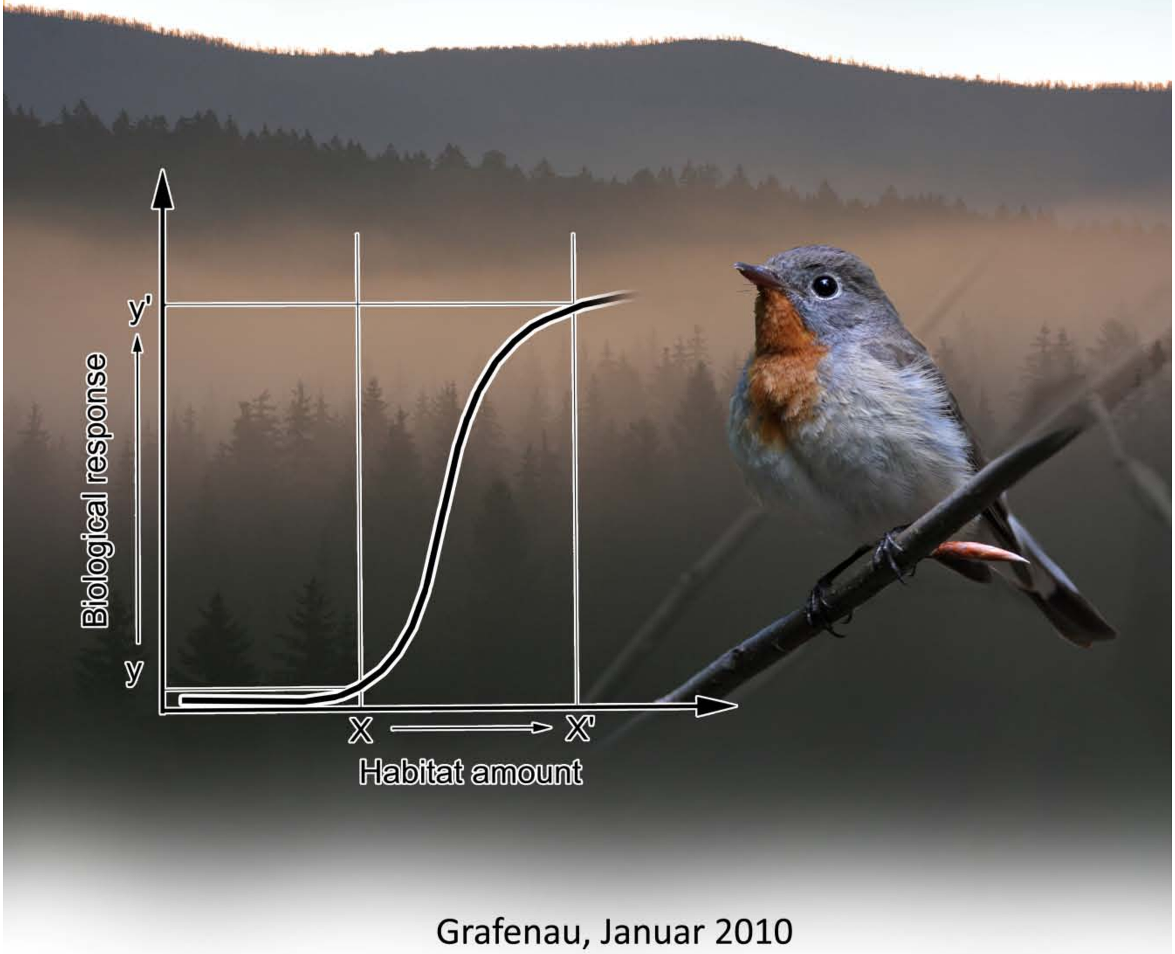
Ökologische Schlüsselwerte in Bergmischwäldern als Grundlage für eine ökologisch nachhaltige Waldnutzung

- Abschlussbericht -



Grafenau, Januar 2010

Projektbeginn: 01.03.2007 – Projektende: 31.01.2010

Aktenzeichen 25227-33/0

Verfasser: Christoph Moning, Jörg Müller

DBU
LWF

Deutsche Bundesstiftung Umwelt

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Verfasser: Christoph Moning, Jörg Müller

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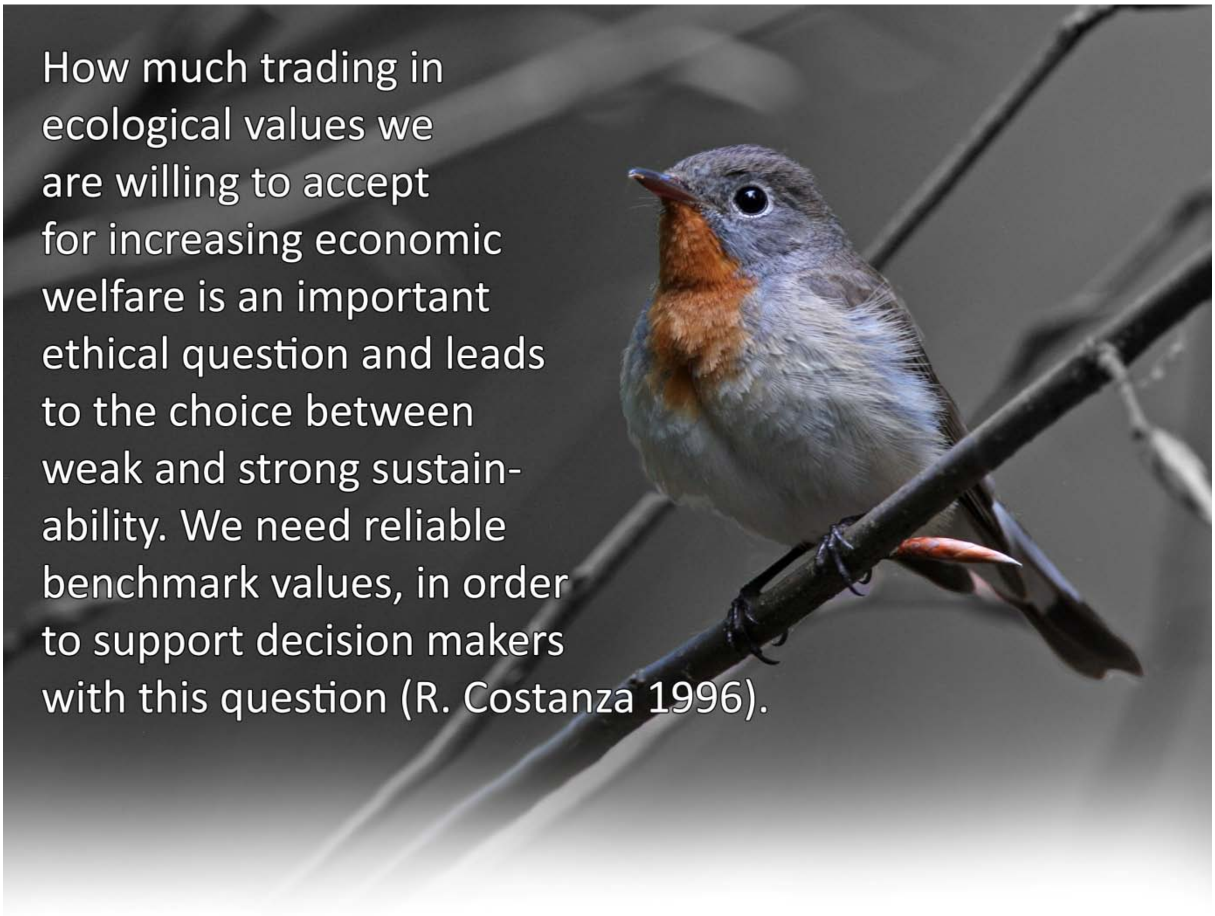
Projektbeginn: 01.03.2007 – Projektende: 31.01.2010

Laufzeit: 2 Jahre 11 Monate



How much trading in ecological values we are willing to accept for increasing economic welfare is an important ethical question and leads to the choice between weak and strong sustainability. We need reliable benchmark values, in order to support decision makers with this question (R. Costanza 1996).

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Zusammenfassung

Trotz der erheblichen Bedeutung, die Bergmischwälder für den Naturschutz in Mitteleuropa haben, existierten bislang keine überregional gültigen Schwellenwerte, die als Richtlinien für die Forstwirtschaft dienen könnten. In diese Lücke stößt das hauptsächlich von der Deutschen Bundesstiftung Umwelt finanzierte Projekt „Ökologische Schlüsselwerte in Bergmischwäldern als Grundlage für eine ökologisch nachhaltige Forstwirtschaft“.

Das Projekt hat zwei Beitragsebenen. Auf der übergeordneten Planungsebene liefert es Beiträge für Naturschutzkonzepte in Bergmischwäldern und hier in erster Linie auf der betrieblichen Ebene. Dies geschieht in Form von Schwellenwerten u.a. zu Bestandsalter, Totholzmengen und -dimensionen, Kronendachdeckung und Höhlenbaumdichten. Diese fließen in ein Verfahren zur Klassifizierung der naturschutzfachlich wertvollen Bereiche auf Betriebsebene ein. Dabei wird auf Basis der Forstinventurdaten ein Interpolationsverfahren angewendet.

Die zweite Beitragsebene sind Empfehlungen für Maßnahmen auf Bestandsebene. Hier vermittelt das Projekt wichtige Schlüssel- und Schwellenwerte und liefert Empfehlungen zur Umsetzung der Schwellenwerte und zwar in Form eines Fortbildungsmoduls und als anschauliche Zusammenfassung in gedruckter Form. Letztere stellt eigens erstellter Band der Wissenschaftlichen Reihe des Nationalparks Bayerischer Wald dar, der auch im Rahmen des Fortbildungsmoduls als Fortbildungsunterlage dient.

Dieser Band fasst die wesentlichen Schlüsselstrukturen und Schwellenwerte auf der Landschaftsebene, auf der Bestandsebene und auf der Ebene der einzelnen Objekte (z.B. Einzelstamm) zusammen. Des Weiteren werden, die aus dem Projekt gewonnenen Rückschlüsse in Handlungsempfehlungen für die Forstwirtschaft umgesetzt. Darauf basierend wird skizziert, wie sich die Schwellenwerte in einem betrieblichen Naturschutzkonzept umsetzen lassen. Den Abschluss bildet eine Zusammenstellung von Indikatorarten, welche die Schlüsselstrukturen in Bergmischwäldern in anschaulicher Weise repräsentieren. Dieses Kapitel entstand unter der Hilfe anerkannter Artenexperten. Der Band liegt dem Abschlussbericht bei.

In diesem Bericht werden darüber hinaus die wesentlichen Projektergebnisse zusammengefasst. Der Darstellung der Arbeitsschritte und der Diskussion ist zu entnehmen, dass der Arbeits- und Zeitplan des Projektes zu den anvisierten Kosten realisiert werden konnte. Änderungen der Zielsetzung waren zu keinem Zeitpunkt der Projektlaufzeit notwendig. Im Kapitel Öffentlichkeitsarbeit werden die Grundzüge des erarbeiteten Fortbildungsmoduls skizziert. Ebenso werden die zahlreichen erarbeiteten Publikationen, die aus dem Projekt entstanden sind, summarisch dargestellt und hinsichtlich der Zielgruppen eingeordnet. Die Publikationen sind im Anhang des Berichtes wiedergegeben.

Bericht

Anlass und Beiträge des Projektes

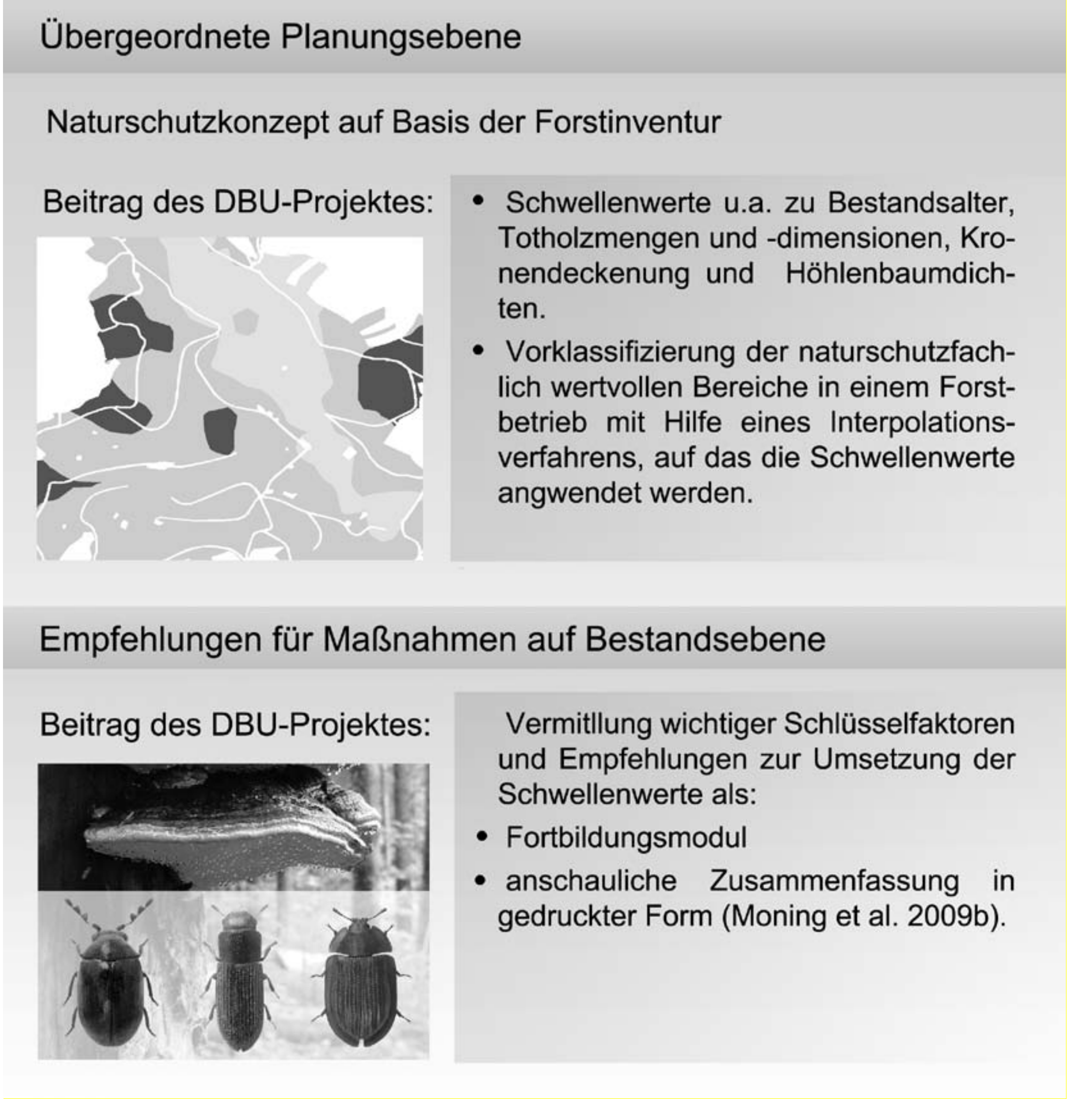
Neben den Buchenwäldern stellen die Bergmischwälder im südlichen Mitteleuropa den größten Anteil der naturnahen und somit auch naturschutzrelevanten Waldfläche. Der Großteil der mitteleuropäischen Bergmischwälder unterliegt einer forstlichen Nutzung mit naturschutzfachlichen Ansprüchen, da sie als Naturparks, Landschaftsschutzgebiete, Schutzwälder, Naturwaldreservate, Naturschutzgebiete oder Nationalparks ausgewiesen sind. Jedoch ist über die nutzungsbedingten Einflussfaktoren (Schlüsselfaktoren) und Schlüsselwerte (Umweltfaktoren, die als Habitatparameter über das Auftreten von Arten und Zönosen entscheiden) für die Lebensgemeinschaften und deren Auswirkungen auf die Artenvielfalt in diesen Wäldern wenig bekannt. Bislang wurde noch nicht versucht, den Lebensraumkomplex des Bergmischwaldes in einem breiten und umfassenden Ansatz zu erklären.

Als Basis für Nutzungskonzepte in der Forstwirtschaft werden seit vielen Jahren eine Reihe von Kenngrößen wie z.B. Durchmesser- und Baumartenverteilung, Vorratsstruktur und Altersklassenverteilung im Rahmen der Forsteinrichtung erhoben. Entsprechende Größen als Basis für naturschutzfachliche Konzepte liegen dagegen erst ansatzweise vor. Fehlende Schlüssel-, Schwellen- und Grenzwerte sind generell ein großes Defizit bei der Erstellung von Naturschutzkonzepten, stellen jedoch, wo verfügbar, ein herausragendes Planungsinstrument dar. Das mangelhafte Wissen um die ökologisch wirksamen Schlüsselwerte mag auch ein Grund dafür sein, dass bisher kein überregionales, die Naturschutzziele integrierendes Bewirtschaftungskonzept für Bergmischwälder existiert. Dies steht im drastischen Widerspruch zu der hohen naturschutzfachlichen Bedeutung von Bergmischwäldern. Um diese Lücke zu schließen, wurde im Nationalpark Bayerischer Wald dieses von der Deutschen Bundesstiftung Umwelt finanzierte Projekt „Ökologische Schlüsselwerte in Bergmischwäldern als Grundlage für eine nachhaltige Waldwirtschaft“ (nachfolgend als DBU-Bergmischwaldprojekt bezeichnet) ins Leben gerufen. In diesem Projekt wurde mit Hilfe der ermittelten Schlüsselwerte am Beispiel des Forstbetriebs Neureichenau der Bayerischen Staatsforsten ein Konzept zur nachhaltigen Nutzung des Bergmischwaldes entworfen, welches sich als Modul in bestehende forstplanerische Instrumente der Forsteinrichtung einfügen lässt. Dadurch wurde eine verbesserte Entscheidungsgrundlage für eine naturschutzorientierte nachhaltige Bergwald-Bewirtschaftung geschaffen.

Abbildung 1. Der Blick vom Bayerischen Wald in die Alpen. Mittelgebirge dominieren weite Teile Mitteleuropas. Sie werden von Bergmischwäldern charakterisiert, die einen überproportional hohen Anteil an naturschutzfachlich bedeutenden Wäldern aufweisen. (Foto: Pöhlmann)

Parallel zur konzeptionellen Arbeit werden die gewonnenen Ergebnisse und Managementempfehlungen durch eine Fortbildungsreihe, die durch die Bayerische Landesanstalt für Wald und Forstwirtschaft (LWF) organisiert und durchgeführt wird, an die Forstleute weitergegeben.

Zusammenfassend lässt sich festhalten, dass die Ergebnisse des DBU-Bergmischwaldprojektes Beiträge zu zwei Handlungsebenen innerhalb der naturschutzorientierten forstlichen Praxis liefern (Abbildung 2). Auf der übergeordneten Planungsebene liefert das Projekt Daten zur naturschutzorientierten Planung auf Basis der Forstinventur. Die zweite Ebene sind konkrete Vorgaben für forstliche Maßnahmen auf Bestandsebene.



Übergeordnete Planungsebene

Naturschutzkonzept auf Basis der Forstinventur

Beitrag des DBU-Projektes:

- Schwellenwerte u.a. zu Bestandsalter, Totholzmengen und -dimensionen, Kronendeckenung und Höhlenbaumdichten.
- Vorklassifizierung der naturschutzfachlich wertvollen Bereiche in einem Forstbetrieb mit Hilfe eines Interpolationsverfahrens, auf das die Schwellenwerte angwendet werden.

Empfehlungen für Maßnahmen auf Bestandsebene

Beitrag des DBU-Projektes:

Vermitllung wichtiger Schlüsselfaktoren und Empfehlungen zur Umsetzung der Schwellenwerte als:

- Fortbildungsmodul
- anschauliche Zusammenfassung in gedruckter Form (Moning et al. 2009b).

Abbildung 2. Die wesentlichen Ergebnisse des Projektes.

Darstellung der Arbeitsschritte und der angewandten Methoden

Grundlage der Analysen des DBU-Bergmischwald-Projektes sind rund 300 Probeflächen, die entlang von vier Transekten arrangiert wurden (Abbildung 3). Der Höhengradient reicht von 655 m bis 1420 m. Zwei der Transekte liegen im Altpark und zwei im Erweiterungsgebiet des Nationalparks. Während die Forschungsflächen im Altpark der unbeeinflussten Entwicklung unterliegen, findet im Erweiterungsgebiet auf Teilen der untersuchten Flächen noch ein Borkenkäfermanagement statt.

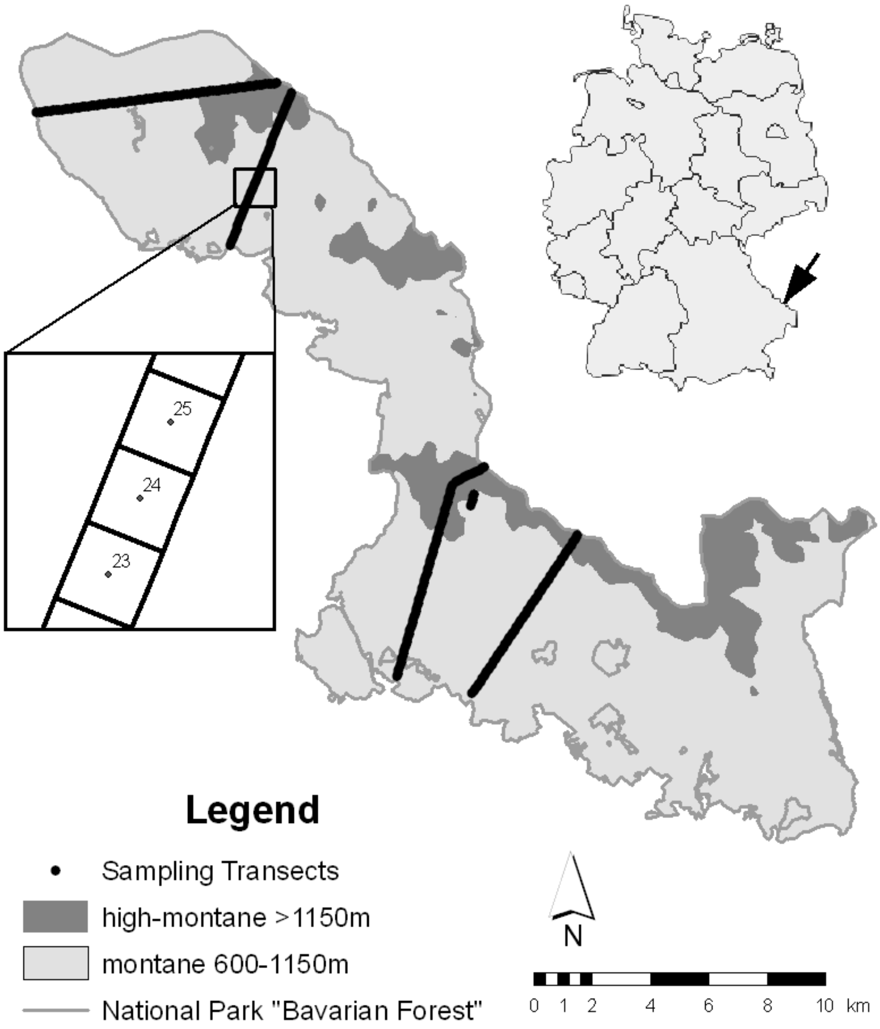


Abbildung 3. Lage des Nationalparks Bayerischer Wald und der Transekte.

Exkurs: Schwellenwertforschung im Nationalpark Bayrischer Wald

Der Nationalpark Bayerischer Wald wurde 1970 als erster Nationalpark in Deutschland gegründet. Damit stellte Bayern eine einmalige Wald- und Mittelgebirgslandschaft an der Landesgrenze zur Tschechischen Republik unter Schutz. Der größte Teil des Parks ist mit Bergmischwald bedeckt. Im Jahr 1997 erweitert, umfasst der Nationalpark mittlerweile eine Fläche von über 240 km². Auf nahezu der gesamten Fläche des Nationalparks erstrecken sich ausgedehnte Wälder, die heute in weiten Teilen einer vom Menschen weitgehend unbeeinflussten Entwicklung überlassen bleiben. Das Wirken natürlicher Umweltkräfte und eine ungestörte Dynamik der Lebensgemeinschaften werden gewährleistet. Als erster in Deutschland hat sich der Nationalpark Bayerischer Wald aufgrund seiner konsequenten Naturschutz-Zielsetzung die internationale Anerkennung der Weltnaturschutz Union (IUCN) erworben.

Der Nationalpark Bayerischer Wald bietet für die Forschung an Schlüsselstrukturen in Bergmischwäldern günstige Rahmenbedingungen, denn

1. Er stellt einen repräsentativen Ausschnitt des Bergmischwaldes in Mitteleuropa entlang eines weiten Höhengradienten von 800 m und in verschiedensten Ausprägungen (Bodentypen, Borkenkäferbefall unterschiedlicher Intensität, usw.) dar.
2. Auch seit Jahrhunderten ungenutzte Bestände stehen für Untersuchungen zur Verfügung.
3. Das Gebiet ist groß genug, um räumlich unabhängige und somit statistisch belastbare und auf größere Regionen übertragbare Ergebnisse zu erzielen.

****

Alle Details der Aufnahmen an dieser Stelle darzustellen, würde den Rahmen dieser Publikation sprengen. Aus diesem Grund sind die aufgenommenen Daten und die angewandten Methoden in Tabelle 1 und Tabelle 2 zusammenfassend dargestellt. Eine umfassende Darstellung der im Projekt angewandten Methoden findet sich bei BÄSSLER et al. (2008, Anhang) und in der Wissenschaftlichen Reihe des Nationalparks Bayerischer Wald (MONING et al. 2009, liegt dem Bericht bei).

Tabelle 1. Zusammenfassung der angewandten Methoden und Auflistung der untersuchten Artengruppen sowie Anzahl und Größe der jeweilig untersuchten Probeflächen.

Taxonomische Gruppe	293 1ha PF*	293 0,1 ha PF*	293 0,02 ha PF*	180 0,1 ha PF*	113 0,1 ha PF*	113 0,1 ha PF*	36 0,1 ha PF*	Methode
Samenpflanzen			X					Kartierung
Farne			X					
Moose			X					
Flechten			X					
Pilze		X						
Vögel	X							
Fledertiere					X			Rufanalyse
Schnecken				X		X		Standardisiertes Sammeln, über 100 Bodenfallen
Nacht-schmetterlinge							X	Lichtfalle
Käfer				X		X	X	180 Flugfensterfallen, 36 Malaise-Fallen, 180 Bodenfallen, 113 Probeflächen mit standardisiertem Sammeln
Wanzen				X			X	180 Flugfensterfallen, 36 Malaise-Fallen, 180 Bodenfallen
Netzflügler				X			X	
Schwebfliegen				(X)			X	
Pflanzenwespen				X			X	
Stechimmen				X			X	
Ameisen				X				180 Bodenfallen
Spinnen				X			(X)	
Weberknechte				X				
Hundertfüßer				X				
Tausendfüßer				X				
Springschwänze				X				
Asseln				X				
Schnabelfliegen							X	36 Malaise-Fallen

* PF=Probeflächen

Tabelle 2. Untersuchte abiotischen Umweltvariablen und Methoden zu deren Erfassung.

Variable	Definition	Punkt	0,02 ha	0,1 ha	1,0 ha	50 ha	Messmethode
Allgemeine Information							
Geografische Koordinaten	Gauß-Krüger Koordinaten	x					GIS Model (DTM 25)
Höhe	Höhe in Metern über dem mittl. Meeresniveau	x					
Exposition	Grad	x					
Hangneigung	Grad	x					
Strahlung	Potenzielle Summe der Strahlung während der Vegetationsperiode (kwh/m^2)	x					
Klimaparameter							
Temperatur	Jahresmittel (1980-2006) in °C	x					GIS Model (ArcEgmo)
Niederschlag	Jahresmittel (1980-2006) in mm	x					
Globalstrahlung	Jahresmittel (1980-2007) in kwh/m^2	x					
Bestandsstruktur							
Deckung der Kronenschicht	Von Bäumen beschatteter Anteil der Probefläche (Anteile der einzelnen Kronenschichten) separiert nach Baumarten in %		x		x	x	Visuelle Schätzung, Luftbildanalyse, Laserdaten (LIDAR)
Deckung von Felsen	Anteil der von Felsen bedeckten Probefläche		x		x	x	
Deckung von Wasserflächen	Anteil der von Wasser bedeckten Probefläche		x		x	x	
Deckung von Lücken	Anteil der von Lücken bedeckten Probefläche		x		x	x	
Maximaler Brusthöhen-Durchmesser (DBH) in der Probefläche	DBH in 1,3 m Höhe				x		Messung
Bestandsalter	Mittleres Bestandsalter in Jahren aus Forstinventurdaten			x			Bohrprobe
Krautschichtdeckung	Deckung der Vegetation unter 1 m Höhe auf der Probefläche		x				Visuelle Schätzung
Kronenschicht: max. Höhe	Digitales Oberflächen-,		x	x	x	x	Flugzeugbasierter Laserscanner
Kronenschicht: mittl. Höhe			x	x	x	x	

Variable	Definition	Punkt	0,02 ha	0,1 ha	1,0 ha	50 ha	Messmethode
Kronenschicht: Standardabweichung der Höhe	Gelände- und Kronenschichtmodel (DSM, DTM, DCM)		x	x	x	x	
Totholz	Zersetzungsgrad, Länge, Durchmesser			x			Messung, visuelle Schätzung
Bodenvariablen							
Bodenwasserbilanz	Index, berechnet nach Ewald (2000)		x				Berechnung
pH Wert-Laubstreu	4 Bodenproben pro Probefläche (Bundesministerium für Ernährung 1990)		x				1 M KCl, Hamilton Glas-Elektrode
pH Wert-Oberboden			x				1 M KCl, Hamilton Glas-Elektrode
Humusformen	4 Proben aus der Humusschicht, Klassifizierung nach AK Standortskartierung (1996)		x				Visuelle Schätzung
Podsolierungsgrad	4 Proben aus 30 cm Oberboden, Klassifizierung nach AK Standortskartierung (1996)		x				Visuelle Schätzung
Austauschbare Nährstoffe	Unterteilt in Streuschicht und Oberboden (µeq/g); Al, Ca, Fe, K, Mg, Mn, Na		x				ICP-IES (Perkin Elmer Optima 3000), CHN-analyser LECO CHN-1000
Basensättigung	Unterteilt in Streuschicht und Oberboden (µeq/g and %)		x				
Kationen-Austausch-Kapazität (CEC)	CEC unterteilt in Streuschicht und Oberboden (µeq/g)		x				
C/N-Verhältnis	Kohlenstoff (%) / Stickstoff (%)-Verhältnis		x				

Die umfangreichen Arterfassungen bedurften eines großen Expertenkreises und der Anwendung vielfältiger Erfassungsmethoden.

Abbildung 4. Flechtenexperte und Forstdienststellenleiter Johannes Bradtka bei der Arbeit. (Foto: Schiener)

Abbildung 5. Sortierung der Schmetterlingsfänge. (Foto: Müller)

Abbildung 6. Windwürfe erschweren das Vorankommen entlang der Transekte. (Foto: Kergalve)

Abbildung 7. Käferexperte Heinz Bussler ist seinen Zielorganismen mit dem Klopfschirm auf der Spur. (Foto: Stephan)

Zeitlicher Ablauf

Dem Zeit- und Arbeitsplan entsprechend konnten die Arbeitsschritte wie in Tabelle 3 dargestellt bewältigt werden.

Tabelle 3. Zeit- und Arbeitsplan.

1. Vorbereitung der Freilandarbeiten	**Zeitrahmen**	**Beteiligte Projektteilnehmer**
Literaturrecherche Festlegung und Einrichtung der Transekte und Probekreise Erste Probeaufnahmen und Probeauswertungen Befliegung mit Laserscanner	Sommer bis Dezember 2006	Nationalpark Bayerischer Wald durch Dr. Jörg Müller, Claus Bässler 1 Wissenschaftlicher Mitarbeiter (1/2 Stelle, BAT IIa)
2. Durchführung der Freilandarbeiten	**=> eigentlicher Projektbeginn 01.03.2007**	
Kartierung der Fauna - Betreiben 170 Flugfensterfallen - Betreiben von 36 Malaisefallen - Betreiben von 180 Barberfallen - Betreiben von 36 Lichtfallen - Kartierung von 100 Probekreisen Holzkäfer - Zeitnahe Sortierung der -Monatsfänge durch Hilfskräfte oder Werkvertrag - Kartierung der Mollusken auf 112 Probekreisen - Kartierung Spinnen auf 170 Probekreisen - Kartierung der Avifauna auf allen Probequadranten - Kartierung der Flechten auf 112 Probekreisen - Kartierung der Moose auf 112 Probekreisen - Kartierung der Pilze auf 293 Probekreisen - Kartierung der Gefäßpflanzen auf 293 Probekreisen	Frühjahr bis Herbst 2007	Nationalpark Bayerischer Wald durch Dr. Jörg Müller, Claus Bässler und 1 Wiss. Mitarbeiter (1/2 Stelle, BAT IIa): Christoph Moning LWF: Heinz Bußler; sowie Werkvertrag mit Gutachterbüros
3. Erarbeitung der Ergebnisse		
- Bestimmung der Fänge - Dateneingabe - statistische Auswertungen	August 2007 bis Mitte 2008	Nationalpark Bayerischer Wald durch Dr. Jörg Müller, Christoph Moning, externe Experten
4. Erstellung eines Zwischenberichts und Publikation der ersten Ergebnisse	**Mitte 2008 bis Ende 2008**	Nationalpark Bayerischer Wald durch Dr. Jörg Müller, Christoph Moning
5a. Erstellung und Umsetzung der Ergebnisse in ein Konzept für den Modellbetrieb Neureichenau.	**Ende 2008 bis Anfang 2009**	Nationalpark Bayerischer Wald: Christoph Moning, Dr. Jörg Müller BaySF: Michael Held, Neureichenau; Markus Kölbel, Regensburg
- Analyse der Forsteinrichtungsdaten bezüglich der Ergebnisse im NP - Erstellung von Planungseinheiten für		Nationalpark Bayerischer Wald: Christoph Moning, Dr. Jörg Müller

Naturschutzfachliche Konzeption - Entwicklung eines Moduls naturschutzfachliche Bewertung anhand von Inventurdaten		BaySF: Andreas Füller
5b Erstellung eines Fortbildungskonzeptes und anschließende Durchführung desselben	**Ende 2008 bis Oktober 2009**	Bayerische Landesanstalt für Wald und Forstwirtschaft: Dr. Helge Walentowski, Nationalpark Bayerischer Wald: Christoph Moning, Dr. Jörg Müller Freiberufliches Büro, Forstbetrieb Neureichenau
Erstellung einer Fortbildungsmappe und eines Datenträgers mit einem Block Fachvorträge und einem Block Praxisempfehlungen (Powerpoint Präsentationen)		Gutachterbüro: Opus, Franz Moder
6 Organisation und Durchführung eines Abschlusskolloquiums im Nationalpark Bayerischer Wald	**Oktober 2009 bis Januar 2010**	Nationalpark Bayerischer Wald: Christoph Moning, Dr. Jörg Müller

Ergebnisse

Es fällt schwer aus der Fülle der Forschungsergebnisse heraus, die dieses Projekt erbracht hat, eine zusammenfassende Darstellung zu erstellen ohne wesentliche Zusammenhänge zu vernachlässigen. Dennoch werden im Folgenden wichtige konkrete Fakten, die aus den Forschungen des DBU-Projekts errechnet werden konnten, dargestellt. Simple Botschaften verleiten zur unreflektierten Zitation, weshalb wir daran erinnern möchten, die folgenden Ergebnisse nur aus dem Zusammenhang der entsprechenden Publikationen heraus zu zitieren.

Beschaffenheit des Kronendaches

- 1641 Arten aus allen untersuchten Artengruppen zeigen, dass 661 Arten also rund 40 % aller Arten eine statistisch nachweisbar positive Beziehung zur Auflichtung aufweisen. Rund 215 Arten (13 %) des Artenspektrums zeigen hingegen eine statistisch nachweisbare Abhängigkeit zum Waldinneren auf.

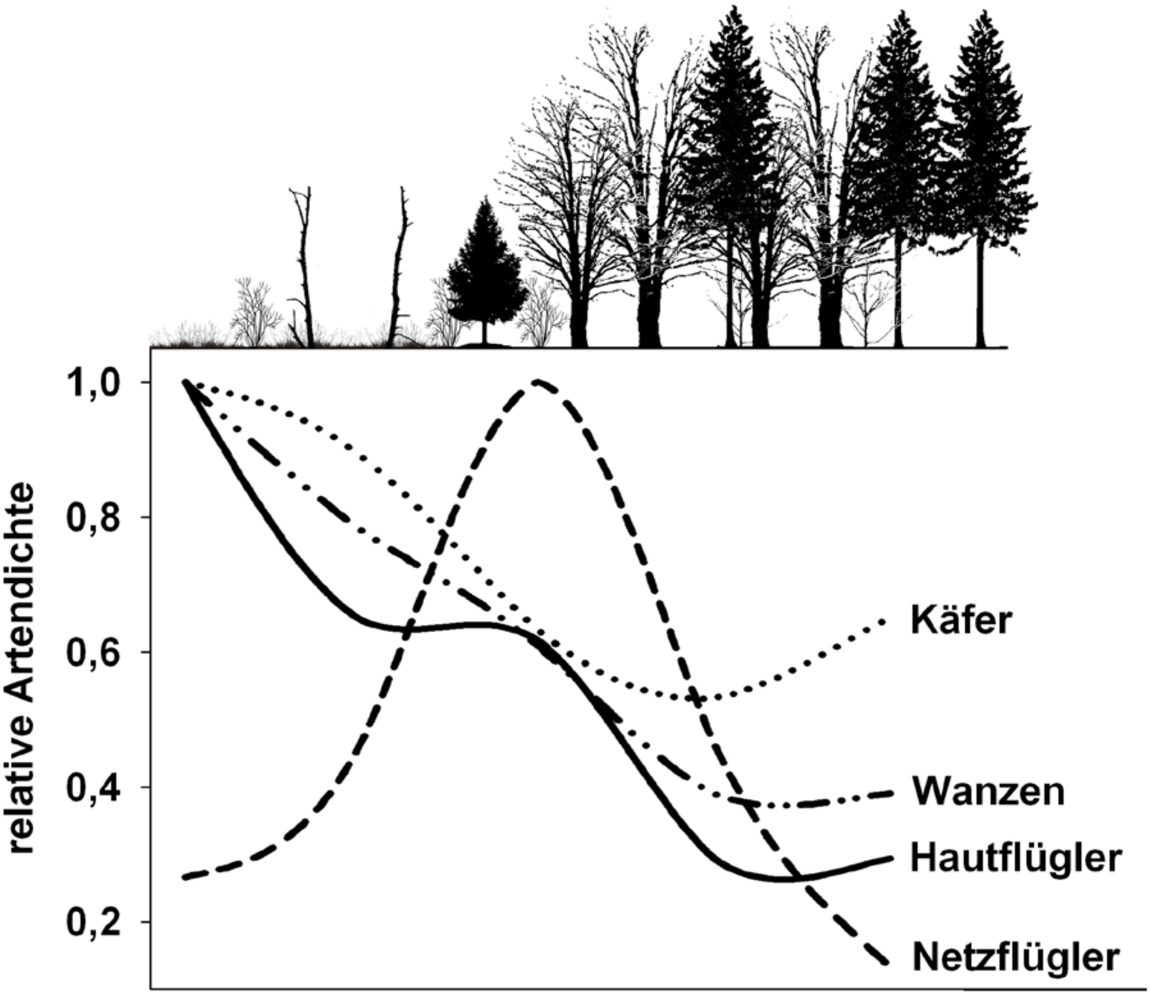


Abbildung 8. Relative Artenvielfalt von Käfern (240 Arten), Wanzen (96 Arten), Hautflüglern (Bienen und Wespen, 65 Arten) und Netzflüglern (20 Arten) entlang des Waldrandgradienten. Die zugrunde liegenden Daten entstammen einem eigenen Forschungsprojekt, dass sich mit der Bedeutung der Waldränder in Bergmischwäldern für xylobionte Käfer im Nationalpark Bayerischer Wald befasst hat (MÜLLER et al. 2007).

Abbildung 9. Malaisefallen und die zugehörigen August-Leerungen auf einem Standort mit geschlossenem Kronendach (oben) und in einer Waldlücke (Käferloch, unten). (Fotos: Merkel-Wallner)

- Die Holzpilzartenvielfalt ist statistisch nachweisbar größer auf Totholz, das maximal gut 30 % besonnt ist bzw. auf Totholz, das mindestens 70 % beschirmt ist.

- Vergleich Hochlagen mit abgestorbenem Kronendach mit Hochlagen mit lebendem Kronendach (Tabelle 4): Das Resultat dieses Vergleichs zeigt deutlich die Zunahme bei den licht- und wärmebedürftigen Arten in den Hochlagen mit abgestorbenen Altfichten, insbesondere bei den Insekten. Zudem profitieren Totholzbewohner. Dem reicheren Nahrungsangebot in den Wäldern mit abgestorbenen Altbäumen folgen auch räuberisch lebende Arten. Die Zahl der Gefäßpflanzenarten nimmt durch großflächige Auflichtungen hingegen signifikant ab, da die hohen Streuauflagen der Hochlagen-Fichtenwälder durch das erhöhte Lichtangebot und die erhöhten Temperaturen schnell umgesetzt werden, was zu einer Anhebung des pH-Wertes führt, was wiederum konkurrenzstarke Arten wie das Berg-Reitgras (*Calamagrostis varia*) oder die Rasenschmiele (*Deschampsia cespitosa*) fördert. Zwergsträucher wie die *Vaccinium*-Arten hingegen nehmen in Folge der pH-Wert-Erhöhung ab. Insgesamt nimmt jedoch die Biomasse in der Krautschicht zu, wodurch pflanzenfressende Arten insgesamt zunehmen.

Tabelle 4. Vergleich der Artenausstattung bei verschiedenen Artengruppen zwischen Hochlagen mit lebenden Altbäumen und Hochlagen mit abgestorbenen Altbäumen. Aussagen beziehen sich auf Untersuchungen aus dem Nationalpark Bayerischer Wald.

Artengruppe	Hochlagen mit lebenden Altbäumen	Hochlagen mit abgestorbenen Altbäumen
Flechten	– –	+ +
Moose	+	–
Holzpilze	+ +	– –
Gefäßpflanzen	–	+
Mollusken	0	0
Spinnen	–	+
Weberknechte	0	0
Käfer-Pilzfresser	0	0
Käfer-Kotfresser	0	0
Käfer-Fäulnisfresser	0	0
Käfer-Aasfresser	–	+
Käfer-räuberisch	–	+
Käfer-Pflanzenfresser	– –	+ +
Käfer-Holzbewohner	– –	+ +
Wanzen-räuberisch	–	+
Wanzen-Pflanzenfresser	– –	+ +
Stechimmen (Bienen und Wespen)	– –	+ +
Nachtschmetterlinge	– –	+ +
Vögel	+	–

Erläuterung zu der Tabelle: 0 bedeutet kein Unterschied, +/- etwas mehr bzw. weniger Arten, ++/-- deutlich mehr oder weniger Arten.

Das Resultat dieses Vergleichs zeigt deutlich die Zunahme bei den licht- und wärmebedürftigen Arten in den Hochlagen mit abgestorbenen Altfichten, insbesondere bei den Insekten. Zudem profitieren Totholzbewohner. Dem reicheren Nahrungsangebot in den Wäldern mit abgestorbenen Altbäumen folgen auch räuberisch lebende Arten. Die Zahl der Gefäßpflanzenarten nimmt durch großflächige Auflichtungen hingegen signifikant ab, da die hohen Streuauflagen der Hochlagen-Fichtenwälder durch das erhöhte Lichtangebot und die erhöhten Temperaturen schnell umgesetzt werden, was zu einer Anhebung des pH-Wertes führt, was wiederum konkurrenzstarke Arten wie das Berg-Reitgras (*Calamagrostis varia*) oder die Rasenschmiele (*Deschampsia cespitosa*) fördert. Zwergsträucher wie die *Vaccinium*-Arten hingegen nehmen in Folge der pH-Wert-Erhöhung ab. Insgesamt nimmt jedoch die Biomasse in der Krautschicht zu, wodurch pflanzenfressende Arten insgesamt zunehmen.

- Die Schwellenwerte für die Waldlückengröße, ab der sich Effekte auf die Tierwelt nachweisen lassen, liegen in einer Spannweite zwischen 0,3 und 0,6 ha. Somit kann eine Lückengröße von rund 0,5 ha als ein sinnvolles Maß für das Ziel einer maximale Vielfalt im Bergmischwald angenommen werden. Auf der Landschaftsebene ist es wichtig, dass auch die großflächig offenen und großflächig geschlossenen alten Wälder bestehen.

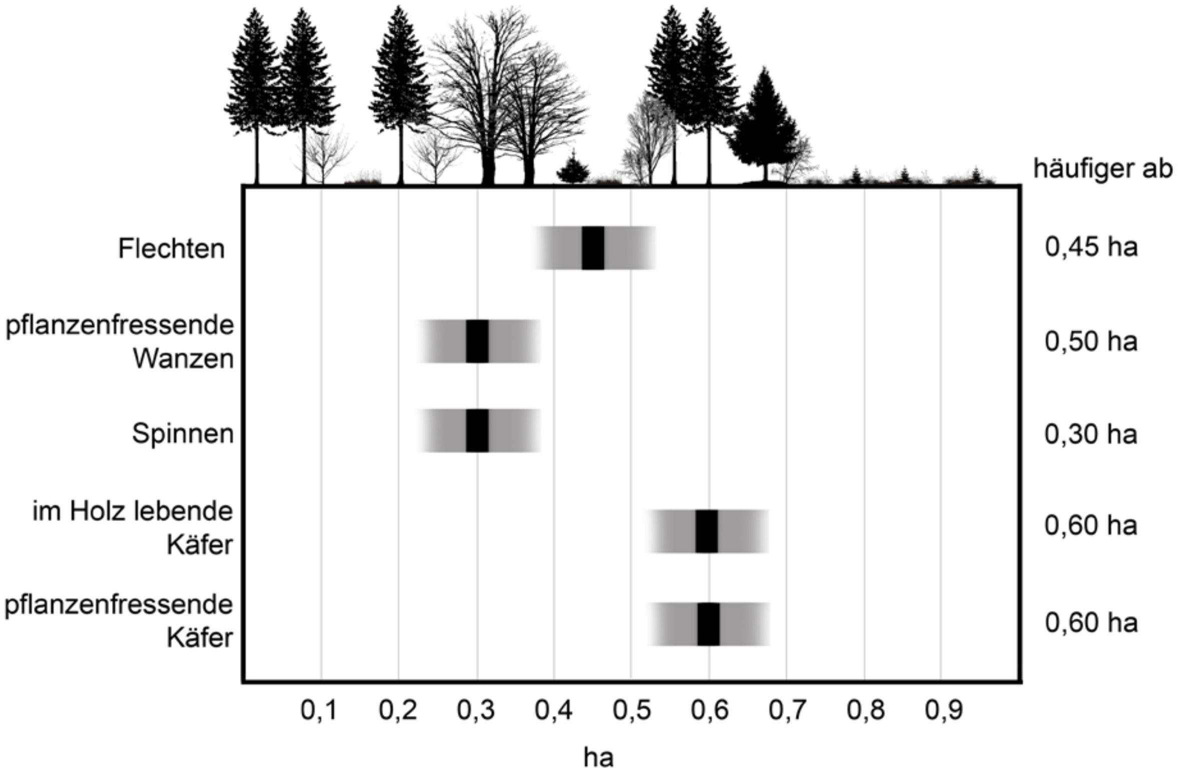


Abbildung 10. Schwellenwerte für Lückengößen im Kronendach, ab denen die dargestellten Artengruppen statistisch nachweisbar häufiger auftreten.

- Effekt der Kronendachöffnung auf Singvögel: Ein breiter Gradient der Kronendachöffnung zwischen 15 und 50 % über eine größere Fläche bewirkt, dass alle ökologischen Nischen bei den Strauchbewohnern bedient werden und somit eine hohe Artenvielfalt erzeugt wird.

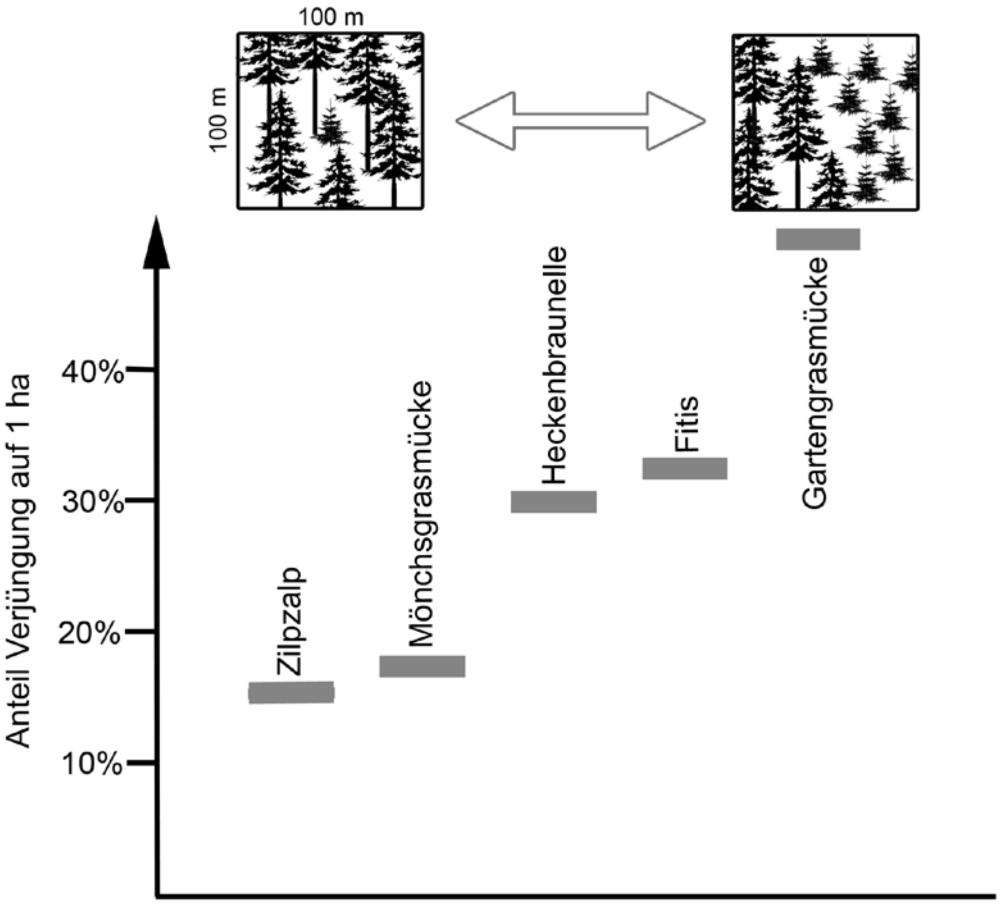


Abbildung 11. Schwellenwerte, für Vogelarten die statistisch nachweisbar auf Auflichtung in Form von Verjüngung reagieren. Die abgebildeten Schwellenwerte bedeuten, dass die jeweilige Vogelart ab dem jeweiligen Schwellenwert häufiger auftritt, der Zilpzalp also ab 15% Anteil Verjüngungsfläche an den untersuchten 1ha-Quadranten.

Habitattraditionen - Waldalter

- Pilze: Auf 293 Probekreisen wurden rund 150 makroskopierbare (Makroskopie = „grobe Betrachtung“) Pilzarten bestimmt und hinsichtlich ihrer Artendichte untersucht. Dabei zeigen sich deutliche Unterschiede in der Artenzahl zwischen seit Jahrhunderten völlig ungenutzten Waldflächen mit Habitattradition, Nationalparkflächen, die sich im Management (Borkenkäferbekämpfung wird durchgeführt) befinden und Nationalparkflächen, die dem Prozessschutz (kein Einfluss seit wenigen Jahrzehnten) unterliegen. Obwohl die Artenzahl der Flächen mit Habitattradition überdurchschnittlich hoch ist, ist lediglich der Unterschied zwischen Flächen mit Habitattradition und Managementflächen statistisch signifikant. Dies zeigt einerseits die hohe Bedeutung von Waldflächen mit Habitattradition für die Pilze auf, andererseits zeigt die Auswertung, dass der Prozessschutz auch anspruchsvollen Pilzarten Lebensraum schafft.

- Die Daten aus dem Projekt zeigen, dass Holzpilze in Bergmischwäldern erst ab 235 Jahren signifikant höhere Artendichten also Artenzahlen pro Fläche erreichen. Dies gilt für alle Arten wie auch für die gefährdeten Arten allein (Rote-Liste Arten).

- Die hohen Artendichten bei den gefährdeten holzbewohnenden Käfern der alten Wälder unterscheiden sich signifikant von denen der Management- und Prozessschutzflächen.

- Vergleicht man die im Rahmen des DBU-Bergmischwald-Projektes erhobenen Artenzahlen von Brutvögeln, Mollusken und Flechten je Probefläche, so zeigt sich, dass bei allen Artengruppen die Artenzahl mit dem Waldalter zunimmt. Diese Beobachtung trifft auf die gesamte Artengemeinschaft genau so zu wie auf die gefährdeten Arten alleine. Die statistisch ermittelte Schwelle, die artenreiche von artenarmen Waldbeständen trennt, liegt bei den Bergmischwäldern des Bayerischen Waldes zwischen 160 und 220 Jahren. Allgemein kann festgehalten werden, dass Bergmischwälder für Artengruppen die auf Strukturen alter Wälder angewiesen sind, ab rund 200 Jahren einen statistisch nachweisbar höheren Wert haben.

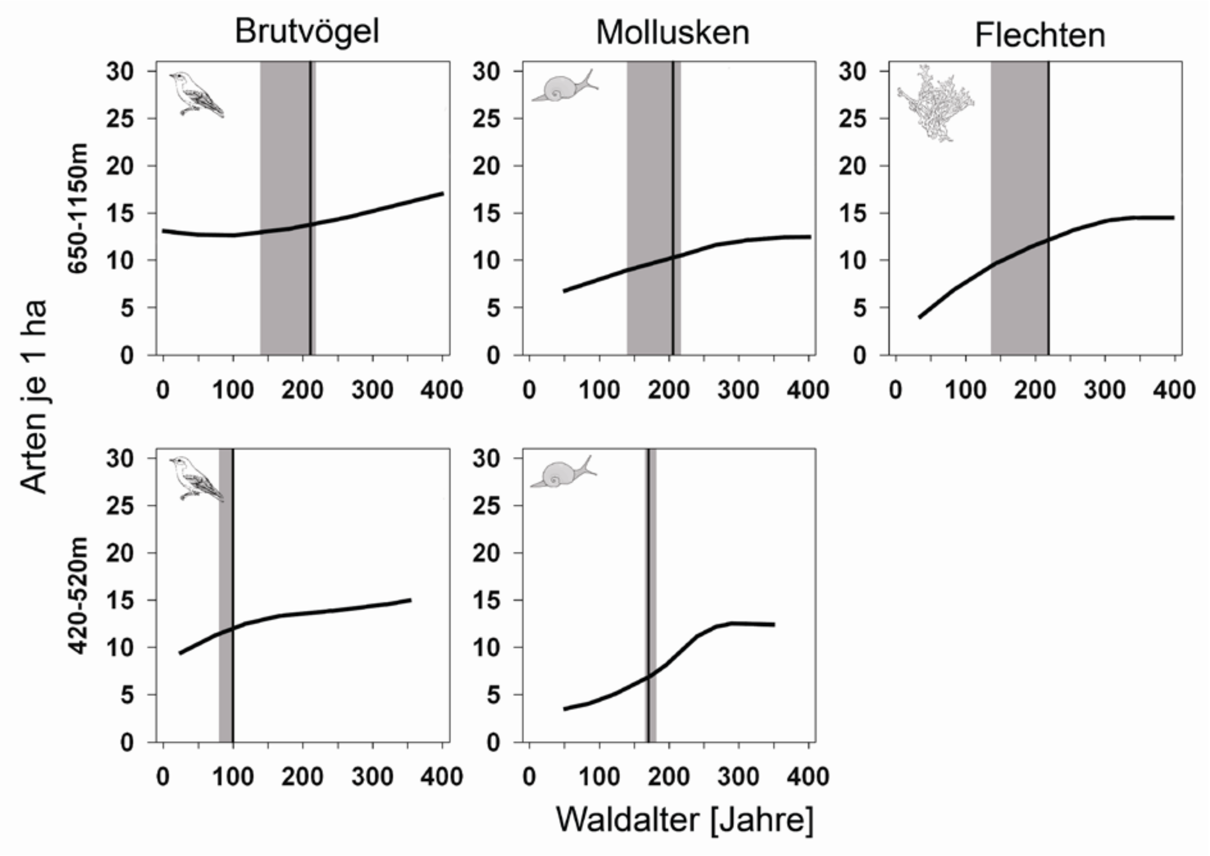


Abbildung 12. Zusammenhang zwischen Anzahl der Arten von Brutvögeln, Mollusken und Flechten je ha (X-Achse) und Bestandsalter (Y-Achse). Die Daten der oberen Reihe stammen aus dem Bergmischwald im Nationalpark Bayerischer Wald (650-1150 m) und die der unteren Reihe aus den kollinen Buchenwäldern des Steigerwaldes (420-520 m). Die vertikalen schwarzen Linien stellen die jeweiligen Schwellenwerte dar. Sie liegen in grauen vertikalen Balken (Schwellenwertkorridore), die das statistisch niedrige Artenniveau (jeweils links) von den statistisch hohen Niveaus (jeweils rechts) trennen (MONING & MÜLLER 2009).

Die Vogelarten, die aus den Daten des DBU-Bergmischwaldprojektes statistisch nachweisbar mit einem hohen Waldalter zusammenhängen, weisen einen ähnlichen Schwellenwert auf. Ab rund 200 Jahren kommen die dargestellten Arten häufiger vor. Eine Ausnahme bildet der Zwergschnäpper, der erst in Wäldern ab 300 Jahren häufiger auftritt (Abbildung 13).

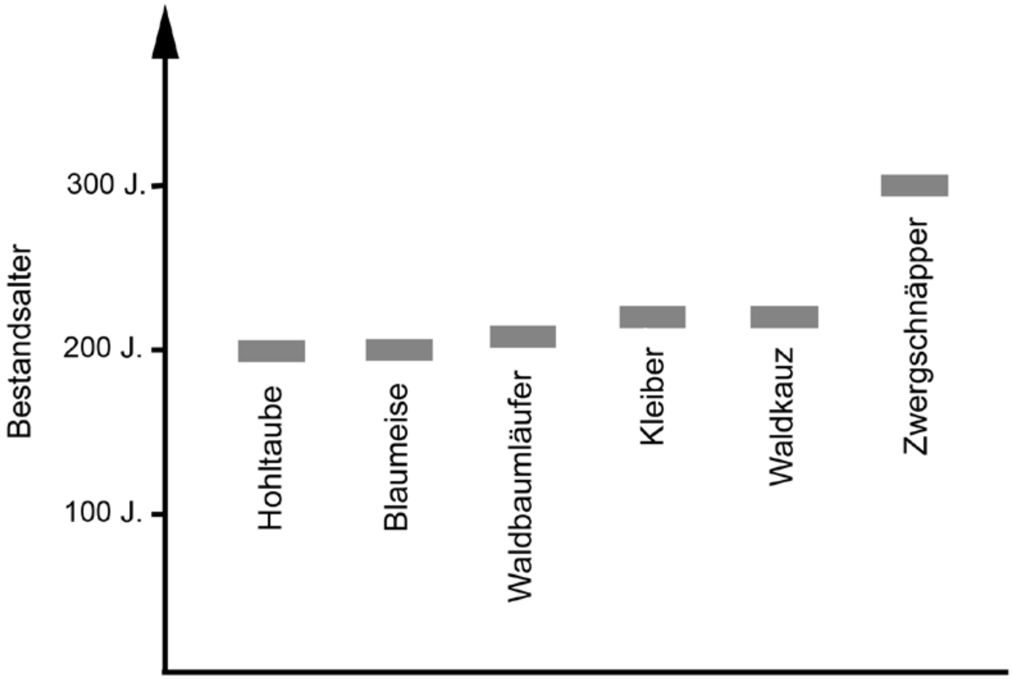


Abbildung 13. Die Vogelarten, die aus den Daten des DBU-Bergmischwaldprojektes statistisch nachweisbar mit einem hohen Waldalter zusammenhängen, weisen einen ähnlichen Schwellenwert auf. Ab rund 200 Jahren kommen die dargestellten Arten häufiger vor. Eine Ausnahme bildet der Zwergschnäpper, der erst in Wäldern ab 300 Jahren häufiger auftritt.

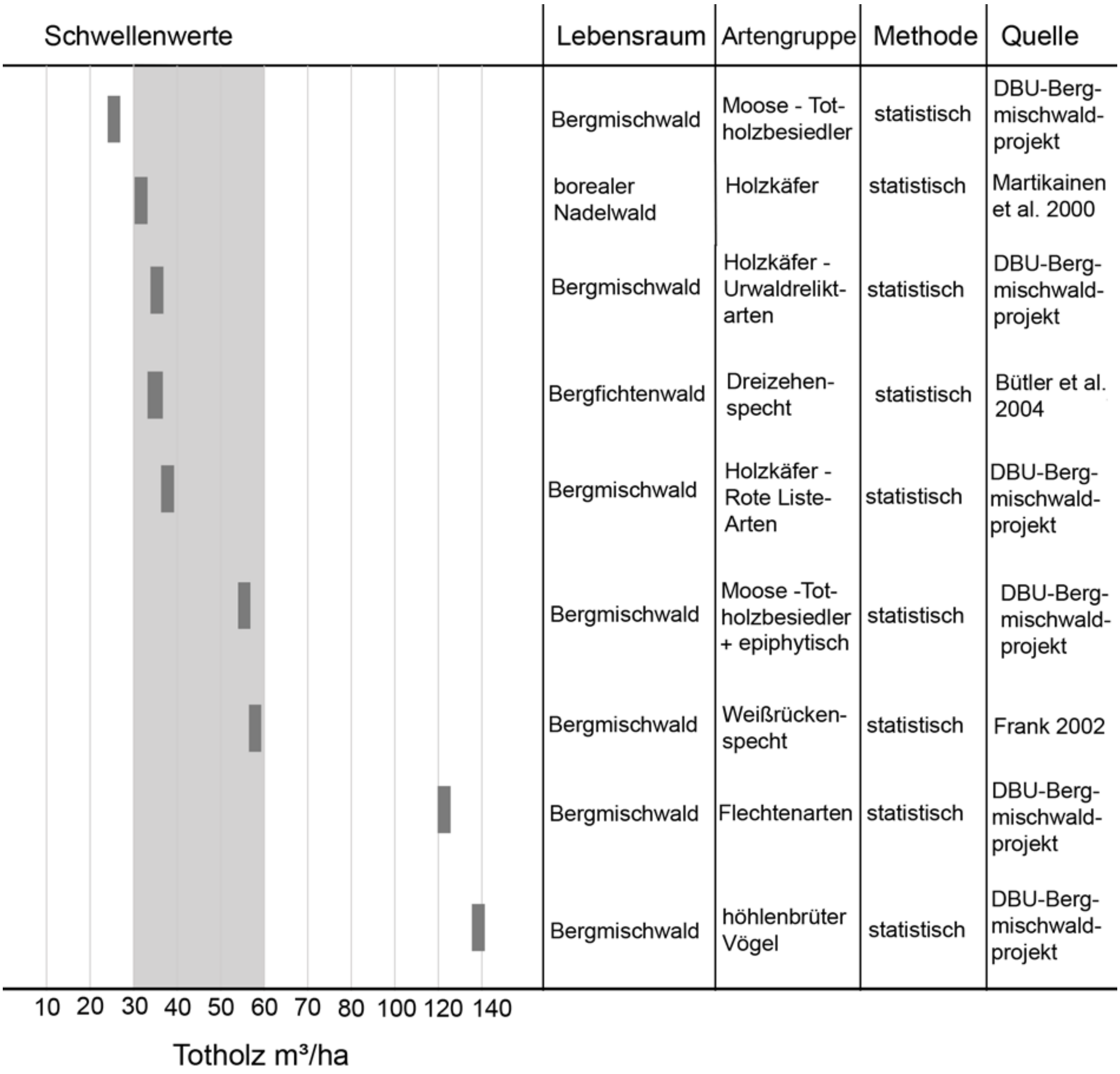
Abbildung 14. Beispiel einer Zwergschnäpperbrut aus dem Nationalpark Bayerischer Wald (Watzlikhain). Die Brut fand innerhalb des Urwaldbestandes in einer nebenständigen abgestorbenen Erle mit einem ausgefaulten Streifschaden statt. Solche Strukturen entstehen erst in sehr alten Wäldern in größerer Zahl. (Fotos: Moning)

Totholz

- Die Untersuchungen aus dem DBU-Bergmischwaldprojekt zeigen für die Bergmischwälder des Nationalparks Bayerischer Wald, dass Urwaldreliktarten (8 Arten) der Holzkäfer ab 34 m³ Totholz je Hektar und ab rund 160 Jahren Bestandsalter signifikant häufiger auftreten. Für die Rote Liste-Arten unter den Holzkäfern (350 Arten) ergibt sich ein Schwellenwert von 37 m³ Totholz je Hektar.

- Die Schwelle des statistisch nachweisbar höheren Auftretens von Moosen, die nahezu ausschließlich Totholz besiedeln, liegt im untersuchten Gebiet im Nationalpark Bayerischer Wald bei 18 m³ liegendem Totholz/ha (entspricht im Durchschnitt 25 m³ Gesamttotholz/ha). Eine zweite Schwelle für Moose, die Totholz besiedeln, aber auch an Wurzelansätzen und epiphytisch auf lebenden Bäumen gefunden werden können, liegt bei 29 m³ Laubtotholz je ha (entspricht im Durchschnitt 55 m³ Gesamttotholz/ha).

- Stellt man die Totholzschwellen, die aus den Projektdaten gewonnen wurden, mit solchen aus der Literatur zusammen, so erkennt man, dass ab einer Spannweite von 30 bis 60 m³ Totholz je ha eine ganze Reihe Artengruppen von dem Totholzangebot profitiert (Abbildung 15).



Lebensraum	Artengruppe	Methode	Quelle
Bergmischwald	Moose - Totholzbesiedler	statistisch	DBU-Bergmischwaldprojekt
borealer Nadelwald	Holzkäfer	statistisch	Martikainen et al. 2000
Bergmischwald	Holzkäfer - Urwaldreliktarten	statistisch	DBU-Bergmischwaldprojekt
Bergfichtenwald	Dreizehenspecht	statistisch	Bütler et al. 2004
Bergmischwald	Holzkäfer - Rote Liste-Arten	statistisch	DBU-Bergmischwaldprojekt
Bergmischwald	Moose -Totholzbesiedler + epiphytisch	statistisch	DBU-Bergmischwaldprojekt
Bergmischwald	Weißrückenspecht	statistisch	Frank 2002
Bergmischwald	Flechtenarten	statistisch	DBU-Bergmischwaldprojekt
Bergmischwald	höhlenbrüter Vögel	statistisch	DBU-Bergmischwaldprojekt

Abbildung 15. Gegenüberstellung von Schwellenwerten für Totholzmengen in Wäldern. Die grauen Balken geben die Schwellen wieder. Der hellgraue Bereich stellt einen Taxonomie-übergreifend wirksamen Korridor dar, ab dem viele Artengruppen von einer Totholzanreicherung profitieren.

- Aus den Daten für Höhlen bewohnende Vögel und Flechtenarten ergeben sich sehr hohe Totholz-Schwellen von 141 m³/ha bzw. 127 m³/ha. Diese Artengruppen treten signifikant häufiger in Flächen auf, in denen der Altholzbestand abgestorben ist, wo sie dann durch die hohen Totholzmengen und das gute Lichtangebot profitieren.

- Das Fichtentotholz erreicht bedingt durch massive Borkenkäfergradationen und Sturmereignisse sein Maximum bereits zwischen 150 und 200 Jahren. Buchen- und Tannentotholz entsteht auch im Nationalpark mit seinen ungestörten Abläufen erst in über 200 Jahre alten Wäldern in nennenswertem Umfang (Abbildung 16).

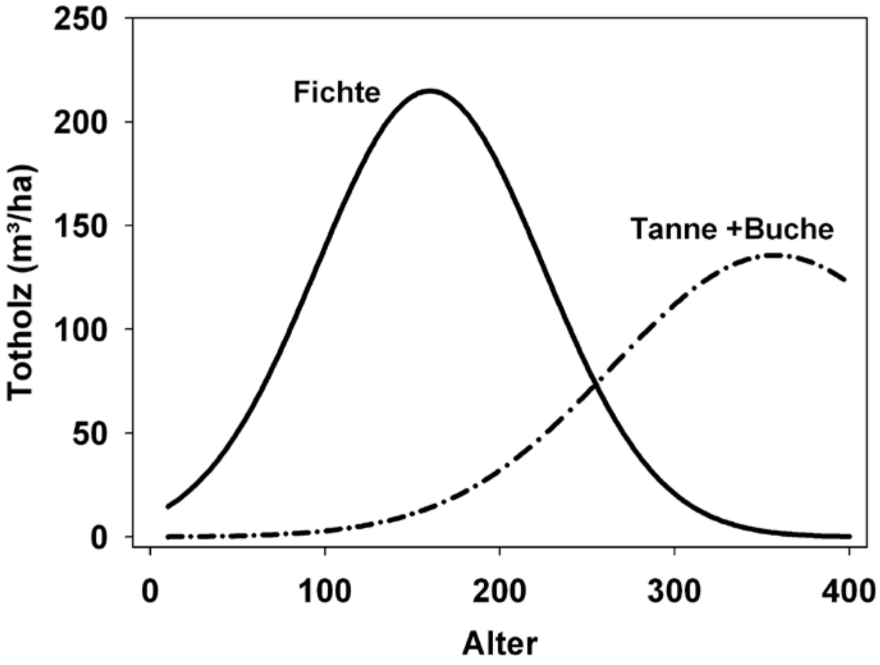


Abbildung 16. Totholzmengen im Nationalpark Bayerischer Wald in der Zone unterhalb 1150 m (Bergmischwald der Buchenwaldzone) von Fichte einerseits und Buche und Tanne zusammen andererseits, bezogen auf das Waldalter.

- Bei kleinen Totholzmengen steigt mit geringer Zunahme der Totholzmenge die Totholz-Strukturvielfalt rasch an, um dann bei großen Totholzmengen in eine Sättigung überzugehen (sigmoidale Sättigung, Abbildung 17). Schon eine geringe Zunahme der Totholzmenge auf rund 30 bis 40 m³ Totholz/ha hat demnach einen großen Einfluss auf die Verfügbarkeit von Totholzstrukturen, die wiederum für eine vielfältige Lebewelt von großer Bedeutung ist.

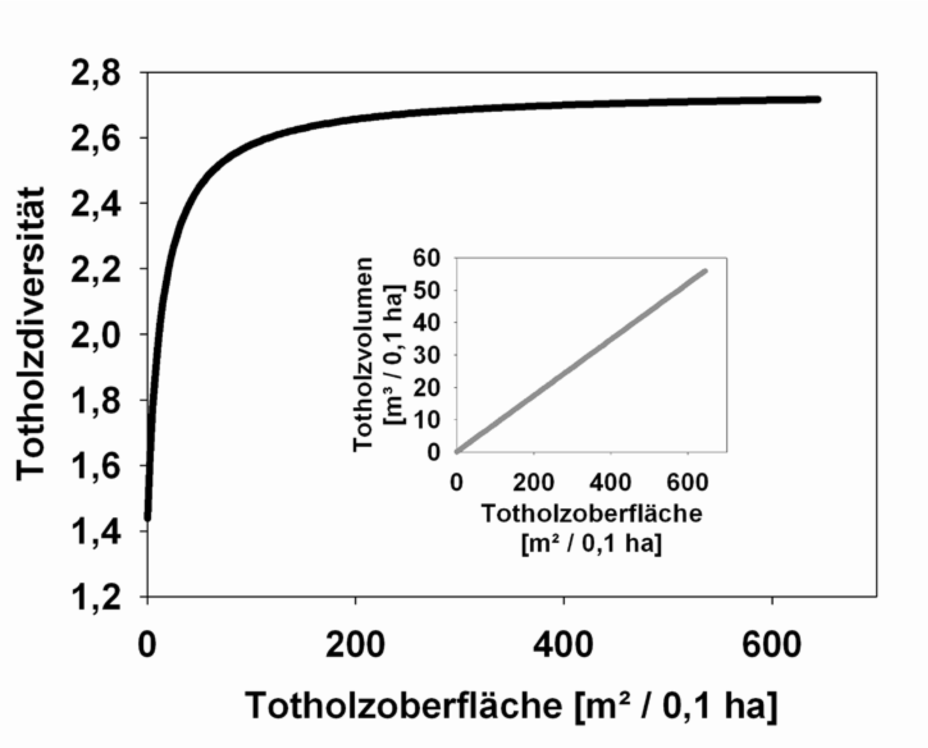


Abbildung 17. Zusammenhang zwischen Totholzoberfläche und Totholzdiversitätsindex (groß) sowie zwischen Totholzoberfläche und Totholzvolumen (klein). Daten entstammen dem DBU-Bergmischwaldprojekt, von den Transekten im Nationalpark Bayerischer Wald. Untersuchungen aus Finnland zeigen, das der Anstieg der Artenzahl der Totholzkäfer genau dem Verlauf des Totholzdiversitätsindex folgt (MARTIKAINEN et al. 2000).

Abbildung 18. Als eine für die Artenvielfalt im Bergmischwald herausragend wichtige Struktur können alte lebende und vor allem auch tote Weißtannen (*Abies alba*) gelten. Eine ganze Reihe Käferarten finden in kränkelnden und absterbenden Weißtannen hervorragende Entwicklungsbedingungen. Zu ihnen zählen Tannenrüsselkäfer (*Pissodes piceae*), Krummzähniger Tannenborkenkäfer (*Pityokteines curvidens*), Mittlerer Tannenborkenkäfer (*Pityokteines vorontzowi*) und Kleiner Tannenborkenkäfer (*Cryphalus piceae*). Ihnen folgen Räuber und Schmarotzer wie der schlanke Kurzflügler *Metoponcus brevicornis*, der Leistenkopf-Plattkäfer (*Laemophloeus alternans*) oder die Brackwespe *Eubazus atricornis*. Aber man findet an stärker zersetztem Tannentotholz auch Urwald reliktarten, die dem Tannentotholz seine besondere Bedeutung für den Artenschutz verleihen. (Foto: Müller)

Stammdimension

- Aus den Daten des DBU-Bergmischwaldprojektes lässt sich berechnen, dass sich stark dimensioniertes Totholz positiv auf die Artendichte bei den Flechten auswirkt. Insbesondere kommen hier seltene Arten hinzu.

- Untersucht man die Pilzvielfalt auf die Totholzdimension hin, so zeigt sich bei der Fichte, dass sich ein Wechsel in der Artengemeinschaft bei geringen Zersetzungsgraden schon ab 20 cm Totholzdurchmesser ergibt. Bei stärker zersetztem Totholz liegt der Artenwechsel bei rund 30 cm Durchmesser. Es rentiert sich also aus Artensicht auch schwaches Totholz im Wald zu belassen. Nichts desto trotz ist der Anteil bedrohter Arten an stark dimensioniertem Totholz besonders hoch. Tanne und Buche sind ab 50 cm Durchmesser artenreicher. Auf die Frage, ab wann ein Totholzstumpf als dick im Sinne von naturschutzfachlich bedeutender gilt, muss man folglich je nach Baumart antworten (Abbildung 19).

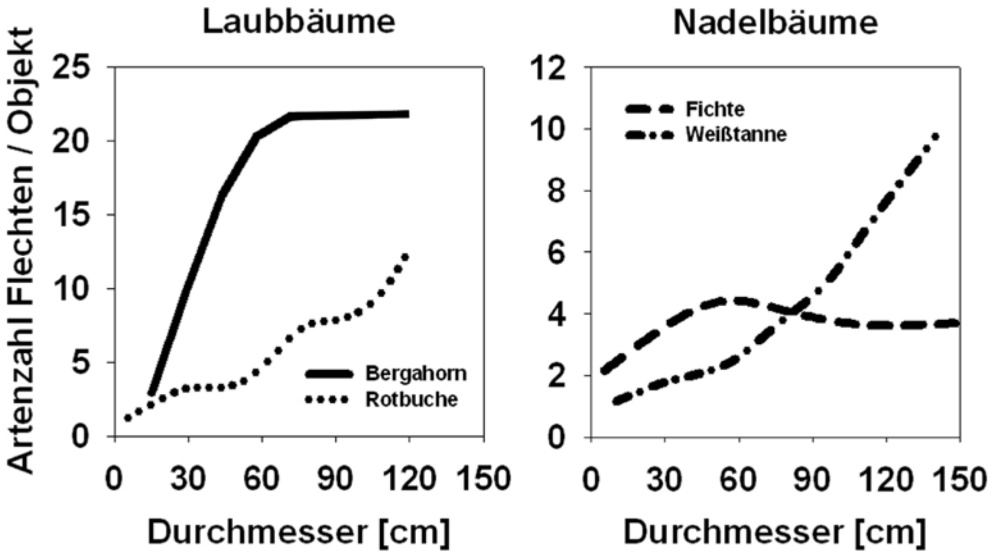


Abbildung 19. Artenzahl bei Flechten hinsichtlich einzelner Baumarten in Bezug auf die Stammdimension. Daten aus den Projekt-Untersuchungsflächen im Nationalpark Bayerischer Wald.

Abbildung 20. Stark dimensioniertes liegendes Totholz weist eine kontinuierliche Feuchtigkeit auf. Lebensbedingungen, die von den darauf spezialisierten Arten Rindenschröter (*Ceruchus chrysomelinus*), *Lacon fasciata* und *Ampedus auripes* bevorzugt werden (Fotos: Hintergrund: Arndt; Käfer: Jeniš)

Baumarten

- Mit Hilfe statistischer Methoden lassen sich beispielsweise unter den Vögeln Arten mit deutlichen Präferenzen für Laubwald herausarbeiten. Hierzu zählen Kernbeißer, Blaumeise, Waldlaubsänger und Kleiber. Der statistische Schwellenwert für das Vorkommen dieser Arten im Bergmischwald liegt bei einem Laubbaum-Mindestanteil in der Kronenschicht von 60 %.
- Der Bergahorn (*Acer pseudoplatanus*) wird schon bei relativ kleinen Dimensionen (ab BHD 60 cm) durch eine artenreiche Flechtengemeinschaft besiedelt. Auch Buche und Tanne erreichen bei starken Dimensionen artenreiche Flechtengemeinschaften. Die Fichte weist hingegen über die ganze Breite der Stammdurchmesser ein relativ ausgeglichenes, vergleichsweise niedriges Artenniveau bei den Flechten auf. Durch das Belassen rauborkiger Laubbäume, besonders Bergahorn, lässt sich bei vergleichsweise geringem Aufwand ein hoher Artenreichtum bei den Flechten sichern (Abb. 19).

Abbildung 21. Alte Bergahorne stellen besonders wertvolle Refugien unter anderem für eine artenreiche und bedrohte Flechtengemeinschaft dar. Sie sind im Bergmischwald unverzichtbare Bausteine für die Artenvielfalt und sollten keinesfalls wirtschaftlich genutzt werden. Da der Bergahorn nur einen kleinen Anteil des Bergmischwaldes ausmacht, lässt sich die grundsätzliche Nicht-Nutzung dieser Baumart auch mit wirtschaftlichen Interessen vereinen. (Foto: Schiener)

Baumhöhlen

- Die Berechnung des Einflusses von Höhlen auf die Höhlenbrüter ergab einen signifikanten Schwellenwert bei vier Höhlenbäumen je Hektar. Darüber, also ab fünf Höhlenbäumen verdoppelt sich die Zahl der Vogelarten mit Bruten in Baumhöhlen. Dies gilt sowohl für die Arten als auch für die Individuen. Soll die Zahl der höhlenbrütenden Vogelarten ein nachhaltiges Niveau erreichen, so müssen mindestens fünf Höhlenbäume pro Hektar belassen werden.

Abbildung 22. Der Sperlingskauz zählt im Bergmischwald zu den typischen Folgenutzern von Bunt- und Dreizehenspechthöhlen. (Foto: Moning)

- Im Nationalpark Bayerischer Wald konnten im Rahmen des DBU-Bergmischwald-Projektes durchschnittlich 1,5 Höhlenbäume bzw. 2,5 Höhlen je Hektar gefunden werden. Maximal wurden auf einem Hektar 12 Höhlenbäume und 31 Höhlen gefunden. Von den 850 kartierten Höhleneingängen konnten 78,6 % Spechten zugeordnet werden. Als überragende Faktoren für das Vorkommen von Höhlen wurden das Volumen an Totholz und das Alter des Baumbestandes identifiziert. Die höchsten Höhlendichten konnten folglich in alten Wäldern gefunden werden. In den Hochlagen-Fichtenwäldern findet man in den Prozessschutzflächen signifikant mehr Höhlen als in den Flächen, in denen der Borkenkäfer noch bekämpft wird. Der negative Einfluss von Wegen auf das Höhlenangebot konnte bestätigt werden.

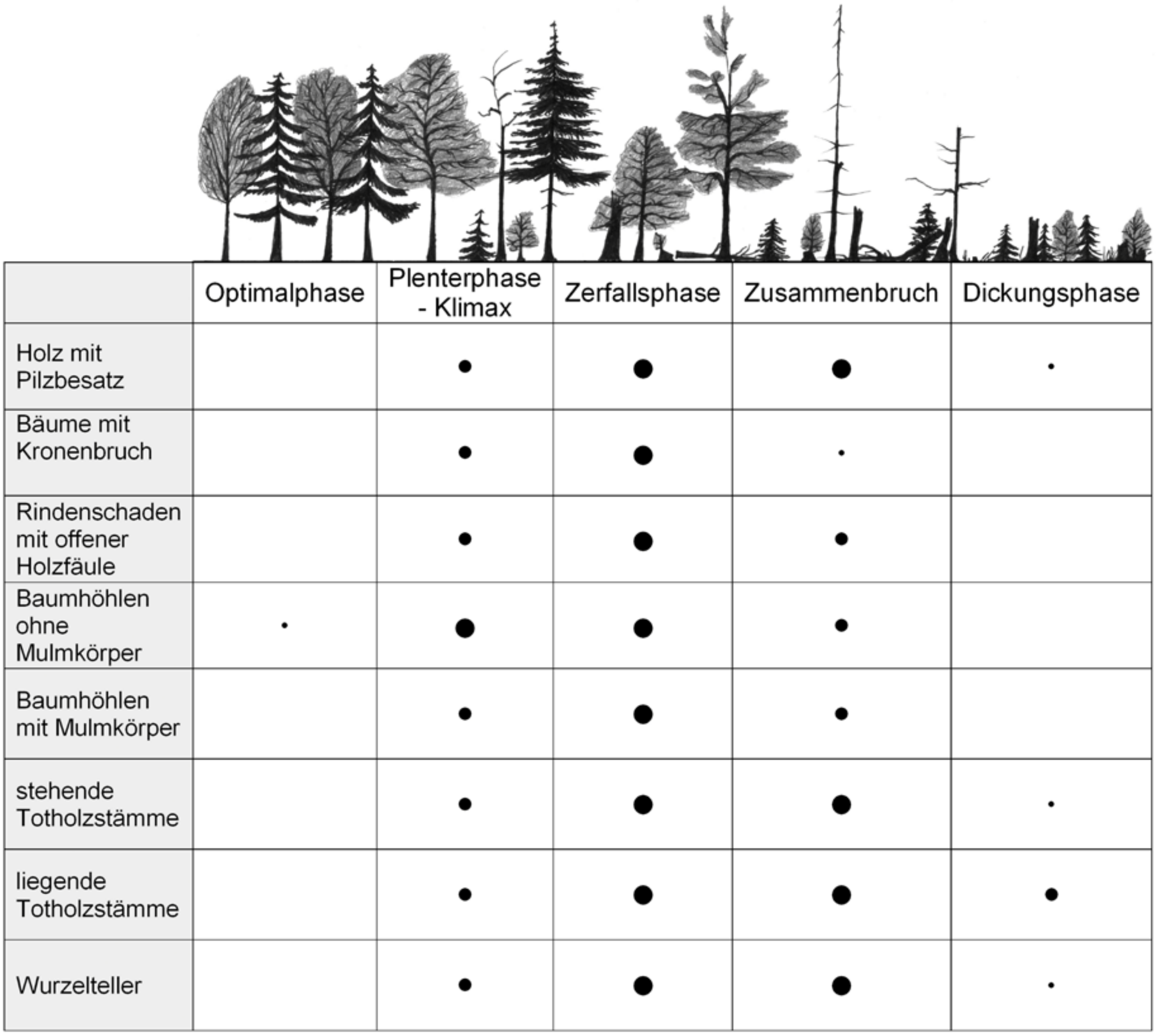
Rückschlüsse und Handlungsempfehlungen für die Forstwirtschaft

Aus dem DBU Projekt und der Literatur heraus ergibt sich eine Reihe von Schwellenwerten als Grundlage für eine Umsetzung von naturschutzfachlichen Verbesserungen in der Waldbewirtschaftung. Diese lassen sich nach verschiedenen Umweltvariablen differenzieren.

Totholz

Totholz besiedelnde Artengruppen und insbesondere bedrohte Arten unter den Totholzbesiedlern profitieren ab Totholzmengen von rund 30 m³/ha. Auf Flächen, die diesen Schwellenwert erreichen, sollte diese Menge auch zukünftig nicht unterschritten werden. Unter anderem auch, um eine fortwährende Habitattradition zu gewährleisten. Insbesondere in Beständen mit einem verhältnismäßig hohem Bestandsalter ab rund 140 Jahren sollte angestrebt werden, mindestens 30 m³ Totholz je ha zu erreichen. Diese Bestände müssen, um von anspruchsvollen Arten besiedelt zu werden, durch Korridore vernetzt sein.

Tabelle 5. Schematische Darstellung der Verfügbarkeit von Totholzstrukturen in den verschiedenen Waldentwicklungsphasen. Die Größe der Punkte gibt die verhältnismäßige Menge der einzelnen Strukturen wider.



	Optimalphase	Plenterphase - Klimax	Zerfallsphase	Zusammenbruch	Dickungsphase
Holz mit Pilzbesatz		•	●	●	·
Bäume mit Kronenbruch		•	●	·	
Rindenschaden mit offener Holzfäule		•	●	•	
Baumhöhlen ohne Mulmkörper	·	●	●	•	
Baumhöhlen mit Mulmkörper		•	●	•	
stehende Totholzstämme		•	●	●	·
liegende Totholzstämme		•	●	●	•
Wurzelteller		•	●	●	·

Empfehlungen zur Sicherung der notwendigen Mindestmengen Totholz:

- Durch Sommerstürme, Schneebruch und Windwurf gebrochene und absterbende Bäume sind im Wirtschaftswald gezielt zu belassen.

- Gerade ganze Bäume, vor allem bei Absterben über einen langen Zeitraum, liefern eine hohe Zahl an verschiedenen Totholztypen und -dimensionen, besonders diese belassen.
- Bevorzugt Baumteile, die nach Stürmen anfallen mit Durchmessern bei Fichtentotholz >20 cm und Buchen- und Tannentotholz >50 cm belassen.
- Auf Windwürfen mit aufgestelltem Wurzelteller Hochstubben belassen, Wurzelteller nicht zurückklappen.
- Im Zuge aller Hiebsmaßnahmen gezielt Starkkronen oder ökonomisch weniger wertvolle Stammteile liegen lassen.
- Brennholzwerber weniger in Altholzhieben, sondern bevorzugt in Pflegebestände mit geringeren Altern und Dimensionen einsetzen.
- Bei Windwurfflächen mindestens auf 0,5 ha Größe Totholzstrukturen erhalten.

Abbildung 23. Für die Verjüngung von Fichten spielt Totholz eine herausragende Rolle. Die jungen Fichten genießen auf stärker vermoderten Baumstämmen eine geringere Konkurrenz gegenüber Gräsern und krautigen Pflanzen, eine optimale Wärme- und Lichtversorgung sowie eine günstige Nährstoffversorgung. Am Boden liegendes Totholz wirkt ausgleichend für das Mikroklima. Die dunkle Oberfläche und die geringe Wärmeleitfähigkeit von Holz führen dazu, dass Totholz gegenüber der Umgebung bei Sonneneinstrahlung eine erhöhte Temperatur aufweist. Andererseits kann Totholz seine unmittelbare Umgebung auch vor Überhitzung schützen, da es infolge des erhöhten Wassergehalts Temperaturschwankungen auszugleichen vermag. Somit ist auch der umgebende Boden besser vor Austrocknung geschützt. (Foto: Pöhlmann)

Waldalter

Ab einem Baumalter von rund 200 Jahren erreicht die Artendichte bei verschiedenen Artengruppen wie Flechten, Mollusken und Vögeln ein dauerhaft statistisch signifikant höheres Niveau. Der ansteigende Trend beginnt bei einem Bestandsalter von 140 Jahren im Bergmischwald. Daher sollten neben der Nicht-Nutzung von Einzelbäumen in einem räumlich möglichst engmaschigen Netz immer wieder alte Bestände als Trittsteine und Refugien für Arten, die auf Urwaldstrukturen angewiesen sind, ungenutzt bleiben. Dies kann beispielsweise in Form von Naturwaldreservaten bei größeren Flächen aber auch durch Klassifizierung von Beständen als Naturschutzvorrangfläche (z.B. arB-Flächen) erfolgen. Durch höhere Totholzmengen und Baumartenvielfalt bieten sich häufig auch Fließgewässer begleitende Bestände als Vernetzungsstrukturen an. Die größte Bedeutung weisen heute sehr alte Bergmischwälder mit einem Alter von über 200 Jahre auf.

Empfehlungen zur Sicherung alter Bäume und Bestände:

- In den meisten Waldgebieten sind alte Bestände (>200 Jahre) nur noch in Resten vorhanden. Daher sollten sie von einer weiteren Nutzung verschont bleiben.
- Wo auf Grund größerer Flächen eine Nutzung unverzichtbar erscheint, sollte diese auf wenige ökonomisch besonders wertvolle Bäume beschränkt bleiben. Letztere sind ökologisch meist von untergeordneter Bedeutung.
- In reifen (>140 Jahre) Beständen sollten gerade ältere Einzelbäume und alle Baumindividuen, die Höhlen, Stammschäden, Kronenbrüche und andere deutliche Merkmale von Biotopbäumen aufweisen, in einem Umfang von mindestens 10 pro ha erhalten werden.
- In jüngeren Beständen (<140 Jahre) sollten bei der Auswahl von Erntebäumen gezielt Individuen mit ersten Verletzungen belassen werden, um daraus später Biotopbäume entstehen zu lassen.
- Wo immer die Zahl geeigneter Biotopbäume auf Grund der langen Nutzungstradition sehr gering ist, sollten durch aktive Maßnahmen Biotopbäume induziert werden.

Waldlücken

Wie oben gezeigt, treten unter den kühlen klimatischen Bedingungen von Bergwäldern lichtbedürftige Arten erst ab Lückengrößen von mindestens 0,5 ha signifikant zahlreicher auf. Für eine maximale Artenvielfalt sollte diese Lückengröße bei der Planung forstlicher Maßnahmen berücksichtigt werden. Dabei gilt es zu bedenken, dass einige Artengruppen wie Flechten und holzbewohnende Käfer in diesen Waldlücken erst bei ausreichendem Substrat- also Totholzangebot auftreten. Ein breiter Gradient der Kronendachöffnung zwischen 15 und 50 % über eine größere

Fläche bewirkt, dass alle ökologischen Nischen bei den Strauchbewohnern unter den Vögeln bedient werden und somit eine hohe Artenvielfalt erzeugt wird.

Empfehlungen zur Sicherung licht- und wärmeliebender Bergmischwaldarten:

- Lücken im Bergwald sind nach natürlichen Dynamiken aber auch im Rahmen der Holzernte zu zulassen und zu schaffen. Dabei gilt es markante Öffnungen (mindestens 0,5 ha) in der Waldlandschaft regelmäßig aktiv und passiv anzubieten.
- Um die positiven Effekte solcher Lücken tatsächlich ausreichend zu erzielen, ist immer wieder auf Pflanzung zu verzichten. Nur so kann das wärmebegünstigte Kleinklima auch über mehrere Jahre hinweg erhalten bleiben.
- Für wärmeliebende Totholzbewohner ist gezielt in diesen Lücken Totholz zu belassen.
- Generell bietet ein breites Angebot an verschiedenen Auflichtungsgraden in der Waldlandschaft die beste Grundlage für das Überleben einer Vielzahl anspruchsvoller Arten. Ereignisse wie Borkenkäferbefall, Windwürfe können dabei genutzt werden.

Abbildung 24. Windwürfe, wie hier im Nationalpark Bayerischer Wald, verändern die Lichtsituation am Boden schlagartig. Bis zur Wiederbewaldung stellen solche Flächen besonders bei Belassen des Totholzes Zentren der Artenvielfalt in Bergmischwäldern dar. (Foto: Stephan)

Baumhöhlen

Mindestens fünf Höhlenbäumen je Hektar gewährleisten signifikant hohe Niveaus bei Arten und Individuen bei den höhlenbrütenden Vögeln. Dabei handelt es sich nicht zwangsläufig um starke Bäume. Gerade Zwischenständer die im Laufe der Jahre immer wieder Streifschäden erlitten haben, sind häufig als Höhlenbäume ebenso wichtig. Daher ist sowohl auf die leicht erkennbaren stärkeren Höhlenbäume, wie sie die Spechte anlegen, zu achten, aber auch gezielt nach dünnen Höhlenbäumen zu suchen.

Empfehlungen zur Sicherung eines ausreichenden Höhlenangebotes:

- Je Hektar sind mindestens 5 Höhlenbäume, wo vorhanden, dauerhaft zu markieren und von einer Nutzung zu verschonen.
- Nachdem Höhlen generell Mangelware sind, sollten bei Höhlenkonzentrationen lokal auch deutlich höherer Werte erhalten werden.
- Nachdem Spechthöhlen viele Folgenutzer haben, sollten sie auch langfristig erhalten bleiben, da an ihnen im Laufe der Zeit wichtige Totholzstrukturen wie Mulmhöhlen entstehen.
- Stehendes Totholz ist eine wichtige Grundlage für die Anlage von Höhlen und sollte aus diesem Grund im Zuge der Totholzanreicherung (s. oben) belassen werden.
- Der Bergahorn bietet überdurchschnittlich oft Höhlen und Halbhöhlen bereits auch bei schwächeren Dimensionen. Daher ist er besonders zu berücksichtigen.

Baumartenzusammensetzung

Das besondere Merkmal von Bergmischwäldern ist das natürliche gemeinsame Vorkommen von Laub- und Nadelbäumen. Natürliche Bergmischwälder weisen in Deutschland einen hohen Buchen- und Tannenanteil auf. Arten, die Laubwälder bevorzugen sind hier häufig in ihrer Verbreitung durch die Förderung der Fichte zurückgedrängt worden. Alte Bergahorne stellen besonders wertvolle Refugien unter anderem für eine artenreiche und bedrohte Flechtengemeinschaft dar.

Empfehlungen zur Sicherung der Baumartenvielfalt

- Bergahorne sind im Bergmischwald besonders unverzichtbare Bausteine für die Artenvielfalt und sollten daher nur in Ausnahmefällen wirtschaftlich genutzt werden.
- Um das Vorkommen Laubwald-bevorzugender Vogelarten zu gewährleisten, ist auf Bestandsebene ein Laubbaumanteil von mindestens 60 % erforderlich.
- Die Tanne als ökologisches Bindeglied von Laub- und Nadelbaumbewohnern wird besonders im hohen Alter bedeutsam für viele gefährdete Arten. Daher ist die Sicherung von Alttannen mit über 300 Jahren anzustreben.

Umsetzung der Schwellenwerte in ein betriebliches Naturschutzkonzept

Viele der aus dem Projekt resultierenden Schwellenwerte liegen weit über dem Flächendurchschnitt der meisten Betriebe im Bergmischwaldbereich. Diese auf ganzer Fläche in einem ökonomisch orientierten Forstbetrieb zu überschreiten, kommt als Ziel demnach nicht in Frage. Die Schwellenwerte lassen sich vielmehr zur Identifikation der naturschutzfachlichen „Hotspots“ sowie weiterer Flächen in denen vorrangig Naturschutzziele verfolgt werden sollen, innerhalb der Gesamtbetriebsfläche verwenden.

Forstinventurdaten bieten hier eine hervorragende Grundlage, um Schwellenwerte in flächige Naturschutzkonzepte umzusetzen. Sie sind überregional flächig verfügbar, wurden bislang jedoch erst wenig für naturschutzfachliche Anwendungen genutzt (z.B. MÜLLER et al. 2009). Obwohl Forstinventurdaten aus einem groben Raster bestehen (die Entfernung zwischen den Stichprobepunkten beträgt 100-200 m) können sie für betriebliche Gesamtkonzeptionen (Durchschnitt Betriebsfläche Bayerische Staatsforsten (reine Waldfläche): 17.500 ha) eine ausreichend genaue Übersicht liefern.

In dem DBU-Bergmischwaldprojekt wurden die Schwellenwerte (Tabelle 6) auf Basis der Inventurdaten in ein Naturschutzkonzept für bergmischwald-dominierte Betriebe exemplarisch umgesetzt (Tabelle 7). Dazu musste in einem ersten Schritt aus den Inventurpunkt-Daten eine flächige Information erstellt werden. Zu diesem Zweck wurde das so genannte Kriging-Verfahren angewendet, bei dem Inventur-Punktdaten auf die Fläche interpoliert werden.

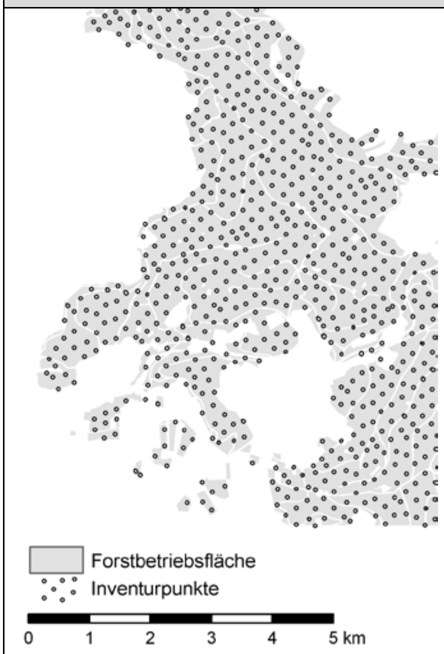
Das Kriging-Verfahren liefert für die einzelnen Schlüsselwerte flächige und stufenlose Daten. Diese wurden dann gemäß den Schwellenwerten klassifiziert (Tabelle 6), so dass sich folgende Flächenkategorien abbilden lassen (Tabelle 7):

1. Flächen, in denen die Schwellenwerte überschritten sind.
2. Flächen, in denen nur Teile der Schwellenwerte überschritten sind.
3. Flächen, in denen keiner der Schwellenwerte überschritten ist.

Tabelle 6. Für das Kriging-Verfahren genutzte Schwellenwerte.

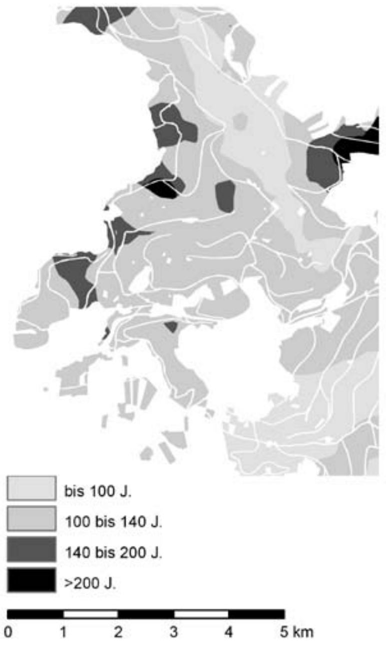
Alter	Ab 140 Jahren tritt bei vielen Artengruppen eine statistisch nachweisbar höhere Artendichte auf, der Schwellenwertbereich ist ab einem Bestandsalter von 200 Jahren überschritten.
Totholz	Ab 30 m³/ha bis 60 m³/ha treten Totholz nutzende und besiedelnde Arten häufiger auf. Der Schwellenwertbereich ist ab 60 m³/ha überschritten. Nach CHRISTENSEN et al. (2005) wurde die Schwelle für Totholzmengen durch den Faktor 1,19 dividiert, um die Totholzschwellen, die auf der Kluppschwelle 12 cm basieren auf 20 cm der Forstinventur anzupassen.
Laubholzanteil	Die Schwelle für laubbaumabhängige Vogelarten liegt bei 60 % Laubholzanteil.

Tabelle 7. Ablaufschema des Bewertungsverfahrens: Von den Inventurpunkten bis zu den Handlungsempfehlungen. Dargestellt ist ein Ausschnitt eines bayerischen Bergmischwald-dominierten Betriebes.

Schritt 1: Forstinventur	
	Die Forstinventurpunkte geben die Grundinformationen vor. In einem Raster von 100 m (bzw. 200 m in Montanlagen) Probepunktabstand werden auf konzentrischen Probekreisen (0,05 ha) Daten wie Baumarten, Altersstrukturen, Wachstums- und Holzvorräte erfasst.

Schritt 2: Die Darstellung der Schwellenwerte mit Hilfe des Kriging Verfahrens (Schwellenwertanalyse)

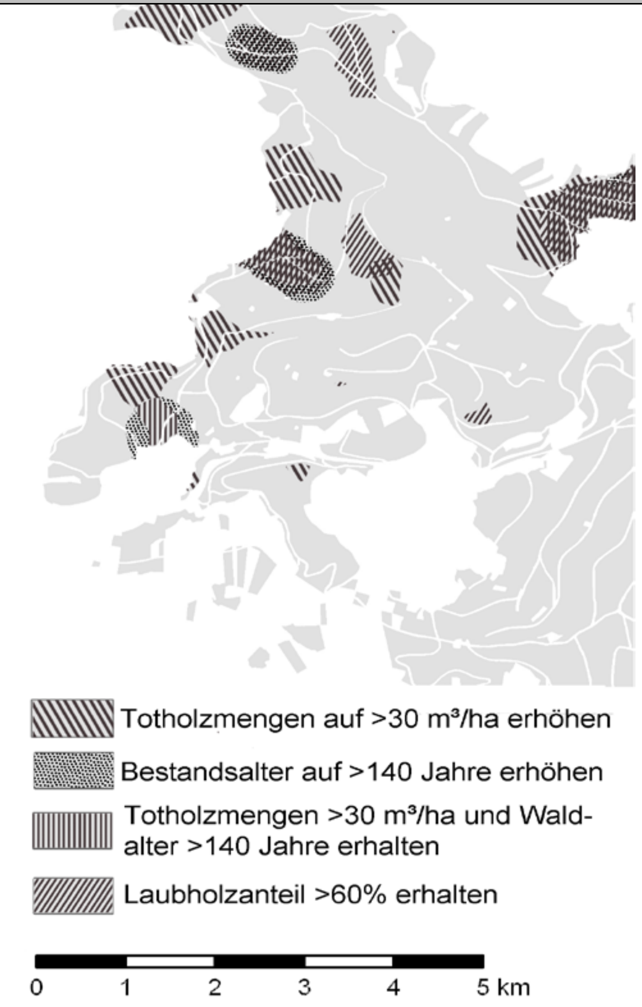
Waldalter



Totholz

Laubholzanteil

Schritt 3: Handlungsempfehlungen aus der Verschneidung der Schwellenwertanalyse



In der Synthese der überlagerten Flächen aus der Schwellenwertanalyse werden Managementempfehlungen abgeleitet. In Bereichen, die den Alters-Schwellenwertbereich von 140 Jahren erreichen, wird eine Totholzanreicherung auf über 30 m³/ha empfohlen. In Bereichen mit hohen Totholzsummen von über 30 m³/ha wird ein Belassen des überschirmenden Bestandes bis in ein Waldalter von über 140 Jahren empfohlen. In Bereichen, die bereits einen Laubholzanteil von über 60 % aufweisen, wird empfohlen, den hohen Laubbaumanteil zu erhalten.

Auf diesen Flächenkategorien basierend konnten Handlungsempfehlungen abgeleitet werden (Schritt 3, Tabelle 7). Flächen der Kategorie 1 sind naturschutzfachliche Kernflächen. In ihnen steht der Erhalt der Qualität der vorliegenden Schwellenwerte im Vordergrund. Flächen der Kategorie 2 sind Entwicklungsflächen. In ihnen wird das Überschreiten der Schwellenwerte angestrebt. Dabei sollte insbesondere in Beständen mit einem verhältnismäßig hohen Bestandsalter ab rund 140 Jahren angestrebt werden, mindestens 30 m^3 Totholz je ha zu erreichen. Diese Bestände bieten eine große Nischenvielfalt, die durch die alten Bäume entsteht. Im Zusammenhang mit hohen Totholzmengen können sie Lebensraum gerade für hoch spezialisierte Tier- und Pflanzengruppen bieten. Flächen der Kategorie 3 sind schließlich ökonomische Vorrangflächen. Dies soll nicht bedeuten, dass dort langfristig nicht auf naturnähere Waldbestände hingearbeitet werden soll (z.B. Laubholzeinbringung in Fichtenreinbeständen, Entwicklung von Biotopbäumen, Erhalt und Markierung von Höhlenbäumen).

Auf Basis der naturschutzfachlichen Kernflächen und der Entwicklungsflächen können auch Empfehlungen für die Etablierung von Habitatkorridoren abgeleitet werden, denn wenn naturschutzfachlich wertvolle Flächen von anspruchsvollen Arten besiedelt werden sollen, müssen sie durch Korridore vernetzt sein. Dazu bieten sich vor allem die Flächen der Kategorie 2 an, soweit diese zwischen Flächen der Kategorie 1 vorhanden sind. Neben dem Anstreben der Schwellenwerte lässt sich die Vernetzung auch durch weitere Einzelmaßnahmen verbessern, z.B. den Erhalt oder die Schaffung von Biotopbäumen, oder den Erhalt und die Verbesserung bachbegleitender Baumbestände, die meist baumarten- und totholzreicher als die Durchschnittsbestände sind.

Die Umsetzung der Schwellenwerte in ein Naturschutzkonzept, lässt sich in die laufende Forsteinrichtung integrieren, die Grundlage für die zukünftige Behandlung der Waldflächen ist. Dabei bietet die kartografische Darstellung der Schwellenwerte und Flächenkategorien den Vorteil, dass sich im Rahmen der fortlaufenden Forstinventur nachvollziehen lässt, ob sie berücksichtigt bzw. umgesetzt wurden, was sich anderweitig bei flächig angewandten Naturschutzkonzepten nicht immer feststellen lässt. Das Verfahren kann jederzeit mit neuen Variablen (bei neuem Wissenszuwachs) ergänzt bzw. in einer Region nicht relevante Variablen weggelassen werden. Daneben kann auf diese Weise zu ersten Mal ein objektives Controlling von Naturschutzbelangen in die allgemeine Betriebsplanung integriert werden.

Die bisherigen Erfahrungen aus der Anwendung des vorgestellten Verfahrens in drei Forstbetrieben der Bayerischen Staatsforsten zeigt, dass man selbst in Betrieben mit sehr hohem naturschutzfachlichen Potenzial über die Schwellenwerte zu einer flächendifferenzierten Planung kommen kann, wo vorher noch das „Schreckgespenst“ einer durch flächenhaften Naturschutz unmöglichen Nutzung im Raum stand.

Diskussion

Dem Ergebnisteil und den zahlreichen Publikationen, die auch im Anhang wiedergegeben sind, ist zu entnehmen, dass die anvisierten Projektziele vollends erreicht wurden. Es konnten nicht nur zahlreiche und repräsentative Schwellen- und Schlüsselwerte für Bergmischwälder erarbeitet werden. Auch wurden durch die Publikationen sowohl der Wissenschaftszweig als auch der Anwenderzeig (Förster) erfolgreich adressiert. Darüber hinaus gelang es gemäß dem Arbeitsplan ein Fortbildungsmodul für die Bayerischen Staatsforsten zu erproben und über die Landesanstalt für Wald und Forstwirtschaft für die Zukunft zu etablieren (siehe Kapitel Öffentlichkeitsarbeit). Dass die Projektergebnisse Eingang in das Naturschutzkonzept der Bayerischen Staatsforsten fanden, ging sogar über die Projektziele hinaus.

Die Zusammenarbeit mit den Kooperationspartnern war stets zielführend, unbürokratisch und von durchgehend konstruktivem Charakter. An der Tatsache, dass die Bayerische Landesanstalt für Wald und Forstwirtschaft das Fortbildungsmodul in Kooperation mit den Bayerischen Staatsforsten fortführt und dass die Bayerischen Staatsforsten die erarbeiteten Werte und Konzepte in die eigenen Naturschutzkonzepte integriert, ist deutlich abzulesen, dass die Projektpartner stets großes Interesse an der Umsetzung der Projektergebnisse hatten.

Öffentlichkeitsarbeit

Neben zahlreichen öffentlichen Vorträgen fanden die Ergebnisse des Projektes Eingang in viele wissenschaftliche Publikationen. Diese sind ein wesentliches Ergebnis des Projektes. Eine Übersicht ist in Tabelle 8 zusammengestellt.

Über die Publikation wissenschaftlicher Arbeiten hinaus zielte das Projekt auf die Vermittlung der Ergebnisse in Forstkreisen. Viele der Schwellenwerte werden durch forstliche Maßnahmen auf Bestandsebene beeinflusst. Es ist daher unerlässlich, dass Forstleute die Schlüsselstrukturen sehen und schätzen lernen. Dies wird durch ein Fortbildungsmodul erreicht, das exemplarisch für die Revierleiter im Forstbetrieb Neureichenau im Herbst 2009 durchgeführt wurde: Der Vormittag bestand aus einer Reihe von Vorträgen, welche die wesentlichen Ergebnisse des Projektes vermittelt haben. Den Nachmittag bildete ein praktischer Teil. Dabei wurden drei Beispielbestände im Forstbetrieb Neureichenau besucht. Für diese wurden zuvor die wesentlichen Bestandsdaten ausgemessen. Die Revierleiter mussten nun diese Bestandsdaten schätzen. Anschließend wurden die Einschätzungen miteinander verglichen und diskutiert. So entstand bei den Revierleitern ein „Gefühl“ für Totholzmengen. Gleichzeitig konnten Details wie Wegesicherheit, Höhlenbaumangebot und die Auszeichnung von Waldbeständen (Selektion naturschutzfachlich wichtiger Bäume) diskutiert werden. Erst wenn Revierleiter und Waldarbeiter Waldbilder richtig einschätzen lernen, können

Schwellenwerte wirklich Eingang in die forstliche Praxis finden. Dieses Fortbildungsmodul wurde für 2010 für die Bayerischen Staatsforsten als zweitägiges Ausbildungsmodul von der Bayerischen Landesanstalt für Wald und Forstwirtschaft angemeldet.

Der Exkursionsführer mit Angaben zu den Beispielbeständen, die Kernpunkte der erarbeiteten Fortbildung sind, findet sich im Anhang dieses Berichtes. Der Band 19 der Wissenschaftlichen Reihe des Nationalparks Bayerischer Wald fasst die wesentlichen Ergebnisse des Projektes in allgemeinverständlicher Form zusammen. Er dient als Fortbildungsunterlage und wurde neben dem Kontingent, das der Nationalpark regulär drucken lässt, auch in 500 Stück auf Projektkosten gedruckt, so dass er im Rahmen der Fortbildung verteilt werden kann. Für diesen Band wurde großer Aufwand getrieben, ihm eine ansprechende Gestalt und Bebilderung zu geben. Der Band liegt dem Bericht bei.

Tabelle 8. Artikel, die im Rahmen des Projektes entstanden sind.

Autoren	Jahr	Titel	Publikationsorgan	Nr., Seitenzahl	Zielgruppe
Bässler, C., B. Förster, C. Moning & J. Müller	2008	The BIOKLIM Project: Biodiversity research between climate change and wilding in a temperate montane forest- The conceptual framework	Waldökologie, Landschaftsforschung und Naturschutz	7, 21-33	Wissenschaft, interessierte Förster
Kanold, A., N. Rohrmann & J. Müller	2008	Einflussfaktoren auf das Baumhöhlenangebot und dessen Auswirkungen auf die Arten und Dichten von Höhlenbrütern in Bergwäldern	Ornithologischer Anzeiger	47, 116-129	Wissenschaft, interessierte Förster
Moning, C. & J. Müller	2008	Environmental key factors and their thresholds for the avifauna of temperate montane forests	Forest Ecology and Management	256, 1198-1208	Wissenschaft, interessierte Förster
Moning, C. & J. Müller	2009	Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests	Ecological Indicators	9, 922-932	Wissenschaft, interessierte Förster
Moning, C., S. Werth, F. Dziock, C. Bässler, J. Bradtka, T. Hothorn & J. Müller	2009	Lichen diversity in temperate montane forests is influenced by forest structure more than climate	Forest Ecology and Management	258, 745-751	Wissenschaft, interessierte Förster
Müller, J. & R. Brandl	2009	Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages	Journal of Applied Ecology	46, 897-905	Wissenschaft, interessierte Förster
Müller, J., C. Bässler, C. Strätz, B. Klöcking & R. Brandl	2009	Molluscs and climate warming in a low mountain range national park	Malacologia	5, 89-109	Wissenschaft, interessierte Förster
Müller, J., C. Moning, C. Bässler, M. Heurich & R. Brandl	2009	Using airborne laser scanning to model potential abundance and assemblages of forest passerines	Basic and Applied Ecology	-	Wissenschaft, interessierte Förster
Müller, J., J. Stadler & R. Brandl	2009	Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of LiDAR	Remote Sensing of Environment	-	Wissenschaft, interessierte Förster
Moning, C., R. Moshammer & J. Müller	2009	Umsetzung ökologischer Schwellenwerte in betriebliche Naturschutzkonzepte in Bergmischwäldern	Naturschutz und Landschaftsplanung	-	Förster und Planer
Moning, C., H. Bussler & J. Müller	2009	Schlüsselwerte in Bergmischwäldern als Grundlage für eine nachhaltige Forstwirtschaft	Wissenschaftliche Reihe des Nationalparks Bayerischer Wald	19, 100 S.	Förster, Planer, interessierte Laien

Abbildung 25. Waldbilder mit den zugehörigen Totholzmengen. Für die effiziente Umsetzung von Totholzkonzepten ist die korrekte Ansprache von Totholzmengen unverzichtbar. (Bilder v.l.n.r.: Schiener, Becker, Moning, Arndt, Müller)

Fazit

Abschließend lässt sich feststellen, dass sich das anvisierte Konzept vollends bewährt hat. Wie dem Arbeitsplan (Tabelle 3) zu entnehmen ist, wurden die im Antrag festgelegten Arbeitsschritte im beantragten Zeitrahmen bewältigt. Während der gesamten Projektlaufzeit wurden keine Änderungen der Zielsetzung notwendig. Dies war nicht zuletzt durch die Mitarbeit zahlreicher Experten möglich. Auch die Kooperation mit dem BIOKLIM-Projekt, das im selben Sachgebiet innerhalb der Nationalparkverwaltung angesiedelt ist, hat sich sehr bewährt. Aus diesem Projekt konnte unter anderem auf Klima-, Struktur- und Vegetationsdaten zurückgegriffen werden, die bei der Analyse der im DBU-Projekt erarbeiteten Daten von großer Bedeutung waren.

Es hat sich auch bewährt, die wesentlichen Auswertungsschritte schon vorab festzulegen. Nur so konnten die Ergebnisse in wissenschaftlichen Publikationen verbreitet werden. Gleichzeitig blieb durch die zeitnahe Umsetzung der Ergebnisse in wissenschaftliche Publikationen genügend Zeit, auch Fortbildungen, Vorträge und populärwissenschaftliche Publikationen zu erarbeiten.

Nicht zuletzt war es auch durch die unbürokratische Zusammenarbeit mit der DBU, namentlich Dr. Stock möglich, im Rahmen einer kostenneutralen Projektverlängerung ein Abschlusskolloquium zu organisieren und durchzuführen. Dabei konnte ein weiter Expertenkreis erreicht werden. Neben den Publikationen dürfte der Eingang der Ergebnisse in das Naturschutzkonzept der Bayerischen Staatsforsten einer der Haupterfolge des Projektes sein.

Das langfristig bedeutendste Ergebnis des Projektes sind die zahlreichen Schlüssel- und Schwellenwerte, die eine wichtige Lücke für die forstliche Praxis schließen. Sie könnten darüber hinaus auch Anwendung in der Landschaftsplanung im Rahmen der Ausgleichsplanung finden.

Literaturangaben

Die folgenden Literaturangaben beziehen sich nur auf die in diesem Bericht zitierte Literatur. Da viele der Projektergebnisse publiziert wurden, und der Bericht auf diese Quellen zurückgreifen kann, ist die Aufstellung bei weitem nicht vollständig. Für eine umfassende Literaturübersicht zu dem Thema Schwellenwerte in Wäldern sind die Literaturangaben der publizierten Artikel heranzuziehen. Diese sind im Anhang wiedergegeben.

BÄSSLER, C., B. FÖRSTER, C. MONING & J. MÜLLER (2008): The BIOKLIM Project: Biodiversity research between climate change and wilding in a temperate montane forest – The conceptual framework. – Waldökologie, Landschaftsforschung und Naturschutz 7, 21-33.

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MÜLLER, J. & R. BRANDL (2009): Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. - Journal of Applied Ecology 46, 897-905.

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MÜLLER, J., J. STADLER & R. BRANDL (2009): Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of LiDAR. - Remote Sensing of Environment, in Druck.

Anhang

Artikel, die im Rahmen des Projektes entstanden sind

Im Folgenden sind die in Tabelle 8 aufgezählten Publikationen zusammengestellt. Der Band 19 aus der Wissenschaftlichen Reihe des Nationalparks liegt diesem Bericht jedoch gesondert bei.

Artikel 1: The Bioklim Project: Biodiversity research between climate change and wilding in a temperate montane forest – The conceptual framework

Status: Publiziert in Waldökologie, Landschaftsforschung und Naturschutz 7, 2008.

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Waldökologie, Landschaftsforschung und Naturschutz | Heft 7 | Seite 21-33 | 5 Fig., 4 Tab. | Freising, August 2008

The BIOKLIM Project: Biodiversity Research between Climate Change and Wilding in a temperate montane forest – The conceptual framework

Claus Bässler, Bernhard Förster, Christoph Moning and Jörg Müller

Abstract

To understand the rapid rate of change in global biodiversity, it is necessary to analyse the present condition of ecosystems and to elucidate relationships of species to their environment. The BIOKLIM Project (Biodiversity and Climate Change Project) is intended to close this gap in our knowledge of montane and high montane forests of Central European low mountain ranges, one of the most threatened mixed montane systems worldwide. The Bavarian Forest National Park is characterised by its altitude range of ca. 800 m and a strongly developed gradient of forest structure. Relicts of old growth forests (areas of former local nature reserves) and dead stands, mostly killed by bark beetles, are accompanied by widely varying levels of woody debris and light. The gradients comprise a wide range of abiotic and forest structure factors, making the study area well suited for a multidisciplinary investigation of biodiversity. Unconstrained ordination (CA) of six taxa (vascular plants, wood inhabiting fungi, birds, carabids, spiders and molluscs) indicate the altitudinal gradient to be the main driver for distribution patterns of species assemblages.

Objectives, structure, study design and data sampling of the BIOKLIM Project are described in detail. We set up 293 sampling plots along four main straight transects following the altitudinal gradient. All abiotic and stand structure data regarded as relevant are available for each plot. Vascular plants, wood inhabiting fungi and birds were sampled or mapped on all 293 plots. For the other 22 investigated taxa we used subsamples pre-stratified according to the sampling methods. The necessity of dealing with spatial autocorrelation, arising from sampling along linear transects, is described. Finally, study approach of our biodiversity project is compared with others involving altitudinal gradients. Worldwide, only a few multidisciplinary biodiversity studies have been previously conducted on long altitudinal gradients. However, in most cases sampling techniques were similar to ours, which allows comparison of results between continents.

Keywords: Climate Change, Biodiversity, species-environment relationships

Zusammenfassung

Um die rasante Veränderung globaler Biodiversität zu verstehen, ist es erforderlich, den gegenwärtigen Zustand von Ökosystemen zu analysieren und die Zusammenhänge zwischen Arten und deren Umwelt aufzulösen. Das BIOKLIM-Projekt (Biodiversität und Klima Projekt) hat zum Ziel, diese Wissenslücken für Wälder montaner und hochmontaner Mittelgebirge zu schließen. Der Nationalpark Bayerischer Wald ist neben dem Höhengradient (ca. 800 m) durch einen starken Strukturgradient geprägt. Dieser resultiert aus Restvorkommen sehr alter Bestände (ehem. Naturschutzgebiete) sowie dem Wirken des Borkenkäfers seit ca. zwei Jahrzehnten und einem dadurch verbundenen z.T. sehr hohen Totholzvorrat. Die Gradienten umfassen eine breite Spanne von abiotischen Faktoren und Bestandesstrukturen und machen den Nationalpark zu einem gut geeigneten Untersuchungsgebiet für interdisziplinäre Biodiversitätsforschung. Korrespondenzanalysen (CA) für 6 taxonomische Gruppen (Gefäßpflanzen, Holzpilze, Vögel, Laufkäfer, Spinnen und Mollusken) machen die starke Abhängigkeit der Artengruppen vom Höhengradienten deutlich.

Es werden detailliert die Zielsetzungen, Projektaufbau, das Untersuchungsdesign sowie die Erfassungsmethoden des BIOKLIM-Projektes beschrieben. 293 Probepunkte wurden entlang von 4 Transekten, welche dem Höhengradienten folgen, eingerichtet. Zu jedem Probekreis stehen alle als relevant erachteten Daten zur Abiotik und Bestandesstruktur zur Verfügung. Gefäßpflanzen, Holzpilze und Vögel wurden auf allen 293 Probepunkten erfasst. Für die anderen 22 untersuchten Artengruppen wurde in Abhängigkeit von der Methode ein stratifiziertes Design gewählt. Lösungsansätze zum Umgang mit Autokorrelation, die durch die Anordnung von Probekreisen entlang von Linien (Transekte) bedingt ist, werden dargestellt. Schließlich wird das BIOKLIM-Projekt mit den wenigen weltweiten Biodiversitätsprojekten verglichen und diskutiert. In den meisten Fällen sind die Erhebungsmethoden ähnlich, sodass Vergleiche der Ergebnisse zwischen verschiedenen Kontinenten möglich werden.

Schlüsselwörter: Klimawandel, Biodiversität, Arten-Umwelt-Beziehung

Introduction

Loss of habitat and living space has accelerated enormously in the last few decades, caused by changes in land use and global climate. Destruction takes place faster than our understanding of natural systems improves (Wilson 1992). Global biodiversity is changing at an unprecedented rate as a complex response to several changes induced by humans in the global environment (Sala et al. 2000, Travis 2002, Hooper et al. 2005). As a result of this rapid rate of change there is a growing need to record and analyse the present state of ecosystems, to establish relationships of species to the environment, and to use this data for assessing and predicting further changes caused by anthropogenic influence (land use and climate change). It follows that a major challenge is to determine how biodiversity dynamics, ecosystem processes and abiotic factors correlate (Loreau et al. 2001). Furthermore, there is a clear need to increase our ability to predict the consequences of environmental change (Sutherland 2006). Averaged across all biomes (Boreal, Arctic, Grassland etc.), land use change and climate change are the driving factors which are expected to have the largest global impact on biodiversity by the year 2100 (Sala et al. 2000). Global air temperature increased in the 20th century by about 0.74K. The global trend is reflected in rapid atmospheric warming during the last decades. 11 of the last 12 years were the warmest since the measurement of climate parameters began (IPCC 2007b). This development has most probably been caused by anthropogenic greenhouse gas emissions, especially carbon dioxide (IPCC 2007b). Latest scenarios predict further warming (IPCC 2007b). The probable value for the lowest scenario until the end of this century is an increase of 1.8 K (1.1 - 2.9 K) and for the highest 4.0 K (2.4 - 6.4 K). According to this assessment, the northern hemisphere has been most affected by the past temperature increase and will be strongly affected in future. It is difficult to measure the impacts of increasing air temperature on biodiversity. Despite this, there is broad evidence that anthropogenic climate change will lead to massive species extinction (Bakkenes et al. 2002, Leuschner & Schipka 2004, Schröter et al. 2004, Thomas et al. 2004, IPCC 2007a). Changes in plant or animal phenology as a result of climate change have already been made clearly evident by reliable long-term data (Beebee 1995, Crick et al. 1997, Ahas 1999, Crick & Sparks 1999, Menzel & Fabian 1999, Parmesan et al. 1999, Sparks 1999, Walther et al. 2002, Menzel 2003, Menzel et al. 2006). Many studies reveal a coherent shift in distribution of species (Parmesan et al. 1999, Frahm & Klaus 2000, Hill et al. 2002, Parmesan 2003, Walther et al. 2005), but the potential effect on complex communities is little understood. The conventional approach of making assumptions and deriving models to make predictions about the consequences of environmental change is often unsatisfactory for complex problems and includes considerable uncertainties (Harrington et al. 1999, IPCC 2001, Sutherland 2006). We need significantly improved models of the effects of climate change on the distribution of species and habitats. To achieve this, ecological research on climatic tolerances of species and habitats needs to be intensified (Sutherland et al. 2006). Furthermore, according to the latter study there is an urgent need to find out which species are the best indicators of the effects of climate change on natural communities, which habitats and species might be lost completely because of climate change, what time lags can be expected between climate change and ecological change, and what the likely relationship will be between the extent of climate change and the pattern of species extinction.

Current climate change predictions for the study area at a regional scale show increasing temperatures until the end of the 21st century. Hence a temperature increase of 1.7 - 2.1 K is expected (mean 2071-2100 compared to mean 1961-1990) (Spekat et al. 2007). Changes in precipitation will be moderate, decreasing by a maximum of about 6 % (Spekat et al. 2007).

More than half of Central Europe consists of mountain areas and most of these are low ranges covered by forest (Cipra 2007). The aim of our studies is to contribute to the knowledge of expected effects of climate change on these low mountain range forest ecosystems in Central Europe. The biodiversity and climate-change project described here includes an altitudinal gradient representative of a considerable part of Central European forests (Cipra 2007). Despite much discussion and a high level of research activity on assessing the impact of global change caused by temperature increase on biodiversity and natural systems in various disciplines there is still a major lack of knowledge on temporal and spatial scales as described by Sutherland et al. 2006. To remedy this, biodiversity projects have recently been started worldwide. Despite its relevance to policy makers, only a few studies involve integrated, multidisciplinary biodiversity research along altitudinal gradients (Epa 2007, Ibisca 2007, Doran et al. 2003).

Because mainly of the expected increase in temperature, a powerful effect on biological systems is very likely (IPCC 2007a) and the most significant effects of climate change will occur on a regional scale in the next 50 years.

1. Aims and structure of the BIOKLIM Project

The fundamental objective of our study is to quantify the dependency of various taxa on the environmental factors which are main determinants of their local distribution. The two dominant spatial gradients in the study area are altitude and frequency of forest structures. By the latter we mean characteristic structures that emerged through the protection of natural processes, such as areas rich in dead wood or alterations in canopy structure mainly created by the activity of bark beetles. The subjects addressed by the project may be divided into the complexes “Climate Change” and “Habitat Factors”.

The steep altitudinal gradient recommends the study area for research work on the impacts of climate change, because changes will take place within a small area. Geographical variation in species assemblages is known to be tied strongly to climate (Wildenow 1805). Distribution of many species is limited by altitude, as an expression of response to climate parameters or limitation of resources (Grabherr et al. 1994, Theurillat & Guisan 2001). The main priority of our study is to identify, through intensive study of the widest possible range of organisms, which species or groups are responding with greatest sensitivity to climate change. In this context the first step is to identify climate sensitive zones, in order to then focus on areas which are most sensitive to temperature increase. Climate sensitive zones are climate-induced ecological thresholds (Muradin 2001) represented by defined altitudinal zones. The monitoring of these zones allows for early quantification of climate change effects because the most obvious changes take place here first as warming proceeds. On the basis of the data gathered we can model the impacts of climate change and verify scenarios by conducting effective monitoring in the region. Prediction of the extinction risk for high montane species using habitat modelling techniques (e.g. generalized linear models, for more detail see Lawler et al. 2006) is one example of the possible uses for such data.

The second main objective of the project is to assess habitat factors responsible for species response variation; in particular, gradients in forest structure resulting from different types of management (from the extremes of continuous logging activity to process protection) affecting biodiversity are to be examined. The study site consists of extensive areas of forest which have not been used for decades or even for about a hundred years. Relicts of old growth forests and stands, parts of which have been killed by bark beetle attack, allow a broad span of woody debris availability and light conditions to be investigated. The significance of habitat parameters as drivers of biodiversity change revealed by our studies considerably improves the understanding of montane forest ecosystems. Based on this knowledge we can derive implications for management. The main questions are (i) how is terrestrial biodiversity affected by the protection of the natural processes that facilitate massive bark beetle infestations? (ii) What effect do huge amounts of coarse woody debris have on the build up of donor populations of highly endangered relict species of virgin forest, or endangered species in general? (iii) What are the consequences for biodiversity of measures against bark beetles? And finally (iv) Which habitat factors account for the oc-

currence of typical montane species and endangered species in low mountain range forest ecosystems and what conclusions can be drawn for multifunctional silvicultural treatment of these ecosystems?

After detecting the principal determinants in the system as a whole, it may be possible to answer further questions such as the impacts of climate change on taxonomical or functional groups. The ultimate aim of the study is to establish an empirical-statistical model of how species assemblages of different groups of organisms react to various scenarios of environmental change in low mountain range forests.

The well-documented samples and standardized sampling methods, together with the sensitive groups and species which these reveal (indicators), form a solid foundation for long term monitoring to detect environmental change and its impacts on a broad spectrum of forest inhabitants.

2. Study Area - Model Region

The Bavarian Forest National Park is situated in the German part of the Bohemian Forest, forming a homogenous landscape with the contiguous forests in the Czech Republic. This forest landscape is one of the largest in Central Europe. The highest ridges of the low mountain range form the watershed between the Danube and Elbe catchment areas. The Bavarian part of the Bohemian Massif is called the Inner Bavarian Forest.

The Bavarian Forest National Park (24235 ha) is located in the centre of the Inner Bavarian Forest and is about 98% covered by forest (Elling et al. 1987).

The region is characterized by montane and high montane areas within a vertical range of approximately 800m (from 650 m to 1420 m a.s.l.). Slopes in the National Park have mainly a southwestern exposition. Long-term phases of weathering and erosion have led to rounded, elevated landforms. Below 900m a.s.l., typical geomorphological elements are foothills, between 900 und 1100 m a.s.l. flat hillsides and valleys with steep hillsides dominate and between 1100 und 1400 m a.s.l. flat ridges are overtopped by summits

Geologically, the Bavarian Forest is the south-western part of the Bohemian Massif (Variscian basement) and consists essentially of granite and gneiss. Accordingly, soils are acidic, with dominantly sandy and loamy soils (particularly brown earths and podsols), and are partly covered with rocks. All altitudinal levels, but especially the valleys, are characterized by a persistent or intermittent water-table in both mineral and organic soils.

On a larger scale the Bavarian Forest belongs to the temperate zone and is characterized by atlantic and continental influences. The total annual precipitation is between 1200 und 1800 mm depending on altitude. Annual mean air temperature varies between 5.1°C per year in the valley sites, 5.8°C on hillsides and 3.8°C in the higher montane zones (Noack 1979, Bässler 2004).

At the lowest sites forest is characterized by *Picea abies* (83%), *Fagus sylvatica* L. (5%), *Abies alba* Mill. (5%) and *Sorbus aucuparia* L. (2.4%). The montane forest zone consists of *Picea abies* L. H.Karst (58%), *Fagus sylvatica* L. (34%) and *Abies alba* Mill. (3%). The high montane zone is characterized by *Picea abies* L. H.Karst (90%), *Sorbus aucuparia* L. (8%) and *Fagus sylvatica* L. (2%).

3. Study Design

We set up a total of 288 plots (Fig. 1) along four straight transects (Meyer et al. 2001) following the altitudinal gradient (Fig.2). Five additional plots were installed beside the main transects to compensate for the lack of old growth forest samples at higher altitude. Thus the plots comprise various altitudinal ranges and forest structures. The four transects were selected by using a stratified random scheme. First imperative was to include within the straight transects from valleys to mountain tops the entire vertical gradient of the study area. As a result of the division of the National Park into two main areas of wilding and continuous management, we planned to set up two transects in each category. Finally, we balanced the lines in order to avoid autocorrelation in forest structure. We thus avoided, for example, a continuous or discrete change in the ages of stands along the altitudinal gradient. In general, the sampling design should contain an adequate number of replications (Bernstein and Zalinski 1983), but design is also influenced by criteria of practicability and feasibility (Leyer and Wesche 2006). The use of 293 plots ensures that the dataset contains gradual structural differences, which is not so with case studies. The number of plots investigated was decided upon as a result of the estimation of the expected range of environmental variables. A recommendation exists that use of 10 random samples per environmental explanatory variable is sufficient to ensure a balanced data frame (Steyerberg et al. 2001). This equates the $p/10$ rule of thumb with $p = \min[\Sigma(\text{presences}, \Sigma(\text{absences})]$ (Guisan & Zimmermann 2000). Our use of 293 sample plots and consideration of approximately 30 main explanatory variables (Tab.3) satisfies these conditions. Due to difficult accessibility in the wilderness areas and the involvement of many specialists, we decided to set up transects with a simple design which enables effective execution of sampling and mapping. A small path, cleared by chainsaw, connects all plots of a transect,

Tab.1: Number of replications within the altitudinal range (100 m steps) for the entire sample plot design and the pre-stratified subsample plot designs.

Altitudinal range	293 sample plots	180 subsamples	113 subsamples	36 subsamples
< 700	31	14	7	2
700 - 799	64	31	22	5
800 - 899	60	20	12	5
900 - 999	23	22	14	3
1000 - 1099	27	25	17	6
1100 - 1199	33	23	15	5
1200 - 1299	31	25	13	6
1300 - 1399	24	20	13	4

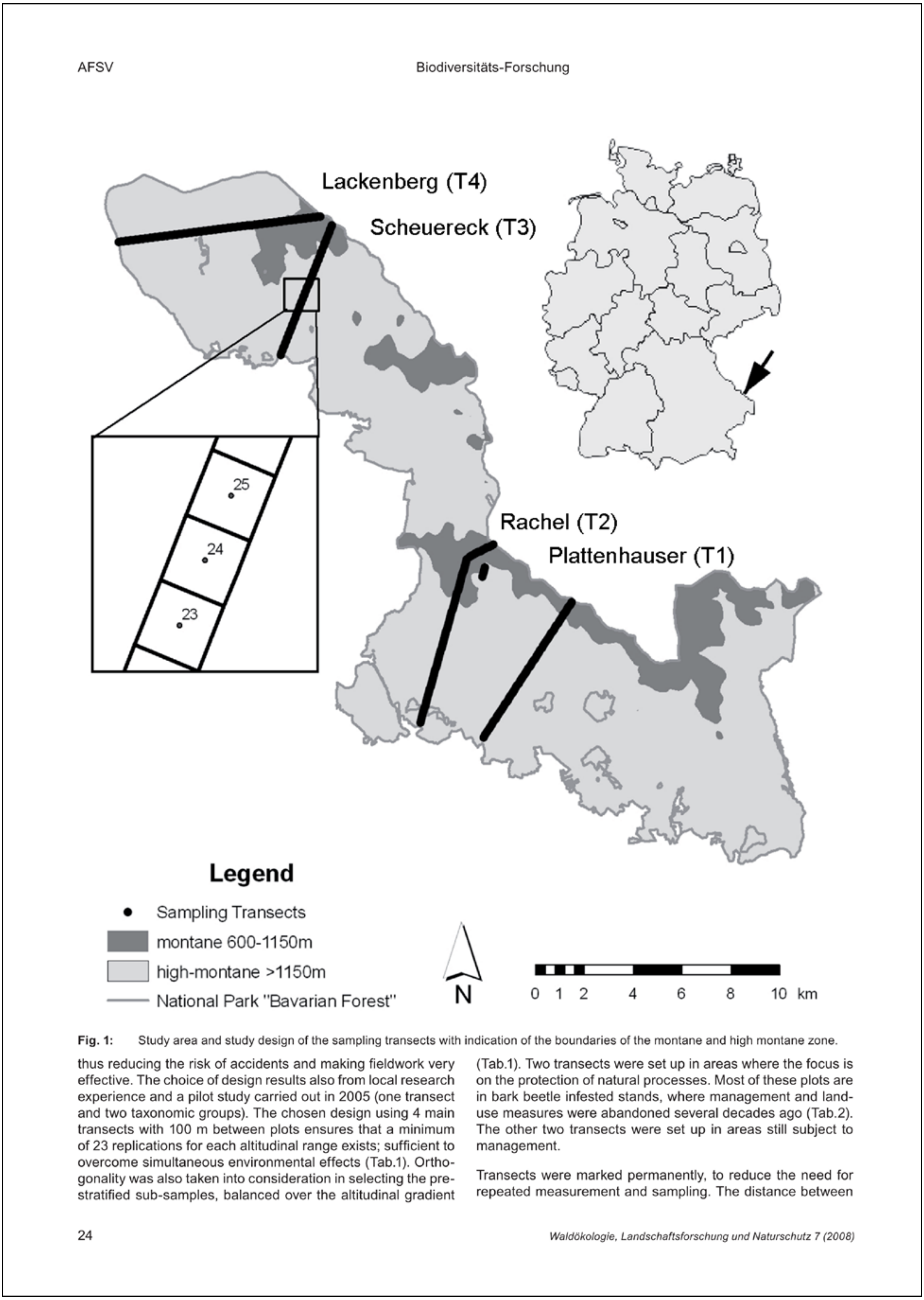

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Fig. 1: Study area and study design of the sampling transects with indication of the boundaries of the montane and high montane zone.

thus reducing the risk of accidents and making fieldwork very effective. The choice of design results also from local research experience and a pilot study carried out in 2005 (one transect and two taxonomic groups). The chosen design using 4 main transects with 100 m between plots ensures that a minimum of 23 replications for each altitudinal range exists; sufficient to overcome simultaneous environmental effects (Tab.1). Orthogonality was also taken into consideration in selecting the pre-stratified sub-samples, balanced over the altitudinal gradient (Tab.1). Two transects were set up in areas where the focus is on the protection of natural processes. Most of these plots are in bark beetle infested stands, where management and land-use measures were abandoned several decades ago (Tab.2). The other two transects were set up in areas still subject to management.

Transects were marked permanently, to reduce the need for repeated measurement and sampling. The distance between

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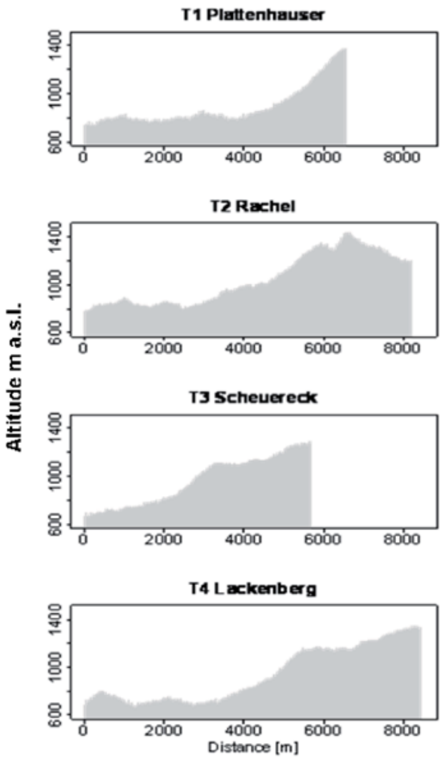


Fig. 2: Vertical profiles of the four transects, from airborne laser scanner data.

Tab. 2: Number of plots, degree of management and core zone affected plots for the transects.

Transect	Number of plots		
	Wilding	Management	Old growth
Plattenhauser	62	4	0
Rachel	73	8	0
Scheuereck	17	38	2
Lackenberg	22	48	14
Rachelsee	0	0	5
Total	174	98	21

the plots is 100 m (Fig.1). The plots represent fairly well the main plant communities of the National Park (Fig.3).

4. Data sampling

The marked plot centre is the basic reference point for any data collection. The scale of data collection depends on the taxonomic group (Tab. 4). The goal is to obtain data of all types from the same sampling plots from all disciplines, in contrast to the frequently applied approaches concentrating on individual species, which often present problems in interpretation within projects with a greater scope (Legendre & Legendre 1998). Every investigation in the project was therefore conducted essentially on the same plots, to enable proper comparability in studies on the relationships between the different kinds of data (Henle et al. 2006).

4.1 Abiotic

All environmental variables derived from field measurement, aerial photographs (LIDAR data) and climate stations are listed in Tab. 3. General information comprises, i. e., geographical coordinates and altitude, both generated using geographic information systems (GIS). Basis of calculation was a digital terrain model (DTM) with a cell size of 50 m.

Climate parameters result from geostatistical modelling using ArcEGMO (Becker et al. 2002, Pfützner 2002). To obtain reliable climate data we set up 30 data loggers with temperature and humidity registration and 10 rain gauges arranged on geomorphologically representative plots on the transects. Additionally, data are included from five main meteorological stations with extended climatological programs in the study area.

Variables on stand structure were recorded by measuring and estimation at each plot supplemented by interpretation of aerial photographs using the stereo analyst tool (Mc Grath et al. 2004). This was applied at different spatial scales (0.02 ha, 0.1 ha, 1 ha and 50 ha). In addition to the terrestrial measurement of stand structures, we used airborne laser scanning to get more detailed information on terrain and the canopy and its variation. Ages of stands are based on forest inventory (2002) using core samples. This information is also available in GIS.

Four soil samples from each plot were mixed together to provide two samples separated as humus layer and mineral soil up to 30 cm depth. Before chemical analysis the samples were dried at 65°C for 5 days and sieved through a 2 mm sieve. An aliquot of the mixed sample was milled. Soil pH was measured in 1 M KCl, using a Hamilton glass electrode (Bundesministerium für Ernährung 1990). C and N were analysed according to the Dumas method with the CHN analyser LECO CHN-1000 after complete oxidative combustion. Total elemental content of cations was measured following HNO_3 digestion (Bundesministerium für Ernährung, Landwirtschaft und Forsten 1990) with an ICP-IES (Perkin Elmer Optima 3000). The cations of all substrates were extracted with 1 M NH_4Cl for 2 hours on a rotation shaker (Bundesministerium für Ernährung, Landwirtschaft und Forsten 1990, Luehr & Böhmer 2000). Finally, cation exchange capacity, base saturation and C/N ratio were calculated.

Chemical analysis provides data on pH value, cations, anions, base saturation and cation exchange capacities. Additionally, we assessed visual soil parameters (e.g. soil texture) for the humus layer and the mineral soil up to 30cm depth. Based on these data a soil water balance index was calculated for each plot following Ewald et al. (2000).

4.2 Biotic

All taxonomic groups, methods and number of sampled plots (replications) are presented in Tab. 4. Altogether we collected data on 25 higher taxa. The number of plots to be sampled depends on the nature of the scientific enquiry and on the target group. For this reason we stratified 293 sample plots, selecting pre-stratified sub-samples with respect to the two main gradients (altitude and forest structure) for some groups. Plants, ferns, wood inhabiting fungi and birds were mapped on all 293 plots. 180 of these plots were chosen for flight intercep-

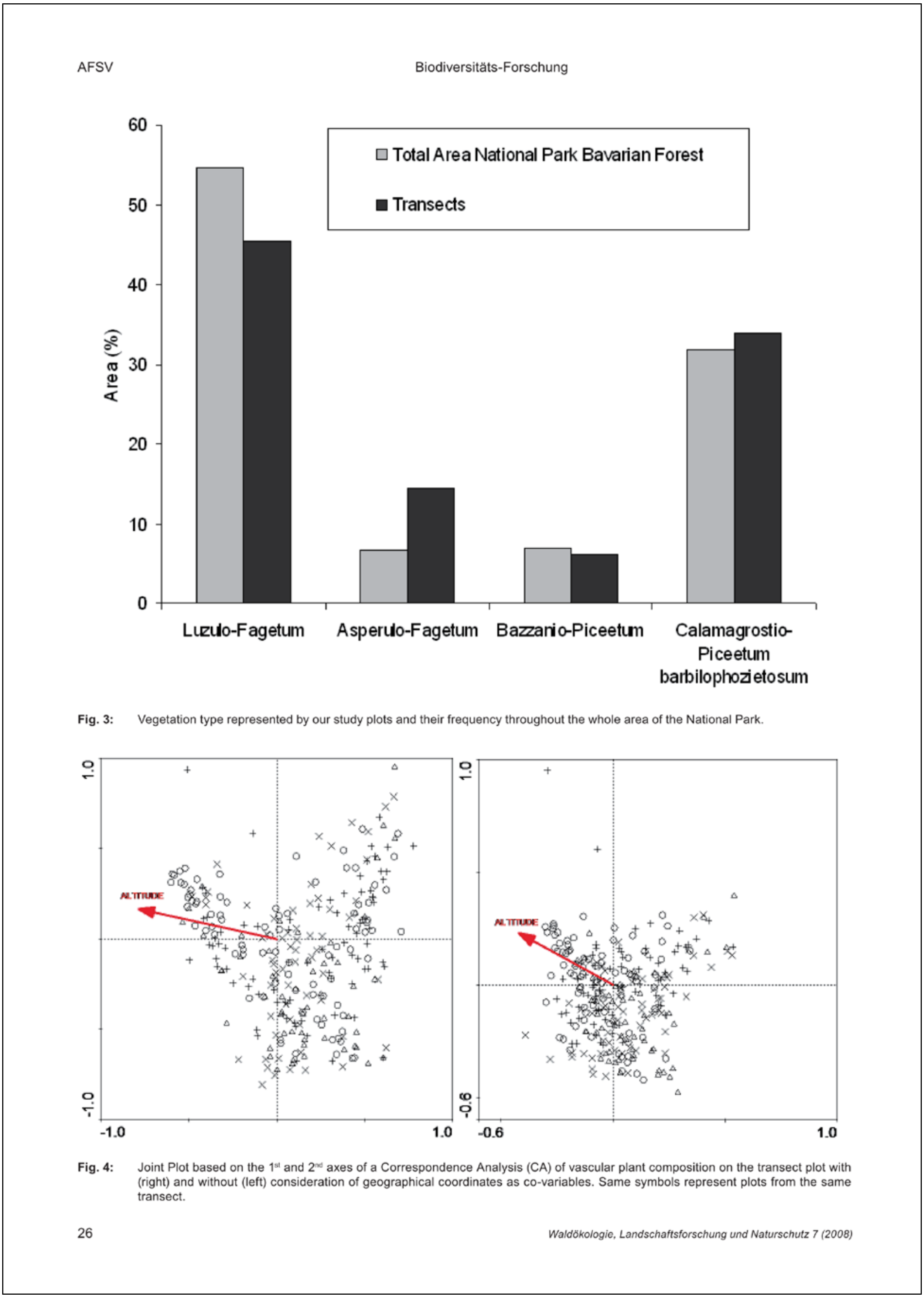
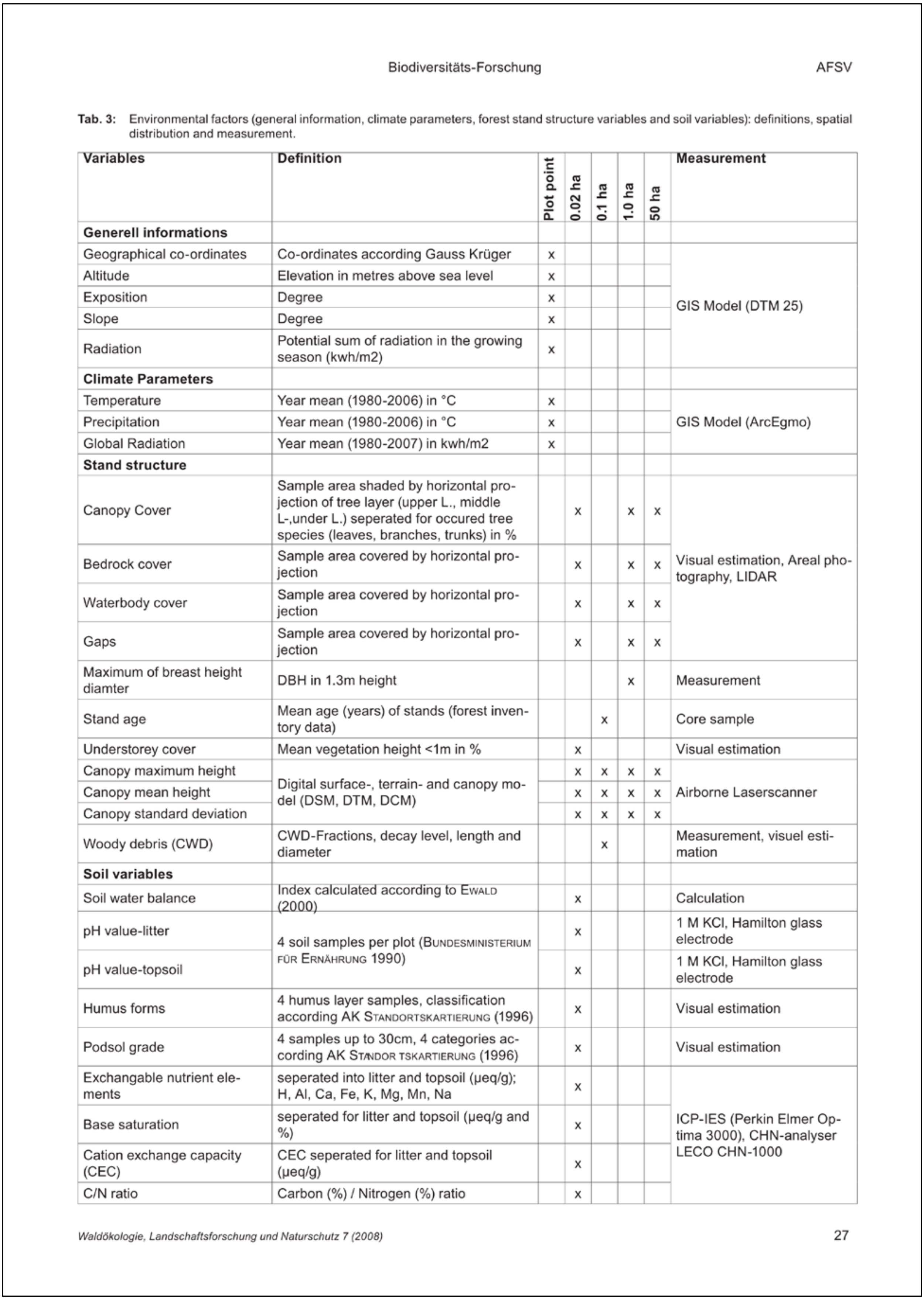


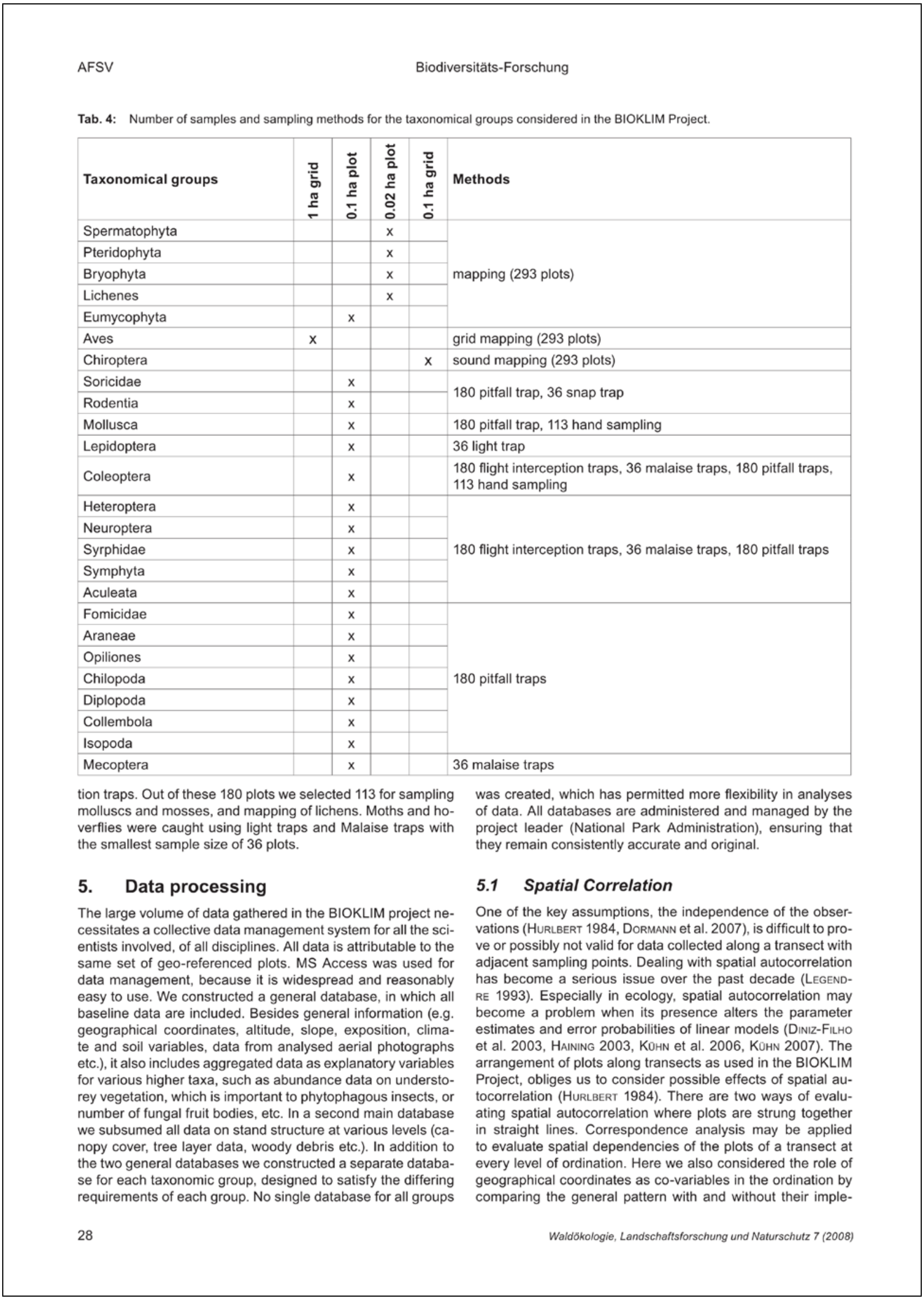
Fig. 3: Vegetation type represented by our study plots and their frequency throughout the whole area of the National Park.

Fig. 4: Joint Plot based on the 1st and 2nd axes of a Correspondence Analysis (CA) of vascular plant composition on the transect plot with (right) and without (left) consideration of geographical coordinates as co-variables. Same symbols represent plots from the same transect.



Tab. 3: Environmental factors (general information, climate parameters, forest stand structure variables and soil variables): definitions, spatial distribution and measurement.

Variables	Definition	Plot point	0.02 ha	0.1 ha	1.0 ha	50 ha	Measurement
Generell informations							
Geographical co-ordinates	Co-ordinates according Gauss Krüger	x					GIS Model (DTM 25)
Altitude	Elevation in metres above sea level	x					
Exposition	Degree	x					
Slope	Degree	x					
Radiation	Potential sum of radiation in the growing season (kwh/m2)	x					
Climate Parameters							
Temperature	Year mean (1980-2006) in °C	x					GIS Model (ArcEgmo)
Precipitation	Year mean (1980-2006) in °C	x					
Global Radiation	Year mean (1980-2007) in kwh/m2	x					
Stand structure							
Canopy Cover	Sample area shaded by horizontal projection of tree layer (upper L., middle L-,under L.) seperated for occured tree species (leaves, branches, trunks) in %		x		x	x	Visual estimation, Areal photography, LIDAR
Bedrock cover	Sample area covered by horizontal projection		x		x	x	
Waterbody cover	Sample area covered by horizontal projection		x		x	x	
Gaps	Sample area covered by horizontal projection		x		x	x	
Maximum of breast height diamter	DBH in 1.3m height				x		Measurement
Stand age	Mean age (years) of stands (forest inventory data)			x			Core sample
Understorey cover	Mean vegetation height <1m in %		x				Visual estimation
Canopy maximum height	Digital surface-, terrain- and canopy model (DSM, DTM, DCM)		x	x	x	x	Airborne Laserscanner
Canopy mean height			x	x	x	x	
Canopy standard deviation			x	x	x	x	
Woody debris (CWD)	CWD-Fractions, decay level, length and diameter			x			Measurement, visuel estimation
Soil variables							
Soil water balance	Index calculated according to Ewald (2000)		x				Calculation
pH value-litter	4 soil samples per plot (Bundesministerium für Ernährung 1990)		x				1 M KCl, Hamilton glass electrode
pH value-topsoil			x				1 M KCl, Hamilton glass electrode
Humus forms	4 humus layer samples, classification according AK Standortskartierung (1996)		x				Visual estimation
Podsol grade	4 samples up to 30cm, 4 categories according AK Standortskartierung (1996)		x				Visual estimation
Exchangable nutrient elements	seperated into litter and topsoil (µeq/g); H, Al, Ca, Fe, K, Mg, Mn, Na		x				ICP-IES (Perkin Elmer Optima 3000), CHN-analyser LECO CHN-1000
Base saturation	seperated for litter and topsoil (µeq/g and %)		x				
Cation exchange capacity (CEC)	CEC seperated for litter and topsoil (µeq/g)		x				
C/N ratio	Carbon (%) / Nitrogen (%) ratio		x				



Tab. 4: Number of samples and sampling methods for the taxonomical groups considered in the BIOKLIM Project.

Taxonomical groups	**1 ha grid**	**0.1 ha plot**	**0.02 ha plot**	**0.1 ha grid**	**Methods**
Spermatophyta			x		mapping (293 plots)
Pteridophyta			x		
Bryophyta			x		
Lichenes			x		
Eumycophyta		x			
Aves	x				grid mapping (293 plots)
Chiroptera				x	sound mapping (293 plots)
Soricidae		x			180 pitfall trap, 36 snap trap
Rodentia		x			
Mollusca		x			180 pitfall trap, 113 hand sampling
Lepidoptera		x			36 light trap
Coleoptera		x			180 flight interception traps, 36 malaise traps, 180 pitfall traps, 113 hand sampling
Heteroptera		x			180 flight interception traps, 36 malaise traps, 180 pitfall traps
Neuroptera		x			
Syrphidae		x			
Symphyta		x			
Aculeata		x			
Fomicidae		x			180 pitfall traps
Araneae		x			
Opiliones		x			
Chilopoda		x			
Diplopoda		x			
Collembola		x			
Isopoda		x			
Mecoptera		x			36 malaise traps

tion traps. Out of these 180 plots we selected 113 for sampling molluscs and mosses, and mapping of lichens. Moths and hoverflies were caught using light traps and Malaise traps with the smallest sample size of 36 plots.

5. Data processing

The large volume of data gathered in the BIOKLIM project necessitates a collective data management system for all the scientists involved, of all disciplines. All data is attributable to the same set of geo-referenced plots. MS Access was used for data management, because it is widespread and reasonably easy to use. We constructed a general database, in which all baseline data are included. Besides general information (e.g. geographical coordinates, altitude, slope, exposition, climate and soil variables, data from analysed aerial photographs etc.), it also includes aggregated data as explanatory variables for various higher taxa, such as abundance data on understorey vegetation, which is important to phytophagous insects, or number of fungal fruit bodies, etc. In a second main database we subsumed all data on stand structure at various levels (canopy cover, tree layer data, woody debris etc.). In addition to the two general databases we constructed a separate database for each taxonomic group, designed to satisfy the differing requirements of each group. No single database for all groups was created, which has permitted more flexibility in analyses of data. All databases are administered and managed by the project leader (National Park Administration), ensuring that they remain consistently accurate and original.

5.1 Spatial Correlation

One of the key assumptions, the independence of the observations (Hurlbert 1984, Dormann et al. 2007), is difficult to prove or possibly not valid for data collected along a transect with adjacent sampling points. Dealing with spatial autocorrelation has become a serious issue over the past decade (Legendre 1993). Especially in ecology, spatial autocorrelation may become a problem when its presence alters the parameter estimates and error probabilities of linear models (Diniz-Filho et al. 2003, Haining 2003, Kühn et al. 2006, Kühn 2007). The arrangement of plots along transects as used in the BIOKLIM Project, obliges us to consider possible effects of spatial autocorrelation (Hurlbert 1984). There are two ways of evaluating spatial autocorrelation where plots are strung together in straight lines. Correspondence analysis may be applied to evaluate spatial dependencies of the plots of a transect at every level of ordination. Here we also considered the role of geographical coordinates as co-variables in the ordination by comparing the general pattern with and without their imple-

mentation. This is illustrated using vascular plant data in Fig. 4. According to this analysis, the importance of altitude as main driver is not obscured by spatial dependency.

A further approach to evaluation of autocorrelation is the use of semiparametric spatial generalised linear models. In this method, spatial autocorrelation is alleviated by including a spatial surface in the regression model. Assuming asymptotic normality of the estimated regression coefficients, confidence bands and p-values can be computed from the standard deviations obtained from the Fisher information matrix as implemented in the package "BayesX" , described in more detail in Fahrmeir et al. 2004, Kneib & Fahrmeir 2006.

6. Altitude as the main driver for communities

We expected altitude to be the main driver of distribution patterns for the taxonomic groups considered. Amongst abiotic variables, the altitudinal gradient within the study area is strongly characterised by temperature decrease with increasing altitude (Elling et al. 1987, Bässler 2004). It can therefore be concluded, that conditions for studying the impacts of global warming are appropriate within the study area.

Preliminary unconstrained ordination (CA) of data for the first six taxonomic groups (carabids, breeding birds, wood inhabiting fungi, molluscs, plants and spiders) reveal the altitudinal gradient as the main driver for communities: this follows the first axis (Fig.5). For this analysis we used CANOCO (Ter Braak & Smilauer 2002). The basis of the analysis was the data as specified in Tab.4. Where appropriate, the data were preliminary prepared such as e.g. square root transformation of the vascular plant species data. These ordination patterns are intended only to illustrate the strong influence of altitude on the selected assemblages and are not intended as a substitute for further analysis where other explanatory variables are relevant. Distribution of taxonomic assemblages is limited by altitude, as an expression of climate parameters or limitation of resources (Grabherr et al. 1994, Theurillat & Gui san 2001). Altitude is therefore a surrogate gradient representing many climate factors affecting species directly and is thus correlated with resources and regulators of species development (Austin 1980). The many components of climate, including for example temperature, precipitation and seasonality, vary in a non-random fashion along most elevation gradients (Lomolino 2001). A further component of the proxy altitude is the change in forest structures along the gradient. Alterations in tree species composition correlated with altitude are obvious in forests both of high and low mountain ranges (Doležal & Šrůtek 2002, Walentowski et al. 2004, Lee et al. 2005). A great challenge to the project is to establish the importance of the directly operating physiological factors hidden within the proxy altitude and to deal with confounding environmental effects. To this end, different multivariate approaches such as partial variance (Økland 2003), hierarchical partitioning (Chevan & Sutherland 1991), the application of generalized linear models (McCullough & Nelder 1989) or maximally selected rank statistics (Hothorn & Lausen 2003) could for example be adopted.

A comparable approach to studying biodiversity along an altitudinal gradient is taking place in Queensland, Australia. The IBISCA Queensland Project is a major international collaborative effort to survey different taxonomic groups in southeast Queensland's Lamington National Park (Epa 2007, Ibisca 2007). The vertical gradient spans 800m (300 – 1100 m.a.s.l.) within undisturbed, continuous subtropical rainforest, featuring a gradual transition from the highly diverse mixed broadleaved forests at the lower elevations to the almost pure southern beech forests at the highest levels. As for BIOKLIM, the purpose of IBISCA is to identify the species or groups that respond with greatest sensitivity to climatic change (Ibisca 2007). Field work began simultaneously to that of BIOKLIM in 2006, with establishment of permanent research plots. Following the vertical gradient, IBISCA set up five study sites at different altitudes with a total of 20 permanent plots arranged in a nested design. Plants, ferns and mosses were mapped on all 20 plots. Insects were sampled with pitfall traps in an array of nine traps per plot (180 traps on 20 plots). Two light traps (total 40 traps) and 3 yellow pans (total 60 pans) per plot were installed. Furthermore, one Malaise trap and one flight interception trap is operated on each plot (total 20 traps of each type) and litter sampling is also carried out. This methodology will be augmented by bark spraying, canopy knockdown and hand collection. Despite similar project aims, the chosen designs represent different approaches (for review of sampling design techniques see Green 1979). IBISCA works with a single transect laid out quite differently to the chains of sample plots used in the BIOKLIM project, but also oriented on the altitudinal gradient. Replications in different altitudinal ranges result from parallel sampling on the nested plots. The BIOKLIM design and the relatively high number of plots should ensure adequate representation of the variability in environmental and structural conditions within the sampling plots, with a minimum risk of spatial autocorrelation (see 5.1) and avoiding pseudo-replication (Hurlbert 1984).

A second study with a similar approach was set up in Tasmania, Australia. The program aims at monitoring distributional changes in vegetation and invertebrate assemblages along an altitudinal gradient (1230 m) in response to climate change and other environmental events (Doran et al. 2003). During the first two years baseline data were collected, as in BIOKLIM, to obtain long term comparative information. The research concept is based on four transects with a total of 24 plots and 240 subplots (nested design as described for the IBISCA project). Plots were set up in 100 m altitudinal ranges between 70 and 1300 m a.s.l. Focus of this study is on vegetation and invertebrate taxa. Vegetation was mapped on all 240 subplots. Altogether 84 pitfall traps were set up on 14 plots. One Malaise trap was set up on each of six plots.

With a special focus on plants, particularly endemic species, the Global Observation Initiative in Alpine Environments (GLORIA) was set up in the 1990's. GLORIA aims at the establishment of an internationally coordinated network focussed on monitoring global warming at a global scale (Grabherr et al. 2000). In this project, alpine environments refer to areas from the timberline to the top of high mountains. Thus there is no consideration of the complete altitudinal gradient from valley floor upwards. Although it can not be doubted that alpine summits are very sensitive to climate change (Grabherr et al. 1994, Kazakis et al. 2007, Pauli et al. 2007), important changes are expected on a wider vertical scale, and there is also a definite need to consider a wider range of taxonomic groups.

Some existing studies deal with responses of selected biological groups to climate change along altitudinal gradients, but most of these consider only a few taxonomic groups. For example Wilson et al. (2007) studied altitudinally restricted communities of Schizophoran flies (Diptera) using Malaise traps, to assess the impacts of further warming. Other studies focus on species richness patterns along altitudinal gradients without considering aspects of climate change. Such studies have be-

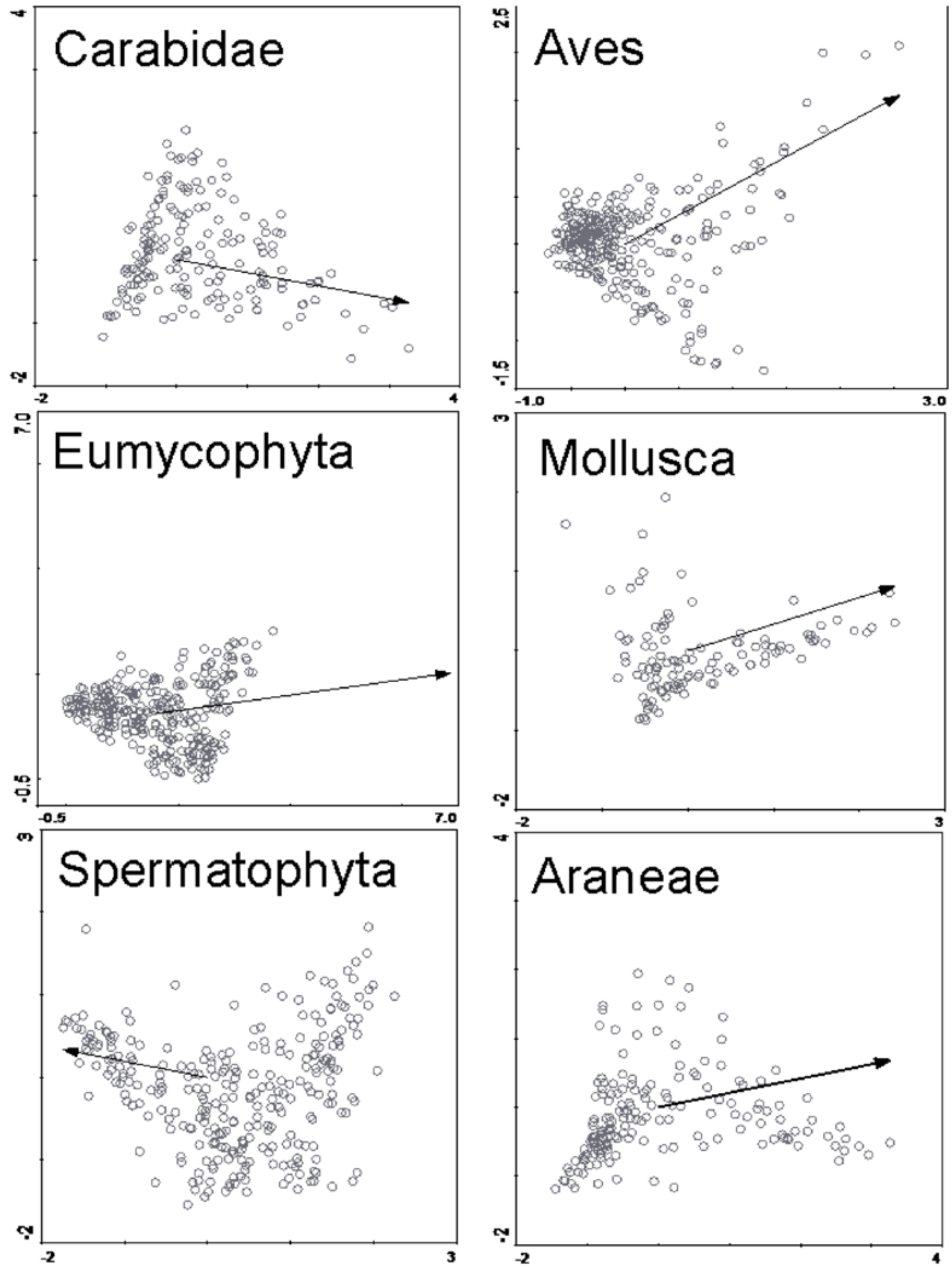


Fig. 5: Wood inhabiting fungi, vascular plant, bird, mollusc, spider and carabid communities and their dependence on the altitudinal gradient. Joint Plots based on an unconstrained correspondence analysis (CA). The circles represent the assemblages, the vector (arrow) represents the factor altitude.

en presented for vascular plants (Grytnes 2003), bryophytes and lichens (Grytnes et al. 2006) and ferns (Bhattarai et al. 2004).

Aims and sampling methodology of our research project are essentially similar to those of other projects, using an integrative approach to answering questions about the relationships between biodiversity change and climate change. Despite differences in design and structure of the projects, there is great fundamental similarity in the approach to studying biodiversity along an altitudinal gradient. The sampling methods used (e.g. use of permanent plots, types of traps used, methods of mapping) and the type of taxonomic groups selected for study are also similar. However, with respect to the number of groups considered and number of sampling replications, our project belongs to those few which are based on a large volume of original data.

Conclusions

As a first preliminary result, altitude was revealed as the main factor driving occurrence of the selected taxonomic groups. Due to the strong dependency of temperature on altitude we expect a strong dependency of the taxonomic groups on temperature. This would qualify the project as suitable for studying the impacts of global warming. A special attribute of the BIOKLIM Project is the concentration of studies by specialists on various taxa within the same study design and time frame. This secures availability of complete and reliable baseline information on biota and abiotic factors. A further valuable attribute is the innovative way in which data on environmental and structural variables were obtained. Use of high resolution airborne laser-scanning data for each plot has not previously been applied in investigating the relationships between environmental and structural variables and local distribution of taxonomic groups. Neither has a previous project considered as many as 293 plots, with the resultant high level of replication.

Studies of changes along gradients of altitude and structure are of both high scientific and practical interest. The strong structural gradient caused by varying amounts of woody debris is unique in Central Europe. This allowed modelling of different management intensities to be based on a stock of data sufficient to obtain adequate decision support. It is thus possible to derive thresholds and key criteria for montane forests managed to integrate the requirements of nature conservation with the imperatives resulting from climate change. We hope to obtain long term comparative information from the project by setting up a monitoring program with a continuous record of sampling and mapping results.

Acknowledgement

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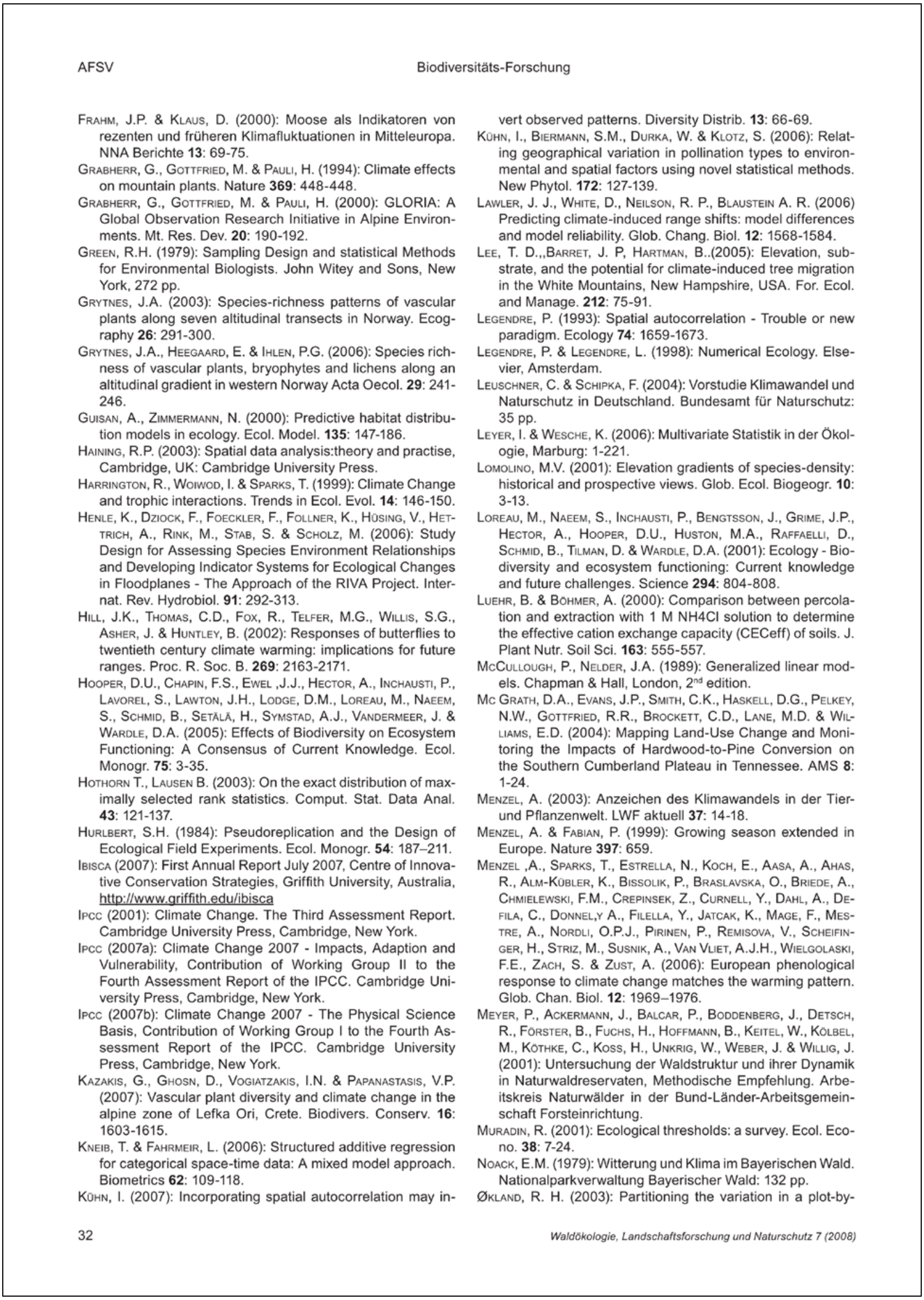

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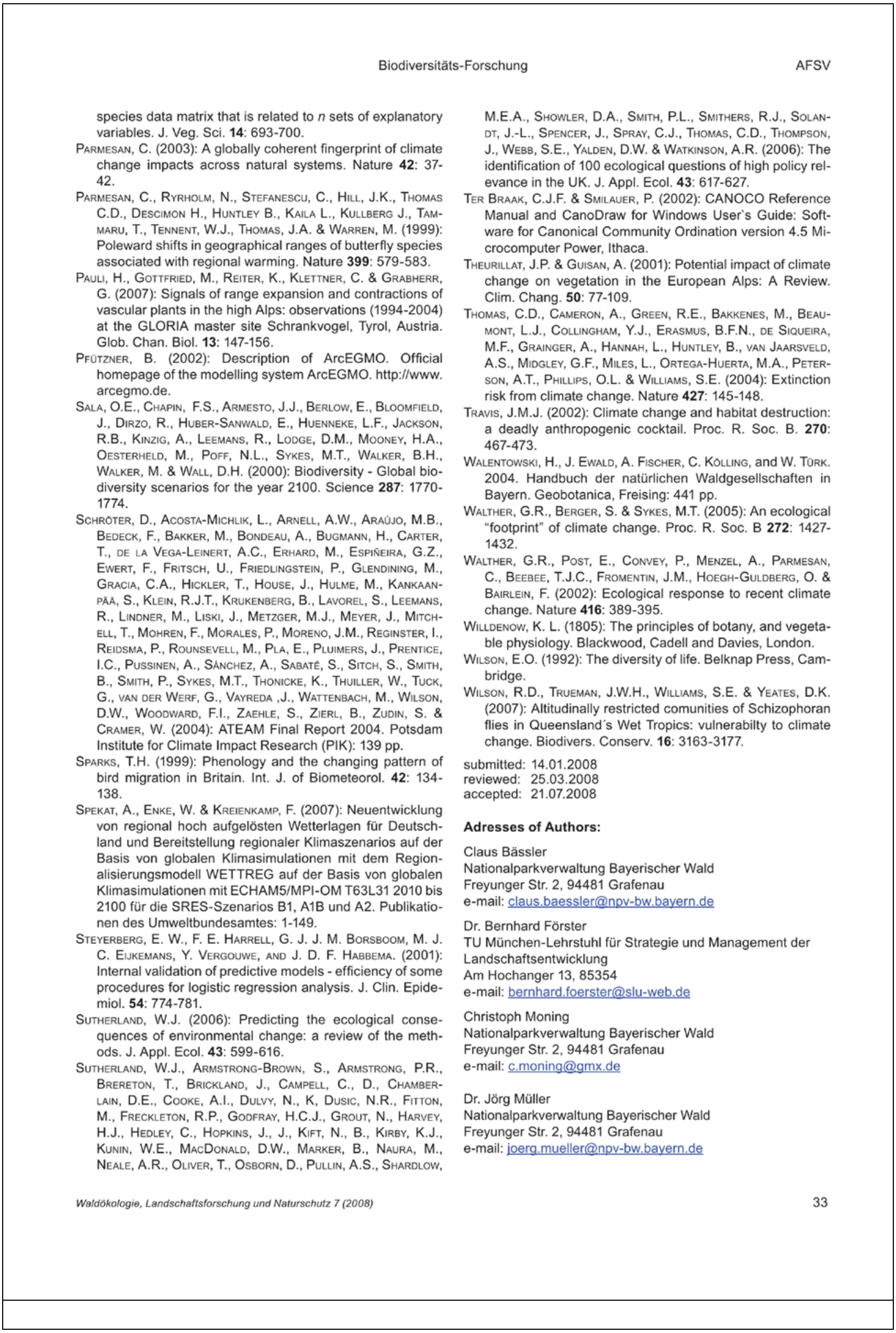

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Artikel 2: Einflussfaktoren auf das Baumhöhlenangebot und dessen Auswirkungen auf die Arten und Dichten von Höhlenbrütern in Bergwäldern.

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Einflussfaktoren auf das Baumhöhlenangebot und dessen Auswirkungen auf die Arten und Dichten von Höhlenbrütern in Bergwäldern

Anna Kanold, Nils Rohrmann und Jörg Müller

Factors influencing the supply of tree cavities and the effects of supply on species composition and population density of cavity breeders in montane forests

To find out more about factors which influence cavities in trees, all such holes were recorded along five transects covering 293 hectares in the Bavarian Forest National Park. Age of woodland and amount of dead wood were found to be positive parameters and density of roads / paths and altitude to be negative parameters. In the montane mixed woodland zone, analysis of management types indicated significantly higher numbers of cavities in old woods and in non-intervention trial areas compared with managed areas. At higher altitudes also, supply of cavities is better in non-intervention areas. Use of a regression tree showed that presence of 5 cavities per hectare led to approximately double the number of cavity-breeding species. The analyses substantiate not just the outstanding role of old woods in providing an abundance of cavities, but also that of the non-intervention areas. Although management in the latter stopped only a few decades ago, they are developing into natural woods, with better conditions for woodpeckers and cavity-breeders.

Key words: Woodpeckers, cavity, cavity-breeding birds, cavit tree, montane forest.

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Einleitung

Baumhöhlen stellen eine Schlüsselstruktur für eine Vielzahl von Lebewesen in Wäldern dar (Jarzabek 2005, Martin & Eadie 1999, Ranius & Heding 2001, Scherzinger 1996, Scott 1978, Scott, Whelan & Svoboda 1980, Swallow, Gutierrez & Howard 1986). Erst durch die Bewirtschaftung sind sie vielerorts selten geworden, weil Bäume, aus ökonomischen Gründen, bereits lange vor der Entstehung von Höhlen gefällt werden (Ducasse & Brustel 2008, Scherzinger & Schumacher 2004, Speight 1989). So wurden Höhlenbäume zu einer knappen Ressource und folglich zu Zielgrößen im Waldnaturschutz. Sie finden sowohl in der Planung von Forstbetrieben Berücksichtigung als auch bei der Bewertung von Natura-2000-Lebensräumen. Spechte gelten dabei als die Hauptproduzenten von Baumhöhlen und deren Initialstadien (Scherzinger 1982, Scherzinger 1998).

Einige Vogelarten, vor allem Höhlenbrüter und Spechte, reagieren sehr empfindlich auf strukturelle Veränderungen im Wald und gelten daher als Indikatoren für naturnahe Waldbestände (Scherzinger 1985, Müller, Hothorn & Pretzsch 2007). Durch das Aufhacken fester Holzstrukturen können Spechte, Kleiber und einige Meisenarten Nahrungsquellen erschließen, die für viele andere Vogelarten unzugänglich sind. Darüber hinaus schaffen sie durch den Höhlenbau Quartiere, in denen eine Vielzahl verschiedener Vögel, Säugetiere und Insekten leben (Kaule 1991, Blume 1996). Auch Pilze nutzen diese Höhlen als Eintrittspforten in noch lebende Bäume.

Der Nationalpark Bayerischer Wald wurde

1970 mit dem Ziel ausgewiesen, das Gebiet der natürlichen Sukzession zu überlassen. Durch eine Vielzahl unterschiedlich stark anthropogen überprägter Waldbestände und inzwischen großräumig ablaufender Dynamiken wie altersbedingtes Absterben, Windwurf und Borkenkäfergradation, ist ein vielfältiges Mosaik an Waldzuständen und Strukturen in den ehemaligen Forsten wieder entstanden.

Ein Teil der Fläche wurde in historischer Zeit nicht oder wenig genutzt. Aus diesem Grund ist ihre Baumarten- und Alterszusammensetzung, mit bis zu 400–600-jährigen Buchen und Tannen, osteuropäischen Bergurwäldern noch sehr ähnlich (Scherzinger 1985). Dieser Teil der Fläche wird im Folgenden als „Alte Wälder" bezeichnet. Die totholzreichen Strukturen dieser Wälder beherbergen diverse Spechtarten, deren Folgenutzer sowie zahllose Totholzbewohner. Rund ein Drittel aller im Wald lebenden Arten ist von absterbenden und toten Bäumen abhängig (Schmidt 2006, Utschick 1991).

Ziel der vorliegenden Studie war, die folgenden Fragen zur Entstehung von Höhlen und deren Bedeutung für die Avifauna zu untersuchen:

1. Wie hoch ist der Anteil der Baumhöhlen im Bergwald, die von Spechten gemeißelt wurden?
2. Welche weiteren, nicht anthropogenen Umweltfaktoren bestimmen das Baumhöhlenangebot im Bergmischwald?
3. Welchen Einfluss haben die verschiedenen Managementtypen im Nationalpark auf das Baumhöhlenangebot?
4. Ab welchem Schwellenwert des Höhlenbaumangebots treten mehr Höhlenbrüter im Bergwald auf?

Das Untersuchungsgebiet

Der Nationalpark Bayerischer Wald liegt in Niederbayern an der Grenze zur Tschechischen Republik, in den Landkreisen Freyung-Grafenau und Regen. 1970 wurde der Nationalpark mit 13.100 ha gegründet (Altgebiet) und 1997 um 11.126 ha erweitert (Erweiterungsgebiet), womit der Nationalpark heute insgesamt 24.226 ha umfasst.

Die Höhenlagen des Nationalparks reichen von 598 m bis 1.453 m, die Jahresniederschläge von 1.100 mm in den Tallagen bis zu 1.800 mm in den Hochlagen (Nationalpark Bayerischer Wald 2008). Die Jahresmitteltemperaturen liegen in den Tallagen bei 5–6 °C und sinken mit steigender Höhe auf bis zu 3–5 °C (NPV Bay. Wald 2008).

Die natürliche Vegetation des Nationalparks bildet einerseits die hochmontanen Bergmischwälder in den Hanglagen und andererseits die Fichtenwälder der tiefsubalpinen Höhenstufen (Walentowski et al. 2004). Generell finden menschliche Eingriffe im Nationalpark nur noch im ‚Erweiterungsgebiet' und in den Pufferzonen in Form von Borkenkäferbekämpfungsmaßnahmen statt. In den Kernzonen des ‚Altgebietes' wird nicht mehr in die natürlichen Prozesse eingegriffen. Für eine ausführliche Darstellung der Konzeption siehe Scherzinger (2007). Auf dieser Basis lassen sich vereinfacht drei Managementkategorien unterscheiden: Die bereits zuvor erwähnte Kategorie „Alte Wälder", die Kategorie „Prozessschutz" mit strukturreichen Beständen, hervorgegangen durch Dynamiken der letzten 30 Jahre und die Kategorie „Management" mit Flächen, in die weithin forstlich eingegriffen wird. Diese drei Kategorien lassen sich noch in die beiden

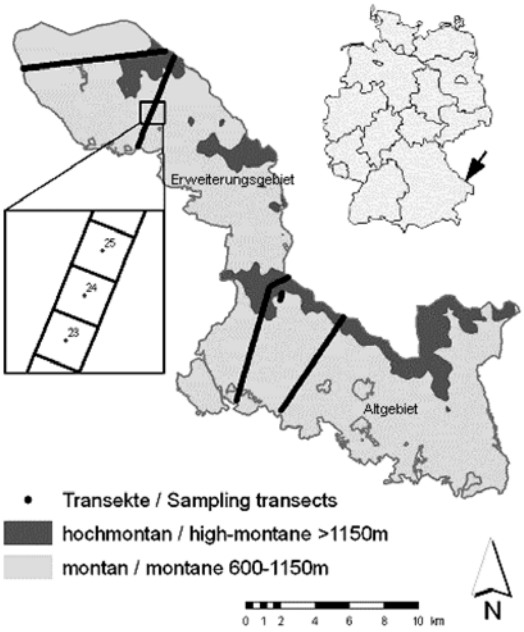
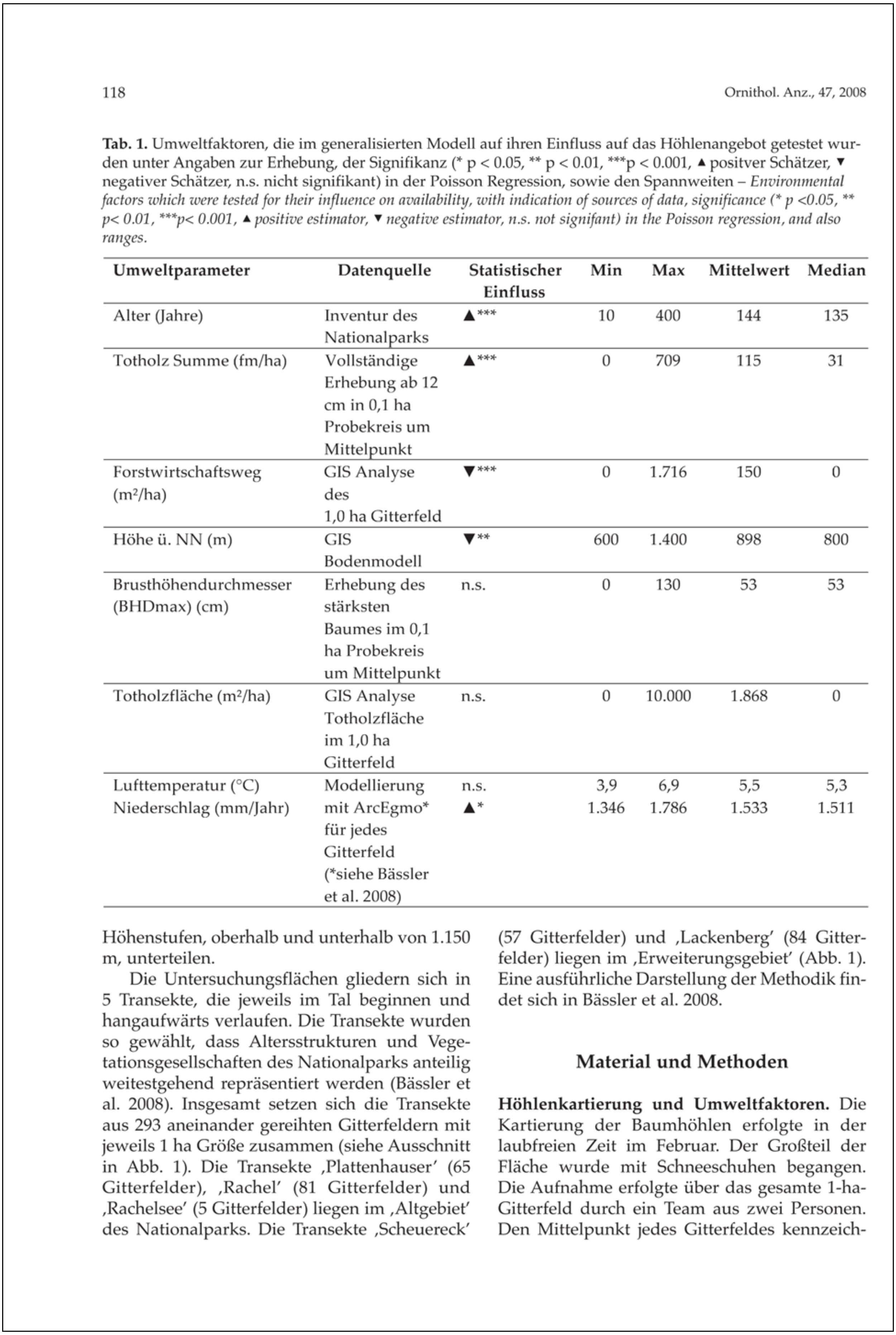


Abb. 1. Lage der fünf Untersuchungs-Transekte im Nationalpark Bayerischer Wald. – *Position of the five study transects in the Bavarian Forest National Park.*



Tab. 1. Umweltfaktoren, die im generalisierten Modell auf ihren Einfluss auf das Höhlenangebot getestet wurden unter Angaben zur Erhebung, der Signifikanz (* p < 0.05, ** p < 0.01, ***p < 0.001, ▲ positver Schätzer, ▼ negativer Schätzer, n.s. nicht signifikant) in der Poisson Regression, sowie den Spannweiten – *Environmental factors which were tested for their influence on availability, with indication of sources of data, significance (* p <0.05, ** p< 0.01, ***p< 0.001, ▲ positive estimator, ▼ negative estimator, n.s. not signifant) in the Poisson regression, and also ranges.*

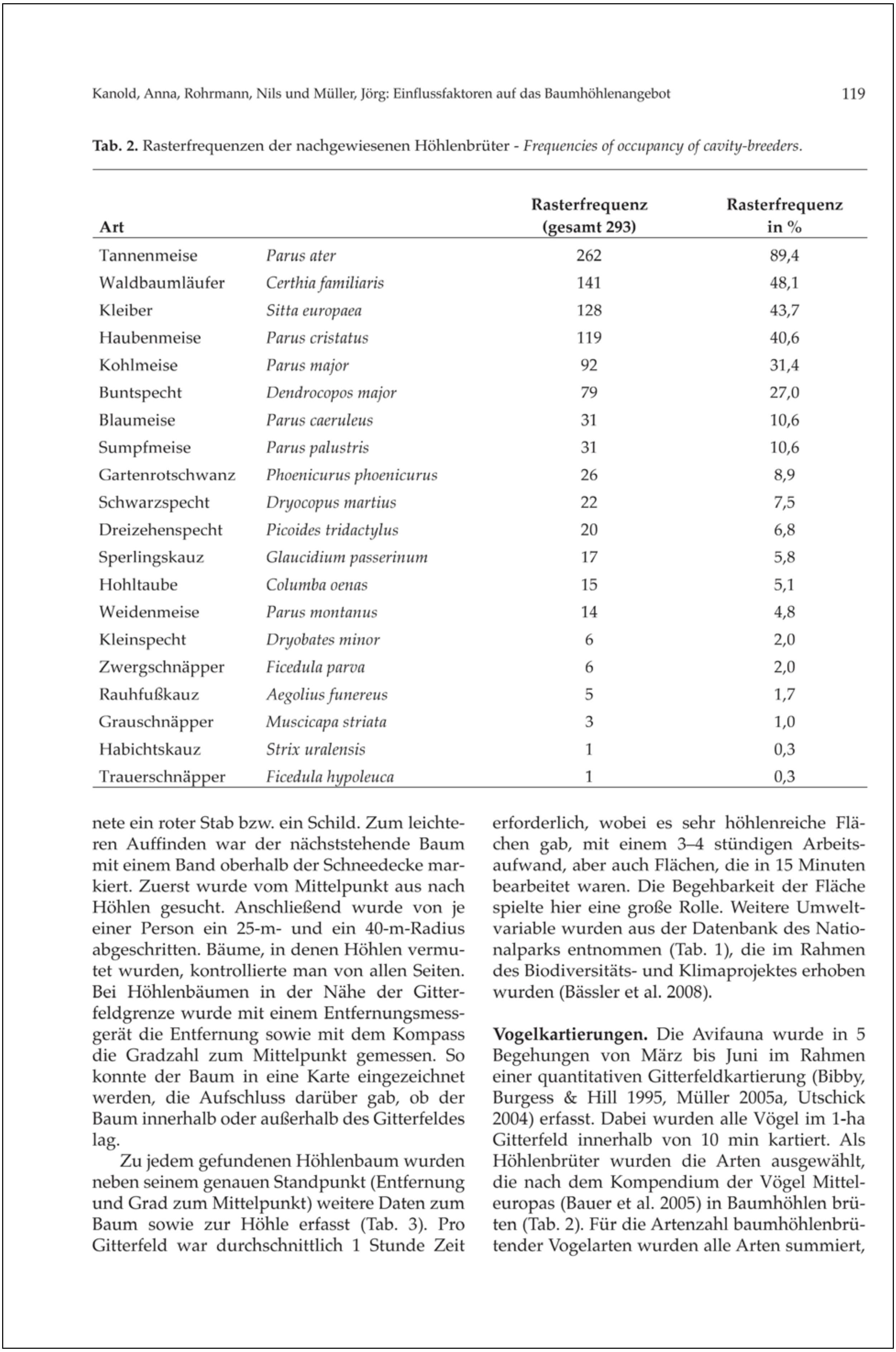
Umweltparameter	Datenquelle	Statistischer Einfluss	Min	Max	Mittelwert	Median
Alter (Jahre)	Inventur des Nationalparks	▲***	10	400	144	135
Totholz Summe (fm/ha)	Vollständige Erhebung ab 12 cm in 0,1 ha Probekreis um Mittelpunkt	▲***	0	709	115	31
Forstwirtschaftsweg (m²/ha)	GIS Analyse des 1,0 ha Gitterfeld	▼***	0	1.716	150	0
Höhe ü. NN (m)	GIS Bodenmodell	▼**	600	1.400	898	800
Brusthöhendurchmesser (BHDmax) (cm)	Erhebung des stärksten Baumes im 0,1 ha Probekreis um Mittelpunkt	n.s.	0	130	53	53
Totholzfläche (m²/ha)	GIS Analyse Totholzfläche im 1,0 ha Gitterfeld	n.s.	0	10.000	1.868	0
Lufttemperatur (°C)	Modellierung mit ArcEgmo* für jedes Gitterfeld (*siehe Bässler et al. 2008)	n.s.	3,9	6,9	5,5	5,3
Niederschlag (mm/Jahr)		▲*	1.346	1.786	1.533	1.511

Höhenstufen, oberhalb und unterhalb von 1.150 m, unterteilen.

Die Untersuchungsflächen gliedern sich in 5 Transekte, die jeweils im Tal beginnen und hangaufwärts verlaufen. Die Transekte wurden so gewählt, dass Altersstrukturen und Vegetationsgesellschaften des Nationalparks anteilig weitestgehend repräsentiert werden (Bässler et al. 2008). Insgesamt setzen sich die Transekte aus 293 aneinander gereihten Gitterfeldern mit jeweils 1 ha Größe zusammen (siehe Ausschnitt in Abb. 1). Die Transekte ‚Plattenhauser' (65 Gitterfelder), ‚Rachel' (81 Gitterfelder) und ‚Rachelsee' (5 Gitterfelder) liegen im ‚Altgebiet' des Nationalparks. Die Transekte ‚Scheuereck' (57 Gitterfelder) und ‚Lackenberg' (84 Gitterfelder) liegen im ‚Erweiterungsgebiet' (Abb. 1). Eine ausführliche Darstellung der Methodik findet sich in Bässler et al. 2008.

Material und Methoden

Höhlenkartierung und Umweltfaktoren. Die Kartierung der Baumhöhlen erfolgte in der laubfreien Zeit im Februar. Der Großteil der Fläche wurde mit Schneeschuhen begangen. Die Aufnahme erfolgte über das gesamte 1-ha-Gitterfeld durch ein Team aus zwei Personen. Den Mittelpunkt jedes Gitterfeldes kennzeich-



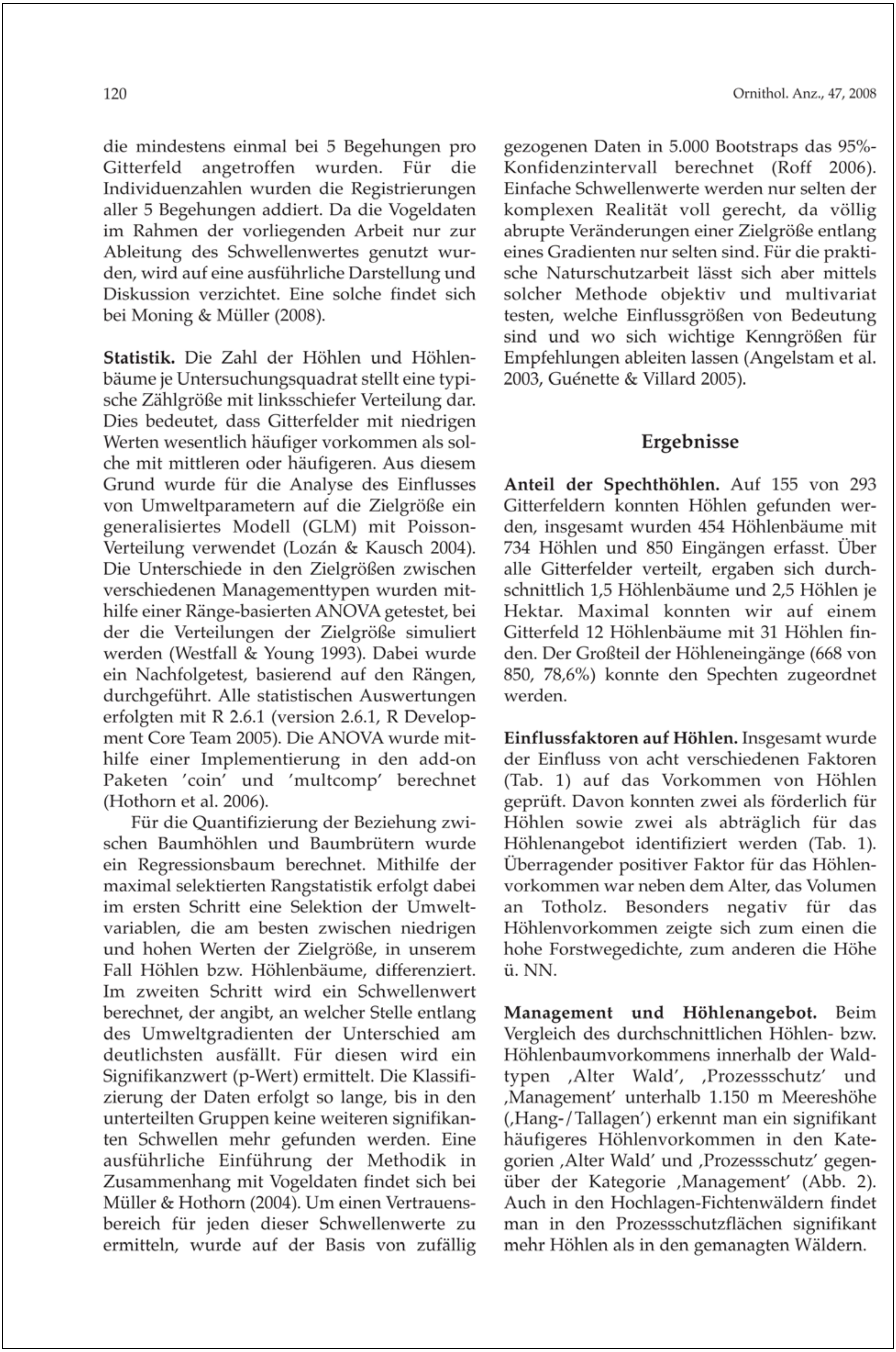
Tab. 2. Rasterfrequenzen der nachgewiesenen Höhlenbrüter - *Frequencies of occupancy of cavity-breeders.*

Art		Rasterfrequenz (gesamt 293)	Rasterfrequenz in %
Tannenmeise	*Parus ater*	262	89,4
Waldbaumläufer	*Certhia familiaris*	141	48,1
Kleiber	*Sitta europaea*	128	43,7
Haubenmeise	*Parus cristatus*	119	40,6
Kohlmeise	*Parus major*	92	31,4
Buntspecht	*Dendrocopos major*	79	27,0
Blaumeise	*Parus caeruleus*	31	10,6
Sumpfmeise	*Parus palustris*	31	10,6
Gartenrotschwanz	*Phoenicurus phoenicurus*	26	8,9
Schwarzspecht	*Dryocopus martius*	22	7,5
Dreizehenspecht	*Picoides tridactylus*	20	6,8
Sperlingskauz	*Glaucidium passerinum*	17	5,8
Hohltaube	*Columba oenas*	15	5,1
Weidenmeise	*Parus montanus*	14	4,8
Kleinspecht	*Dryobates minor*	6	2,0
Zwergschnäpper	*Ficedula parva*	6	2,0
Rauhfußkauz	*Aegolius funereus*	5	1,7
Grauschnäpper	*Muscicapa striata*	3	1,0
Habichtskauz	*Strix uralensis*	1	0,3
Trauerschnäpper	*Ficedula hypoleuca*	1	0,3

nete ein roter Stab bzw. ein Schild. Zum leichteren Auffinden war der nächststehende Baum mit einem Band oberhalb der Schneedecke markiert. Zuerst wurde vom Mittelpunkt aus nach Höhlen gesucht. Anschließend wurde von je einer Person ein 25-m- und ein 40-m-Radius abgeschritten. Bäume, in denen Höhlen vermutet wurden, kontrollierte man von allen Seiten. Bei Höhlenbäumen in der Nähe der Gitterfeldgrenze wurde mit einem Entfernungsmessgerät die Entfernung sowie mit dem Kompass die Gradzahl zum Mittelpunkt gemessen. So konnte der Baum in eine Karte eingezeichnet werden, die Aufschluss darüber gab, ob der Baum innerhalb oder außerhalb des Gitterfeldes lag.

Zu jedem gefundenen Höhlenbaum wurden neben seinem genauen Standpunkt (Entfernung und Grad zum Mittelpunkt) weitere Daten zum Baum sowie zur Höhle erfasst (Tab. 3). Pro Gitterfeld war durchschnittlich 1 Stunde Zeit erforderlich, wobei es sehr höhlenreiche Flächen gab, mit einem 3–4 stündigen Arbeitsaufwand, aber auch Flächen, die in 15 Minuten bearbeitet waren. Die Begehbarkeit der Fläche spielte hier eine große Rolle. Weitere Umweltvariable wurden aus der Datenbank des Nationalparks entnommen (Tab. 1), die im Rahmen des Biodiversitäts- und Klimaprojektes erhoben wurden (Bässler et al. 2008).

Vogelkartierungen. Die Avifauna wurde in 5 Begehungen von März bis Juni im Rahmen einer quantitativen Gitterfeldkartierung (Bibby, Burgess & Hill 1995, Müller 2005a, Utschick 2004) erfasst. Dabei wurden alle Vögel im 1-ha Gitterfeld innerhalb von 10 min kartiert. Als Höhlenbrüter wurden die Arten ausgewählt, die nach dem Kompendium der Vögel Mitteleuropas (Bauer et al. 2005) in Baumhöhlen brüten (Tab. 2). Für die Artenzahl baumhöhlenbrütender Vogelarten wurden alle Arten summiert,



die mindestens einmal bei 5 Begehungen pro Gitterfeld angetroffen wurden. Für die Individuenzahlen wurden die Registrierungen aller 5 Begehungen addiert. Da die Vogeldaten im Rahmen der vorliegenden Arbeit nur zur Ableitung des Schwellenwertes genutzt wurden, wird auf eine ausführliche Darstellung und Diskussion verzichtet. Eine solche findet sich bei Moning & Müller (2008).

Statistik. Die Zahl der Höhlen und Höhlenbäume je Untersuchungsquadrat stellt eine typische Zählgröße mit linksschiefer Verteilung dar. Dies bedeutet, dass Gitterfelder mit niedrigen Werten wesentlich häufiger vorkommen als solche mit mittleren oder häufigeren. Aus diesem Grund wurde für die Analyse des Einflusses von Umweltparametern auf die Zielgröße ein generalisiertes Modell (GLM) mit Poisson-Verteilung verwendet (Lozán & Kausch 2004). Die Unterschiede in den Zielgrößen zwischen verschiedenen Managementtypen wurden mithilfe einer Ränge-basierten ANOVA getestet, bei der die Verteilungen der Zielgröße simuliert werden (Westfall & Young 1993). Dabei wurde ein Nachfolgetest, basierend auf den Rängen, durchgeführt. Alle statistischen Auswertungen erfolgten mit R 2.6.1 (version 2.6.1, R Development Core Team 2005). Die ANOVA wurde mithilfe einer Implementierung in den add-on Paketen 'coin' und 'multcomp' berechnet (Hothorn et al. 2006).

Für die Quantifizierung der Beziehung zwischen Baumhöhlen und Baumbrütern wurde ein Regressionsbaum berechnet. Mithilfe der maximal selektierten Rangstatistik erfolgt dabei im ersten Schritt eine Selektion der Umweltvariablen, die am besten zwischen niedrigen und hohen Werten der Zielgröße, in unserem Fall Höhlen bzw. Höhlenbäume, differenziert. Im zweiten Schritt wird ein Schwellenwert berechnet, der angibt, an welcher Stelle entlang des Umweltgradienten der Unterschied am deutlichsten ausfällt. Für diesen wird ein Signifikanzwert (p-Wert) ermittelt. Die Klassifizierung der Daten erfolgt so lange, bis in den unterteilten Gruppen keine weiteren signifikanten Schwellen mehr gefunden werden. Eine ausführliche Einführung der Methodik in Zusammenhang mit Vogeldaten findet sich bei Müller & Hothorn (2004). Um einen Vertrauensbereich für jeden dieser Schwellenwerte zu ermitteln, wurde auf der Basis von zufällig gezogenen Daten in 5.000 Bootstraps das 95%-Konfidenzintervall berechnet (Roff 2006). Einfache Schwellenwerte werden nur selten der komplexen Realität voll gerecht, da völlig abrupte Veränderungen einer Zielgröße entlang eines Gradienten nur selten sind. Für die praktische Naturschutzarbeit lässt sich aber mittels solcher Methode objektiv und multivariat testen, welche Einflussgrößen von Bedeutung sind und wo sich wichtige Kenngrößen für Empfehlungen ableiten lassen (Angelstam et al. 2003, Guénette & Villard 2005).

Ergebnisse

Anteil der Spechthöhlen. Auf 155 von 293 Gitterfeldern konnten Höhlen gefunden werden, insgesamt wurden 454 Höhlenbäume mit 734 Höhlen und 850 Eingängen erfasst. Über alle Gitterfelder verteilt, ergaben sich durchschnittlich 1,5 Höhlenbäume und 2,5 Höhlen je Hektar. Maximal konnten wir auf einem Gitterfeld 12 Höhlenbäume mit 31 Höhlen finden. Der Großteil der Höhleneingänge (668 von 850, 78,6%) konnte den Spechten zugeordnet werden.

Einflussfaktoren auf Höhlen. Insgesamt wurde der Einfluss von acht verschiedenen Faktoren (Tab. 1) auf das Vorkommen von Höhlen geprüft. Davon konnten zwei als förderlich für Höhlen sowie zwei als abträglich für das Höhlenangebot identifiziert werden (Tab. 1). Überragender positiver Faktor für das Höhlenvorkommen war neben dem Alter, das Volumen an Totholz. Besonders negativ für das Höhlenvorkommen zeigte sich zum einen die hohe Forstwegedichte, zum anderen die Höhe ü. NN.

Management und Höhlenangebot. Beim Vergleich des durchschnittlichen Höhlen- bzw. Höhlenbaumvorkommens innerhalb der Waldtypen ‚Alter Wald', ‚Prozessschutz' und ‚Management' unterhalb 1.150 m Meereshöhe (‚Hang-/Tallagen') erkennt man ein signifikant häufigeres Höhlenvorkommen in den Kategorien ‚Alter Wald' und ‚Prozessschutz' gegenüber der Kategorie ‚Management' (Abb. 2). Auch in den Hochlagen-Fichtenwäldern findet man in den Prozessschutzflächen signifikant mehr Höhlen als in den gemanagten Wäldern.

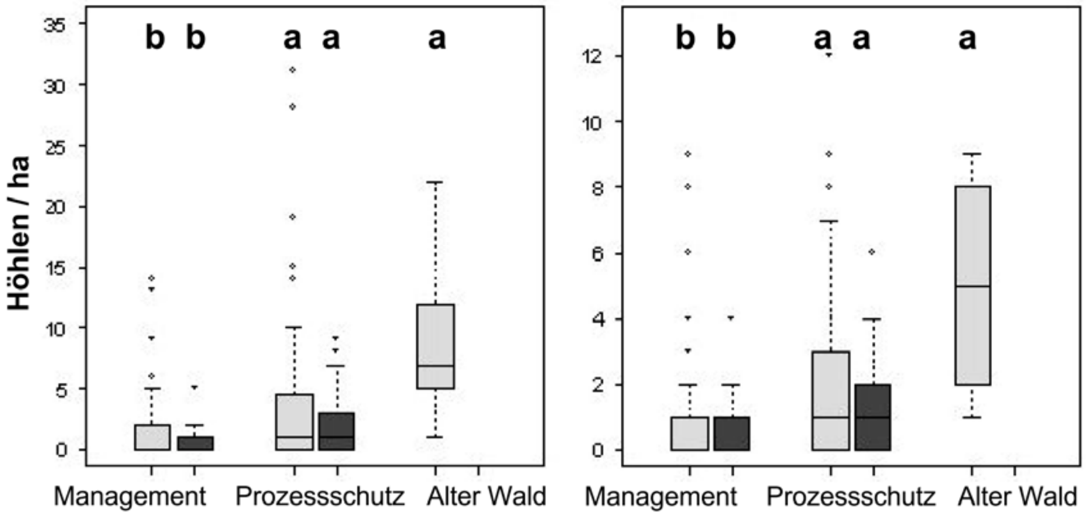


Abb. 2. Boxplot der Höhlen und Höhlenbaumanzahlen pro ha getrennt nach Managementtypen und Höhenlage (Hochlagenfichtenwälder >1.150 m NN sowie Fichten-Tannen-Buchenwäldern darunter). Statistische Unterschiede (p<0,05) in den Posthoc-Tests sind durch unterschiedliche Buchstaben gekennzeichnet. Kategorien, die keinen gemeinsamen Buchstaben aufweisen, sind signifikant unterschiedlich. Beachte, alle Tests wurden nur innerhalb einer Höhenstufe getestet. Die Boxen zeigen die 25- und 75%-Quartile, die Whisker die 95%-Quartile. Die leeren Kreise stellen Ausreißer dar. Der Balken zeigt den Median. – *Boxplots of the cavities and cavity trees per hectare separated according to management types and altitude (high altitude spruce forest >1.150m a.s.l., as well as spruce-fir-beech woods below this). Statistically significant differences (p<0,05) in the posthoc tests are indicated by different letters. Note that testing was always carried out within a single altitudinal zone.*

Höhlenbaumangebot und Höhlenbrüter. Beim Vergleich des Höhlenangebotes mit dem Vorkommen höhlenbrütender Vogelarten je Gitterfeld ergab sich ein signifikanter Schwellenwert von 4 Höhlenbäumen pro Hektar (95%-Konfidenzintervall 4–5). Dies bedeutet, dass in Flächen mit mindestens 5 Höhlenbäumen die Zahl der Höhlenbrüter deutlich ansteigt. Vergleicht man die Mediane der Gruppe unter und ab 5 Höhlenbäumen pro ha, so liegt der Median bei letzterem etwa doppelt so hoch (Abb. 3). Dies gilt sowohl für die Artenzahl als auch für die Individuenzahl (nicht dargestellt).

Diskussion

Methodendiskussion. Da die Kartierungen nur vom Boden aus durchgeführt wurden, besteht die Gefahr, Höhlen übersehen oder falsch beurteilt zu haben. Da bei den meisten Studien Höhlen vom Boden aus kartiert werden, ist der Anteil der zu Unrecht angesprochenen Höhlen jeweils vergleichbar. Eine Kontrolle durch Besteigen der Bäume oder mit dem TreeTop Peeper (eine Kamera an einer Teleskopstange) wäre mit zu viel Aufwand verbunden gewesen. Durch ein Absuchen der Bäume bei unterschiedlichen Lichtverhältnissen, wie in anderen Studien (Weggler & Aschwanden 1999), hätte das Kartierergebnis noch verbessert werden können. Die Geländebedingungen und die Ausdehnung der Probeflächen mit mehr als 29 km ließen eine mehrfache Begehung innerhalb der vorgegebenen Zeit nicht zu. In der Rhön konnte in einer Studie festgestellt werden, dass ¼ der kartierten Höhlen nicht für Höhlenbewohner nutzbar waren (Zahner 1993). Insgesamt wurden die Kartierarbeiten aber bei gleichbleibender Kartiereffizienz durchgeführt, da es nur sehr wenige Gitterfelder gab, die aufgrund ihrer schlechten Begehbarkeit und schlechten Sicht durch hohe Verjüngung ungenauer kartiert wurden. An Tagen mit starkem Nebel oder Schnee-/Regenschauern wurden die Kartierarbeiten abgebrochen.

Ein weiterer Schwachpunkt des Kartiervorgangs auf einem 1,0-ha-Gitterfeld kann die Einhaltung des äußeren Kartierradius von 40 m, vor allem in unzugänglichem Gelände, darstellen. Im Bereich zwischen diesem Radius und der Gitterfeldgrenze wird die nach außen

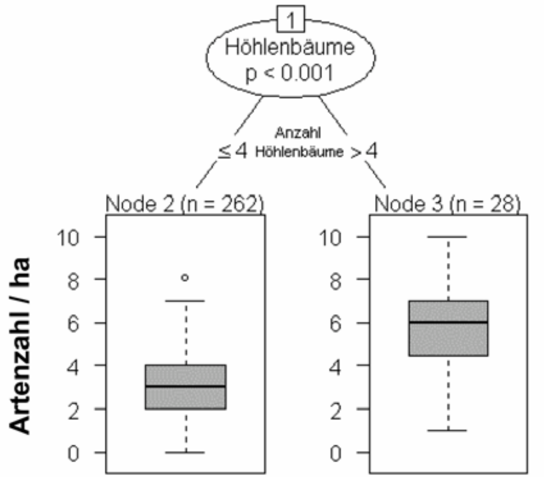


Abb. 3. Regressionsbaum für die Artenzahl höhlenbrütender Vogelarten in Abhängigkeit von der Zahl der Höhlenbäume. Dabei wird dargestellt, an welcher Stelle der Höhlenbaumzahl (hier > 4) die Zielgröße Vogelarten sich am deutlichsten zwischen niedrigen und hohen Werten trennen lässt. Für jede dadurch gebildete Untergruppe wird die Artenzahl als Boxplot (s. Erläuterung Abb. 2) dargestellt. Der Balken zeigt den Median der höhlenbrütenden Vogelartenzahl. – *Regression tree for the species number of cavity-breeding birds as determined by the number of cavity trees. For each subgroup built by the regression tree the values of species number of cavity-breeding birds is shown as boxplot.*

gerichtete Stammseite nicht eingesehen. Um diesen Fehler auszuschließen, könnte ein größerer Radius von ca. 70 m begangen werden, hier wäre der Abstand zwischen den beiden Radien aber zu groß und unübersichtlich, was wiederum zu einer neuen Fehlerquelle führen könnte.

Anteil der Spechthöhlen. Spechte sind mit ihren Schnäbeln und ihrer Anatomie die einzige Vogelfamilie, die über speziell angepasstes Werkzeug verfügt, um aktiv Höhlen in Holz zu zimmern (Miranda & Bürgi 2005). So überrascht es nicht, dass der Großteil (ca. 80%) der Höhleneingänge den Spechten zugeordnet werden kann. Gelegentlich nutzen Spechte auch Faulhöhlen, die sich durch Holzzersetzer gebildet haben. Meistens entsprechen Faulhöhlen jedoch nicht den Ansprüchen der Spechte in Bezug auf Stabilität und Größe.

Einflussfaktoren auf Höhlen. Das Ergebnis, dass das Bestandesalter eine wichtige Größe für das Baumhöhlenangebot ist, findet sich in vielen Arbeiten zu diesem Thema. Alte Wälder sind aus zwei Gründen für Höhlenbauer von Vorteil: Zum einen häufen sich Strukturen wie Spalten, Risse und Höhlen (Müller 2005b). Darin leben Insekten; die Hauptnahrung der Spechte. In Schweden wurde ein für Spechte deutlich reduziertes Nahrungsangebot in jüngeren Beständen festgestellt (Petterson et al. 1995). Daneben sind faulende Totholzstrukturen in alten Wäldern für Spechte optimal, da sie viele geeignete Stellen zum Höhlenbau bieten. Nicht nur für die „zimmerschwachen" Spechtarten wie den Kleinspecht *Dryobates minor* und Weißrückenspecht *Dendrocopos leucotos* sind diese weichen Stellen zum Höhlenbau bedeutsam, auch für die kräftigen Arten wie Dreizehenspecht *Picoides tridactylus* und Buntspecht *Dendrocopos major* sind faule Stellen an Bäumen wichtig (Scherzinger 1998). Bei Untersuchungen im Sauerland wurden in Laubholzbeständen, die 140 Jahre alt waren, mehr Höhlenbäume gefunden (Noeke 1991). Nach Blume (1990) setzt die Höhleneignung bereits bei einem Alter von 75–80 Jahren ein. Mosler-Berger (1993) diskutiert weitere Eigenschaften alter Wälder, die diese gerade für Spechte prädestiniert: Durch die dicken, großen Bäume alter Bestände ist der Stammbereich licht, was einen freien Anflug zur Höhle ermöglicht, wenn es die Unter- und Mittelschicht des Bestandes zulässt. Der lichte Stammbereich bietet mehr Sicherheit, da Feinde auf größere Distanz erkannt werden können.

Als weitere, statistisch wichtige Einflussgröße erwies sich das Totholzangebot. Der Höhlenbau der meisten Spechte findet in geschwächtem oder totem Holz statt (siehe auch Noeke 1991, Schumacher 2006). Spechte verständigen sich durch Trommel- und Klopfsignale, wofür Totholz häufig den Resonanzboden bietet (Blume 1993). In einem Waldgebiet im südbayerischen Voralpenland reagierten rund 65% der Vogelarten auf Totholz. Daraus abgeleitet, gilt als optimale Totholzmenge je nach Waldtyp 20–60 m³/ha (Utschick 1991). Für den Dreizehenspecht ist nachgewiesen, dass er stehende Totholzmengen von 20 m³/ha benötigt, um ein Gebiet dauerhaft zu besiedeln (Bütler & Schlaepfer 2004). Eine Steigerung des Totholzanteils von 1 auf 3% der Holzmasse kann zu einer Verdoppelung der Höhlenbrüterdichte führen (Lauterbach & Walentowski

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Foto 1. Brutbaum des Raufußkauzes *Aegolius funereus*. – *Breeding site of Tengmalm's Owl* Aegolius funereus.
Fotos: C. Moning, 2007

Foto 2. Sperlingskauz *Glaucidium passerinum* - *Pygmy Owl* Glaucidium passerinum. Foto: C. Moning, 2007

2006). Stirbt in einem Bestand ein Baum ab, kann mehr Licht und Wärme durch die blattlose Krone an den Stamm und Boden gelangen. Dieser „Lichtschachteffekt“ lockt Insekten an (Noeke 1991). In den Wäldern des Nationalparks steigert das Totholzvorkommen die Dynamiken in mittelalten Beständen. Dies ist sicherlich der Grund, dass sich die Höhlendichte im Altbestand und auf Prozessschutzflächen gleicht. Damit lässt sich gut der fehlende Unterschied in den Höhlendichten zwischen Alter Wald und Prozessschutz erklären (Abb. 3).

Der negative Einfluss der Wegedichte konnte (Tab. 1) auch in anderen Studien festgestellt werden (Bütler et al. 2004). Die Ursache liegt dabei aber nicht im Vorhandensein der Wege, sondern in der wesentlich verbesserten Nutzungsmöglichkeit der Waldbestände innerhalb ihres Umfelds. Dadurch wurden in so nutzbaren Waldbereichen potenzielle Höhlenbäume bereits frühzeitig entfernt. Eine zusätzliche Ursache für das verminderte Höhlenvorkommen an Wegen stellt auch die Verkehrssicherungspflicht dar. Bei ihrer Ausführung

Foto 3. Kartierter Höhlenbaum mit brütendem Habichtskauz *Strix uralensis*. – *Recorded cavity-tree with breeding Ural Owl* Strix uralensis. Foto: Göggelmann, 2008

werden vor allem anbrüchige Bäume entnommen, die häufig die höhlenreicheren sind. Direkte negative Einflüsse der Wege sind gering. Sogar das Gegenteil ist der Fall: viele der Höhlenbauer, z. B. der Grünspecht *Picus viridis*, bevorzugen diesen „Ersatzlebensraum" für Urwaldlücken wegen des erhöhten Sonnen- und damit verbundenen Nahrungsangebots (Müller 2005b).

Mit zunehmender Höhenlage zeigt sich ein hoch signifikant negativer Einfluss auf die Höhlendichte. Mit steigender Höhe nimmt der Jahresniederschlag zu und die Jahresmitteltemperatur sinkt. So verkürzt sich in den höheren Lagen die Vegetationsperiode, und das Nahrungsspektrum für Spechte verknappt sich, besonders in den langen schneereichen Wintern, die zu hohen Populationsverlusten führen können (Scherzinger 2007). Daneben sinkt der allgemeine Holzvorrat, somit die Anzahl der Bäume, in denen Höhlen gebaut werden können. Auch kann die niedere Temperatur im Zusammenspiel mit größerer Feuchtigkeit die Mortalität der Spechtbruten erhöhen. Aus diesem Grund werden die Hochlagen zum Höhlenbau gemieden. Eine tatsächliche Präferenz für die Fichtenhochlagenwälder zeigt im Wesentlichen nur der Dreizehenspecht, durch seine Bindung an totholzreiche Fichtenwälder, während andere Arten vorrangig in mittleren Hanglagen zu finden sind (Krištin 2003). Bei einer Untersuchung in der Mittelslowakei konnte eine Abnahme der Abundanz der gesamten Spechtgemeinschaft bei steigender Höhe (Untersuchungsrahmen 460 – 1.458 m ü. NN) beobachtet werden (Krištin 2001). Man konnte sogar für alle Vogelarten eine abnehmende Vogelartenzahl bei steigender Höhe feststellen (Scherzinger 1985).

Eine weitere Ursache ist der Anteil an Laubbäumen, der im Nationalpark über 1.150 m rasch absinkt. Generell wird Laubholz von Spechten bevorzugt, da es nicht harzt, Höhlenöffnungen langsamer überwallt und häufiger Totäste aufweist (Zahner 1993). Darüber hinaus bilden die Bäume in den höheren Lagen engere Jahrringe und dadurch eine höhere Holzdichte. So ist dieses Holz für Spechte schwerer zu bearbeiten. Ein häufigeres Vorkommen bestimmter Arten wie dem Schwarzspecht kann in höheren Gebirgslagen auftreten (Bauer, Bezzel & Fiedler 2005). Sie sind aber meist das Ergebnis eines von unten nach oben ansteigenden Strukturangebots. Denn durch unzugängliche Waldungen in höheren Gebirgslagen findet man z. B. in den Alpen höhere Totholzvorräte als in niederen Lagen.

Foto 4. Kleinspecht *Dryobates minor* – *Lesser Spotted Woodpecker* Dryobates minor. Foto: J. Müller, 2007

Höhlenbaumangebot und Höhlenbrüter. Diese Untersuchung zeigt, dass auf den Gitterfeldern mit mindestens 5 Höhlenbäumen/ha doppelt so viele höhlenbrütende Vogelarten vorkommen, als auf den Feldern mit weniger Höhlenbäumen/ha. Diese statistische Ableitung eines kritischen Schwellenwertes ist vor einer Verallgemeinerung kritisch zu hinterfragen. Generell ist ein statistisch abgesicherter Zusammenhang zwischen Höhlenbrütern und Höhlenbäumen nicht überraschend. Höhlenbäume sind zentrale Schlüsselstrukturen für deren Nutzer. In der Regel handelt es sich um alte oder tote und somit strukturreiche Bäume mit einer Vielzahl an Nischen (z. B. Höhlen, Spalten, abstehende Rinde). Dabei können zwei bis fünf Quartiere gleichzeitig an einem Höhlenbaum besetzt werden (Frank 1997). Für verschiedene Höhlenbewohner ist das breite

Angebot an Höhleneigenschaften wichtig, z. B. Volumina, Feuchtigkeit/Trockenheit und die Anzahl der Eingänge (Frank 1997). Die Chance, viele Arten oder Individuen mit den gleichen Ansprüchen zu befriedigen, steigt mit der Höhlenbaumanzahl. Damit sinkt die bestehende Quartierkonkurrenz um eine geeignete Höhle (Frank 1997). Erst durch ein insgesamt hohes Angebot an Höhlen haben auch konkurrenzschwache Arten wie die Blaumeise *Parus caeruleus*, der Gartenrotschwanz *Phoenicurus phoenicurus*, der Zwergschnäpper *Ficedula parva* oder der Trauerschnäpper *Ficedula hypoleuca* die Chance, geeignete Höhlen beziehen zu können (Müller 2005b, Sachslehner 1995). Dass der Mangel an Höhlenbäumen die Nistmöglichkeiten für Höhlenbrüter limitiert, wurde nicht nur in vielen empirischen Arbeiten bereits beschrieben, sondern auch experimentell, über ein künstlich gesteigertes Nistplatzangebot nachgewiesen (Löhrl 1957).

Konkrete Empfehlungen zur Anzahl notwendiger Höhlen sind relativ selten. Schumacher (2006) gibt aus avifaunischer Sicht als Bewirtschaftungsempfehlung ein Belassen von 5 Altbäumen/ha in Wirtschaftswäldern und 7 Höhlenbäumen/ha in Naturschutzgebieten. Für kolline Buchenwälder werden 5 Höhlenbäume als kritische Untergrenze für eine Besiedlung durch den Halsbandschnäpper *Ficedula albicollis* angegeben (Müller 2005b). Die Schwierigkeit, hier valide Empfehlungen zu geben, drückt Frank (1997) durch seinen Ratschlag aus „Ein Zuviel dürfte es nicht geben“. Damit soll der in der vorliegenden Arbeit ermittelte Schwellenwert, als einer aus den Daten eines Nationalparks mit langen Gradienten (keine bis viele Höhlen pro Hektar) angesehen werden, der sich aber durchaus in den Rahmen bestehender Arbeiten einreiht.

Schlussfolgerungen

Die Analyse des Höhlenangebotes im Nationalpark Bayerischer Wald ergibt im Wesentlichen zwei wichtige Ergebnisse. Zum einen sind in Prozessschutzflächen durch natürliche Dynamiken bereits Höhlendichten entstanden, die sich nicht mehr statistisch von alten Wäldern unterscheiden lassen. Damit ist belegt, dass der Schritt, die Flächen sich selbst zu überlassen zu einer Annährung an urwaldartige Bestände geführt hat. Zum anderen hat sich gezeigt, dass für eine deutliche Erhöhung von Höhlenbrütern in bewirtschafteten Bergwäldern eine Etablierung von mindestens 5 Höhlenbäumen pro Hektar notwendig ist.

Zusammenfassung

Um mehr über die Einflussfaktoren auf das Baumhöhlenangebot herauszufinden, wurden im Nationalpark Bayerischer Wald auf 293 Hektar entlang von fünf Transekten alle Baumhöhlen kartiert. Alter und Totholzmenge erwiesen sich als positive, Forstwegedichte und Höhenlagen als negative Einflussfaktoren für das Vorhandensein von Baumhöhlen.

Der Vergleich der drei Managementtypen ergab signifikant höhere Baumhöhlenzahlen in alten Wäldern und Prozessschutzflächen gegenüber den gemanagten Flächen in der Stufe der Bergmischwälder. Auch in den Hochlagen ist das Höhlenangebot in Prozessschutzflächen signifikant größer. Mithilfe eines Regressionsbaumes konnte ermittelt werden, dass sich ab fünf Höhlenbäumen pro Hektar die Zahl der Höhlenbrüterarten in etwa verdoppelt.

Die Analysen belegen eine überragende Rolle alter Wälder für den Höhlenreichtum. Aber auch die Prozessschutzflächen, obwohl erst einige Jahrzehnte aus der Nutzung, entwickeln sich zu Naturwäldern mit besseren Voraussetzungen für Spechte und andere Höhlenbrüter.

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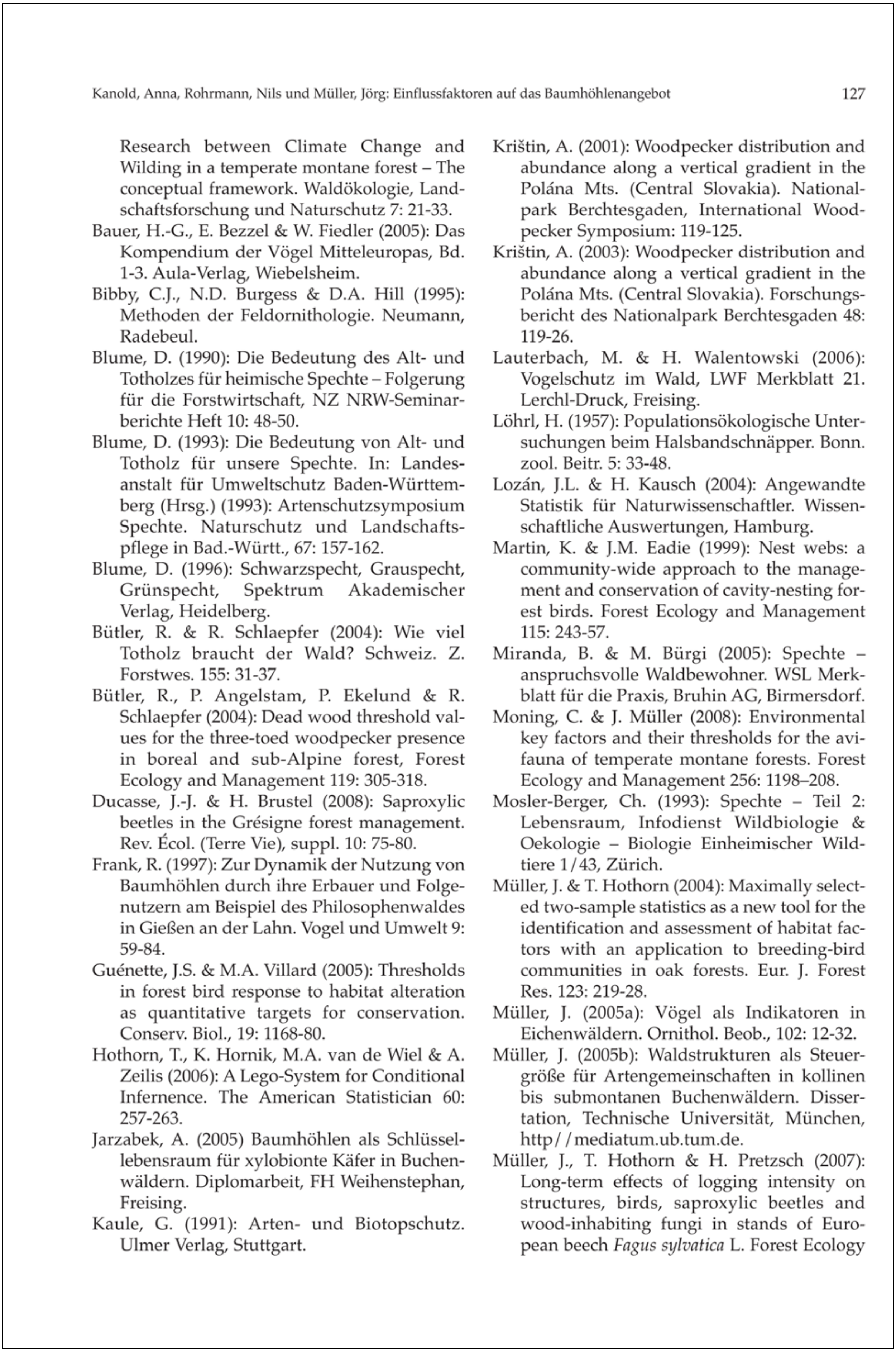

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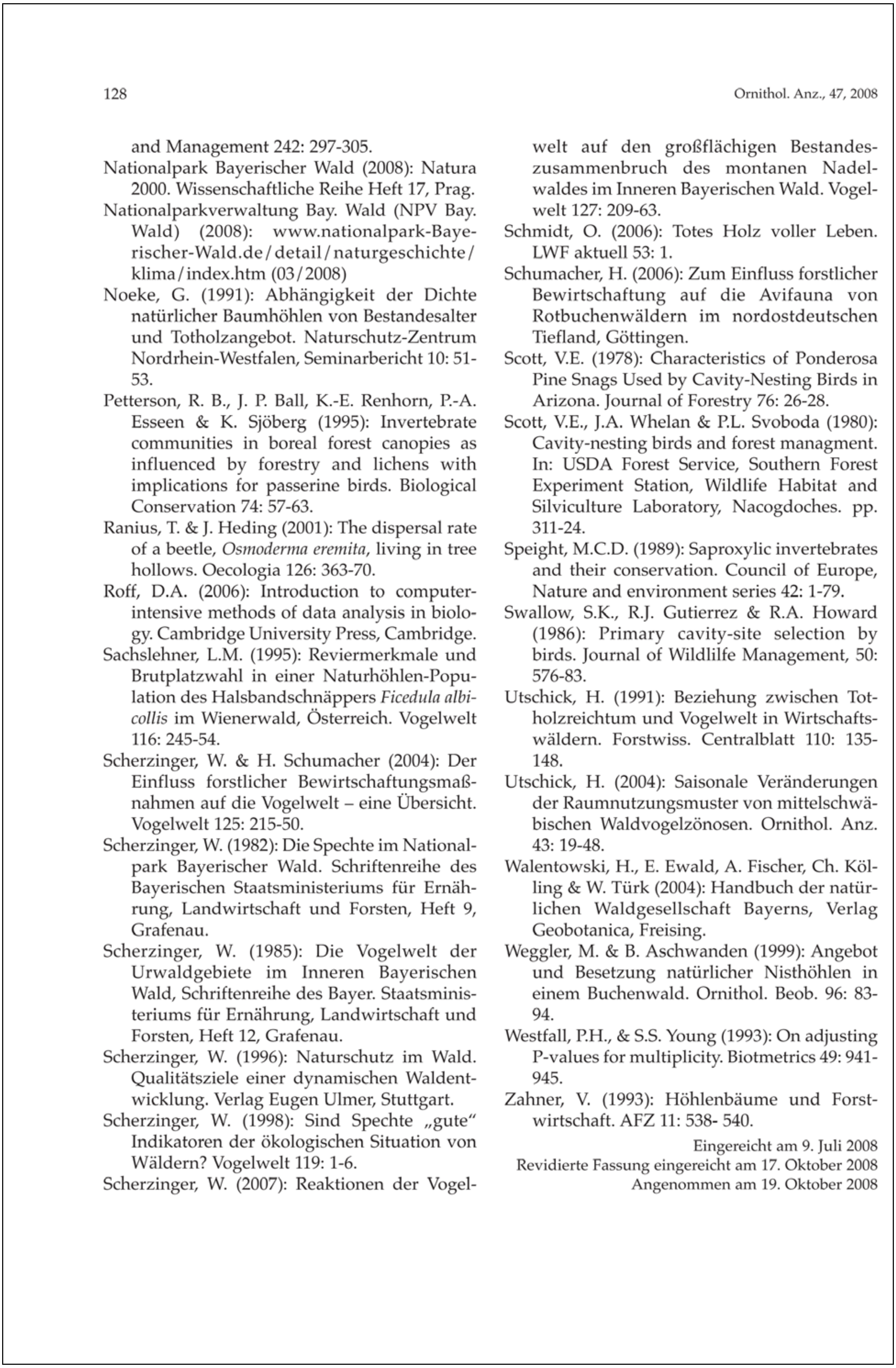

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Environmental key factors and their thresholds for the avifauna of temperate montane forests

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ABSTRACT

Mixed montane forests cover large tracts of the low mountain ranges that dominate Central Europe and also contain much of the area that is important to forest related nature conservation. However, beyond general patterns little is known about ecologically effective driving factors in this habitat. This results in a lack of precise values that can be used to formulate guidelines for nature conservation oriented management strategies. To improve this situation, we used birds as indicators for forest habitat qualities.

The avifauna of the Bavarian Forest National Park was investigated on 293 plots of 1 ha along four transects ranging from 655 to 1420 m a.s.l. The investigated forest includes a wide structural gradient ranging from very open, grass dominated areas of the high montane zone, where mature spruce trees have died after bark beetle infestation, to mature mixed montane forests at lower elevations. Altitude is the main factor driving composition of bird assemblages in the montane forests. We analysed occurrence of species using a subdivided dataset, in which the altitude could be eliminated as an important influencing factor, by implementation of General Linear Models under consideration of spatial effects and utilising maximally selected rank statistics. Our analysis identified canopy cover as the most influential factor in montane and high montane forests. Forest age is the second most important gradient in montane forests. The tree species composition has an influence on a limited number of species. In high montane forests, bark beetle infestations have led to a complete change in the avifauna composition. The distinct, species-poor group that is found here includes some species that are generally decreasing in abundance in Central Europe. By calculating threshold values for the environmental variables which were identified as important, we were able to formulate the following concrete management recommendations:

(1) To create conditions suitable for the whole range of species associated with openings in the canopy, the full spectrum of canopy-openness ranging from 5% to 70% should be realized on the stand scale throughout a whole forest landscape.
(2) To sustain the whole range of cavity-breeding species and species of mature forests, the age of Central European mixed montane forests needs to surpass 200–220 years.
(3) To support the deciduous forest species in mixed montane stands a minimum of 60% cover of deciduous trees at least in single stands that are maximally few kilometres apart is required.

Among the threshold values, we identified cascade-like threshold sequences that represent the ecological niches of the individual species with respect to the environmental variables, which contrasts with species groups where the collective threshold value is a universal threshold that applies to the whole group.

1. Introduction

More than half of Central Europe is covered by low mountain areas, most of which are clothed in forests (CIPRA, 2007). These montane forests contain much of the area that is important for forest related nature conservation such as special protected areas (SPA), nature protection areas, natural parks, national parks, etc. In contrast to oak forests at lower altitudes (e.g. Bühlmann, 1993;

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Wesołowski and Tomiałojć, 1995; Wesołowski et al., 2002) and despite their great importance for conservation, little is known about the ecologically effective driving factors in montane forests.

Forest birds have proved to be good indicators of forest habitat qualities (e.g. Flade, 1994; Müller, 2005). Generally, they have been very well studied worldwide (e.g. Askins et al., 1987; Terborgh et al., 1990; del Hoyo et al., 1992–2008; Schmiegelow et al., 1997; Sekercioglu, 2002) and have also been subject to various surveys that revealed distribution patterns in montane forests worldwide (e.g. Loiselle and Blake, 1991; Watson and Townsend Peterson, 1999). For example, in temperate montane forests the winter distribution of birds has been linked to solar radiation (Huertas and Díaz, 2001) and the presence of old growth and unlogged patches (Beese and Bryant, 1999). The change in the bird species composition at various successional stages has also been investigated in Central Europe (Glutz von Blotzheim, 2001; Christen, 2003; Scherzinger, 2006). In general, interrelated effects of climate, habitat physiognomy (mainly vegetation cover and diversity of stratification: Rov, 1975; Cueto and de Casenave, 1999), competitive interactions, food resources, wintering habits and biogeographic origin of the avifaunas have been considered to be the most important factors determining the avian species composition and niche structures in a variety of montane habitats (Sabo and Holmes, 1983).

Beyond the general patterns, little is known about specific ecologically effective threshold values of montane forest bird assemblages (but see, e.g. Bütler et al., 2004; Guenette and Villard, 2005; Müller and Bußler, 2007). However, there is abundant evidence of discontinuities and threshold effects arising as the consequence of human disturbance also in forest systems. Yet due to the complexities involved, the predictive capacity of ecology is limited and large uncertainties still remain (Muradian, 2001). This has led to a serious lack of precise guideline values for temperate mixed montane forests that can be implemented in management procedures. One of the reasons is that in many cases only a limited array of environmental parameters is involved in the analysis, which interferes with an unprejudiced analysing process and finally leads to inconclusive results. There is also a shortage of investigations that rely on bird mapping data and habitat parameter data that originate within the same time frame. Only statistically verified data of this type can eventually yield statistical threshold values (Angelstam et al., 2003; Lindenmayer and Luck, 2005).

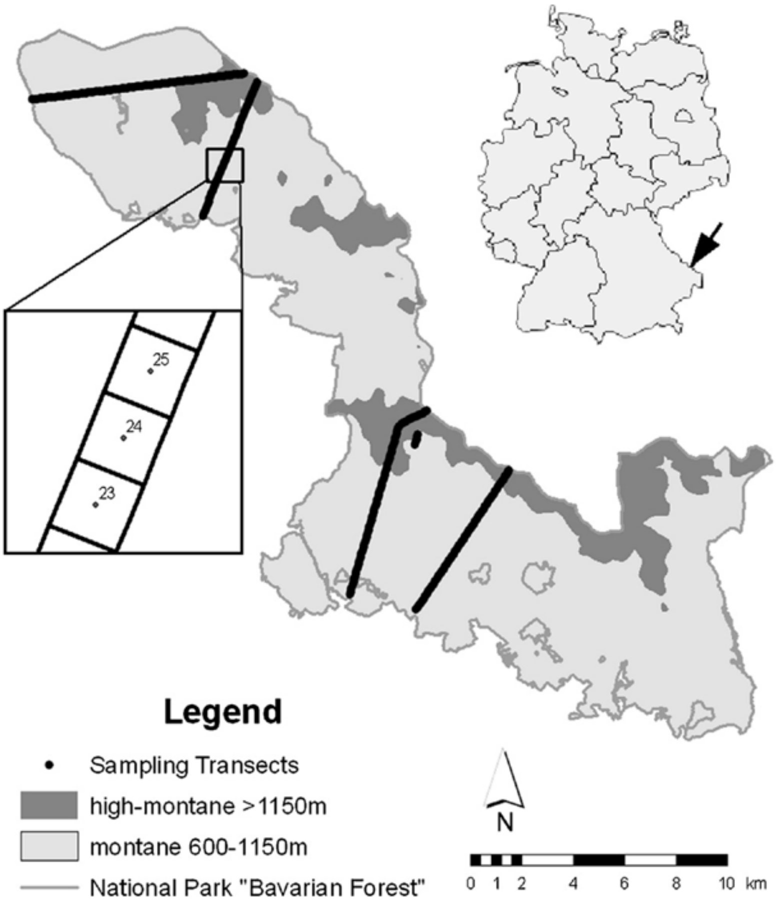


Fig. 1. Location of the National Park "Bavarian Forest" and the sampling transects in the National Park. The sampling design includes a short transect situated in an old mixed montane forest east of the Rachel mountain.

Threshold values are a key feature in controlling environment–economy interactions (Muradian, 2001). For example, threshold values are recommended for implementation in biodiversity conservation (e.g. Perrings and Pearce, 1994) and sustainable development strategies (e.g. Rennings and Wiggering, 1997).

In order to improve management guidelines for the montane forest avifauna in Central Europe, these bird assemblages have to be characterized by means of statistically meaningful threshold values. We therefore carried out appropriate research in the Bavarian Forest National Park, which is well suited to this purpose because of its large forest area and long structural gradients. The aims of this study are: (1) identification of the main driving environmental parameters for forest-breeding birds under consideration of a comprehensive assemblage of parameters including the altitude gradient, (2) to explain species abundances by dint of the identified environmental driving factors using a subdivided dataset that allows the elimination of the effect of altitude, which is an important but not a manageable factor, (3) to identify threshold values, and (4) indicator species for the important environmental factors and (5) to derive from these results recommendations relevant to management with respect to various aspects of avian diversity in temperate montane forests.

2. Methods

2.1. Study site and field methods

The Bavarian Forest National Park is situated in south-east Germany and forms part of the trans-border park system Bavarian Forest/Šumava (Fig. 1). In order to sample the breeding birds, 293 square plots were arranged along four transects in the National Park (Fig. 1). The two eastern transects are situated in the old part of the National Park, where no forest management operations have taken place since the beginning of the 1980s. Most of the high montane spruce trees in this part have been killed by bark beetles, mainly *Ips typographus*, largely since the mid 1990s. The other two transects in the west are situated in the newer part of the National Park established in 1997, where active forest management, mainly control of bark beetles, is still taking place extensively. The altitude ranges from 655 to 1420 m a.s.l. This includes a wide structural gradient ranging from very open, grass dominated high montane areas where mature spruce trees have died due to bark beetle infestation, to denser, mature, mixed montane forests at lower elevations.

The avifauna was investigated on each transect at the end of March, in mid-April, at the beginning and at the end of May and at the beginning of June. During each investigation, every transect was mapped on one morning from sunrise to 11 a.m. The weather on these days was without or with little wind, without rain and was more or less sunny (Bibby et al., 2000; Müller et al., 2007). Each transect is composed of a line of square plots abutting on each other with each plot measuring 100 m × 100 m (=1 ha, Fig. 1). Every plot was investigated for 10 min on each occasion. The locations of all bird individuals seen and/or heard during this period were recorded precisely on a field map based on aerial photographs from the year 2005, updated to 2006, which also depicted the habitat types in the plot. The records could thus later be linked with the habitat categories. Only birds that were recorded within the plots were included in the analysis.

The basic dataset was the sum of all registered individuals for each species for each plot. This reflects the abundance of the various species on the plots during the investigations and is not

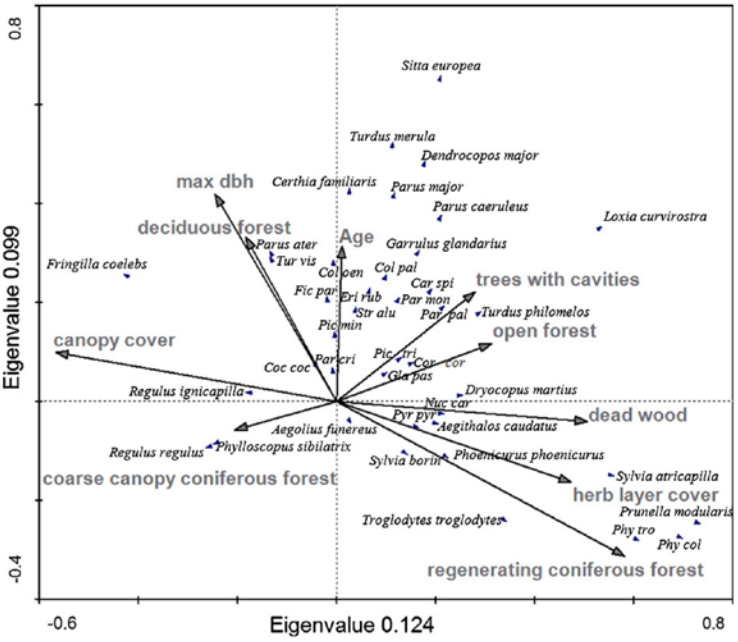


Fig. 2. Location within two-dimensional ordination space of species of the montane forest avifauna from 600 to 1150 m a.s.l. including the ten most important environmental variables. Abbreviations used in this figure are Car spi (*Carduelis spinus*), Coc coc (*Coccothraustes coccothraustes*), Col oen (*Columba oenas*), Col pal (*Columba palumbus*), Cor cor (*Corvus [corone] corone*), Eri rub (*Erithacus rubecula*), Fic par (*Ficedula parva*), Gla pas (*Glaucidium passerinum*), Nuc car (*Nucifraga caryocatactes*), Par cri (*Parus cristatus*), Par mon (*Parus montanus*), Phy col (*Phylloscopus collybita*), Phy tro (*Phylloscopus trochilus*), Pic min (*Picoides minor*), Pru mod (*Prunella modularis*), Pyr pyr (*Pyrrhula pyrrhula*), Str alu (*Strix aluco*) and Tur vis (*Turdus viscivorus*).

necessarily linked to the number of territories present on the plots. However, the number of individuals is the most objective obtainable data unit and is the most reliable indicator for the habitat use of the species (see also, e.g. Haila et al., 1996). As the species are not compared with each other, the differences in the ease of detection of species do not represent a problem.

2.2. Statistical analysis

The bird data in the main as well as the subdivided datasets was square-root transformed, because a few species are recorded very frequently. In order to identify meaningful underlying variables in the complete dataset, a principal component analysis (PCA) was first used, chosen because of the length of the first gradient (1.5S.D., Leps and Smilauer, 2003). The PCA, in which 25 environmental variables were considered, revealed that the altitude gradient has a fundamental impact on the montane forest avifauna. For further analysis, concentrating on the role of stand structures as manageable factors, it was therefore necessary to eliminate altitude as an environmental factor. Thus, the dataset was subdivided into segments in which the altitude would play a subordinate role. This was achieved by recursive partitioning (Müller and Hothorn, 2004; Hothorn and Zeileis, 2008) of the PCA score-values for axis 1, which essentially represents the altitude gradient. The basic principle of recursive partitioning is use of maximally selected two-sample statistics in which a value may be identified that marks the greatest difference between two data packs along an environmental gradient. The method resembles a *t*-test applied to a complete set of values along a gradient. The given *p*-value indicates the quality of the threshold value and is also a limitation criterion for the subsequent calculation that proceeds for every data subset until no *p*-value is found.

For the analysis of the data subsets, a comprehensive set of environmental variables was available. To avoid multicolinearity, we applied a two-sided rank correlation test after Spearman on the selected set of variables, setting a limit for considering both correlated variables of $r_s = |0.7|$ (Fielding and Haworth, 1995). Based on the remaining environmental variables, a PCA using a cut-off r^2-value of 0.1 was performed for each data subset in order to select the most meaningful parameters (Appendix C).

Following this procedure, we reduced the environmental variables for the dataset below 1150 m a.s.l. to 10 (Fig. 2) and for the dataset above this altitude to 8 (Fig. 3) meaningful variables.

To assess the influence of the previously selected environmental parameters on the species, a Generalized Linear Model (GLM) was used. Due to the character of the bird census data, a Poisson Regression Model with log link function was applied (Quinn and Keough, 2002; Everitt and Hothorn, 2006). However, the independence of the observations, one of the key assumptions of Generalized Linear Models (Hurlbert, 1984), is difficult to prove if not inappropriate with data collected along a transect with adjacent grid cells (Fig. 1). To overcome this difficulty, we utilised a general approach based on semi-parametric spatial Generalized Linear Models that allows the use of spatially correlated data for the routine analysis. The approach is implemented in the free software package "BayesX" and is described in detail in Fahrmeir et al. (2004) as well as in Kneib and Fahrmeir (2006).

To derive threshold values of species abundances relating to meaningful environmental variables that were compiled in the GLM, maximally selected rank statistics were applied (Lausen and Schumacher, 1992; Hothorn and Lausen, 2002; Müller and Hothorn, 2004; Hothorn and Zeileis, 2008). Threshold values are calculated for the most meaningful environmental variables by recursive partitioning (see above). On the basis of 5000 bootstrap samples, the 95% confidence intervals were calculated on the function of density for the threshold values. These calculations were performed using the statistical software R 2.4.1 (R DevelopmentCoreTeam, 2006) with the add-on package 'party' (Hothorn et al., 2006).

The confidence intervals of many of the threshold values show a wide range (Table 2). These are included because threshold values

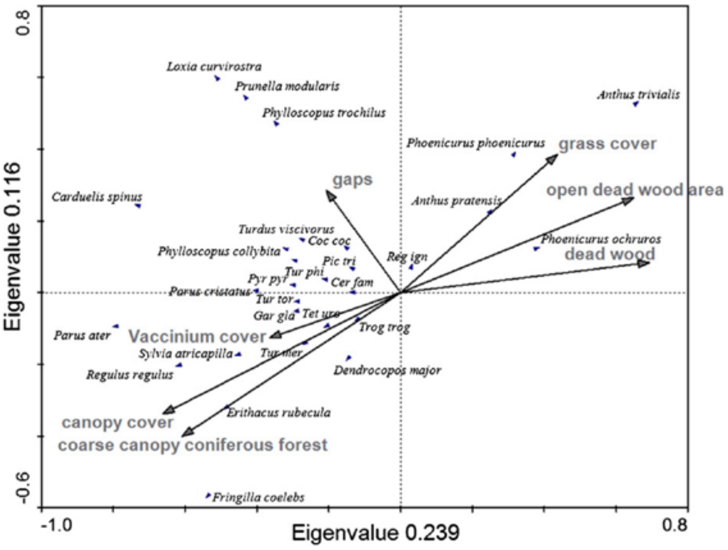
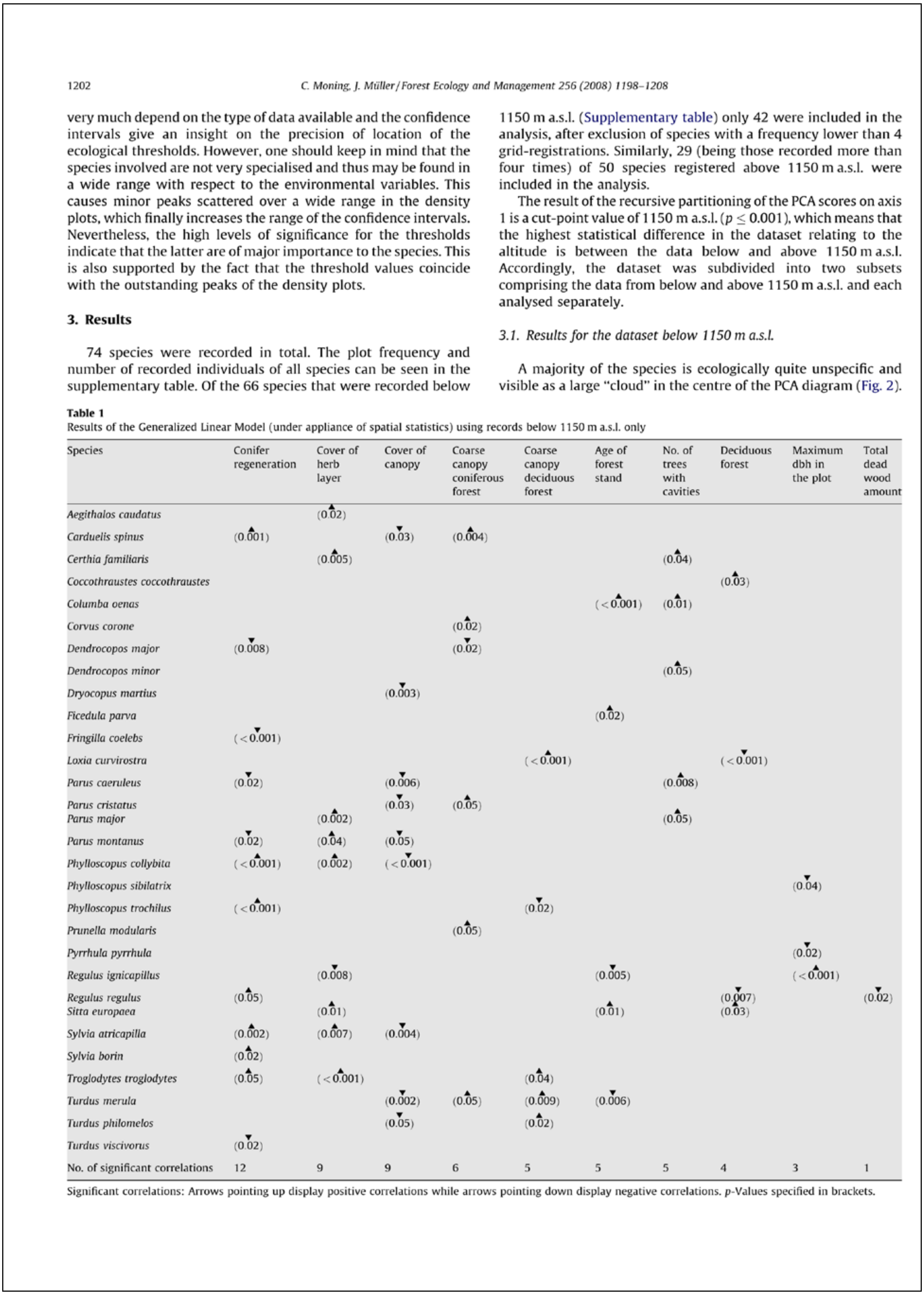


Fig. 3. Location within two-dimensional ordination space of species of the high montane forest avifauna from 1150 to 1420 m a.s.l. including the eight most important environmental variables. Abbreviations used in this figure are Cer fam (*Certhia familiaris*), Coc coc (*Coccothraustes coccothraustes*), Gar gla (*Garrulus glandarius*), Pic tri (*Picoides tridactylus*), Pyr pyr (*Pyrrhula pyrrhula*), Reg ign (*Regulus ignicapillus*), Tet uro (*Tetrao urogallus*), Trog trog (*Troglodytes troglodytes*), Tur mer (*Turdus merula*), Tur phi (*Turdus philomelos*) and Tur tor (*Turdus torquatus*).



very much depend on the type of data available and the confidence intervals give an insight on the precision of location of the ecological thresholds. However, one should keep in mind that the species involved are not very specialised and thus may be found in a wide range with respect to the environmental variables. This causes minor peaks scattered over a wide range in the density plots, which finally increases the range of the confidence intervals. Nevertheless, the high levels of significance for the thresholds indicate that the latter are of major importance to the species. This is also supported by the fact that the threshold values coincide with the outstanding peaks of the density plots.

3. Results

74 species were recorded in total. The plot frequency and number of recorded individuals of all species can be seen in the supplementary table. Of the 66 species that were recorded below 1150 m a.s.l. (Supplementary table) only 42 were included in the analysis, after exclusion of species with a frequency lower than 4 grid-registrations. Similarly, 29 (being those recorded more than four times) of 50 species registered above 1150 m a.s.l. were included in the analysis.

The result of the recursive partitioning of the PCA scores on axis 1 is a cut-point value of 1150 m a.s.l. ($p \leq 0.001$), which means that the highest statistical difference in the dataset relating to the altitude is between the data below and above 1150 m a.s.l. Accordingly, the dataset was subdivided into two subsets comprising the data from below and above 1150 m a.s.l. and each analysed separately.

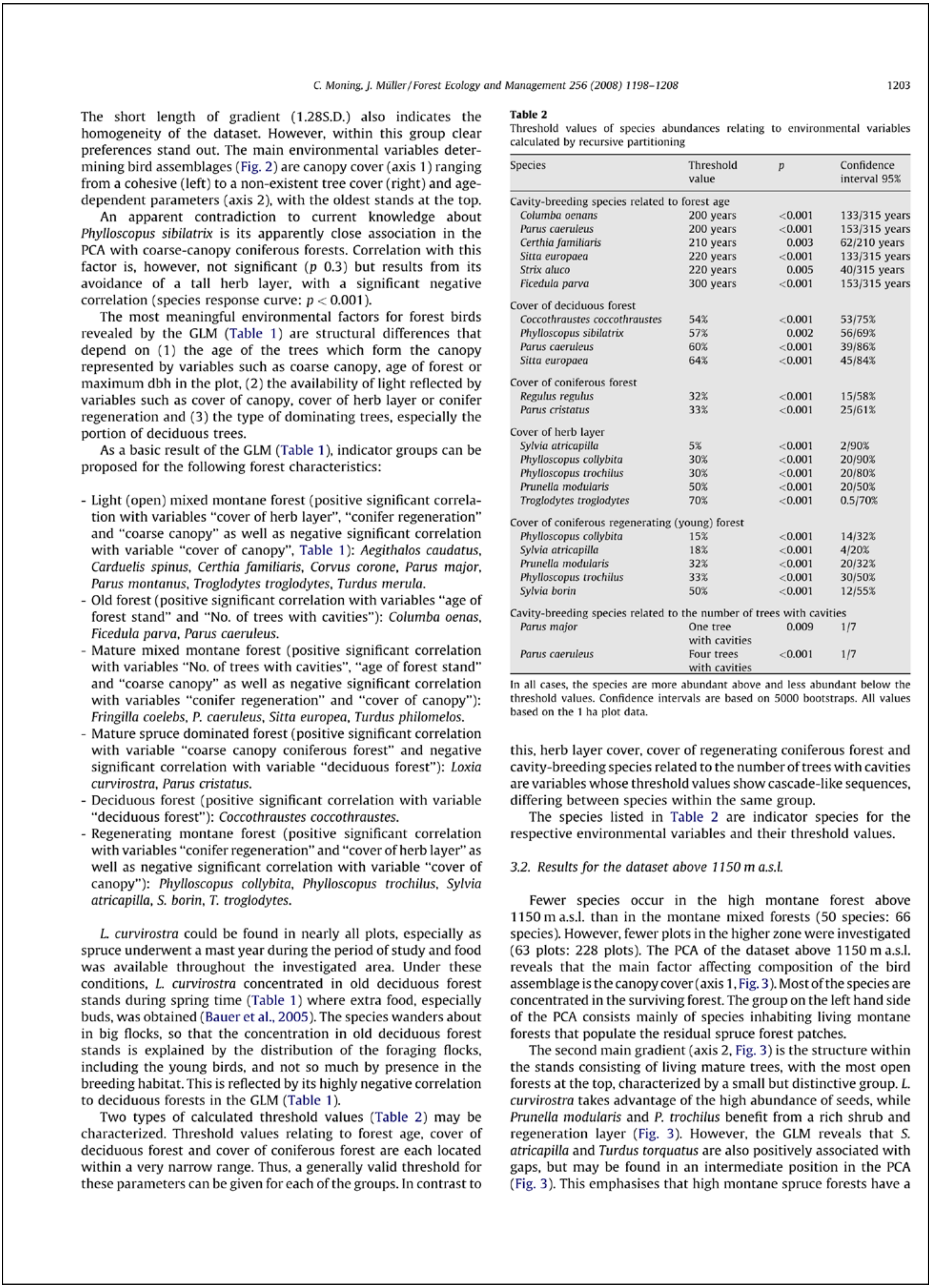
3.1. Results for the dataset below 1150 m a.s.l.

A majority of the species is ecologically quite unspecific and visible as a large “cloud” in the centre of the PCA diagram (Fig. 2).

Table 1
Results of the Generalized Linear Model (under appliance of spatial statistics) using records below 1150 m a.s.l. only

Species	Conifer regeneration	Cover of herb layer	Cover of canopy	Coarse canopy coniferous forest	Coarse canopy deciduous forest	Age of forest stand	No. of trees with cavities	Deciduous forest	Maximum dbh in the plot	Total dead wood amount
Aegithalos caudatus		▲(0.02)								
Carduelis spinus	▲(0.001)		▼(0.03)	▲(0.004)						
Certhia familiaris		▲(0.005)					▲(0.04)			
Coccothraustes coccothraustes								▲(0.03)		
Columba oenas						▲(<0.001)	▲(0.01)			
Corvus corone				▲(0.02)						
Dendrocopos major	▼(0.008)			▼(0.02)						
Dendrocopos minor							▲(0.05)			
Dryocopus martius			▼(0.003)							
Ficedula parva						▲(0.02)				
Fringilla coelebs	▼(<0.001)									
Loxia curvirostra					▲(<0.001)			▼(<0.001)		
Parus caeruleus	▼(0.02)		▼(0.006)				▲(0.008)			
Parus cristatus			▼(0.03)	▲(0.05)						
Parus major		▲(0.002)					▲(0.05)			
Parus montanus	▼(0.02)	▲(0.04)	▼(0.05)							
Phylloscopus collybita	▲(<0.001)	▲(0.002)	▼(<0.001)							
Phylloscopus sibilatrix									▼(0.04)	
Phylloscopus trochilus	▲(<0.001)				▼(0.02)					
Prunella modularis				▲(0.05)						
Pyrrhula pyrrhula									▼(0.02)	
Regulus ignicapillus		▼(0.008)				▼(0.005)			▲(<0.001)	
Regulus regulus	▲(0.05)							▼(0.007)		▼(0.02)
Sitta europaea		▲(0.01)				▲(0.01)		▲(0.03)		
Sylvia atricapilla	▲(0.002)	▲(0.007)	▼(0.004)							
Sylvia borin	▲(0.02)									
Troglodytes troglodytes	▲(0.05)	▲(<0.001)			▲(0.04)					
Turdus merula			▼(0.002)	▲(0.05)	▲(0.009)	▼(0.006)				
Turdus philomelos			▼(0.05)		▲(0.02)					
Turdus viscivorus	▼(0.02)									
No. of significant correlations	12	9	9	6	5	5	5	4	3	1

Significant correlations: Arrows pointing up display positive correlations while arrows pointing down display negative correlations. *p*-Values specified in brackets.



The short length of gradient (1.28S.D.) also indicates the homogeneity of the dataset. However, within this group clear preferences stand out. The main environmental variables determining bird assemblages (Fig. 2) are canopy cover (axis 1) ranging from a cohesive (left) to a non-existent tree cover (right) and age-dependent parameters (axis 2), with the oldest stands at the top.

An apparent contradiction to current knowledge about *Phylloscopus sibilatrix* is its apparently close association in the PCA with coarse-canopy coniferous forests. Correlation with this factor is, however, not significant (p 0.3) but results from its avoidance of a tall herb layer, with a significant negative correlation (species response curve: $p < 0.001$).

The most meaningful environmental factors for forest birds revealed by the GLM (Table 1) are structural differences that depend on (1) the age of the trees which form the canopy represented by variables such as coarse canopy, age of forest or maximum dbh in the plot, (2) the availability of light reflected by variables such as cover of canopy, cover of herb layer or conifer regeneration and (3) the type of dominating trees, especially the portion of deciduous trees.

As a basic result of the GLM (Table 1), indicator groups can be proposed for the following forest characteristics:

- Light (open) mixed montane forest (positive significant correlation with variables "cover of herb layer", "conifer regeneration" and "coarse canopy" as well as negative significant correlation with variable "cover of canopy", Table 1): *Aegithalos caudatus, Carduelis spinus, Certhia familiaris, Corvus corone, Parus major, Parus montanus, Troglodytes troglodytes, Turdus merula.*
- Old forest (positive significant correlation with variables "age of forest stand" and "No. of trees with cavities"): *Columba oenas, Ficedula parva, Parus caeruleus.*
- Mature mixed montane forest (positive significant correlation with variables "No. of trees with cavities", "age of forest stand" and "coarse canopy" as well as negative significant correlation with variables "conifer regeneration" and "cover of canopy"): *Fringilla coelebs, P. caeruleus, Sitta europea, Turdus philomelos.*
- Mature spruce dominated forest (positive significant correlation with variable "coarse canopy coniferous forest" and negative significant correlation with variable "deciduous forest"): *Loxia curvirostra, Parus cristatus.*
- Deciduous forest (positive significant correlation with variable "deciduous forest"): *Coccothraustes coccothraustes.*
- Regenerating montane forest (positive significant correlation with variables "conifer regeneration" and "cover of herb layer" as well as negative significant correlation with variable "cover of canopy"): *Phylloscopus collybita, Phylloscopus trochilus, Sylvia atricapilla, S. borin, T. troglodytes.*

L. curvirostra could be found in nearly all plots, especially as spruce underwent a mast year during the period of study and food was available throughout the investigated area. Under these conditions, *L. curvirostra* concentrated in old deciduous forest stands during spring time (Table 1) where extra food, especially buds, was obtained (Bauer et al., 2005). The species wanders about in big flocks, so that the concentration in old deciduous forest stands is explained by the distribution of the foraging flocks, including the young birds, and not so much by presence in the breeding habitat. This is reflected by its highly negative correlation to deciduous forests in the GLM (Table 1).

Two types of calculated threshold values (Table 2) may be characterized. Threshold values relating to forest age, cover of deciduous forest and cover of coniferous forest are each located within a very narrow range. Thus, a generally valid threshold for these parameters can be given for each of the groups. In contrast to this, herb layer cover, cover of regenerating coniferous forest and cavity-breeding species related to the number of trees with cavities are variables whose threshold values show cascade-like sequences, differing between species within the same group.

Table 2
Threshold values of species abundances relating to environmental variables calculated by recursive partitioning

Species	Threshold value	p	Confidence interval 95%
Cavity-breeding species related to forest age			
Columba oenans	200 years	<0.001	133/315 years
Parus caeruleus	200 years	<0.001	153/315 years
Certhia familiaris	210 years	0.003	62/210 years
Sitta europaea	220 years	<0.001	133/315 years
Strix aluco	220 years	0.005	40/315 years
Ficedula parva	300 years	<0.001	153/315 years
Cover of deciduous forest			
Coccothraustes coccothraustes	54%	<0.001	53/75%
Phylloscopus sibilatrix	57%	0.002	56/69%
Parus caeruleus	60%	<0.001	39/86%
Sitta europaea	64%	<0.001	45/84%
Cover of coniferous forest			
Regulus regulus	32%	<0.001	15/58%
Parus cristatus	33%	<0.001	25/61%
Cover of herb layer			
Sylvia atricapilla	5%	<0.001	2/90%
Phylloscopus collybita	30%	<0.001	20/90%
Phylloscopus trochilus	30%	<0.001	20/80%
Prunella modularis	50%	<0.001	20/50%
Troglodytes troglodytes	70%	<0.001	0.5/70%
Cover of coniferous regenerating (young) forest			
Phylloscopus collybita	15%	<0.001	14/32%
Sylvia atricapilla	18%	<0.001	4/20%
Prunella modularis	32%	<0.001	20/32%
Phylloscopus trochilus	33%	<0.001	30/50%
Sylvia borin	50%	<0.001	12/55%
Cavity-breeding species related to the number of trees with cavities			
Parus major	One tree with cavities	0.009	1/7
Parus caeruleus	Four trees with cavities	<0.001	1/7

In all cases, the species are more abundant above and less abundant below the threshold values. Confidence intervals are based on 5000 bootstraps. All values based on the 1 ha plot data.

The species listed in Table 2 are indicator species for the respective environmental variables and their threshold values.

3.2. Results for the dataset above 1150 m a.s.l.

Fewer species occur in the high montane forest above 1150 m a.s.l. than in the montane mixed forests (50 species: 66 species). However, fewer plots in the higher zone were investigated (63 plots: 228 plots). The PCA of the dataset above 1150 m a.s.l. reveals that the main factor affecting composition of the bird assemblage is the canopy cover (axis 1, Fig. 3). Most of the species are concentrated in the surviving forest. The group on the left hand side of the PCA consists mainly of species inhabiting living montane forests that populate the residual spruce forest patches.

The second main gradient (axis 2, Fig. 3) is the structure within the stands consisting of living mature trees, with the most open forests at the top, characterized by a small but distinctive group. *L. curvirostra* takes advantage of the high abundance of seeds, while *Prunella modularis* and *P. trochilus* benefit from a rich shrub and regeneration layer (Fig. 3). However, the GLM reveals that *S. atricapilla* and *Turdus torquatus* are also positively associated with gaps, but may be found in an intermediate position in the PCA (Fig. 3). This emphasises that high montane spruce forests have a

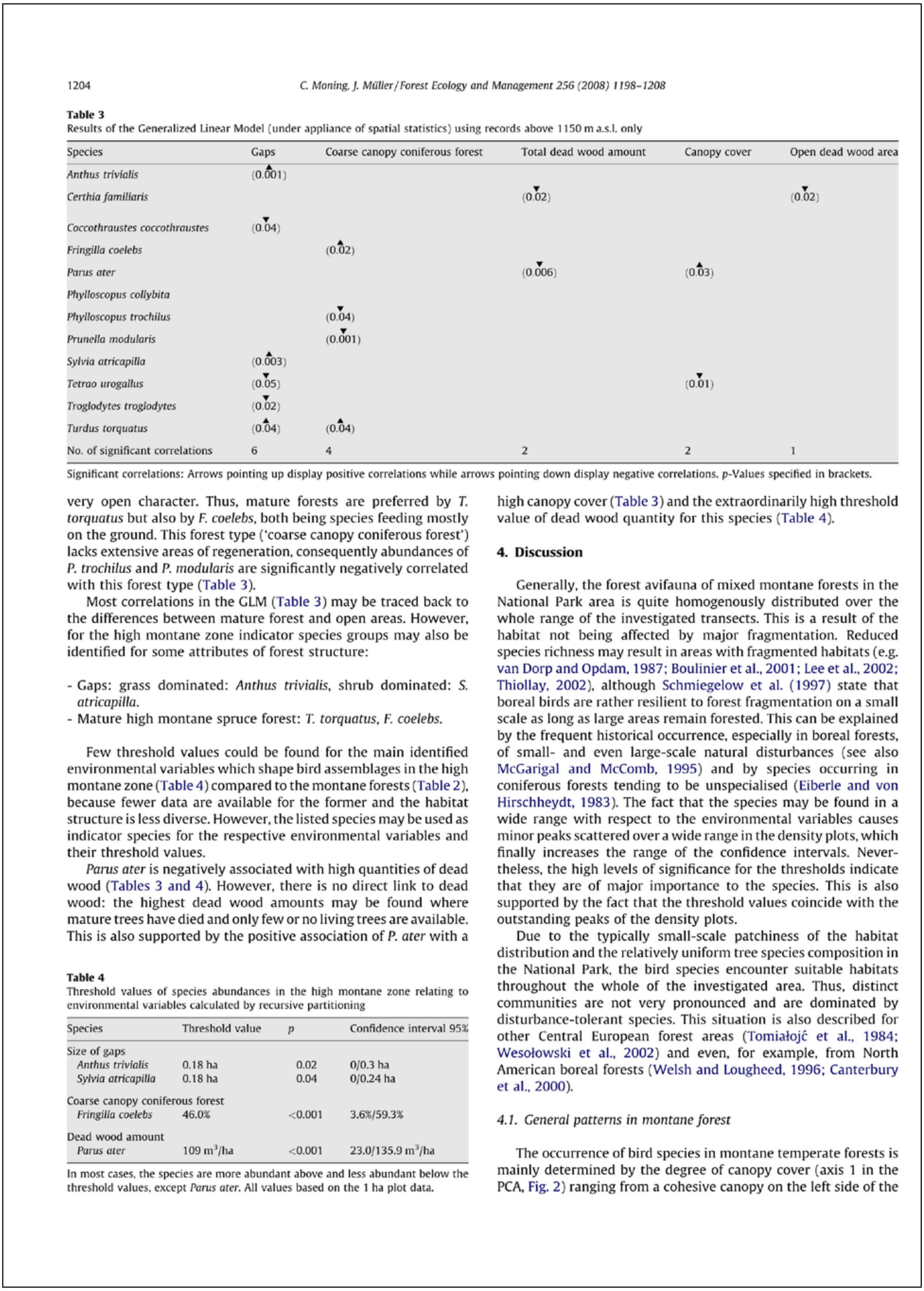


Table 3
Results of the Generalized Linear Model (under appliance of spatial statistics) using records above 1150 m a.s.l. only

Species	Gaps	Coarse canopy coniferous forest	Total dead wood amount	Canopy cover	Open dead wood area
Anthus trivialis	▲ (0.001)				
Certhia familiaris			▼ (0.02)		▼ (0.02)
Coccothraustes coccothraustes	▼ (0.04)				
Fringilla coelebs		▲ (0.02)			
Parus ater			▼ (0.006)	▲ (0.03)	
Phylloscopus collybita					
Phylloscopus trochilus		▼ (0.04)			
Prunella modularis		▼ (0.001)			
Sylvia atricapilla	▲ (0.003)				
Tetrao urogallus	▼ (0.05)			▼ (0.01)	
Troglodytes troglodytes	▼ (0.02)				
Turdus torquatus	▲ (0.04)	▲ (0.04)			
No. of significant correlations	6	4	2	2	1

Significant correlations: Arrows pointing up display positive correlations while arrows pointing down display negative correlations. *p*-Values specified in brackets.

very open character. Thus, mature forests are preferred by *T. torquatus* but also by *F. coelebs*, both being species feeding mostly on the ground. This forest type ('coarse canopy coniferous forest') lacks extensive areas of regeneration, consequently abundances of *P. trochilus* and *P. modularis* are significantly negatively correlated with this forest type (Table 3).

Most correlations in the GLM (Table 3) may be traced back to the differences between mature forest and open areas. However, for the high montane zone indicator species groups may also be identified for some attributes of forest structure:

- Gaps: grass dominated: *Anthus trivialis*, shrub dominated: *S. atricapilla*.
- Mature high montane spruce forest: *T. torquatus*, *F. coelebs*.

Few threshold values could be found for the main identified environmental variables which shape bird assemblages in the high montane zone (Table 4) compared to the montane forests (Table 2), because fewer data are available for the former and the habitat structure is less diverse. However, the listed species may be used as indicator species for the respective environmental variables and their threshold values.

Parus ater is negatively associated with high quantities of dead wood (Tables 3 and 4). However, there is no direct link to dead wood: the highest dead wood amounts may be found where mature trees have died and only few or no living trees are available. This is also supported by the positive association of *P. ater* with a high canopy cover (Table 3) and the extraordinarily high threshold value of dead wood quantity for this species (Table 4).

Table 4
Threshold values of species abundances in the high montane zone relating to environmental variables calculated by recursive partitioning

Species	Threshold value	p	Confidence interval 95%
Size of gaps			
Anthus trivialis	0.18 ha	0.02	0/0.3 ha
Sylvia atricapilla	0.18 ha	0.04	0/0.24 ha
Coarse canopy coniferous forest			
Fringilla coelebs	46.0%	<0.001	3.6%/59.3%
Dead wood amount			
Parus ater	109 m^3/ha	<0.001	23.0/135.9 m^3/ha

In most cases, the species are more abundant above and less abundant below the threshold values, except *Parus ater*. All values based on the 1 ha plot data.

4. Discussion

Generally, the forest avifauna of mixed montane forests in the National Park area is quite homogenously distributed over the whole range of the investigated transects. This is a result of the habitat not being affected by major fragmentation. Reduced species richness may result in areas with fragmented habitats (e.g. van Dorp and Opdam, 1987; Boulinier et al., 2001; Lee et al., 2002; Thiollay, 2002), although Schmiegelow et al. (1997) state that boreal birds are rather resilient to forest fragmentation on a small scale as long as large areas remain forested. This can be explained by the frequent historical occurrence, especially in boreal forests, of small- and even large-scale natural disturbances (see also McGarigal and McComb, 1995) and by species occurring in coniferous forests tending to be unspecialised (Eiberle and von Hirschheydt, 1983). The fact that the species may be found in a wide range with respect to the environmental variables causes minor peaks scattered over a wide range in the density plots, which finally increases the range of the confidence intervals. Nevertheless, the high levels of significance for the thresholds indicate that they are of major importance to the species. This is also supported by the fact that the threshold values coincide with the outstanding peaks of the density plots.

Due to the typically small-scale patchiness of the habitat distribution and the relatively uniform tree species composition in the National Park, the bird species encounter suitable habitats throughout the whole of the investigated area. Thus, distinct communities are not very pronounced and are dominated by disturbance-tolerant species. This situation is also described for other Central European forest areas (Tomiałojć et al., 1984; Wesołowski et al., 2002) and even, for example, from North American boreal forests (Welsh and Lougheed, 1996; Canterbury et al., 2000).

4.1. General patterns in montane forest

The occurrence of bird species in montane temperate forests is mainly determined by the degree of canopy cover (axis 1 in the PCA, Fig. 2) ranging from a cohesive canopy on the left side of the ordination graph to open plots on the right. The canopy cover governs the availability of light reaching the ground and thus drives the abundance of regenerating trees and herb layer. Most ecological adaptations in the avifauna of temperate forests may be ascribed to these disturbance-dependent forest structures (MacArthur and MacArthur, 1961), which is demonstrated by the fact that species that are significantly correlated with the canopy-dependent variables 'cover of herb layer' and 'cover of regenerating coniferous forest' exhibit cascade-like sequences, reflecting a gradation of adaptation of the bird species (Table 2). Both environmental factors can be regarded as mainly indicative of a rich, open structure, where, for example, *S. atricapilla* and *Phylloscopus collobyta* are less demanding than *P. modularis* (see also Wiens et al., 1986). Cascade-like threshold sequences reflect the ecological niche of the individual species with regard to the environmental variable, which is in contrast to groups where the collective threshold value is a universal threshold that applies to the whole group. Closely related species such as *P. collybita* and *P. trochilus* as well as *S. atricapilla* and *S. borin* are separated by cascade-like threshold sequences, which shows the suitability of these sequences for accurately describing the ecological niche of the species involved (Table 2). The formative effect of the canopy shape is characteristic for forest bird assemblages all over the world (e. g. Rov, 1975; James and Wamer, 1982; Jokimaeki and Huhta, 1996). However, the effect of canopy shape on bird species occurrence is generally not characterized by sharp thresholds, a result which was also found, e.g. in North American temperate forests (Villard et al., 1999).

Species inhabiting the most open structures constitute a rather distinct group (Fig. 2). They are mostly insectivorous and inhabit stands with high quantities of dead wood and a rich herb layer or regenerating coniferous stands that are characterized by a high availability of light which in turn enhances the availability of insects as a food source (Hawrot and Niemi, 1996; Bouget and Duelli, 2004; Müller et al., 2007). Although an increase in habitat edges and openings enhances bird species diversity, these disturbance structures mainly support habitat generalists and edge species, especially insectivorous tree-gleaning species (Kroodsma, 1982; Hansson, 1983; Jokimaeki and Huhta, 1996; Robinson and Robinson, 1999; this study), which causes young forests to be rich in bird species but only if older stands are to be found nearby (James and Wamer, 1982). Thus, the small-scale stand patchiness caused by bark beetle infestations in the mixed montane zone of the Bavarian Forest National Park results in a comparatively diverse avifauna.

Stands with a high degree of canopy-cover are middle-aged forest stands mostly with low structural diversity. All species that show statistical dependency on this environmental parameter respond negatively to it in the GLM (Table 1). These species are either those such as *C. spinus*, *P. montanus*, *P. collybita* and *S. atricapilla* that have a high preference for young and/or open, structurally rich forests, or species such as *P. cristatus*, *T. merula* and *T. philomelos* that prefer old and thus structurally rich coniferous or mixed deciduous forest (Bauer et al., 2005).

The second main gradient includes age-dependent structures. The importance of forest age and the associated structural attributes as a main determinant for diversity and density of temperate forest bird communities, especially for hole-nesters, has already been stressed by many authors (e.g. James and Wamer, 1982; Hino, 1984; Repenning and Labisky, 1985; Helle and Jarvinen, 1986; Kornan, 1997). The maximum diversity is found in mature deciduous stands and not in those that have the highest tree species richness, canopy height or tree density (James and Wamer, 1982). Canopy height structure and foraging substrate are important gradients in the organization of forest bird communities (Sabo and Holmes, 1983). The first parameter increases and the latter diversifies in old forest stands, which explains the higher diversity and density values in mature stands, underlined in our study by the majority of species following the age arrow in the ordination (Fig. 2). Structural diversity is greater in mature forests, thus more foraging niches are available (Holmes et al., 1979; Kornan, 1997; Jedicke, 1999). Based on an intercontinental comparison, Homes and Recher (1986) also stress the connection between vegetation structure and food availability, which varies with plant species composition and vertical strata diversity. The main age-dependent structural attribute explaining much of the significant correlation is the variation in the canopy height, which also proved to be a significant factor in North American temperate forests, and may represent a pattern with general validity (James and Wamer, 1982). The partitioning of guilds, especially for insectivorous bird species, is mainly based on foraging height and foraging locations within the canopy (Holmes et al., 1979). This underlines the importance of considering the range of vertical structure in mature stands in comprehensive studies of avian diversity.

In the GLM, many species show mostly positive correlations either to coarse canopy structures of deciduous and/or coniferous forests or old forests in general (Table 1). However, one should keep in mind that coarse-canopy structures, although including mostly old forests, reflect different environmental impacts than the age of the stand does (Förster and Müller, 2006). Some species like *P. modularis* and *T. troglodytes* are bush-dwelling birds that take advantage of the gaps in coarse-canopy structures that allow a rich understorey to grow (Table 1). They may also be found in regenerating stands.

The amount of cavities is linked to the age of the forest (Bürger and Kloubec, 1994) but also to the dead wood amount (Prill, 1991; Hohlfeld, 1995; Martin and Eadie, 1999). This explains the formation of a group consisting of many cavity-breeding species such as most of the *Parus* species, that is situated between the variables 'age' and 'trees with cavities' in the PCA (Fig. 2). Members of this group also show positive correlations with the number of trees with cavities in the GLM (Table 1). Only few threshold values could be found for cavity-breeding species with respect to the number of trees with cavities. However, the values clearly reveal that for the weak competitor *P. caeruleus* the threshold value is higher than for the dominant species *P. major*, which is already significantly more abundant if there are any cavities at all (Table 2; Prill, 1991).

Virgin forest species and hole-nesters showed negative correlations of abundance with large forest openings in other studies (e. g. Jokimaeki and Huhta, 1996; Germaine et al., 1997). At least 70% mean canopy closure and 80 stem/ha are required in North American temperate forests to provide habitat for all sensitive species (Guenette and Villard, 2005). This underlines the importance of extensive mature forest stands, because these are characterized by a distinctive bird assemblage, which can also be seen from the PCA (Fig. 2), the GLM (Table 1) and from the threshold values (Table 2). Occurrence of these species peaks at a stand age of 200–220 years (Table 2). Only *F. parva* seems to have much more demanding habitat requirements than the other species, as this species could only be found significantly more often in forests which were at least 300 years old. This has been postulated before (Bauer et al., 2005) but has not previously been confirmed by a threshold value.

The tree species composition in montane forests does have an influence on a limited number of species. Species that showed a strong association with old deciduous forests are *C. coccothraustes*, *P. caeruleus*, *P. sibilatrix* and *S. europea* (Tables 1 and 2; Mosimann et al., 1987; Prill, 1991; Petersen and Brogger-Jensen, 1992; Jedicke, 1999). A special case in this context is *P. sibilatrix*, a typical colonizer of *Fagus sylvatica* dominated forests. Due to its complex mating system, this species regularly breeds in several aggregated

territories (Bauer et al., 2005). This leads to the problem that due to the scattered but locally accumulated distribution *P. sibilatrix* loses its highly significant positive correlation to deciduous forests in the spatial statistics (Table 1).

L. curvirostra and *Regulus regulus* displayed statistically significant avoidance of deciduous forests, which is totally in agreement with existing knowledge of their habitat requirements (Bauer et al., 2005). In addition to the certainty that a proportion of approximately 55–65% of deciduous tree cover per hectare is required to sustain deciduous forest species (Table 2), the deciduous components must also have a minimum size and need to be connected to each other. For example, the likelihood that *C. coccothraustes* will colonise deciduous stands increases to 100% only when these are of at least 10 ha in area and only if they are no more than 5–10 km apart (Opdam et al., 1984; van Dorp and Opdam, 1987).

The fact that the threshold values for species depending on coniferous trees is with roughly 30% much lower than those for species depending on deciduous trees (Table 2), may not only reflect the natural availability of the different tree types in the montane forest (Korpel, 1995), but may also indicate that species depending on deciduous trees are here at the margin of their ranges, mainly because of suboptimal climatic conditions (Bauer et al., 2005). The latter are thus more demanding with respect to their habitat needs, while birds with boreal distributions find optimal climatic conditions in the National Park and are thus less demanding (Stevens, 1992).

In the GLM (Table 1), none of the investigated species showed a significantly positive correlation to a high amount of dead wood, which debases this variable as an important factor for explaining the composition of the montane forest avifauna. Most probably this is because availability of dead wood is not a limiting factor in the Bavarian Forest. In contrast, Nilsson (1979) found for south Swedish forest bird communities, that standing dead wood is the best predictor for bird community densities and species richness. This does not apply to our study, where the highest amounts of dead wood are found in areas where mature spruce trees died after bark beetle infestation. These areas show the lowest structural diversity and thus hold many fewer species than, for example, mature mixed deciduous forests.

4.2. General patterns in high montane forests

Birds that are dominant in the forest avifauna above 1150 m a.s.l. generally (with few exceptions) exhibit the broadest altitudinal distributions. This result was also found for upland North American temperate forests (Able and Noon, 1976; Sabo and Holmes, 1983), indicating the general applicability of this rule.

The most extreme but least diverse species assemblage of the whole dataset is found in areas of trees that died after bark beetle infestation and that are now dominated by grasses (mainly *Calamagrostis villosa*, Fig. 3). The bird community primarily consists of *Phoenicurus phoenicurus* and *A. trivialis* which may otherwise be found in open forest structures such as gaps or forest margins. *P. phoenicurus* takes advantage of the open habitat that entails high food abundance and increased availability of nesting sites resulting from the low density of competing species (Bauer et al., 2005). Even species that need very open habitats such as *Phoenicurus ochruros* or *Anthus pratensis*, are represented in this group. This assemblage demonstrates how large-scale bark beetle infestations change the avifauna in Central European upland spruce forests. Many typical forest species lose suitable habitats and are replaced by a few species, often endangered such as members of the genus *Anthus* and *P. phoenicurus* which were previously rare in the area. In contrast to the trend of increasing abundance in bark beetle infested montane spruce forests, abundance of *P. phoenicurus* and the *Anthus* species has decreased or is currently decreasing in the lowlands (Sudfeldt et al., 2007).

5. Conclusion

On a large (landscape) scale, the diversity of stand types and on a small (stand) scale the structural diversity of the vegetation play important roles in determining the diversity and composition of the forest avifauna (Annand and Thompson, 1997; Robinson and Robinson, 1999; Müller, 2005).

To achieve the maximum avian diversity in temperate montane forests we suggest that:

(1) To provide for the requirements of the whole range of species depending on openings in the canopy, the full array of canopy-openness ranging from 5% to 70% should be realized at a stand level throughout a forest landscape.
(2) To sustain the whole range of cavity-breeding species and species of mature forests, the age of a part of the stands needs to exceed 200–220 years. In the future, old stands will develop extensively in the National Park. However, in managed forests plans should be developed that allow as many stands as possible to surpass the harvesting age and reach the ecological threshold age of 200–220 years.
(3) To support the deciduous forest species in mixed montane stands a minimum of 60% cover of deciduous trees is required. It is not necessary to establish pure deciduous stands, but rather the development of a forest matrix comprising 60% deciduous trees per hectare is required. Areas containing a deciduous component should however not be too small (some parcels ideally of at least several hectares) and should be more or less connected to each other, or at least not more than approximately 5 km apart.

These conclusions may not be easily transferred to lowland temperate forests. Thus, further research is needed in this habitat.

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Appendix A

Definition, source and measurement of the environmental variables used for the analysis

Environmental variable	Definition, source	Measurement	Range in the dataset
Age of stand	Forest inventory data	Core sample (plot data)	0–400 years
Altitude	Elevation above sea level	GIS Model (centre of plot)	655–1420 m a.s.l.
Canopy cover	Cover estimation (Londo, 1976) of canopy layer (upper third of the vertical forest structure), Sample area shaded by horizontal projection of tree layer, expressed as class means	Areal view interpretation (stereo analyst) [1 ha]	0–100%

Appendix A (*Continued*)

Environmental variable	Definition, source	Measurement	Range in the dataset
Coarse canopy of coniferous forest	Cover of old coniferous forest in the plot [m^2], source: aerial photographs, marked-off visually by structure differences	Visual [1 ha]	0–10,000 m^2
Coarse canopy of deciduous forest	Portion of old deciduous forest in the plot (m^2), source: aerial photographs, marked-off visually by structure differences	Visual [1 ha]	0–9620 m^2
Cover of deciduous forest	Cover of deciduous forest in the plot, source: aerial photographs, marked-off visually by differences in the infra red spectrum	Visual [1 ha]	0–9620 m^2
Cover of grasses	Cover estimation (Londo, 1976) of grasses, expressed as class means	Visual [0.02 ha]	
Cover of herb layer	Cover estimation (Londo, 1976), vascular plants and ferns, expressed as class means	Visual [0.02 ha]	0–97.5%
Cover of regenerating conifer forest	Cover estimation (Londo, 1976) of conifer trees up to 5 m in height, expressed as class means	Visual [0.1 ha]	0–75%
Gaps	Cover of gaps in the plot, source: aerial photographs	Visual [1 ha]	0–8615 m^2
max dbh	Maximum trunk diameter at breast height, measured in a circle shaped plot, 18 m in diameter and centred on the central point of the one-hectare plot	Measured [0.1 ha]	0–130 cm
No. of trees with cavities	Number of trees with cavities, counted in the one-hectare grid-plots	Count [1 ha]	0–12
Open dead wood area/open forest	Area dominated by dead trees without regenerating trees, source: aerial photographs, marked-off visually	Visual [1 ha]	0–10,000 m^2
Dead wood	Estimated total dead wood amount, measured in a circle shaped plot, 18 m in diameter and centred on the central point of the one-hectare plot	Estimate [0.1 ha]	0–709 m^3
Vaccinium cover	Cover estimation (Londo, 1976) of *Vaccinium* spec. (mainly *Vaccinium myrtillus*)	Visual estimation [0.02 ha]	0–100%

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.06.018.

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Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests

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ABSTRACT

Forest age is one of the most simple but ecologically effective key values that may be controlled by forest management. Young and mature but managed forests differ significantly from old-growth forests in species composition, structure and socio-ecological function. Human land-use has already caused the loss or dramatic reduction in occurrence of some entire species assemblages, especially of logging-sensitive species, in Central European forests. These general statements also apply to beech forests, beech (*Fagus sylvatica*) being the naturally dominating tree species in Central Europe. Based on data for breeding birds (from 258 sampling plots in a sub-montane and 228 plots in a montane area), molluscs (36 plots in the sub-montane and 79 plots in the montane area) and lichens (84 plots in the montane forest), this paper aims at identifying significant forest age threshold ranges for the occurrence of these old-growth sensitive taxa. The sampling plots in the sub-montane zone (420–520 m a.s.l.) are in beech-oak forests, plots in the montane zone (650–1150 m a.s.l.) are in beech-spruce-fir forests. Stand ages in both areas range up to around 350–400 years. Threshold values for the total number of species related to stand age were calculated by recursive partitioning.

In all three taxonomic groups the number of species per plot significantly increases with forest age. The same analysis was run for red-listed lichen and mollusc species as well as hole-nesting bird species. The threshold values obtained are very similar to those for the whole species assemblages, except for molluscs where considerably lower threshold values are computed with red-listed species assemblages. Regarding the confidence intervals, the difference pattern between the whole species datasets and the more sensitive species subsets is inconsistent. Threshold values in sub-montane beech forests range from 100 to 170 years and in mixed montane forests from 160 to 220 years.

These threshold levels are clearly incompatible with economic interests that aim on reducing the rotation period in beech stands to less than 140 years to avoid formation of red heartwood. It would therefore seem to be essential to establish a network of trees and stands that are never logged and may thus act as areas for retreat and dispersion for logging-sensitive species.

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1. Introduction

Management guidelines require simple but ecologically effective key values. Among various forest parameters, age is one of the surrogates which can most easily be integrated in forest management. It is well known that old-growth forests differ significantly from young forests in their ecology, particularly with regard to species composition and structure. Old forests are characterized by higher proportions of large, old trees, multiple age-classes and high volumes of fallen and standing dead wood, as well as differences in function such as rate and routes of energy flow and cycling of nutrients and water (Franklin et al., 1981; Helioevaara and Vaeisaenen, 1984; Väisänen et al., 1993; Larsson, 2001; Humphrey, 2005; Liira et al., 2007). Intensive logging of old-growth forest reduces species diversity on the landscape scale by homogenization of forest structures, causing habitat loss and local extinctions of sensitive species (Helioevaara and Vaeisaenen, 1984; Niemela, 1997). In all taxonomic groups, the inhabitants of old forest that are most affected by anthropogenic disturbances are those which are sedentary (Opdam, 1990), have the poorest dispersal abilities (Primm et al., 1988; Bolger et al., 1991; Hermy et al., 1999; Floren and Linsenmair, 2001), have large area requirements (Wilcox, 1980), or are invertebrates associated with micro-habitats of natural old-growth forest, such as coarse woody debris or large broadleaved trees (Niemela, 1997). It is mostly in these groups that some entire species assemblages have already been lost or dramatically reduced in occurrence in Central Europe (Helioevaara and Vaeisaenen, 1984; Speight, 1989; Thomas et al., 1994; Larsson, 2001; Grove, 2002; Cameron and Pokryszko, 2004; Pykälä, 2004). Consequently, remaining old-growth forests have a very high significance for biodiversity conservation and as donor resources for developing mature forests.

In this context the factor of forest continuity has been extensively but controversially debated in biodiversity conservation, especially with regard to spatial and temporal scales at which continuity may influence populations and species (Sverdrup-Thygeson and Lindenmayer, 2003; Paltto et al., 2007). Although species which indicate ecological continuity have been identified, e.g. for lichens (Selva, 1994; Kuusinen, 1996), this practice has been questioned because of the difficulty in defining continuity and separating it from other ecological factors (Nordén and Appelquist, 2001; Rolstad et al., 2002). However, the assumption that forest age is a good integrating parameter for habitat continuity is less disputed (Tibell, 1992; Kuusinen, 1996; Müller et al., 2005b). As stand age is generally readily available information for most forests, we use it as a surrogate factor for habitat continuity in the sense of continuity of habitat structures. It is not regarded as a surrogate for forest continuity. The distinction is important because the latter does not necessarily entail continuity of appropriate habitats, especially for species depending on structures typical of old growth. In this paper we use the term old forest for those forest stands in which old-growth forest structures have developed to such an extent that species are present which are known to depend on such structures.

In Central Europe, beech (*Fagus sylvatica*) would dominate forests under current climatic conditions (Tüxen, 1956; Ellenberg, 1996; Björse and Bradshaw, 1998; Bradshaw and Holmqvist, 1999; Dierschke and Bohn, 2004). Taking Germany as an example, beech would potentially cover 74% of the forested area. However, at present beech forests in Germany, where only 30% of the total land area is still forested, make up 14.8% of the woodland area. Only 6.0% of these beeches are older than 160 years and less than 0.1% of the total German land area is covered by unmanaged beech forests (Schmitz et al., 2004). The situation of old-growth beech forests has accordingly been assessed as critical (Thomas et al., 1995). As Central Europe is the centre of the world distribution of beech-dominated forests, this forest type has attracted a lot of attention in conservation oriented discussions in recent years (Plachter, 1997; Heinrih, 2001; Berg et al., 2002). However, from an economic point of view rotation periods for beech stands are required to be kept short to avoid formation of red heartwood (Knoke, 2003).

Much of the shortfall in applying the results of ecological research in guidelines for land managers results from the highly complex relationships between species and their environment. Clear formulation of descriptive guidelines based on research may be extremely difficult. For this reason, statistically derived threshold values are increasingly recommended as a basis for forest management guidelines (Angelstam et al., 2003; Müller and Hothorn, 2004; Guenette and Villard, 2005; Lindenmayer and Luck, 2005; Ranius and Fahrig, 2006).

Due to the complexities involved, the predictive capacity of threshold values in nature conservation is always a critical theme. Several approaches, including pre-defined threshold values (e.g. Uliczka and Angelstam, 1999), have been attempted. In the present study we have chosen to identify, using recursive partitioning, the data segment along the age gradient that represents the most intense change in species number. The rationale for this method originates in abundant evidence of discontinuities and threshold effects arising as the consequence of human influence on forest systems (e.g. Kuusinen and Siitonen, 1998; Angelstam et al., 2003; Bütler et al., 2004). The large number of threatened species in forests is an indication that ecological age thresholds have already been crossed on a large scale (Scherzinger, 1985; Väisänen et al., 1993; Angelstam and Mikusinski, 1994; Berg et al., 1994, 2002; Fuller, 1995; Gustafsson et al., 2004). This paper aims to identify critical forest age threshold ranges for the two major altitudinal distribution zones of Central European beech forests, with respect to general species density of logging-sensitive taxa and subsets of these taxa which contain species which are presumably even more sensitive.

2. Methods

2.1. Taxa studied

LICHENS are good model organisms for assessing the effects of human impact on ecosystems because of their sensitivity to various types of impact such as logging (Rose, 1992; Wirth, 1995; Uliczka and Angelstam, 1999; Hedenås and Ericson, 2003) or airborne emissions (e.g. sulphur; Garty et al., 1988; Richardson, 1998; Lippo et al., 1995; Ranta, 2001). Old-growth forests possess their own, distinctive lichen communities.

These forests usually contain many specific habitats suitable for the growth of different epiphytic lichens, such as large old trees, logs and snags (Peterson and McCune, 2001; Jüriado et al., 2003; Radies and Coxson, 2004). Numerous lichens, including many red-listed species, are thus observed more frequently on old than on young trees (Neitlich and McCune, 1997; Gustafsson et al., 2004). Furthermore, biomass of epiphytic lichens is strongly related to volume, dimensions and age of branches (Esseen et al., 1996; Fritz et al., 2008). Most of the threatened forest species, many of them being slow colonists (e.g. Sillet et al., 2000), are confined to specific substrates such as deciduous trees, dead wood and old trees (Berg et al., 1994; Esseen et al., 1997; Uliczka and Angelstam, 1999; Nascimbene et al., 2007). The limited amount of substrate available to lichens, and young age of branches which allows only a short time for lichen colonization and growth, are important factors limiting epiphytic lichen abundance in managed forests (Esseen et al., 1996; Kuusinen and Siitonen, 1998; Hilmo and Såstad, 2001; Hilmo, 2002).

Many MOLLUSC species have powers of dispersal too low to enable them to overcome the effects of human-induced fragmentation, making breaks in habitat continuity in conjunction with their dependence on a stable microclimate particularly harmful (Wäreborn, 1979). Thus the snail fauna reacts very sensitively to logging in long undisturbed forest habitats (Tattersfield et al., 2001; Pilāte, 2003a). Although soil moisture and the closely linked soil pH have been pointed out as the strongest determinants of snail density and species richness at undisturbed woodland sites in Central Europe and beyond (Boag, 1985; Waldén et al., 1991; Hotopp, 2002; Martin and Sommer, 2004), the forest snail fauna depends on various forest attributes that are especially frequently encountered in Central European old forests. These include shadiness and humidity, a stable microclimate, adequate calcium content and sufficient amount of coarse woody debris, habitat continuity and richness of vegetation (Müller et al., 2005).

Although many BIRD species prefer a particular stage of growth, bird species richness tends to increase with stand age (Moss, 1978; Helle and Mönkkönen, 1990; Solonen, 1996; Laiolo, 2002). This may even be observed in the distribution of winter birds (Utschick, 2004). Birds are particularly good indicators for forest structures at the stand scale and may therefore function as a superior logging-sensitive indicator group (e.g. James and Wamer, 1982; Cody, 1985; Hagan and Meehan, 2002). For instance, most hole-nesters prefer mature trees (Fuller, 1995) and snags (Zarnowitz and Manuwal, 1985), but bird species which forage on branch surfaces, trunks and on the ground are also more abundant in mature stands (Bürger and Kloubec, 1994; Laiolo, 2002). Apart from the general decrease in bird species diversity in beech forests with increasing logging intensity (Müller et al., 2007), especially with respect to woodpeckers, a negative effect of logging on birds nesting secondarily in cavities and ground-gleaning birds has also been demonstrated (Helle and Jarvinen, 1986; Angelstam and Mikusinski, 1994; Lammertink, 2004; Augenfeld et al., 2008).

2.2. *Study sites*

The data originates from two study sites in Bavaria, south-eastern Germany. The "Northern Steigerwald" is a sub-montane forest area of about 10,000 ha, located in northern Bavaria, dominated by beech and oak (mainly *Quercus petraea*). The altitudinal range extends from 420 to 520 m a.s.l., average daily temperatures range from 7 to 8 °C (Müller et al., 2005a). Some of the beech stands are regarded as among the oldest in Germany, being up to 350 years old (Müller et al., 2007). The selected stands grow on Triassic sandstones of various ages, thus the soils (mainly cambrisols) are rather acid (pH 3.5–5.8). The proportion of coniferous trees in the investigated plots ranges from 0% to 25% and for oak from 0% to 40%. Average tree species number in the canopy layer per plot is 3.3 (range 1–7). Canopy cover varies between 20% and 100% (mean: 72%). Dead wood amounts vary between 3.5 and 500 m^3/ha (mean: 58 m^3/ha).

The Bavarian Forest National Park is situated within the south-western part of the Bohemian Massif, consisting of granite and gneiss. The soils are mainly podsolic cambisols derived from weathering of granite. Thus the soils are rather acidic (pH 2.3–4.8). The park covers approximately 24,000 ha, with an elevation range from 600 to 1430 m a.s.l. Mean annual temperature (1970–2003) varies between 3.8 and 5.8 °C (Bässler, 2004). The investigated area below 1150 m a.s.l. is montane mixed forest dominated by spruce (*Picea abies*), beech and fir (*Abies alba*). Average tree species number in the canopy layer per plot is two (range 0–5). Due to heavy infestation by bark beetles, mainly *Ips typographus*, canopy structure varies widely from open forests, dominated by dead wood, through patchy forest, to more or less dense, closed forest stands (canopy cover: 0–100%, mean: 48%). Dead wood amounts vary between 0 and 709 m^3/ha.

The age of all stands investigated was obtained from the permanent forest inventory data for both areas. Stand ages ranged from 50 to 350 years in the sub-montane area and from 0 to 400 years in the montane area. The age was determined by the age of the oldest tree within each inventory plot (0.05 ha).

2.3. *Species sampling*

Sampling campaigns were accomplished in the sub-montane zone in 2004 and in the montane zone in 2006 (molluscs)/2007 (birds and lichens). Breeding birds were sampled five times during the period March–June, using quantitative plot mapping of 1 ha plots as a standardized area count method on 258 plots in the sub-montane zone in 2004 and 222 plots in the montane zone in 2007. The plots were selected by stratifying them according to altitude, age and canopy cover along the elevation gradient. For details see Müller et al. (2007). Each plot was investigated for 10 min on each occasion. Only birds that were recorded within the plots were included in the analysis. Hole-nesting birds were classified following Bauer et al. (2005).

Molluscs were sampled in the sub-montane area on 37 plots, using 0.1 ha fixed-radius point counts. The minimum distance between the plots was 100 m. At each plot two standard time direct searches were conducted, once in April and once in June 2004. Additionally, litter humus and topsoil was collected from an area of 25 cm × 25 cm per plot. Fresh, empty shells were also counted. Old shells were generally scarce, because of rapid decay and re-use by other organisms. Shells were identified to the species level and individuals counted (for details see Müller et al., 2005a). Sampling methods in the montane area were similar to those in the submontane zone, with the additional installation of one pitfall trap for 3 weeks in July 2006 in the centre of each of the 79 plots. Also, within an area of 0.1 ha around the centre of each sampling plot we collected for 30 min all individuals of living snails and slugs in September 2006. Dead wood structures and trees were primarily sampled, because low pH values cause the snail density to be very low in the litter. A detailed description is given in Müller et al. (in press). Red-listed species were classified following the Bavarian red list (Falkner et al., 2003).

Lichens were investigated in the montane area only. Each of the 84 plots was 8 m in diameter (0.02 ha). All objects carrying lichens in the plots were investigated in 2007. These included living trees, dead wood (standing, lying, snags, stumps, logs and branches) and soil and stones. Particular attention was paid to the main guilds represented. On most plots these were epiphytic lichens growing on living and dead wood. Those specimens that could not be determined in the field were later identified in the laboratory (Culberson and Kristinsson, 1970; White and James, 1985; Huneck and Yoshimura, 1996). Red-listed lichens were classified following the Bavarian red list (Wirth et al., 1996).

2.4. *Statistical analysis*

We used the number of all registered species from all sampling campaigns per plot as the dependent variable. Threshold values were calculated by recursive partitioning (Lausen and Schumacher, 1992; Hothorn and Lausen, 2003; Hothorn and Zeileis, 2008). This approach allows simultaneous identification of a threshold and assessment of its significance by means of a statistical test procedure, i.e. a decision whether or not there is a relationship between independent variable and the response. The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics. Their validity is judged by multiple test procedures. The key results are those in which the difference between high and low values of the dependent variable, here number of species, is largest. After the data set is divided into two subsets by the threshold with highest explanatory power, the subsets are searched for additional thresholds. This method provides a decision tree with p-values for one or more critical thresholds (see example: Supplementary Fig. S1). Based on 5000 bootstrap samples a confidence interval (80%) was calculated for all thresholds. As the density plots of all bootstrapped thresholds show outstanding peaks, the thresholds are characterized by generally high significance levels (see example: Supplementary Fig. S2). In order to display confidence intervals that are meaningful in forest management, the 80% confidence intervals were chosen in preference to 90% intervals because the former are defining more tightly ranges. This methodology is a further development of some currently more popular implementations for 'recursive partitioning' or 'trees', such as 'CART' (Breiman, 1984) or 'C4.5' (Quinlan, 1993), which solves two fundamental statistical problems inherent to the earlier

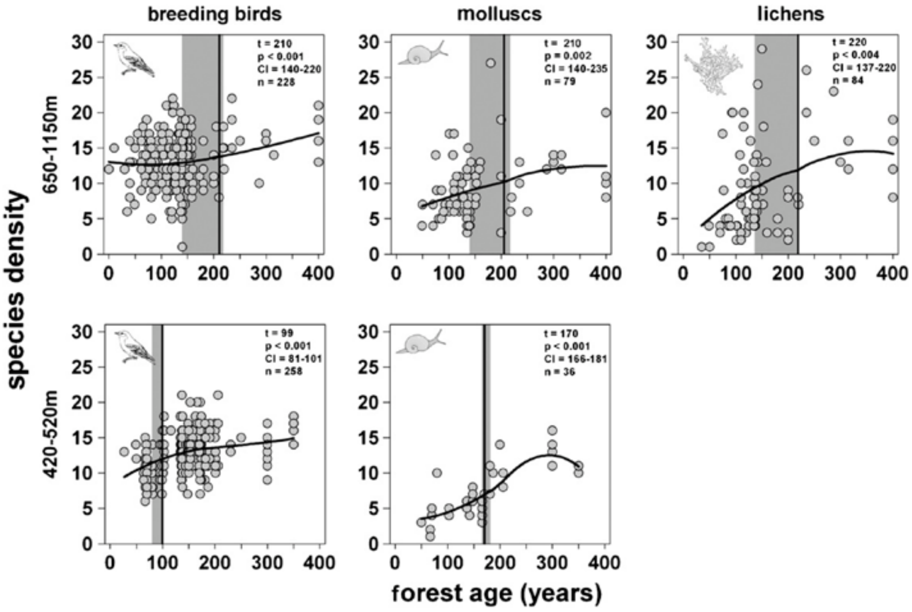

Fig. 1 – Data distribution (scatterplot graphs) for forest age (X-axis) and species density (Y-axis) of breeding birds (1.0 ha plots), mollusks (0.1 ha plots) and lichens (0.02 ha plots) per plot in the zone between 650 and 1150 m a.s.l. of the Bavarian Forest National Park and the zone between 420 and 520 m a.s.l. of the Steigerwald Area, with the appropriate Loess curves (local polynomial regression fitting). The grey boxes indicate the range of the 80% confidence intervals of the threshold values (black vertical lines) calculated by means of recursive partitioning. *t* = threshold value, CI = 80% confidence interval of the threshold, and *n* = number of plots.

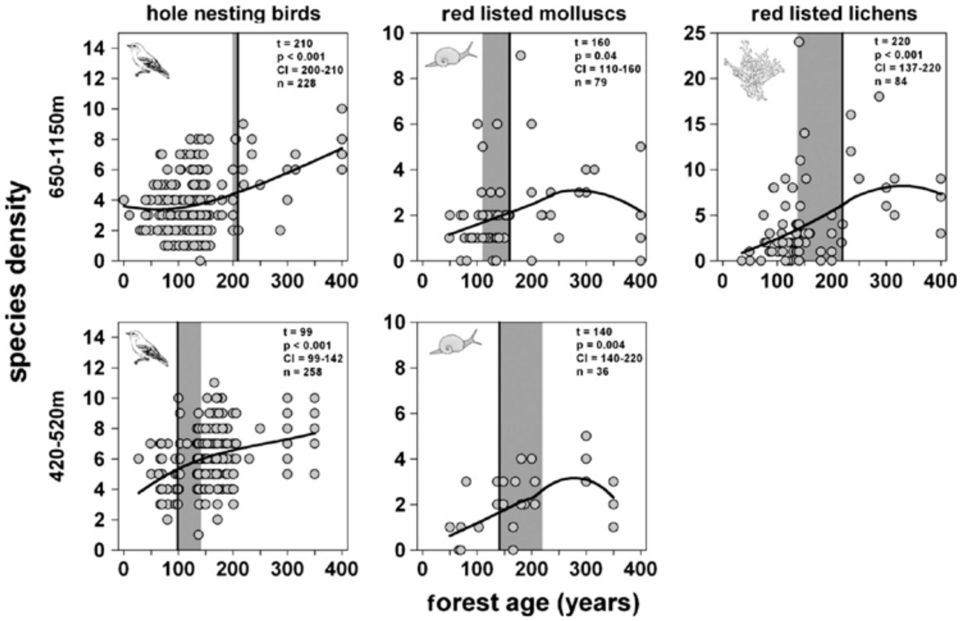

Fig. 2 – Data distribution (scatterplot graphs) for to forest age (X-axis) and species density (Y-axis) of hole-nesting birds (1.0 ha plots), red-listed molluscs (0.1 ha plots) and red-listed lichens (0.02 ha plots) per plot in the zone between 650 and 1150 m a.s.l. of the Bavarian Forest National Park and the zone between 420 and 520 m a.s.l. of the Steigerwald area with the appropriate Loess curves (local polynomial regression fitting). The grey boxes indicate the range of the 80% confidence intervals of the threshold values (black vertical lines) calculated by means of recursive partitioning. t = threshold value, CI = 80% confidence interval of the threshold, and *n* = number of plots.

approaches: overfitting and a selection bias towards covariates with many possible splits or missing values. The method and a comprehensive model comparison are described in Hothorn et al. (2006a).

The calculations were performed using the statistical software R 2.4.1 (RDevelopmentCoreTeam 2006) with the add-on package 'party' (Hothorn et al., 2006b). For details of R-script see Supplementary material S1.

Data distribution was visualized by construction of scatterplot graphs. In order to enhance the visual information on the scatterplots, smoothed points were computed and plotted as loess curves (Figs. 1 and 2). Locally weighted scatterplot smoothing (LOESS) is a method for smoothing a scatterplot, achieved by fitting simple models to localized subsets of the data to build up a function that describes the deterministic part of the variation in the data, point by point. Each smoothed value is expressed as a weighted quadratic least square regression over the span of values of the scatterplot y-axis criterion variable (Cleveland, 1979; Cleveland et al., 1992).

3. Results

In all three taxonomic groups the number of species per plot increases significantly with forest age (Fig. 1). The threshold values in the montane zone for species density of all groups as well as the confidence intervals of the thresholds all fall within the same range, which indicates that forest age reflects similar effects acting on all taxonomic groups in comparable ways (Fig. 1). This does not apply to the sub-montane forest area, where the threshold for birds is at 99 years while that of molluscs is at 170 years. Comparing the results for the sub-montane forest with those for the montane forest, it can be seen that a significantly higher species density level in breeding birds is reached much earlier in the sub-montane than in the montane zone (Fig. 1).

We also tested the number of red-listed lichen and mollusc species as well as hole-nesting bird species per plot for threshold values with respect to forest age (Fig. 2). Nevertheless, the results for threshold values are basically the same as for the whole species assemblages (compare Fig. 1 with Fig. 2), except with molluscs, where abundance of red-listed species reveals threshold values being considerably lower than for all species together. Regarding the confidence intervals, the patterns of difference between the datasets for all species and the subsets for more sensitive species are inconsistent.

4. Discussion

Among the chosen taxonomic groups there are many which would presumably represent good indicators for old-growth forest structures. Saproxylic beetles are a fine example of a group sensitive to presence of such structures. Managed and secondary forests generally support fewer individuals, fewer species and different assemblages to old-growth forests (Grove, 2002). However, this group depends mainly on a single forest attribute (dead wood) and thus its species density is not suitable as a prime indicator of forest age (Müller et al., 2007). Similar results have been obtained for polypores (Penttilä et al., 2004) and amphibians. The latter are represented only by a few species in Central European forests and mainly depend on the occurrence of wetlands, but have been shown to be sensitive to logging of old forest, e.g. in California (Bury, 1983) or tropical forests (Ernst and Rödel, 2005). Hence we selected three taxonomic groups that are known to depend on old-growth structures in multiple ways.

It is well known that in forests the number of logging-sensitive species is higher in the subset of red-listed mollusc and lichen species as well as the subset of hole-nesting birds than in the respective, entire species assemblages (Smith et al., 1985; Thor, 1998; Gustafsson et al., 2004). One would thus expect that the logging-sensitive species subsets display even higher age threshold intervals when compared to the whole species sets (e.g. Uliczka and Angelstam, 1999). However looking at all groups as a whole this trend could not be observed (Figs. 1 and 2). Generally both, generalists as well as the more specialized red-listed lichens/molluscs and hole-nesting birds contribute significantly to the species increase along the age gradient, as demonstrated by highly significant correlations between non-threatened and red-listed species of lichens and molluscs (Supplementary Figs. 3 and 4) and between non-hole nesting and hole-nesting birds (Supplementary Fig. 5, except sub-montane area). This implies that high numbers of generalist species are generally accompanied by high numbers of specialized species. In molluscs the proportion of red-listed species remains the same along the age gradient (Supplementary Fig. 3), while in birds and lichens the proportion of hole-nesting and red-listed species increases with forest age (Supplementary Figs. 4 and 5).

Our results therefore only offer slight support for recommending the use of species diversity of red-listed molluscs/lichens and hole-nesting birds for the identification of ecologically critical forest ages in preference to species numbers of all species. On the other hand, to detect effects of forest age on these taxonomic groups, sampling of only the subsets of logging-sensitive species makes sense, because of the greatly reduced field work effort required.

In nearly every group, instances occur where high numbers of (red listed) species are present below the threshold values. This reflects the high variance level in the datasets, caused by diversity of structure where comparatively small plots are situated within very varied stands. However, comparing larger forest areas with each other would not be a valid alternative, because larger plots vary internally in history and contain areas with widely different numbers of age dependent structures and would thus yield increasingly meaningless averages. Furthermore, it would be methodologically impracticable to obtain standardized mollusc and lichen data from large forest areas. Structures that support typical old-growth forest species may also occur regularly in younger stands (e.g. caused by wind throw, or tree damage resulting in nesting holes). This underlines that in detail and on a short time scale, species diversity is only loosely correlated with forest age. However, in old stands above the threshold values, low species diversity becomes increasingly rare. Although the higher species numbers obtained in very old stands are based on rather few plots, because availability of old forest in the study areas is limited, the positive relation between forest age and species diversity is apparent in every taxonomic group investigated and is valid for the whole altitudinal gradient (Figs. 1 and 2).

The species density increase along the age gradient in the investigated taxonomic groups has been well documented by various previous research projects. Forest structures that are typical for old-growth stands such as rough bark, large amounts of dead wood, nesting cavities and large trees seem to account for the bird species increase in old forests (Moss, 1978; Helle and Mönkkönen, 1990; Solonen, 1996; Laiolo, 2002). Studies suggest that bird community composition and diversity increase as the complexity and variability of forest vertical structures increases (Terborgh, 1977; Rice et al., 1984; MacArthur et al., 1966), an effect which was also demonstrated for pristine beech forests (Kornan, 2000). Although selective logging and clear-cutting in temperate forests in the United States had specific effects only on certain guilds and species, these operations resulted in a marked decrease of total bird abundances and species richness (Thompson and Fritzell, 1990; Probst et al., 1992; Thiollay, 1997; Yahner, 1997). The amplified structural complexity in old-growth stands generally provides a wider diversity of foraging sites and microhabitats upon which birds can specialize, eventually increasing the bird species diversity (Urban and Smith, 1989; Karr, 1990; Cueto and de Casenave, 1999; Kornan, 2000). Dead wood quantities increase in old-growth stands, which thus support a huge invertebrate community that in turn represents a rich food resource for many birds such as woodpeckers (Nilsson, 1979). Additionally, other authors were able detect a strong influence on bird communities of tree volume, a factor that is positively correlated with stand age (Jokimäki and Huhta, 1996). Especially hole-nester abundance increases significantly with stand age, because these species are often confined to the oldest stands with greater availability of holes and crevices in mature trees (Smith et al., 1985).

Bird populations vary from year to year. However, the increase in species number along the age gradient is apparent in both datasets, although they were obtained in different years. Thus we consider the link between forest age and bird species diversity to be generally valid.

A significantly higher bird diversity level is reached much earlier in the sub-montane forest than in the montane forest. This applies to the whole species set as well as to hole-nesting birds (Figs. 1 and 2). In the mixed montane forest area the diversity level remains rather unchanged for the first 150 years, while in the sub-montane area it increases quickly with a threshold value confidence interval resulting already at 81–101 years for all species and at 99–142 years for hole-nesting birds (Figs. 1 and 2). The development of old-growth structures is highly site-dependent and especially elevation-dependent (Dittmar et al., 2003). Thus the critical old-growth forest structures for birds such as cavities increased dead wood amounts and diverse stratification may develop much more

quickly in the area of the sub-montane zone at lower elevations.

Even if donor sites are available to contribute to the colonization of heavily disturbed forest areas (e.g. affected by clear-felling), the snail fauna is only fully restored after decades when large tracts are affected and correspondingly large distances are involved (Reinink, 1979; Suško, 1997; Watters et al., 2005). Colonization may occur considerably more rapidly if only small patches are affected and (micro) refugia remain close by (Shikov, 1984; Strayer et al., 1986). Although precise guidelines still have to be developed for the optimal distribution of snail donor sites in managed beech-dominated forest landscapes, we may conclude from our results that these donor sites should exceed the age range of 180–230 years.

Patterns of forest-age dependent mollusc diversity are little known and far from being consistent. For example, a decrease in average species abundance was found at boreal riparian clear-cutting patches in southern Sweden 2.5 years after harvesting. From 40 to 60 years later, these patches showed higher abundances of individuals and species than the 150-year-old forest stands. However, higher abundances and species richness are in young riparian forests mainly associated with the higher litter pH (Ström, 2004), which does not apply to non-riparian woodlands such as beech-dominated forests. Although there is a slight trend towards a species decrease in very old forests in our data, these were however only obtained from very few plots (Figs. 1 and 2).

Comparing the overall mollusc species increase with age in the montane with that of the sub-montane forest, it becomes apparent that the species increase of the whole species dataset (Fig. 1) in the sub-montane area is steeper, resulting in a much narrower confidence interval. As for birds, the homogeneity of tree species composition might be one reason for this. The confidence intervals of the threshold values for the whole species datasets as well as for the red-listed species datasets are showing overlapping ranges in both areas. In contrast to the birds, mollusc species seem to depend on forest attributes and structures that form in about the same period of time in both areas. These may include shadiness and humidity, a stable microclimate, adequate calcium content and amount of coarse woody debris, habitat continuity and richness of vegetation (Müller et al., 2005). As both areas are essentially semi-natural, populations of old-growth forest snails acting as sources for the colonization of old forests are always close by, which leads to the assumption that the similar threshold intervals reflect the period of time that is generally needed by snails for the immigration of the full species assemblage. If this is so, habitat continuity would have to be regarded as the main driving factor of snail diversity levels in beech forests under the precognition that adjacent populations for the colonization of newly arising habitats are available.

Although no lichen data from the sub-montane beech forests are available, it becomes evident that high lichen diversity levels (all species and red-listed species) are only attained at habitats that are older than 220 years in mixed montane forests (Figs. 1 and 2). This value results for mixed montane forest stands taken as a whole. However, major differences in the lichen species composition and speed of lichen colonization exist between the dominating trees species (Uliczka and Angelstam, 1999). These differences are concealed in our presentation. Although the increase of lichen diversity with increasing age in boreal forests is well documented even for single tree species (e.g. Uliczka and Angelstam, 1999), comparably little is known about forest age dependent thresholds in lichen diversity. For example, species increases were found in stand ages up to 120 years in boreal forests (Kuusinen and Siitonen, 1998; Price and Hochachka, 2001). Uliczka and Angelstam (1999) detected rates of occurrence frequency >20% in lichen species sensitive to habitat change in tree age-classes ranging from 21–40 to 141–160 years in pine and spruce and from 21–40 to 61–80 years in aspen and birch. In beech forests of southern Sweden, lichens associated with very late succession stages were lacking in stands younger than 160 years, while stands older than 350 years had significantly higher lichen species numbers and also contained old-growth species (Fritz et al., 2008).

4.1. *Management implications*

In considering all the scientific discussion about thresholds, one has to keep in mind that only simple threshold values for important surrogates that mirror biodiversity patterns allow the implementation of scientific insights in forest management practices, not least because the use of thresholds has gained wide acceptance (Angelstam et al., 2003; Müller and Hothorn, 2004; Guenette and Villard, 2005; Lindenmayer and Luck, 2005; Ranius and Fahrig, 2006).

Taking Central European beech-dominated sub-montane and montane forests as a whole, a basic guideline for forest management is that these first acquire significantly higher densities of total species as well as of specialized species from the age of about 200 years.

Most of the age threshold values for different taxonomic groups given above exceed by far the economically reasonable maximum rotation age, which is around 120–140 years in beech (Knoke, 2003). Unlike boreal spruce stands (Kuusinen and Siitonen, 1998), the recommendation of prolonged rotation of the stands is feasible for these taxonomic groups only to a limited extent. Apart from the recommendation of the integration of old trees in commercial stands, there is a need to establish a denser network of strict forest reserves than exists today, which can act as refuge and dispersion areas for logging-sensitive taxonomic groups. The effectiveness of such a network has been proven in temperate forests, e.g. for lichens (Sillet et al., 2000; Peterson and McCune, 2001; Rolstad et al., 2001; Pilāte, 2003a; Lõhmus and Lõhmus, 2007). Occasional high diversity levels in younger stands show that it is also possible to enhance their biodiversity. A better understanding of the factors which determine this would possibly permit improved realization of nature protection targets in forests managed primarily for economic production.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2008.11.002.

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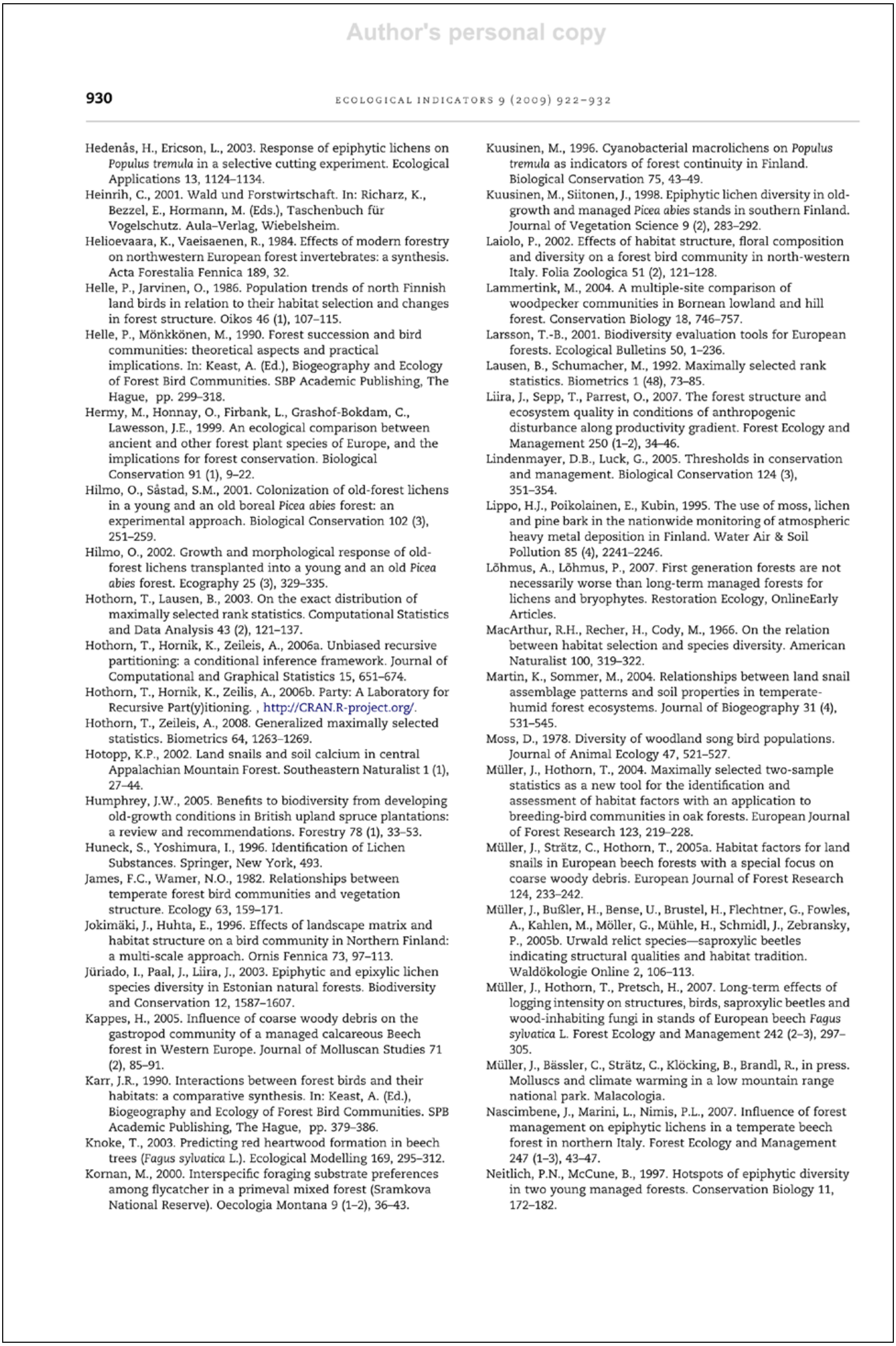

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Lichen diversity in temperate montane forests is influenced by forest structure more than climate

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ABSTRACT

Although the effect of forest management on lichens in temperate forests has been widely examined, little is known about the influence of management-related factors on their biodiversity relative to factors that cannot be altered by management. Here we determined whether forest structure or climate determines lichen diversity in the Bavarian Forest National Park in southeastern Germany, taking spatial variables into account. We investigated 517 single tree stems along 4 transects in 113 pre-stratified plots (8 m in diameter) in this montane forest. We grouped environmental variables into three sets: climate (macroclimate, non-manageable), forest structure (manageable), and space. The explanatory powers of these sets of variables for lichen diversity were compared using variance partitioning for the lichen community, species density, and threatened species density. The relationships of single characteristics of forest structure with lichen species diversity were analyzed using generalized linear models (GLM). Lichen diversity was better explained by stand structures than by climate. Spatial effects influenced the number of species per plot. Among the structural features, the availability of dead wood and sycamore maple as well as forest continuity were most important for the enhancement of lichen diversity. Open canopy structures affected the total diversity positively. Although the availability of large trees was not an influential factor in the GLM at the plot level, high diversity levels were generally associated with large stem diameters at the level of single stems. We provide recommendations for sustainable forest-management practices that aim at specifically enhancing lichen diversity in temperate areas experiencing low levels of air pollution.

1. Introduction

One aim of modern sustainable forest management is the preservation of management-sensitive species. Therefore, a detailed knowledge of the influence of management-related factors on biodiversity as compared to factors that cannot be altered via management is essential. One of the major taxonomical groups sensitive to management are lichens, which are thus important indicators of forests that are close to natural conditions (Ulikzka and Angelstam, 2000). Three major threats are known to have the potential to alter lichen diversity: forest management, air pollution, and climate change (Wirth et al., 1996; Thor, 1998; Ellis et al., 2007a,b).

Temperate forest management influences forest structures, which in turn determine habitat qualities and affect lichen species (Uliczka and Angelstam, 1999; Price and Hochachka, 2001; Gustafsson et al., 2004). Modern forestry has created tree stands with an even age distribution (Gunnarsson et al., 2004). This change in forest continuity through management affects lichen species density, especially the density of threatened species (Tibell, 1992). Especially the conversion of old-growth forest into young, managed stands leads to a significant reduction in the epiphytic lichen biomass (Esseen et al., 1996) and species diversity (Uliczka and Angelstam, 1999). In many managed areas, the rate of disappearance of lichen populations significantly exceeds the rate of establishment of new populations (e.g., Pykälä, 2004).

Epiphytic lichen diversity in temperate forests throughout the northern hemisphere increases with stand age (Neitlich and McCune, 1997; Kuusinen and Siitonen, 1998; Price and Hochachka, 2001; Gustafsson et al., 2004; Nascimbene et al., 2007), which is

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due to limitations in the dispersal and establishment of lichens (Hilmo, 2002; Hilmo and Sastad, 2001; Werth et al., 2006) and slow biomass accumulations of epiphytic lichens (Sillet et al., 2000). Thus, mainly time, i.e. habitat age, comes to the fore as an ecologically effective dimension, especially for threatened lichen species (Tibell, 1992; Goward, 1994; Crites and Dale, 1998; Thor, 1998; Uliczka and Angelstam, 1999). In this context, it is easy to understand why lichen biomass is strongly related to the mass, diameter, and age of branches: many lichen species need long periods to colonize a suitable habitat (Esseen et al., 1996). Thus, the diameter of the substrate is related to the lichen species composition (Esseen et al., 1996), species richness (Humphrey et al., 2002), and especially the abundance of threatened species, which are often weak colonizers (Caruso et al., 2008).

Large stem diameters are a surrogate for various factors, including an obvious species–area effect, i.e., the larger the diameter, the larger the area that may be colonized and the more species that may be expected on the single stem. This species–area effect is well known in ecology (Arrhenius, 1921; Preston, 1962; Rosenzweig, 1995) and may not be clearly separated from other effects that may positively influence lichen diversity on large stems. These other effects include long periods of exposure to large stems and the rough surface of large stems, which may aid lichen colonization (Crites and Dale, 1998; Uliczka and Angelstam, 1999). However, an experimental approach suggests that young bark surfaces are not less favorable for lichen colonization, but old forest stands have a higher propagule density and thus lichen dispersal is more efficient (Hilmo and Sastad, 2001). Nonetheless, as stem size is adequate as a general proxy for compound factors, large stem diameters are an suitable target variable in a forest management that aims at increasing lichen diversity, regardless of how the diversity increase is caused.

Forest management causes a reduction in certain forest structures, such as coarse woody debris (Gibb et al., 2005). This greatly alters the habitat quantity and quality for lichens (Caruso et al., 2008). The substrate volume, e.g., the amount of dead wood, and the type of substrate, e.g., tree species, are among the most important driving environmental factors to explain the density of red-listed lichen species (Ohlson et al., 1997; Lõhmus and Lõhmus, 2001; Gustafsson et al., 2004). Certain tree species are highly preferred because of their specific chemical attributes and bark roughness (Degelius, 1954; Kuusinen, 1996b; Hauck et al., 2001; Uliczka and Angelstam, 1999; Pykälä et al., 2006). Sycamore maple is specifically known to hold high diversity levels in lichens (Macher, 1992). Forest management also influences the cover of the forest canopy layer. This in turn affects the availability of light, which positively affects the growth of lichens (e.g., Ahmadjian, 1993; Uliczka and Angelstam, 1999; Svensson et al., 2005).

The impact of climate change on lichens is a relatively recent issue; however, long-term monitoring suggests that lichens respond to global warming (Insarov et al., 1999; Cezanne et al., 2008). In the Netherlands, arctic-alpine/boreo-montane species appear to be declining, while (sub)tropical species are invading, independent of nutrient demands and decreasing SO_2 emissions (van Herk et al., 2002). In western Europe, more epiphytic species appear to be increasing rather than declining, as a result of global warming (Aptroot and van Herk, 2007). Model predictions indicate major shifts in the distribution of lichen species (Ellis et al., 2007b; Giordani and Incerti, 2008). However, these studies did not separate the influence of climate from the influence of structural and historical variables (Ellis and Coppins, 2007; Ellis et al., 2009). Also these previous lichen bioclimatic studies have focused on target species only, which are expected (a priori) to be responsive to climate change. Such bioclimatic modeling does not pretend to explain 'diversity' at a plot-scale, and has been carried out previously only at a countrywide scale beyond the influence of local forest management. In contrast, our study aims on the assessment of the relative importance of local climate compared to stand structure for characteristics of the whole epiphytic lichen community at a finer local scale that is relevant to forest-management-decisions, and at which the species will most likely response to climate change. However climate–habitat interactions at the landscape-scale are potentially important and the relative importance of their separate effects has not previously been quantified.

Our goal here was to find out whether forest structure variables determine lichen diversity when climate variables are also considered in the same analysis. We chose an area free of air pollution to isolate climatic and stand-structure effects. The following two questions are specifically addressed:

1. To what extent does forest management influence lichen diversity (community, species density, threatened species density) compared to local climatic variation?
2. Which of the forest structure variables included in a multivariate analysis play a key role for lichen diversity among forest structures (i) at the plot (0.1 ha) level and (ii) at the single stem level?

We hypothesized that forest structure variables are the major driving factors for lichen diversity in temperate montane forests. Based on the current knowledge, we assume that among forest structures, (a) old forests retain higher lichen diversity levels than young forests, (b) forests with large amounts of dead wood have higher lichen diversity levels than forests with small amounts of dead wood, (c) an open canopy layer causes higher diversity levels than a closed canopy layer, and (d) high tree species numbers increase lichen diversity.

At the level of a single stem, we tested whether (a) a deciduous substrate has a higher lichen diversity than a coniferous substrate, (b) sycamore maple has a higher lichen diversity than beech, spruce, and fir, (c) dead substrates have a higher lichen diversity than living substrates, and (d) thick stems have a higher lichen diversity than thin stems.

We discuss the results in the context of sustainable forest-management practices, and we suggest management strategies that maximize lichen diversity in temperate forests in areas with little air pollution.

2. Methods

2.1. Study area and lichen sampling

Our study site is within the Bavarian Forest National Park, situated in southeastern Germany along the Czech Republic border. This unmanaged montane forest area contains an altitudinal gradient with a high variety of structures distributed almost independently from elevation and a broad tree age gradient. The rich structural diversity is caused by heavy infestation with bark beetles, mainly *Ips typographus*, since the 1990s (Müller et al., 2008). The study site includes areas that were managed up to a few decades ago, but also remnant primeval forest areas that have never been managed, thereby increasing the length of the management gradient. We established sampling plots every 100 m along four 29.3-km transects from the bottom (650 m a.s.l.) to the top of the mountains (1420 m a.s.l). From these we selected 113 pre-stratified (randomly within altitude classes) plots to sample all types of forest stands with an equal distribution along the altitudinal gradient. For details, see Bässler et al. (2008) and Müller et al. (2009).

At each plot, all epiphytic lichens were recorded from August to November 2007 within a radius of 8 m and up to a height of 2 m, including all trees and dead wood stems and logs (hereafter referred to as stems, total: 517 stems) by an experienced lichenologist (J. Bradtka). At each plot, 1–10 single stems were investigated (average: 5.0 stems per plot), depending on the availability of stems. Lichens growing on the ground and on rocks were not considered in our analysis.

Red lists are widely accepted to present a summary of the status of rare and declining species (Gustafsson et al., 2004) and thus are used here to form the response variable "number of threatened species per sample", where samples refers to plots or single stems. Since no red list has been published for lichens of Bavaria, we used the German red list (Wirth et al., 1996).

Environmental data for all plots were sampled in autumn 2006 and in summer 2007 (Table 1; for details, see Bässler et al., 2008). The variable "altitude" was left out in the data processing in favor of physiologically effective climate variables, such as temperature or precipitation, since the surrogate altitude and these physiologically effective variables were highly correlated along our climatic gradient (Körner, 2007; Müller et al., 2009).

2.2. Statistical analyses

All statistical analyses were conducted in the framework of R, version 2.8.0 (R Development Core Team, 2008). We grouped environmental variables into three basic sets: climate (macro-climate, non-manageable), forest structure (manageable), and space. Our selection of the forest structure variables is an a priori determination based on current knowledge of environmental factors that are known to influence lichen diversity in temperate forests as presented in the introduction. To represent lichen diversity, we chose two univariate response variables (species density and threatened species density) and one multivariate response variable (species community composition). Space was considered to quantify the spatial effects routed in our sampling design and was represented by a second-order trend surface based on the coordinates (compare Table 1 with introduction). Forty-five climate variables were available for all plots. These were subjected to a principal-components analysis (PCA) to maintain full environmental space but avoid colinearity. The first four axes explained 89% of all variance. For the further analyses, the projected axis scores of the first four axes were used to represent the variable 'climate' (Schweiger et al., 2008). The analysis of the main components (PCA) showed that the first four axes represent temperature and precipitation (annual average [°C], means of the vegetation periods [days], extreme temperatures [°C], global radiation [J/(cm^2 days)], and extreme radiation [J/(cm^2 days)] and thus correspond to macro-climatic factors that are effective for lichens (Cezanne et al., 2008). An overview of the investigated variables and their data ranges is given in Table 1.

Species density refers to the number of species per plot or stem (Gotelli and Colwell, 2001). All explanatory variables were standardized to zero mean and unit variance (Oksanen et al., 2006). We used log-transformed density data. Species data for the community matrix were square-root transformed, in order to adjust the high numbers of common species.

To compare the explanatory power of the different environmental variable sets, we partitioned the variation of response table Y with respect to the three explanatory tables using the function *varpart* in *vegan*. This application uses partial redundancy analysis (RDA) for community matrixes as independent variables and partial multiple regression analysis for vector-independent variables. We calculated adjusted *R* square values because this is the only unbiased method (Peres-Neto et al., 2006). Preliminary detrended correspondence analyses (DCA) revealed the length of the first axis gradient as 3.9, which is within the range (2.0–4.0) in which one can select unimodal ordination, such as canonical correspondence analysis (CCA), or linear ordination, such as RDA (Økland, 1990). The same results were obtained with a partial CCA. As only RDA supports adjusted *R* square values for community variance partitioning, we present only the results of RDA.

To test the significance of the influence of our independent fractions on lichen data, we applied a permutation test with 1000 permutations using the function *anova* in *varpart*. This shows whether the particular independent fraction exhibits a significant explanatory power to the corresponding lichen variable (community, species density, threatened species density). To determine the errors of our independent fractions, we used a bootstrapping of the variance partitioning, which allowed us to construct 95%

Table 1
Investigated environmental variables and their variance within the dataset, as well as response variables and their variance.

Environmental variable sets	Data range	Mean
Space		
X	–	–
Y		
X × Y		
X × X		
Y × Y		
Climate (non-manageable factors): projected axis scores of the first four axes of a PCA, based on 45 climate variables	–	–
Forest structure (manageable factors)		
Average stand age from forest inventory grid with 0.1 ha plots [years]. Determined by drill samples.	35–400 years	159 years
Dead wood volume [m^3/0.1 ha] estimated on 0.1 ha plots	0–70.9 m^3/0.1 ha	13.5 m^3/0.1 ha
Maximum diameter at breast height (1.3 m) diameter on 0.1 ha plot [cm]	0–130 cm	53.4 cm
Laser penetration rate (LiDAR measurement) in the space between 2 and 50 m above ground on 0.1 ha plots [%]	0–92.2%	29.4%
Number of tree species on 0.1 ha plots [species]	0–7 species	2.2 species
Diameter of the substrate (stem) [cm]	2–150 cm	37.4 cm
Response variables	Data range	Mean
Species density: number of lichen species per 0.1 ha plot per single stem	Plot: 1–58 species Stem: 1–23 species	Plot: 20 species Stem: 4.2 species
Threatened species density: number of threatened lichen species per 0.1 ha plot per single stem (German Red List data; Wirth et al., 1996)	Plot: 0–39 species Stem: 0–14 species	Plot: 6.7 species Stem: 1.4 species
Community: number of encounters per lichen species per 0.1 ha plot	–	–

confidence bands for our independent effects. The bootstrapping was conducted with 2000 replicates according to Roff (2006).

To analyze the relationships of single characteristics of lichen species diversity with the forest structure variables, we applied generalized linear models (GLM). As our raw data are count data, we selected Poisson error structures (Quinn and Keough, 2002).

When the GLM considered the species or threatened species density on single stems, the dataset consisted of continuous and categorical variables with several classes within the variable "tree species". However, a GLM does not provide a decent insight into the influence of the category variables, although these would be of major interest for practical applications. Therefore, we calculated multiplicity-adjusted Wald-Intervals (following Hothorn et al., 2008a; implemented in the package *multcomp*, Hothorn et al., 2008b) and the corresponding multiplicity-adjusted *p*-values (Fig. 3). Using these inference measures, we restricted the probability of erroneously declaring at least one predictor as influential to alpha = 0.05. This procedure allowed us to fulfil all requirements in multiple testing of the hypothesis even in complex predictor sets (Quinn and Keough, 2002).

Owing to our survey design, spatial autocorrelation needed to be addressed, as one of the key assumptions in statistical models in the present context is the spatial independence of residuals (Dormann et al., 2007). Therefore, in the variance partitioning process, we considered space as a separate environmental variable set (see Table 1). Finally, we checked the residuals of our GLM models for spatial independence using spline (cross)-correlograms (package *ncf*, Dormann et al., 2007).

3. Results

We found 138 lichen species on our plots (see Supplementary table). On our study plots, variance partitioning resulted in a total explained variance of 23.3% for lichen community composition, 36.8% for species density, and 20.6% for threatened species density. The independent explained variance extracted from the data sets for climatic, forest structural, and spatial variances showed that forest structure had the greatest effect and climate had the lowest effect (Fig. 1). This was most apparent for the threatened species density. Spatial correlations for species density had a higher independent effect than for community and threatened species density.

The GLM of the single structural variables at the plot level resulted in similar patterns of significance for both the number of species and the number of threatened species per sample (Table 2). Variables that significantly correlated to both species numbers and threatened species numbers per sample were related to forest continuity (age) and substrate availability (dead wood volume). Open canopy (laser penetration rate) positively affected the total species number per sample at a highly significant level, but did not significantly affect the threatened species number per sample. Tree species diversity (number of tree species) was highly significantly correlated to threatened species number per sample but not to species number per sample. Our assessment of the spatial autocorrelation for residuals of the GLMs by inspection of spline (cross-)correlograms (Fig. 2), indicated no spatial dependence of the residuals for threatened species per sample, but some dependence for the total number species on a scale of around 1 km, which is in agreement with the results shown in Fig. 1.

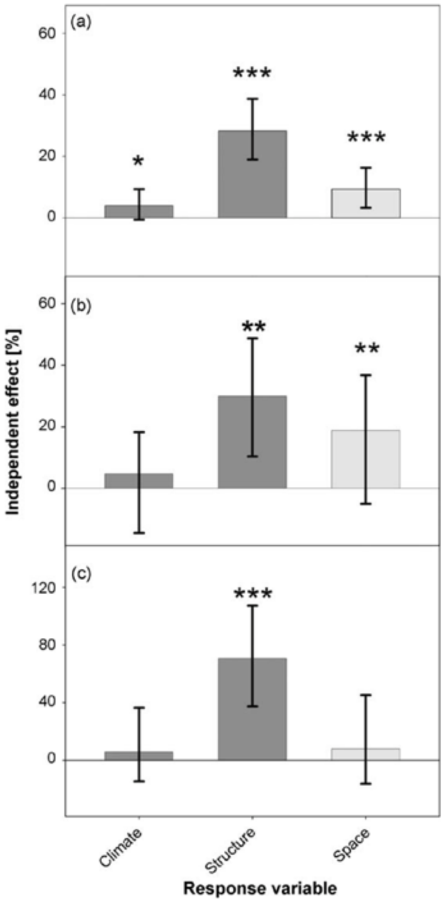

Fig. 1. Exclusive explanatory contribution of climatic, forest-structural, and spatial variable sets of the total explained variance for each dataset based on variance partitioning (function *varpart* in *vegan*, Oksanen et al., 2006). (a) Lichen community composition, (b) species density, and (c) threatened species density, all at the 0.1 ha plot level. To test the significant influence of each independent fraction on the independent variables, a permutation test was applied (function *anova* in *vegan*); significant *p*-values are indicated by asterisks: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. To display the variability of our independent fractions, a bootstrapping of variance partitioning was additionally applied, and the 95% confidence interval is shown in the box plots by whiskers. Note that the significance by permutation and the confidence bands shown by the whiskers are not related to each other. Also note that the target variables differ significantly from each other (vector, community matrix); they cannot be compared quantitatively among each other.

Table 2
Results of the generalized linear model of the forest structural variables at the plot level (0.1 ha). The estimators of the standardized predictors are given. Significant *p*-values are indicated in parentheses; n.s. not significant. For details regarding the variables, see Table 1.

Response variable	No. of species per sample	No. of threatened species per sample
Age	0.089 (**)	0.256 (***)
Dead wood volume	0.200 (***)	0.228 (***)
Maximum diameter at breast height	0.022 (n.s.)	−0.054 (n.s.)
Laser penetration rate	0.218 (***)	0.086 (n.s.)
No. of tree species	0.044 (n.s.)	0.185 (***)

** $p < 0.01$.
*** $p < 0.001$.

Also the GLM of the environmental variables at the level of single stems resulted in similar patterns of significance for both the number of species and the number of threatened species per sample (Fig. 3). The tree species was crucial for both numbers;

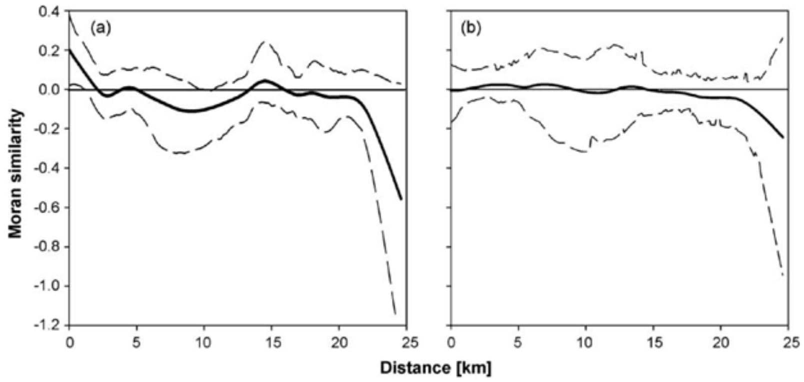

Fig. 2. Spline (cross)-correlogram (Bjørnstad et al., 1999; Bjørnstad and Falck, 2000) of the GLM residuals of (a) the number of all species per sample and (b) the number of threatened species per sample. Both analyses were performed at the plot level (0.1 ha). The non-centered correlogram provides estimates of the spatial correlation for discrete distance classes and is based on Moran's I.

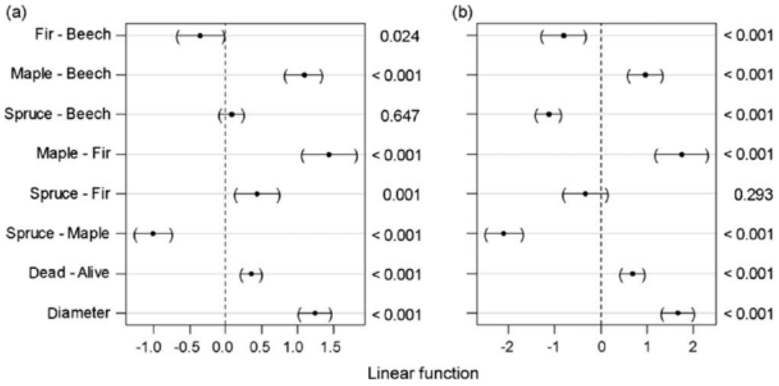

Fig. 3. Generalized linear models with post hoc performance considering (a) the number of species per sample and (b) the number of threatened species per sample, both at the level of single stems ($n = 517$). Multiplicity-adjusted Wald intervals (Laplace, 1812; Landauer, 1997) and the corresponding multiplicity-adjusted p-values are displayed. Fir $n = 23$, maple $n = 14$, beech $n = 177$, spruce $n = 304$, alive $n = 330$, dead $n = 224$. The graphs show the size of the estimators and the confidence intervals. If the confidence interval encloses the zero line, the influence of the environmental variable is not significant. If the value of one category variable is greater than another, the confidence interval lies to the right of the zero line. For example, with maple vs. fir, the confidence interval lies to the right and maple is therefore of higher importance for lichen diversity than fir.

especially sycamore maple (*Acer pseudoplatanus*) was of high importance for lichen diversity. At the single stem level, the substrate diameter and dead wood as the substrate were highly significant for both the number of species and the number of threatened species per sample.

4. Discussion

We did not consider the influence of long-range atmospheric pollution (Hawksworth and Rose, 1970; Ferry et al., 1973) because in the past the influence of SO_2 emissions on lichen diversity in the Bavarian Forest has been rated as low, especially in comparison to northeastern Bavaria (Macher, 1992; Windisch and Vorbeck, 1996). This is exemplified by the wide distribution of SO_2-sensitive species, such as *Alectoria sarmentosa*, *Bryoria nadvornikiana*, *Gyalecta ulmi*, and *Loxospora cismonica*, within the Bavarian Forest National Park and their rarity or uncommonness elsewhere in Bavaria. These species are characteristic for permanent clean air with low SO_2 concentrations, which rate the highest index of atmospheric purity (IAP) values (Ellenberg et al., 1992). Nevertheless, it is important to note that forest management aimed at maintaining or enhancing lichen diversity will only be efficient in places where air pollution levels are sufficiently low, such as in our study area. Large areas of Central Europe still receive considerable amounts of air pollution (van Herk et al., 2007), which is particularly detrimental in dry climates. However, SO_2 emissions have generally decreased in the past decades, and in some areas, lichens have re-invaded "lichen deserts", i.e., areas formerly free of lichens because of intense air pollution (Kandler and Poelt, 1984; van Dobben, 1996). Thus, in contrast to a few decades ago, the influence of forestry on lichen diversity has increased.

Nitrogen depositions have been identified as an important factor that favor nitrophilous lichen species, such as *Xanthoria parietina*, *Xanthoria candelaria*, and *Phaeophyscia orbicularis* (van Herk et al., 2007; Frati et al., 2008). However, since nitrophytes were locally rare among the lichen species we studied, we do not believe that N deposition is a major issue in our study area.

In our study, both the diversity of threatened lichen species and the diversity of total lichen species were mainly affected by forest structure, whereas macroclimatic factors were far less important,

despite the steep elevational gradient investigated. The investigated gradient in the Bavarian Forest National Park ranges from 4.2 °C to 7.8 °C average annual temperature, which also represents a broader regional scale (BayFORKLIM, 1996). Since all of the forest structure variables investigated can be actively influenced by forest management, our results demonstrate that forest management exerts a great effect on the diversity of epiphytic lichens. Our results also indicate the potential for sustainable forest-management strategies, which could actively enhance lichen diversity in temperate forests.

Our results differ from those of a study in northern Norway, where climate as well as forest structure were found to be highly relevant for macrolichen communities (Werth et al., 2005). Climate was likely significant in the Norwegian study because a particularly long gradient comprising humid oceanic and dry inland sites was investigated (Werth et al., 2005). In studies in Great Britain using bioclimatic envelopes, lichen communities had a large potential to react to climate change (Ellis and Coppins, 2008; Ellis et al., 2007a,b), but in these and several other studies, the effects of forest structure as a habitat-defining feature were not considered. Such an approach may lead to an incomplete interpretation of the occurrence patterns of lichens, which are highly forest-structure-dependent organisms. Moreover, the climate warming that started in the last decades is proceeding faster than past climate changes, which means that even if the temperature at a specific altitude increases by +2.0 K within 100 years (IPCC, 2007; Spekat et al., 2007), the creation of dead wood structures, such as those of large broadleaf trees, will not follow at the same pace. This underlines the superior role of forest structures as a decisive influencing factor for lichen species density and community composition within the next decades.

Spatial autocorrelation was detected for the number of species per sample at the plot level, at a scale of up to 1 km. This result indicates that whole mountain slopes are developing characteristic structural features owing to large-scale natural dynamics, such as bark beetle infestations, that cause similar lichen diversity and community patterns to evolve on a scale of a few kilometres (Müller et al., 2008). However, the analysis clearly showed that forest structure results in the greatest exclusive explanatory contribution, which is in line with numerous other studies (Lesica et al., 1991; Hyvärinen et al., 1992; Uliczka and Angelstam, 1999; Cameron, 2002). This was true for community composition, species numbers per sample, and in particular for the number of threatened lichen species per sample. In the majority of European forests, structures are determined directly by forest management. This implies that lichen diversity, including density of threatened species, can be actively managed, and even enhanced, if adequate sylvicultural methods are utilized.

In our study, we found a clearly positive influence of sycamore maple on lichen species densities for both the total number of species and the number of threatened species per sample. This effect is probably caused by more than one factor. First, the chemical attributes of the bark play an important role (e.g., Kuusinen, 1996b; Hauck et al., 2001), as shown for the bark of *Populus tremula*, which offers favorable conditions for cyanobacterial lichens in boreal forests (Kuusinen, 1994, 1996a; Uliczka and Angelstam, 1999). Second, the bark of sycamore maple is rough even in younger trees and thus may be colonized more easily even at an early age.

Regarding to the biogeographic scope and consequently the wider relevance of the results, the findings of other studies of temperate forests all over the northern hemisphere suggest, that the effect of forest structure on forest lichen epiphytes is outstanding (Crites and Dale, 1998; Gustafsson et al., 2004; Hyvärinen et al., 1992; Kuusinen and Siitonen, 1998). Forest structure obviously shapes epiphyte lichen diversity and communities beyond the influence of climate in many montane forests all over the northern hemisphere.

4.1. Management recommendations

From our analyses, we identified those forest structure variables that play a key role for lichen diversity. Thus, we strongly recommend that the amount of dead wood be generally increased by conserving enough veteran trees within a stand, and that along the whole elevation gradient a considerable number of stands should be created with a canopy cover less than 50%, which is typical for all high mountain spruce forests in our study area. To specifically support red-listed species, the portion of native broad-leaved tree species characteristic of a given locality should be enhanced; in low mountain ranges of Central Europe, this is mainly *A. pseudoplatanus*. Additionally, these broad-leaved trees should be allowed to grow to maturity and beyond.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.05.015.

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Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages

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Summary

1. Effective biodiversity management can only be implemented if data are available on assemblage–environment relationships. The level of detail needs to be relevant to the scale of planning and decision making. A number of remote-sensing methods are available, but there are few studies that link information collected at both landscape and local scales. This is particularly true for arthropods even though these organisms are ecologically very important.

2. We assessed the predictive power of habitat variables measured by airborne laser scanning (light detection and ranging; LiDAR) to model the activity, richness and composition of assemblages of forest-dwelling beetles. We compared the results with data acquired using conventional field methods. We sampled beetles with pitfall traps and flight-interception traps at 171 sampling stations along an elevation gradient in a montane forest.

3. We found a high predictive power of LiDAR-derived variables, which captured most of the predictive power of variables measured in ground surveys. In particular, mean body size and species composition of assemblages showed considerable predictability using LiDAR-derived variables. The differences in the predictability of species richness and diversity of assemblages between trap types can be explained by sample size. We expect predictabilities with R^2 of up to 0·6 for samples with 250 individuals on average.

4. The statistical response of beetle data and the ecological interpretability of results showed that airborne laser scanning can be used for cost-effective mapping (LiDAR : field survey : beetles 15 : 100 : 260 € ha^{-1}) of biodiversity even in remote mountain areas and in structurally complex habitats, such as forests.

5. *Synthesis and applications*. The strong relationship between characteristics of beetle assemblages to variables derived by laser scanning provides an opportunity to link data from local ground surveys of hyperdiverse taxa to data collected remotely at the landscape scale. This will enable conservation managers to evaluate habitats, define hotspots or map activity, richness and composition of assemblages at scales relevant for planning and management. In addition to the large area that can be sampled remotely, the grain of the data allows a single tree to be identified, which opens up the possibility of planning management actions at local scales.

Key-words: airborne laser scanning, body size, canopy surface model, disturbance, habitat variables, national park, terrain surface model

Introduction

Biodiversity is diminishing at an accelerating pace (Chapin *et al.* 2000), and, therefore, data on biodiversity and spatial distribution are urgently needed for conservation planning (Margules & Pressey 2000). However, the lack of taxonomists and funds precludes particularly the mapping of hyperdiverse taxonomical groups (Early & Thomas 2007; Basset *et al.* 2008; Vierling *et al.* 2008). Therefore, management strategies concentrate on charismatic vertebrates and only a few conspicuous arthropods (e.g. Buse, Ranius, & Assmann 2008) and ignore most other species (Hammond 1992). However, the diversity of invertebrates is declining even more rapidly than that of plants and vertebrates (Thomas *et al.* 2004), even though

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invertebrates are involved in important ecosystem functions (e.g. pollination and decomposition; Schädler & Brandl 2005; Klein *et al.* 2008). We clearly need methods to rapidly, effectively and cheaply assess the value of sites for all species, including arthropods, at a level of detail or grain (*c.* 1·0–10 000 m^2) and at an extent (ten to thousands of hectare) relevant for management and conservation (Duelli & Obrist 1998; McCleary & Mowat 2002).

Forests are often hotspots of invertebrate diversity (Stork 1988; Lawton *et al.* 1998). The compilation of faunal lists and data from canopy projects have increased our knowledge of insect assemblages living on single tree species (Stork 1987; Basset 2001; Brändle & Brandl 2001, 2006). Patterns of insect assemblages in forests, however, are still poorly understood (Stork, Didham, & Adis 1997; Novotny *et al.* 2007). The three-dimensional structure of the canopy is one of the essential drivers of arthropod diversity in forests (Rinker *et al.* 2001). Measuring the complex canopy structure during ground surveys requires considerable time (Hyde *et al.* 2006), and most forest studies have limited sample sizes and consequently limited statistical power (Nadkarni & Cushing 2002).

Numerous studies have demonstrated the potential of remote sensing to bridge the gap between grain and extent. In entomology, remote sensing is used to monitor insect movement (Osborne *et al.* 1999; Reynolds & Riley 2002) or areas infested by pest species (Solberg *et al.* 2006; Wulder *et al.* 2006). High-resolution multi-spectral imagery has been used to predict ground-dwelling ant and beetle assemblages in Australian forests (Lassau *et al.* 2005b). Despite such promising studies (Lassau & Hochuli 2008), the application of remote sensing for modelling diversity of insects is still underdeveloped. Here, we demonstrate the potential of **L**ight **D**etection **A**nd **R**anging (LiDAR) as a remote-sensing technique (Lefsky *et al.* 2002; Parker, Harding, & Berger 2004) to model assemblage composition, diversity and activity of forest beetles. Although several review articles on the potential of LiDAR in habitat modelling have appeared, the number of applications in real situations is still low, and the studies concentrate on birds (Bradbury *et al.* 2005; Vierling *et al.* 2008).

Among forest insects, beetles are the most prominent group (Grove & Stork 2000) with considerable impact on ecosystem functions (e.g. Grove & Stork 2000; Dennis, Aspinall, & Gordon 2002). The forest canopy is an important driver for the assemblages of beetles. It provides the habitat for many species, and it determines the density, height and composition of the herb layer, which is important for feeding (Böhme 2005). LiDAR provides proxy variables of the structural diversity of the forest, including the density of the canopy layer and forest gaps (Lefsky *et al.* 2002). LiDAR also measures the elevation of a site, which is a proxy for precipitation, temperature and vegetation types (Körner 2007). To examine the potential of variables extracted from LiDAR data sampled from a helicopter for statistical modelling of activity, diversity and composition of beetle assemblages in forests, we selected an area with a broad range of canopy structures. For comparison, we also collected environmental data to characterize habitats from ground surveys. Our analyses have three objectives: (i) to evaluate the predictive power of LiDAR in modelling beetle assemblages in comparison to ground-based measurements, (ii) to evaluate the ecological interpretation of the relationships between single parameters of LiDAR and beetle community characteristics and (iii) to compare the response of the activity of several beetle feeding guilds to LiDAR variables.

Materials and methods

STUDY AREA

Our study was conducted in the Bavarian Forest National Park in south-eastern Germany, a mountainous forest area between 650 and 1400 m a.s.l. (Müller *et al.* 2008b). Owing to a no-take forestry policy (everything was left completely unmanaged) in the core zone of the National Park, wind blows and bark beetle infestations have influenced the canopy structure considerably during the last 25 years (Müller *et al.* 2008b). Forests form a patchy mosaic of habitats (see Fig. S1) differing in structure in a way that is not systematically related to altitude (see also Lomolino 2001). We sampled habitat characteristics as well as beetle assemblages along four transects (T1–T4) from 5·7 to 8·6 km in autumn 2006 and 2007 (total length of 29·3 km; Fig. 1).

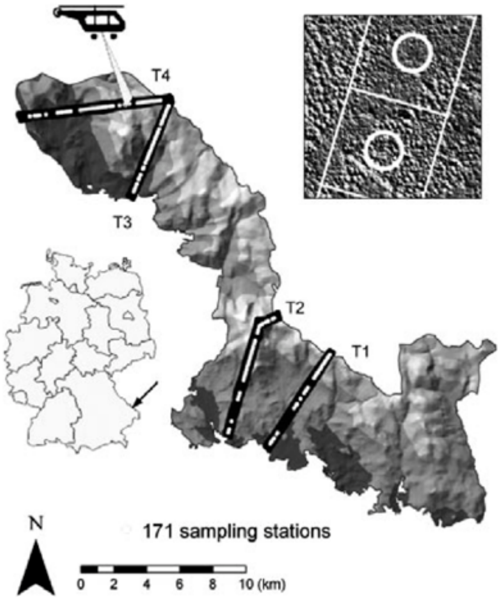

Fig. 1. Study area and sampled transects T1–T4. The map of Germany shows the location of the National Park. The map of the park shows the topography with low (dark) to high (pale) elevations. The 171 sampling stations are shown as white dots. The inset at the top shows an example of the digital surface model generated by LiDAR, with 0·1 ha circles and 1·0 ha squares.

SAMPLING OF BEETLES

Along the transects, we selected 171 sampling stations in 2007 (T1: 35, T2: 44, T3:42 and T4: 50), with a minimum distance between two stations of 100 m. This distance is sufficient to ensure negligible spatial autocorrelation between biodiversity samples (Fig. S3; Baker & Barmutta 2006). At each station centre, we installed one flight-interception trap of a type widely used to survey forest beetle communities (Fig. S2; Grove 2000). Each trap was installed 1 m above the ground between two trees; a 1 L sampling jar containing 3% copper vitriol solution for preservation of specimens was placed at the bottom of the trap funnel (for details, see Müller *et al.* 2008b). We also installed one 0·5-L pitfall trap under each flight-interception trap to sample ground dwellers. Flight-interception traps were set up from May to September, pitfall traps only in May, July and September 2007 and emptied monthly.

Almost complete information is available on the diet, distribution and body size of beetle species in Central Europe (Freude, Harde, & Lohse 1964–1983; Böhme 2005), which enabled us to identify almost all specimens to the species level and to obtain trait data (Table S1). As dependent variables, we used the total number of individuals as well as the number of particular feeding guilds. These are measures of beetle activity at a site (Goßner 2004). Individual feeding guilds were analysed only for guilds with at least 2000 individuals within a trap type. This criterion was met by zoophagous, phytophagous, xylophagous and mycetophagous feeding guilds in flight-interception traps, and zoophagous and phytophagous feeding guilds in pitfall traps. We $\log_{10}$ transformed the number of individuals in each trap for further analyses. We estimated (species) richness according to Gotelli & Colwell (2001) as the residuals of a linear model of $\log_{10}$ (number of species) vs. the $\log_{10}$ (individuals). We calculated the diversity in each trap using the Simpson index as a measure independent from sample size (Lande 1996) and the weighted mean body size (in mm, weighted by relative abundance). To characterize the entire assemblage, we used direct ordinations of a species-abundance matrix with square-root transformation of the number of individuals. For further justification of the choice of dependent variables, see Fig S4.

HABITAT VARIABLES – LIDAR AND GROUND SURVEYS

We used LiDAR and field measurements of abiotic and biotic data to characterize habitats. Our LiDAR data were collected in May 2007 in full waveform after foliation with an average point density of 25 m^{-2} from 400 m above-ground, resulting in a footprint size of 25 cm (for details, see Appendix S1 and Müller *et al.* 2009). One to 11 discrete points were generated per laser shot. With these data, a digital surface model (Fig. 1, inset) and a digital terrain model were calculated. The digital terrain model provided the mean altitude around a trap station. For the digital surface model of the canopy, the raw data points were sorted into a rectangular array of cells ($0{\cdot}25 \times 0{\cdot}25$ m^2) using only the point with the highest value for further calculations. Based on these data, we calculated the SD of canopy height and the maximum tree height at each sampling station. The SD is an index for vertical variation of the canopy height. This is influenced by the mixture of tall and short trees but is also influenced by tree species combination, with generally higher values in plots with conifers than in plots dominated by beech (cf. Müller *et al.* 2009). The maximum tree height provides information about the availability of at least one tall and old tree in a plot, which is a surrogate for habitat continuity (Ohlson *et al.* 1997). We also calculated the penetration rate of the laser echo (in %; number of laser echoes reaching 2 m above-ground divided by the number of laser echoes measured at 50 m above-ground). This is a proxy of microclimatic conditions (e.g. light and temperature) in the lower stratum of forests. All LiDAR variables were calculated for areas of 0·1 ha circles and 1·0 ha squares surrounding the trap stations. Preliminary analyses, however, showed that the variables were correlated across the two scales ($r > 0{\cdot}7$); therefore, we used the 1·0 ha data set for the present analyses. Altogether we derived four environmental variables from LiDAR: (i) altitude, (ii) SD of the canopy height, (iii) maximum tree height and (iv) penetration rate.

For comparison, we sampled abiotic and biotic variables during a ground survey (see also Meyer *et al.* 2001). In 2006, at each site we sampled the vegetation in the herb layer, shrub layer (up to 5 m), tree layer 1 (> 5 to 20 m) and tree layer 2 (> 20 m) within a circular area 200 m^2 around each trap station, and estimated the cover according to Londo (1976). From these raw data, we derived the following five biotic variables: (i) broadleaf tree cover, i.e. the sum of the cover of all individual broadleaf trees in all vegetation layers; (ii) coniferous tree cover, calculated similarly; (iii) number of plant species in the herb layer; (iv) the total cover of the herb layer; and (v) height of the herb layer. We did not include the number of species in the tree layers because the montane forest is dominated by only two to three species. In 2007, we also measured the following abiotic variables (details in Bässler *et al.* 2008): (i) pH value of the humus layer, (ii) ground moisture on a rank scale of 0–10, (iii) mean annual temperature derived from data loggers along the altitudinal gradient (Bässler *et al.* 2008) and (iv) dead wood surface (m^2) estimated from all pieces of dead wood within a 0·1 ha circle around each trap station, based on a ground survey of dead wood in 2006 (for details, see Table S2).

STATISTICAL METHODS

We used canonical correlation analysis to investigate the relationships between our environmental data sets (Hotelling 1936; Krzanowksi 2004). We used the adjusted R^2 and partial R^2 from variance partitioning as implemented in 'vegan' (Oksanen *et al.* 2006) to evaluate the predictive power of LiDAR, and we used the abiotic as well as biotic environmental data sets to define the characteristics of the assemblages of beetles. These analyses extract the unique and joint contribution of each data set for predicting species richness, diversity or community composition (Borcard, Legendre, & Drapeau 1992). We used bootstrapping to estimate the variability of the variance components. Furthermore, we evaluated the percentage of explained variation in the redundancy analyses by randomizing species across plots; this provides a distribution of the expected explained variation when species distributions are independent from the environment.

To study the influence of the variation of individuals on predictive power, we ordered all samples by increasing number of individuals. We calculated the R^2, considering all three environmental data sets for the ordered samples starting with 1–50, 2–51 and so on up to the maximum of 652 individuals in flight-interception traps and 260 in pitfall traps. A window size of 50 was a compromise between sample size and variation between windows.

Finally, we tested the dependent variables against the individual LiDAR variables and estimated the parameters. Predictive power and parameter estimates are two different statistical points of view: predictive power could have the same numerical value, but the signs may be opposite. We applied multiple linear regression models to analyse the relationships of assemblage characteristics and the activity of major feeding guilds with the variables derived from LiDAR (Quinn & Keough 2002). Finally, we checked the residuals of models for spatial independence (Quinn & Keough 2002). However, our models showed no spatial autocorrelation of residuals even at very

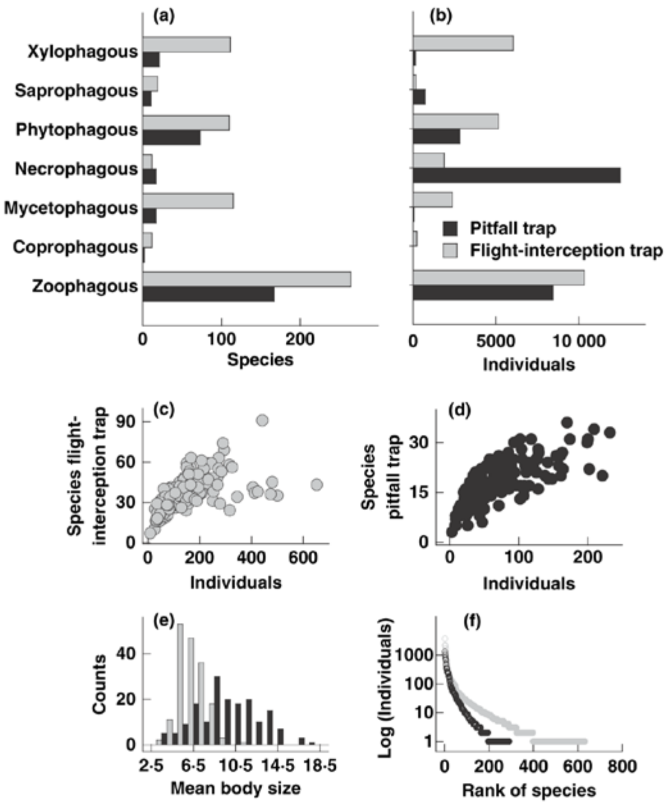

Fig. 2. Distribution of (a) species and (b) individuals across the feeding guilds in the two types of traps. Relationship between the number of sampled individuals and the number of species within (c) the flight-interception traps and (d) the pitfall traps. (e) Distribution of mean body size and (f) rank–abundance plots of the individuals sampled in the two types of traps.

small distances (see Fig. S3), and, therefore, we ignored space in the statistical analyses presented.

Results

Altogether, we collected 50 910 individuals at the 171 sampling stations, representing 782 species (Fig. 2a and b). Only three individuals of *Gabrius* sp. (Staphylinidae) and one individual of *Epurea* sp. (Nitidulidae) could not be identified to the species level and were excluded from subsequent analyses. In both types of traps, we found a curvilinear relationship between the number of individuals and the number of species within a trap (Fig. 2c and d), which became linear after log-transformation (Fig. S4). The body sizes of species showed much more variability, and the mean was higher in the pitfall traps than in the flight-interception traps (Fig. 2e). The rank–abundance relationship was steeper for the pitfall traps than for the flight-interception traps (Fig. 2f). In both trap types, zoophagous species were the most species-rich guild (Fig. 2a). Necrophagous beetles, with 19 species, were not species rich, but high numbers of individuals were present, especially in pitfall traps (Fig. 2b). However, most of these individuals belong to five species (Figs S5 and S6). As necrophagous beetles were attracted to small mammals accidentally caught in the traps, we decided to exclude this guild in our analysis (for further justification, see Figs S5 and S6). The final data set comprised 24 287 individuals in flight-interception traps and 12 216 in pitfall traps.

Canonical correlation analysis between the environmental variables showed clear correlations between the first roots (Fig. 3). Furthermore, the shared information represents a substantial part of the total variance within each data set. This holds true even after excluding the integrative variable altitude from the LiDAR data set (see Appendix S2). Apparently, all three data sets extracted similar environmental gradient patterns from the forest sites.

In general, R^2 values and partial R^2 values were lower for pitfall traps than for flight-interception traps for each of the three independent environmental data sets used to predict activity, richness and diversity of beetles (Table 1). For the assemblages sampled with the flight-interception traps, all variables explained 15–44% of the variance. LiDAR variables contributed >60% to the total predictive power (Table 1). One notable exception to the observation that the predictability of assemblage characteristics is better for samples of flight-interception traps than for pitfall traps was the weighted mean body size. It showed the opposite pattern with higher R^2 for pitfall trap (27·1%) than for flight-interception trap (14·7%). LiDAR variables contributed almost 90% to the explained variance in pitfall traps. For species composition sampled with the pitfall traps, the explained variance was almost 22% (95% confidence

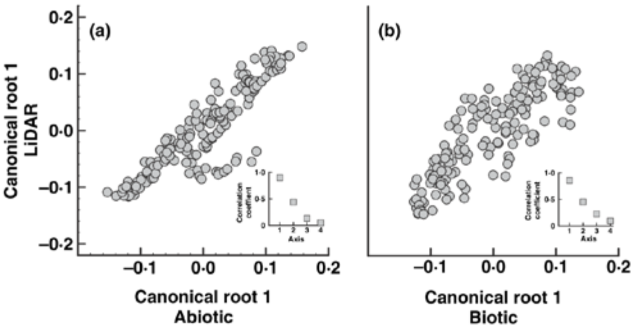

Fig. 3. Correlations between the first roots of a canonical correlation analysis extracted to maximize the correlation between the data sets of (a) abiotic and LiDAR-derived variables and (b) biotic and LiDAR-derived variables. The insets show the decrease of correlation coefficients for the first four roots of each pair of data sets.

Table 1. Partitioning of the explained variance for the three data sets of predictors: LiDAR, biotic and abiotic

	Pitfall traps					Flight-interception traps				
	Total R^2	Total 95% CI	LiDAR R^2	Biotic R^2	Abiotic R^2	Total R^2	Total 95% CI	LiDAR R^2	Biotic R^2	Abiotic R^2
Individuals	8·9	−0·3 to 19·9	17·7	−8·0	54·2	43·8	30·5–55·7	99·8	75·8	54·8
Richness	3·0	−8·7 to 10·7	99·5	99·0	5·9	26·4	13·6–39·4	89·1	30·1	48·4
Diversity (Simpson)	3·7	−6·5 to 19·8	99·0	54·3	−25·7	23·8	14·3–34·0	94·8	60·5	66·5
Body size	27·1	14·3–39·6	87·6	60·6	19·0	14·7	3·9–27·2	66·8	31·0	14·0

For the total explained variance, the 95% confidence intervals (CI) based on bootstraps are given. Note, that 'varpart'-functions frequently give negative estimates of variation. We give the adjusted R^2, which adjusts the number of explanatory terms in a model. Adjusted R^2 can be negative for any fraction, while unadjusted R^2 of testable fractions will always be non-negative (Oksanen *et al.* 2006). Such negative values indicate variability in the data large enough to produce a negative estimate, even though the true value is zero or positive. LiDAR, light detection and ranging.

band: 18·5–25·2), which is much higher than expected by chance (Fig. 4). LiDAR variables contributed 78% to the explained variance. For the assemblage collected with flight-interception traps, the explained variance was around 25% (95% confidence band: 20·4–29·8), and LiDAR contributed 82% to the explained variance (Fig. 4).

Using a window of 50 samples, we tested how sample sizes influenced predictability (Fig. 5). The broad pattern of an increase of R^2 for richness, body size and community with increasing number of individuals was similar for pitfall traps and flight-interception traps, and therefore the low predictability of certain characteristics for pitfall traps is in part due to the lower number of individuals sampled in these traps. Only the Simpson index was, as expected, independent from sample size (see Lande 1996). For traps with a mean of more than 250 individuals, R^2 for species richness and body size reached values of around 40–50%. Note also that despite the low predictability of species richness from pitfalls traps, for a given sample size, the predictability of mean body size and assemblage composition is much better for pitfall traps than for flight-interception traps.

Our linear models showed several significant responses to the LiDAR-derived parameters (Table 2). Species richness in pitfall traps increased with altitude. Individuals, species richness and diversity in flight-interception traps increased, but body size decreased with an increase in the SD. The number of individuals and body size in pitfall traps decreased, but the number of individuals in flight-interception traps increased with an increase in canopy openness. The analysis of the activity of major feeding guilds showed a general decrease of phytophagous and mycetophagous species with an increase in altitude in both trap types. The activity of almost all feeding guilds increased with the increase in the laser penetration rate (Table 2).

Discussion

Our results showed that LiDAR provides useful variables with which to model diversity–habitat relationships with astonishingly few parameters. The main advantage of LiDAR and related methods is that they allow sampling of habitat characteristics with a high resolution at large spatial scales, providing statistically well-behaved data (see skewness and kurtosis in Table S2). Furthermore, remote-sensing techniques such as LiDAR are cost-effective. During our study, we invested *c.* 15 € ha^{-1} for the LiDAR data, which included the flight and sampling from the helicopter (9 € ha^{-1}) and processing of the basic data (6 € ha^{-1}). The costs of collecting the ground-based habitat parameters were *c.* 100 € ha^{-1}, while sampling, sorting and determination of the beetles cost another 260 € per

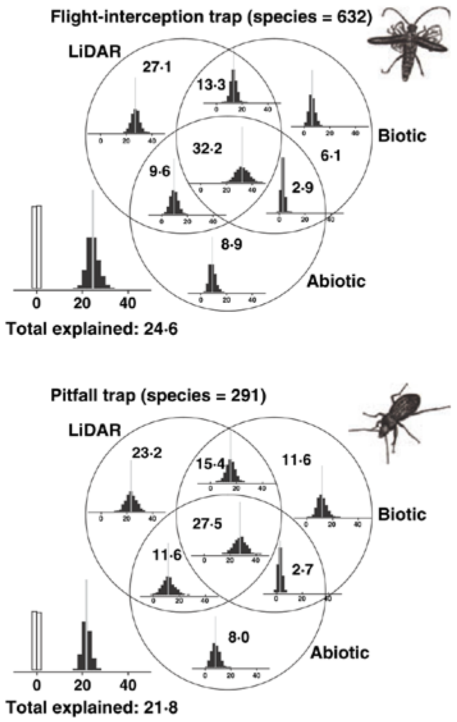

Fig. 4. Variance partitioning of explained variance using three different environmental data sets: variables derived from LiDAR data, biotic and abiotic variables derived from ground surveys, and data from beetle assemblages captured with 171 pitfall traps and 171 flight-interception traps after excluding necrophagous species. Each histogram shows the distribution and the mean (bar) of explained variance components after 10 000 bootstraps. The open histogram shows the result of random distribution of species among plots.

plot (equipment 40 € ha^{-1}, emptying 60 € ha^{-1}, sorting in laboratory 60 € ha^{-1} and identification costs 100 € ha^{-1}). Furthermore, the costs per ha for LiDAR decreases with the area covered during a campaign because of certain fixed costs. Therefore, the advantage of LiDAR compared with ground surveys increases with the extent of a study.

The high costs of collecting hyperdiverse taxa data limit the number of traps or plots that can be sampled during a survey. Published studies in tropical, temperate or boreal forests used between 80 and 240 flight-interception traps and up to 480 pitfall traps (Grove 2002; Martikainen & Kouki 2003; Müller, Bußler, & Kneib 2008a). Sometimes 5–20 traps were set up at one sampling location. Assuming that 240 flight-interception traps are the maximum number of traps that can be handled, a survey across the Bavarian Forest National Park (24 000 ha) would entail 1 trap per 100 ha. This grain of sampling is much too coarse to map relevant spatial patterns of species richness or community composition relevant for the management of the park. Planning is usually carried out at scales of 5–50 ha, while actual management activities, such as felling operations, occur at scales between 0·3 and 1·0 ha (Meyer *et al.* 2001; Burschel & Huss 2003). Clearly, surveys of hyperdiverse insect taxa are too expensive for mapping with the grain and extent needed for management planning. Remote-sensing techniques such as LiDAR provide the means to at least estimate activity, richness or composition of assemblages with the appropriate grain and extent. Nevertheless, ground surveys of biodiversity provide the baseline to derive the parameters needed to model assemblages and their characteristics. Therefore, remote sensing is not an alternative to field surveys, but is rather a valuable technique that allows point data to be transferred to a broader spatial scale.

As LiDAR variables were generated according to the technical possibilities, these variables have no direct and obvious meaning for beetle assemblages. However, phenomenological models are of enormous heuristic value, particularly at larger spatial scales (Vierling *et al.* 2008). Available remote-sensing methods and in particular LiDAR offer a broad array of techniques (Lefsky *et al.* 2002; Turner *et al.* 2003; Bradbury *et al.* 2005; Hinsley *et al.* 2006; Goetz *et al.* 2007). To discuss the value of LiDAR-derived habitat variables for predicting beetle assemblages in more detail, we need to evaluate three important issues: (i) the sampling methods, (ii) the predictive power of our models and (iii) the findings in the context of autecology.

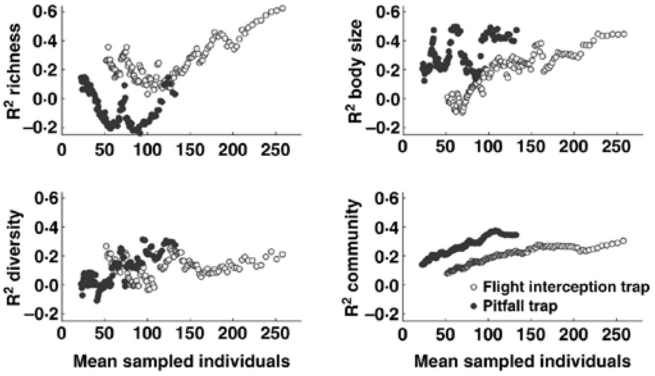

Fig. 5. Adjusted R^2 values for sliding windows of 50 traps moved across the samples sorted from small to large sample sizes and plotted against the mean number of individuals in the 50 traps. R^2 was calculated for samples 1–50, 2–51 and so on. Note that the calculation of the adjusted R^2 by variance partitioning as implemented in 'vegan' can result in negative values. Such negative values indicate variability in the data large enough to produce a negative estimate, even though the true value is zero or positive.

Table 2. Results of multiple linear models using different characteristics for beetle assemblages and diversity

		Altitude		SD of vegetation height		Maximum tree height		Penetration ratio	
	Trap	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Individuals	Flight trap			0·21 ± 0·07	0·005	−0·28 ± 0·10	0·010	0·38 ± 0·06	<0·001
	Pitfall trap	0·026 ± 0·09	0·008						
Richness	Flight trap	−0·08 ± 0·03	0·002	0·12 ± 0·03	<0·001				
	Pitfall trap			0·10 ± 0·03	0·006				
Diversity (Simpson)	Flight trap	−0·14 ± 0·04	<0·001	0·16 ± 0·04	0·001				
	Pitfall trap	0·13 ± 0·04	0·011						
Body size	Flight trap	0·47 ± 0·15	0·003	−0·60 ± 0·18	<0·001	0·68 ± 0·25	0·008		
	Pitfall trap	0·91 ± 0·33	0·008	−0·81 ± 0·39	0·036	1·78 ± 0·55	0·002	−0·93 ± 0·35	0·009
Individuals zoophagous	Flight trap			0·32 ± 0·08	<0·001	−0·30 ± 0·11	0·01	0·30 ± 0·07	<0·001
	Pitfall trap								
Individuals phytophagous	Flight trap							0·37 ± 0·11	<0·001
	Pitfall trap	−0·21 ± 0·09	0·026					0·26 ± 0·10	0·019
Individuals mycetophagous	Flight trap	−0·65 ± 0·09	<0·001	0·38 ± 0·10	<0·001	−0·51 ± 0·14	<0·001		
Individuals xylophagous	Flight trap							0·35 ± 0·11	<0·001

To allow for direct comparisons of the estimators, the predictors were standardized to a mean of 0 and a variance of 1. For the estimated values, the SE are given.

The two trap systems used in our study are standard methods for sampling beetle assemblages (Baker & Barmutta 2006; Grove 2000), but in most studies, more traps were used per site (Martikainen, Kouki, & Heikkala 2006). Resource constraints forced us to use only one trap per site, and the sample size of pitfall traps was often too low for the analysis of certain community characteristics (Fig. 5). We therefore suggest that for calibrating LiDAR variables for monitoring insect communities in temperate forests mean sample sizes of 250 individuals should be used.

Rather unexpectedly, the predictability of mean body size and community composition was not influenced by sample size (individuals) to any degree. Furthermore, in these two cases, the assemblages sampled with pitfall traps had a better predictability than the assemblages sampled with flight-interception traps. These findings have two implications. First, for applied investigations, body size and ordinations may provide reliable patterns of assemblages even with small samples sizes (Basset *et al.* 2008). Secondly, characteristics of assemblages sampled with pitfall traps are more tightly correlated to environmental variables and are therefore more structured than samples of flight-interception traps. The predictability of community characteristics such as richness depends also on 'equilibrium' conditions. If the assemblages of beetles on the ground are not in equilibrium with the local conditions as well as with the regional pool, actual environmental conditions may have nothing to do with actual species composition.

The predictive power of most of our models varied between 10 and 40%. With mean sample sizes of 250 individuals, the predictive power may be almost 60% (Fig. 5). Other studies using R^2 to quantify the predictability of certain characteristics of insect assemblages have found similar values. For ants and beetles in Australian forests, the predictive power was between 30% and 50% for richness and abundance (Lassau *et al.* 2005a; Lassau & Hochuli 2008; Lassau *et al.* 2005b). Note also that the percentage of explained variation dropped to zero when we randomized species across plots (Fig. 4). Despite the sometimes low sample size, sufficient variation in the composition of assemblages was explained by our environmental variables.

Our findings can be placed in the context of autecology using the extensive literature. Based on numerous studies of disturbances in forests, we expected a decrease in body size with the laser penetration ratio, and larger species in closed forests (Peters 1983; Nee & Lawton 1996; Siemann, Tilman, & Haarstad 1996; Weller & Ganzhorn 2004). In temperate and boreal biomes, several xylophagous species need open stands with sunlight and dead wood for feeding and mating (Bouget & Duelli 2004). Therefore, we expected an increase in activity of xylophagous species with an increase of the laser penetration ratio. Last but not least, we expected the activity of mycetophagous and phytophagous species to decrease with altitude because of a reduced availability of hosts. These expectations matched the multiple linear regression models (Table 2), which shows that LiDAR variables are not only suitable for phenomenological models, but can also provide ecological information.

Conclusion

Insects and especially beetles with a body size of < 2 cm act on small spatial scales in most cases, and rugosity may be important for foraging (Kaspari & Weiser 1999). Nevertheless, the canopy structure has important influences on certain habitat characteristics. Therefore, characteristics of species assemblages in forests depend on the structure of the canopy. The high proportion of explained variance by LiDAR-derived variables compared with ground measurements shows the high potential of data from remote sensing for modelling

biodiversity in forests at broad spatial scales, with costs around 5–10% of ground survey costs (Lefsky *et al.* 2002). However, reliable biodiversity data are needed to calibrate and validate the statistical models. After such a modelling exercise, LiDAR provides simple but ecologically meaningful variables for a rapid extrapolation of activity, richness and composition of assemblages across large areas. This enables conservationists to evaluate habitat over large areas and to define diversity hotspots as well as to monitor environmental changes for regional and even countrywide management plans.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1. Field situations along the transect to illustrate the rough terrain.

Fig. S2. Construction of the two trap types used.

Fig. S3. Spline correlograms with average autocorrelation coefficient.

Fig. S4. Correlation of different diversity measurements.

Fig. S5. Necrophagous individuals.

Fig. S6. Abundance of necrophagous species trapped.

Fig. S7. Canonical correlations without altitude.

Table S1. List of all species trapped

Table S2. Detailed results of canonical correlation

Appendix S1. Description of LiDAR variables

Appendix S2. Detailed results of canonical correlation

Artikel 7: Molluscs and climate warming in a low mountain range national park.

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MOLLUSCS AND CLIMATE WARMING IN A LOW MOUNTAIN RANGE NATIONAL PARK

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ABSTRACT

Species restricted to the higher altitudes of low mountain ranges in Central Europe are among the species threatened. To quantify the influence of climate warming, we analysed the altitudinal distribution of mollusc species and modelled the occurrence and distribution of a high montane species under two scenarios of climate warming. Our analysis is based on samples of 3,437 individuals and 46 species collected at 111 localities. Number of individuals and species decreased with altitude. The slope of this decrease changed between 1,100 and 1,200 m a.s.l., which is the ecotone between mixed montane beech-fir-spruce and high-altitude spruce forests. In contrast to the majority of species and the number of species, the occurrence of *Semilimax kotulae* (Westerlund 1883), a Central European endemic, increased with altitude. Again, we found a change in the slope between 1,100 and 1,200 m a.s.l. Using geostatistical models of local temperature as well as spatial GLMs with Poisson and Gaussian errors, we modelled altitudinal distribution of diversity and species under consideration of environmental variables. Especially habitat age was an important predictor for the abundance of many species. For the high montane species *S. kotulae*, our model predicts a decrease in occurrence and abundance with global warming. Although global warming will lead to an overall increase in number of species, species occurring only at higher elevations, such as the *S. kotulae*, will probably become extinct within the study area.

Key words: altitudinal gradient, Bavarian Forest National Park, extinction risk, habitat tradition, *Semilimax kotulae*, BayesX.

INTRODUCTION

Global warming will lead to a latitudinal and altitudinal reorganization of distributional ranges (Parmesan et al., 1999; Parmesan & Yohe, 2003; Root et al., 2003). In extreme, these reorganizations may lead to a regional or even global extinction of species (Bakkenes et al., 2002; Berry et al., 2002; Thomas et al., 2004; IPCC, 2007a, b), and therefore the understanding of the implications of global warming is among the most important tasks for ecologists and conservationists (Sutherland et al., 2006). Despite considerable advances in our understanding of the relations between climate and species distribution at a global scale (Gaston & Blackburn, 2000; Gillooly & Allen, 2007), our knowledge of the local and regional effects of global warming is limited (Grabherr et al., 1994; Kappelle et al., 1999; Travis, 2002; Schrag et al., 2007).

High mountains show long altitudinal gradients that facilitate investigations on the upwards shifts of altitudinal distributions by climate warming (e.g., Kazakis et al., 2007; Pauli et al., 2007). However, the low mountain ranges of Central Europe, with altitudes less than 1,500 m, comprise in total the largest area of all mountains in Europe (CIPRA, 2007). Furthermore, they harbour a number of species with restricted distribution, some relicts from the ice ages (Limondin, 1992; Varga, 1995). Species restricted to the higher zones of these mountains seem to be vulnerable to local and regional extinctions by climate warming for two reasons (Parmesan, 2006): First, the low maximum altitude restricts the possibility to shift ranges upwards to escape the increase of tem-

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perature (Thomas et al., 2004; Thuiller, 2007). Second, the available area decreases with altitude. Any upwards shift leads to a decrease of habitats, to an increase in fragmentation and therefore to a decrease in population size with considerable risk of extinction by demographic stochasticity.

Community composition, species richness as well as location and size of distributional ranges of molluscs depend in particular on climate and soil (Sternberg, 2000; Tattersfield et al., 2001; Aubry et al., 2005; Kappes, 2005; Müller et al., 2005a). This close correlation of mollusc distribution and habitats is in part due to their low dispersal propensity (Waldén, 1981), and therefore molluscs should react very sensitive to global warming. Several species of molluscs are restricted to the upper zone of Central European low mountain ranges (Uminski, 1983). Most of these species are adapted to cold climates, and warming may force a shift of altitudinal distribution with the associated risk of extinction. Beyond this pessimistic scenario, the extinction of local populations may have negative genetic consequences for surviving species. The low dispersal propensity of molluscs leads to considerable genetic variation between populations (Marten et al., 2006). Similar to plants (Matthies et al., 2004), some of this variation may be adaptive (Calosi et al., 2008). The extinction of local populations will probably lead to a reduction in genetic diversity.

Several national parks were established to protect the unique fauna and flora restricted to higher altitudes of the low mountain ranges. The oldest of these national parks in Germany is the Bavarian Forest National Park. Climate warming, however, compromises the protection of high montane assemblages, a major conservation objectives in this and similar parks, of species. Even though the park authorities are unable to influence climate change, it is essential to understand the influence of global warming on the species and habitats for two reasons: Firstly, only if one has some knowledge about species turn-over due to global warming, one is able to detect additional threats. Secondly, the maintenance of habitat diversity is a possibility to decrease the extinction risk due to climate change. Therefore, it is necessary to understand the key resources of the species under consideration to mitigate the effects of climate change. Our study has therefore three main aims:

(1) To assess the influence of altitude and associated environmental variables on number of species and abundance of single species of molluscs in the Bavarian Forest National Park.
(2) To test the influence of site-specific habitat factors on diversity and occurrence of molluscs.
(3) To quantify changes in the extinction risk of high montane species with global warming.

METHODS

Study Area and Study Sites

The Bavarian Forest National Park is located in the southeastern corner of Bavaria, at the border to the Czech Republic (Fig. 1). The park covers approximately 24,000 ha at elevations from 650 m to 1,430 m a.s.l. Total annual precipitation is between 1,200 mm and 1,800 mm depending on altitude. Mean annual temperature (1970–2003) varies between 3.8°C and 5.8°C (Bässler, 2004). Geologically, the Bavarian Forest is the southwestern part of the Bohemian Massif, consisting of granite and gneiss and therefore acidic soils (Table 1). Depending on local conditions, above 1,150 m a.s.l. the vegetation is dominated by almost pure spruce *Picea abies* stands, with only a low proportion of beech, *Fagus sylvatica*, and mountain ash, *Sorbus aucuparia* (high montane forest). Below this, stands are dominated by a mixed montane forest of spruce, beech and fir, *Abies alba* (Walentowski et al., 2004). Due to infestation by bark beetles, mainly *Ips typographus*, large areas of forest have died back, and the resulting structure varies widely from stands with an open canopy, dominated by dead wood, to dense, closed stands (Müller et al., 2008).

We sampled molluscs as part of a more comprehensive program to characterise spatial variation of biodiversity. To get representative samples, we established four transects across the altitudinal range of the park. Along these transects we located a total of 293 plots with a distance of 100 m between adjacent plots. For the sampling of molluscs we randomly selected 111 plots that represented the major forest management types across the altitudinal gradient (Fig. 1). It is important to note that plots were not selected in respect to density or species richness of molluscs. Management types ranged from stands where trees infested by bark beetles are still removed, through stands where management by the forest authorities stopped with the establishment of the national park in 1970, to old-growth forest with veteran trees.

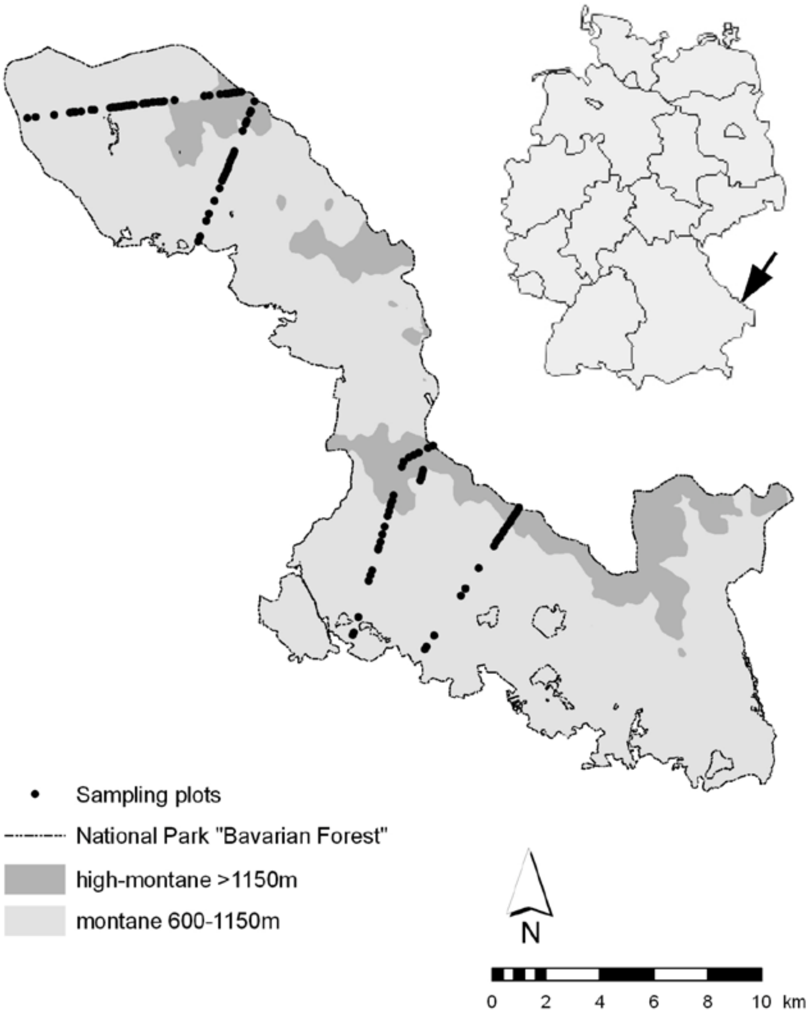

FIG. 1. Study area and location of the 111 plots used to sample molluscs along four altitudinal transects within the Bavarian Forest National Park.

Sampling Methods

Sampling during only one period of the year is not appropriate for all species of molluscs and, for example, early autumn appears to be the best time to sample montane molluscs (Uminski, 1975). Therefore, we used two methods. Firstly, installation of one pitfall traps for three weeks in July 2006 in the centre of each plot. Secondly, hand collection for 30 minutes of all individuals of live snails and slugs within a 0.1 ha area around the centre of each plot in September 2006. Sampling included a few small ephemeral water bodies within forest stands, where we found two *Pisidium* species. When it was not possible to identify an individual in the field, it was stored in 80% ethanol and identified in the laboratory using morphological characters (Wiktor, 1973; Kerney et al., 1983; Jungbluth et al., 1992; Wiktor, 2000). For

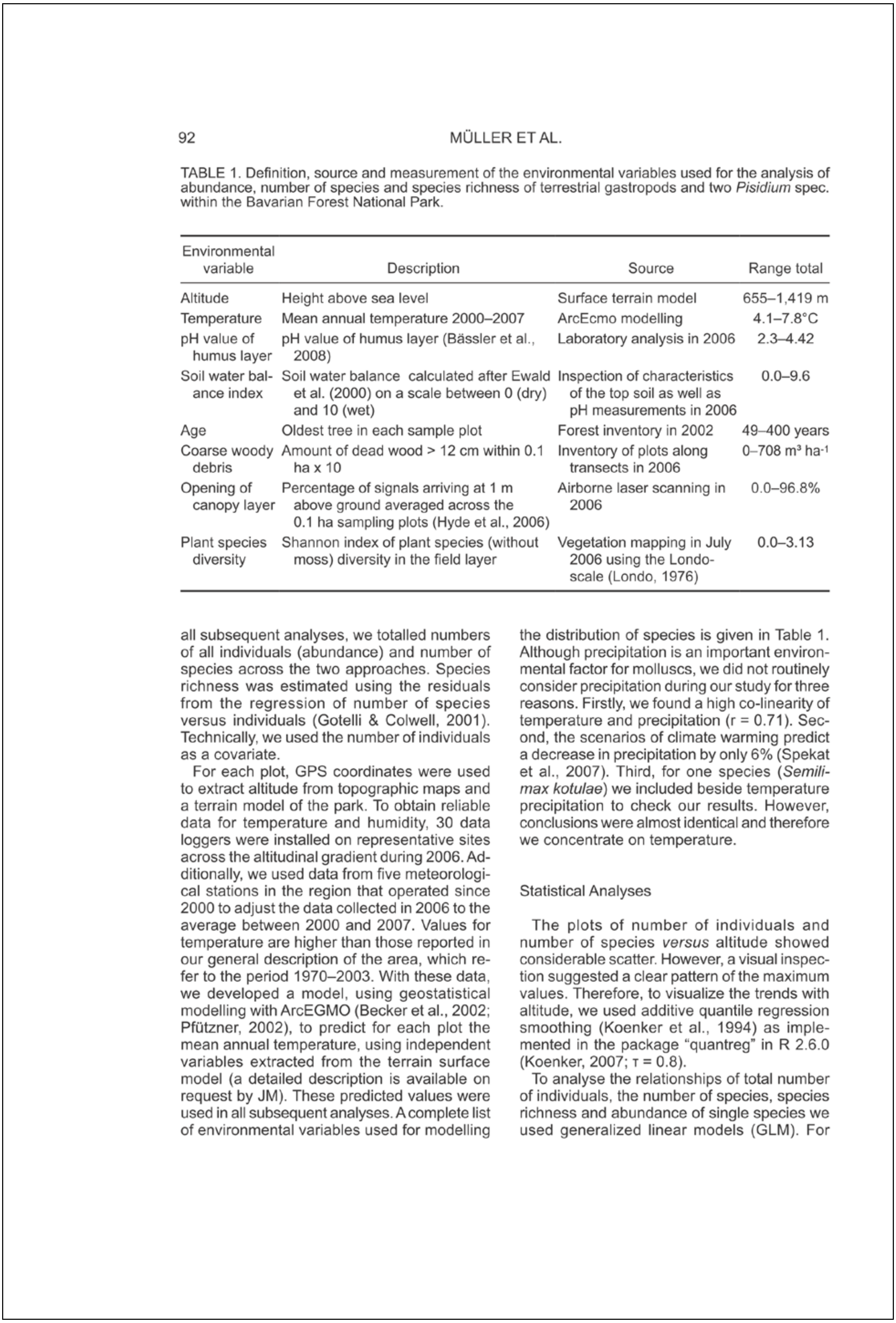

TABLE 1. Definition, source and measurement of the environmental variables used for the analysis of abundance, number of species and species richness of terrestrial gastropods and two *Pisidium* spec. within the Bavarian Forest National Park.

Environmental variable	Description	Source	Range total
Altitude	Height above sea level	Surface terrain model	655–1,419 m
Temperature	Mean annual temperature 2000–2007	ArcEcmo modelling	4.1–7.8°C
pH value of humus layer	pH value of humus layer (Bässler et al., 2008)	Laboratory analysis in 2006	2.3–4.42
Soil water balance index	Soil water balance calculated after Ewald et al. (2000) on a scale between 0 (dry) and 10 (wet)	Inspection of characteristics of the top soil as well as pH measurements in 2006	0.0–9.6
Age	Oldest tree in each sample plot	Forest inventory in 2002	49–400 years
Coarse woody debris	Amount of dead wood > 12 cm within 0.1 ha x 10	Inventory of plots along transects in 2006	0–708 m³ ha-1
Opening of canopy layer	Percentage of signals arriving at 1 m above ground averaged across the 0.1 ha sampling plots (Hyde et al., 2006)	Airborne laser scanning in 2006	0.0–96.8%
Plant species diversity	Shannon index of plant species (without moss) diversity in the field layer	Vegetation mapping in July 2006 using the Londo-scale (Londo, 1976)	0.0–3.13

all subsequent analyses, we totalled numbers of all individuals (abundance) and number of species across the two approaches. Species richness was estimated using the residuals from the regression of number of species versus individuals (Gotelli & Colwell, 2001). Technically, we used the number of individuals as a covariate.

For each plot, GPS coordinates were used to extract altitude from topographic maps and a terrain model of the park. To obtain reliable data for temperature and humidity, 30 data loggers were installed on representative sites across the altitudinal gradient during 2006. Additionally, we used data from five meteorological stations in the region that operated since 2000 to adjust the data collected in 2006 to the average between 2000 and 2007. Values for temperature are higher than those reported in our general description of the area, which refer to the period 1970–2003. With these data, we developed a model, using geostatistical modelling with ArcEGMO (Becker et al., 2002; Pfützner, 2002), to predict for each plot the mean annual temperature, using independent variables extracted from the terrain surface model (a detailed description is available on request by JM). These predicted values were used in all subsequent analyses. A complete list of environmental variables used for modelling the distribution of species is given in Table 1. Although precipitation is an important environmental factor for molluscs, we did not routinely consider precipitation during our study for three reasons. Firstly, we found a high co-linearity of temperature and precipitation (r = 0.71). Second, the scenarios of climate warming predict a decrease in precipitation by only 6% (Spekat et al., 2007). Third, for one species (*Semilimax kotulae*) we included beside temperature precipitation to check our results. However, conclusions were almost identical and therefore we concentrate on temperature.

Statistical Analyses

The plots of number of individuals and number of species *versus* altitude showed considerable scatter. However, a visual inspection suggested a clear pattern of the maximum values. Therefore, to visualize the trends with altitude, we used additive quantile regression smoothing (Koenker et al., 1994) as implemented in the package "quantreg" in R 2.6.0 (Koenker, 2007; $\tau = 0.8$).

To analyse the relationships of total number of individuals, the number of species, species richness and abundance of single species we used generalized linear models (GLM). For

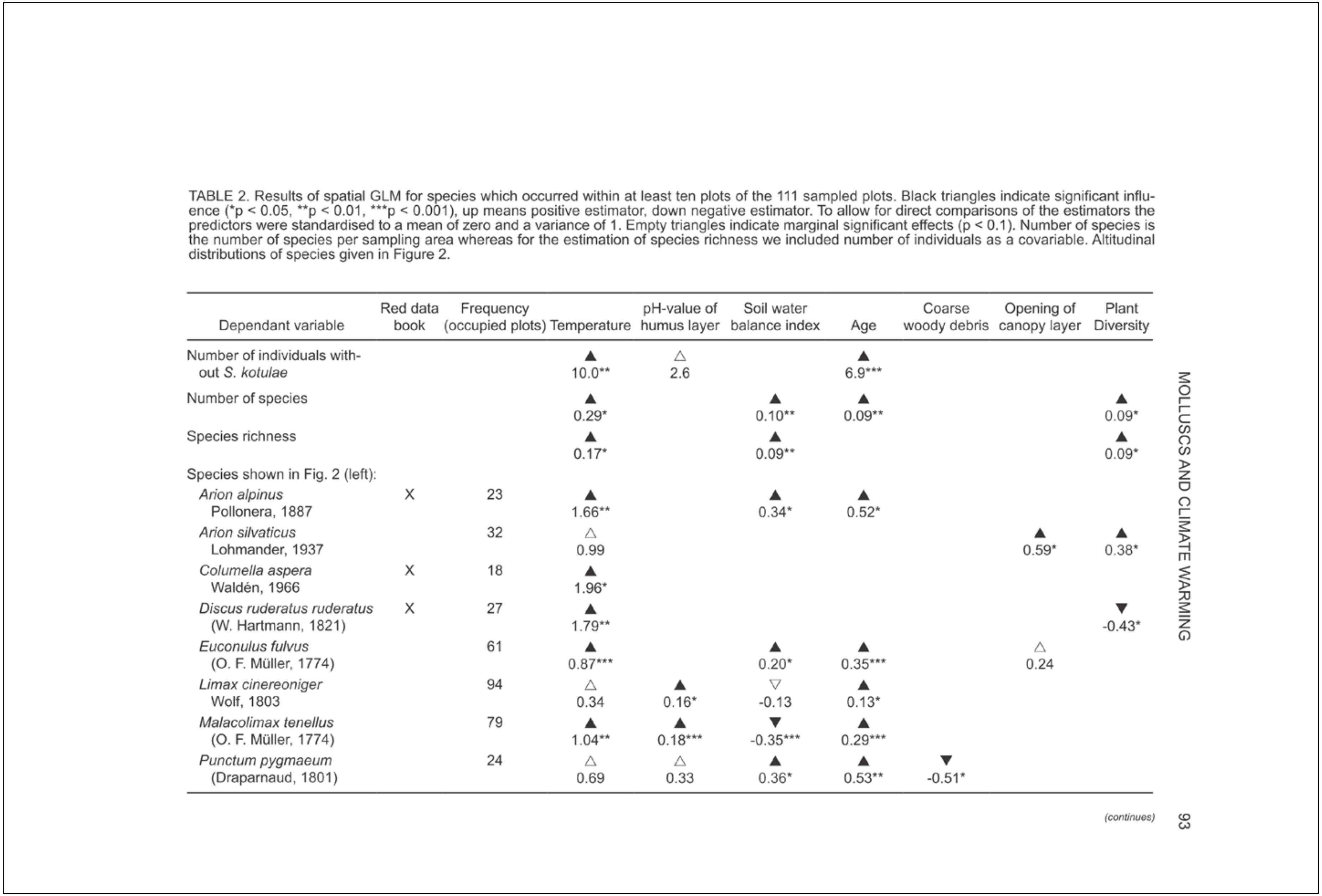

TABLE 2. Results of spatial GLM for species which occurred within at least ten plots of the 111 sampled plots. Black triangles indicate significant influence (*p < 0.05, **p < 0.01, ***p < 0.001), up means positive estimator, down negative estimator. To allow for direct comparisons of the estimators the predictors were standardised to a mean of zero and a variance of 1. Empty triangles indicate marginal significant effects (p < 0.1). Number of species is the number of species per sampling area whereas for the estimation of species richness we included number of individuals as a covariable. Altitudinal distributions of species given in Figure 2.

Dependant variable	Red data book	Frequency (occupied plots)	Temperature	pH-value of humus layer	Soil water balance index	Age	Coarse woody debris	Opening of canopy layer	Plant Diversity
Number of individuals without *S. kotulae*			▲ 10.0**	△ 2.6		▲ 6.9***			
Number of species			▲ 0.29*		▲ 0.10**	▲ 0.09**			▲ 0.09*
Species richness			▲ 0.17*		▲ 0.09**				▲ 0.09*
Species shown in Fig. 2 (left):									
Arion alpinus Pollonera, 1887	X	23	▲ 1.66**		▲ 0.34*	▲ 0.52*			
Arion silvaticus Lohmander, 1937		32	△ 0.99					▲ 0.59*	▲ 0.38*
Columella aspera Waldén, 1966	X	18	▲ 1.96*						
Discus ruderatus ruderatus (W. Hartmann, 1821)	X	27	▲ 1.79**						▼ -0.43*
Euconulus fulvus (O. F. Müller, 1774)		61	▲ 0.87***		▲ 0.20*	▲ 0.35***		△ 0.24	
Limax cinereoniger Wolf, 1803		94	△ 0.34	▲ 0.16*	▽ -0.13	▲ 0.13*			
Malacolimax tenellus (O. F. Müller, 1774)		79	▲ 1.04**	▲ 0.18***	▼ -0.35***	▲ 0.29***			
Punctum pygmaeum (Draparnaud, 1801)		24	△ 0.69	△ 0.33	▲ 0.36*	▲ 0.53**	▼ -0.51*		

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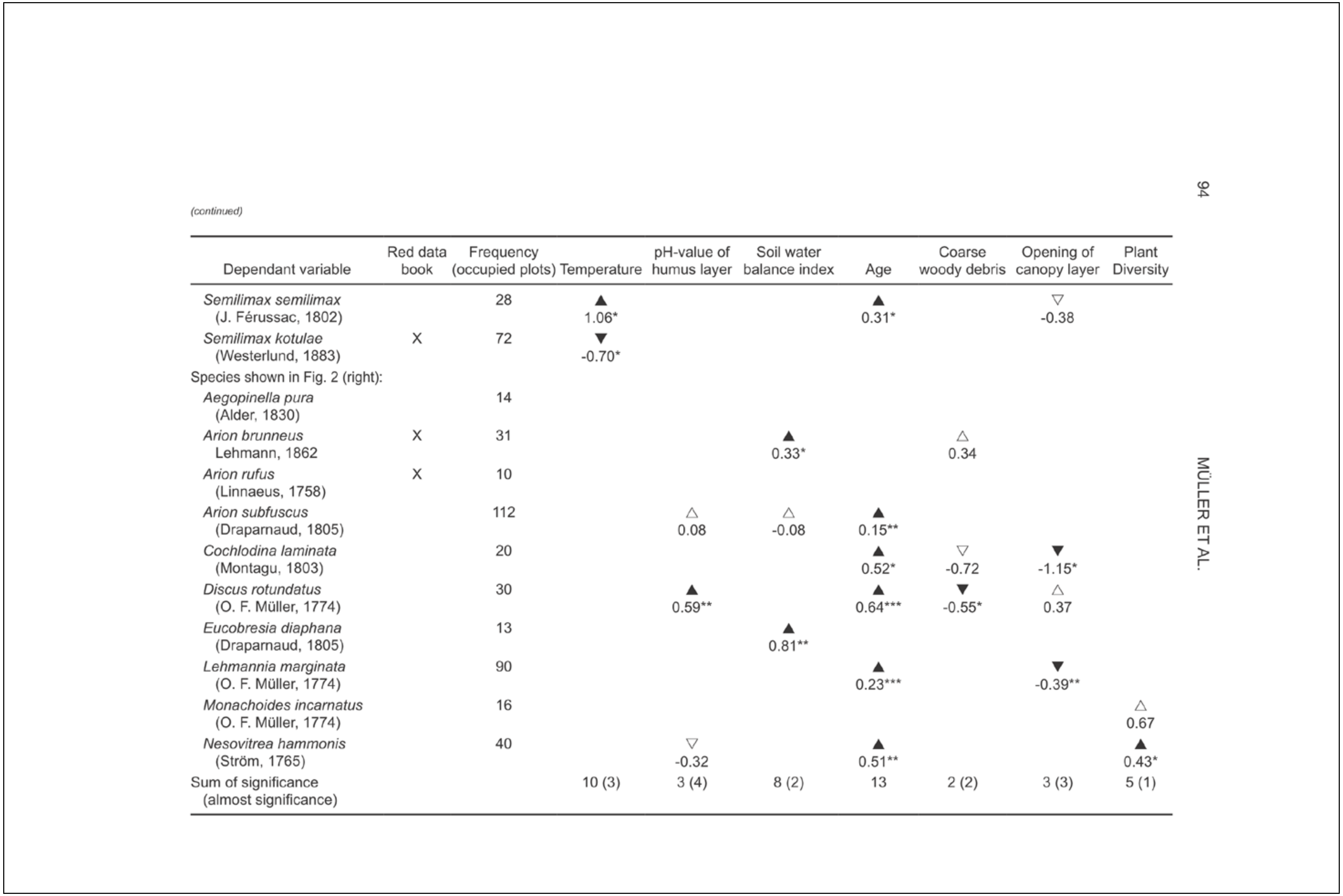
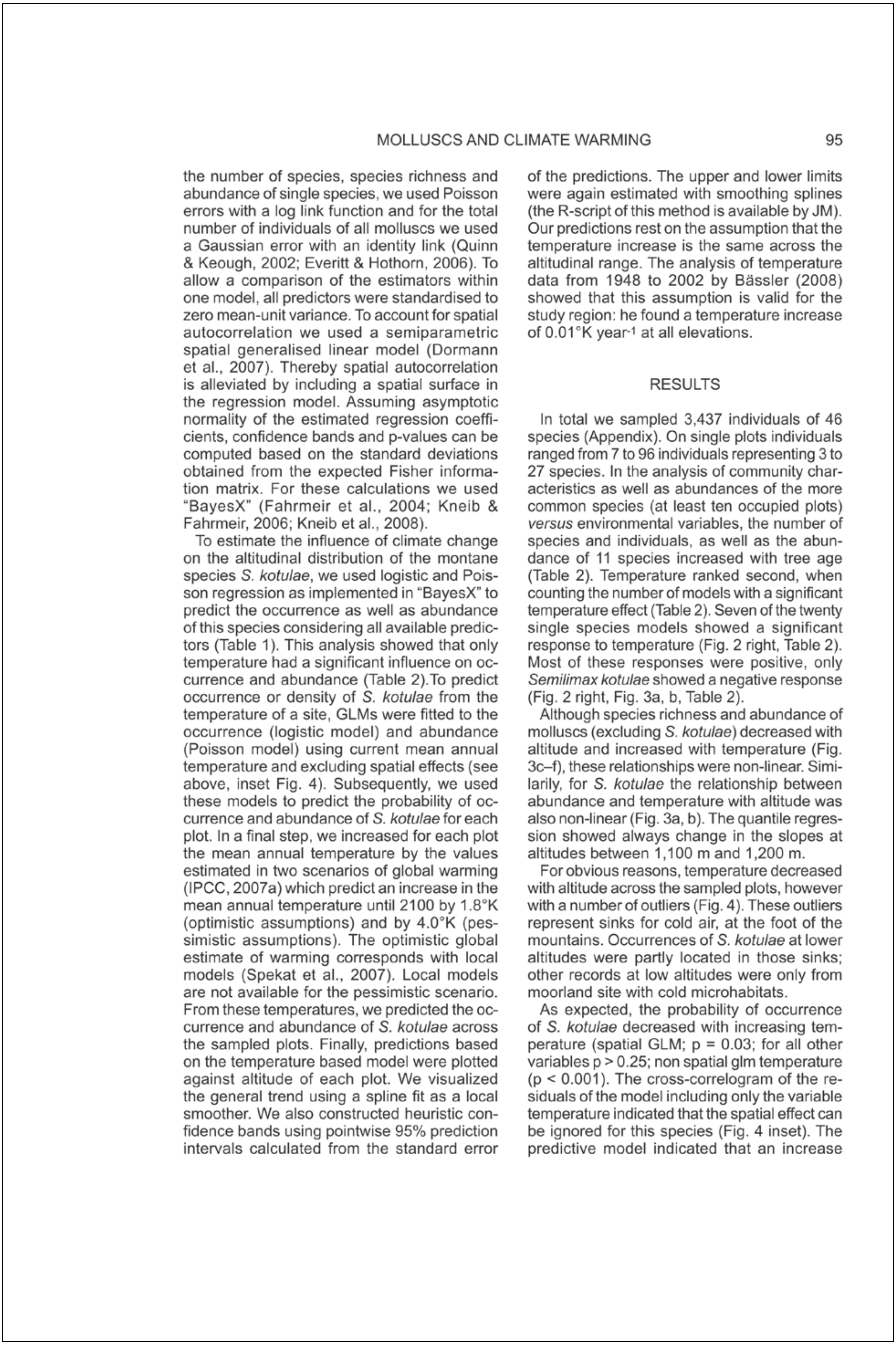


(continued)

Dependant variable	Red data book	Frequency (occupied plots)	Temperature	pH-value of humus layer	Soil water balance index	Age	Coarse woody debris	Opening of canopy layer	Plant Diversity
Semilimax semilimax (J. Férussac, 1802)		28	▲ 1.06*			▲ 0.31*		▽ -0.38	
Semilimax kotulae (Westerlund, 1883)	X	72	▼ -0.70*						
Species shown in Fig. 2 (right):									
Aegopinella pura (Alder, 1830)		14							
Arion brunneus Lehmann, 1862	X	31			▲ 0.33*		△ 0.34		
Arion rufus (Linnaeus, 1758)	X	10							
Arion subfuscus (Draparnaud, 1805)		112		△ 0.08	△ -0.08	▲ 0.15**			
Cochlodina laminata (Montagu, 1803)		20				▲ 0.52*	▽ -0.72	▼ -1.15*	
Discus rotundatus (O. F. Müller, 1774)		30		▲ 0.59**		▲ 0.64***	▼ -0.55*	△ 0.37	
Eucobresia diaphana (Draparnaud, 1805)		13			▲ 0.81**				
Lehmannia marginata (O. F. Müller, 1774)		90				▲ 0.23***		▼ -0.39**	
Monachoides incarnatus (O. F. Müller, 1774)		16							△ 0.67
Nesovitrea hammonis (Ström, 1765)		40		▽ -0.32		▲ 0.51**			▲ 0.43*
Sum of significance (almost significance)			10 (3)	3 (4)	8 (2)	13	2 (2)	3 (3)	5 (1)



the number of species, species richness and abundance of single species, we used Poisson errors with a log link function and for the total number of individuals of all molluscs we used a Gaussian error with an identity link (Quinn & Keough, 2002; Everitt & Hothorn, 2006). To allow a comparison of the estimators within one model, all predictors were standardised to zero mean-unit variance. To account for spatial autocorrelation we used a semiparametric spatial generalised linear model (Dormann et al., 2007). Thereby spatial autocorrelation is alleviated by including a spatial surface in the regression model. Assuming asymptotic normality of the estimated regression coefficients, confidence bands and p-values can be computed based on the standard deviations obtained from the expected Fisher information matrix. For these calculations we used "BayesX" (Fahrmeir et al., 2004; Kneib & Fahrmeir, 2006; Kneib et al., 2008).

To estimate the influence of climate change on the altitudinal distribution of the montane species *S. kotulae*, we used logistic and Poisson regression as implemented in "BayesX" to predict the occurrence as well as abundance of this species considering all available predictors (Table 1). This analysis showed that only temperature had a significant influence on occurrence and abundance (Table 2).To predict occurrence or density of *S. kotulae* from the temperature of a site, GLMs were fitted to the occurrence (logistic model) and abundance (Poisson model) using current mean annual temperature and excluding spatial effects (see above, inset Fig. 4). Subsequently, we used these models to predict the probability of occurrence and abundance of *S. kotulae* for each plot. In a final step, we increased for each plot the mean annual temperature by the values estimated in two scenarios of global warming (IPCC, 2007a) which predict an increase in the mean annual temperature until 2100 by 1.8°K (optimistic assumptions) and by 4.0°K (pessimistic assumptions). The optimistic global estimate of warming corresponds with local models (Spekat et al., 2007). Local models are not available for the pessimistic scenario. From these temperatures, we predicted the occurrence and abundance of *S. kotulae* across the sampled plots. Finally, predictions based on the temperature based model were plotted against altitude of each plot. We visualized the general trend using a spline fit as a local smoother. We also constructed heuristic confidence bands using pointwise 95% prediction intervals calculated from the standard error of the predictions. The upper and lower limits were again estimated with smoothing splines (the R-script of this method is available by JM). Our predictions rest on the assumption that the temperature increase is the same across the altitudinal range. The analysis of temperature data from 1948 to 2002 by Bässler (2008) showed that this assumption is valid for the study region: he found a temperature increase of 0.01°K $year^{-1}$ at all elevations.

RESULTS

In total we sampled 3,437 individuals of 46 species (Appendix). On single plots individuals ranged from 7 to 96 individuals representing 3 to 27 species. In the analysis of community characteristics as well as abundances of the more common species (at least ten occupied plots) *versus* environmental variables, the number of species and individuals, as well as the abundance of 11 species increased with tree age (Table 2). Temperature ranked second, when counting the number of models with a significant temperature effect (Table 2). Seven of the twenty single species models showed a significant response to temperature (Fig. 2 right, Table 2). Most of these responses were positive, only *Semilimax kotulae* showed a negative response (Fig. 2 right, Fig. 3a, b, Table 2).

Although species richness and abundance of molluscs (excluding *S. kotulae*) decreased with altitude and increased with temperature (Fig. 3c–f), these relationships were non-linear. Similarly, for *S. kotulae* the relationship between abundance and temperature with altitude was also non-linear (Fig. 3a, b). The quantile regression showed always change in the slopes at altitudes between 1,100 m and 1,200 m.

For obvious reasons, temperature decreased with altitude across the sampled plots, however with a number of outliers (Fig. 4). These outliers represent sinks for cold air, at the foot of the mountains. Occurrences of *S. kotulae* at lower altitudes were partly located in those sinks; other records at low altitudes were only from moorland site with cold microhabitats.

As expected, the probability of occurrence of *S. kotulae* decreased with increasing temperature (spatial GLM; p = 0.03; for all other variables p > 0.25; non spatial glm temperature (p < 0.001). The cross-correlogram of the residuals of the model including only the variable temperature indicated that the spatial effect can be ignored for this species (Fig. 4 inset). The predictive model indicated that an increase

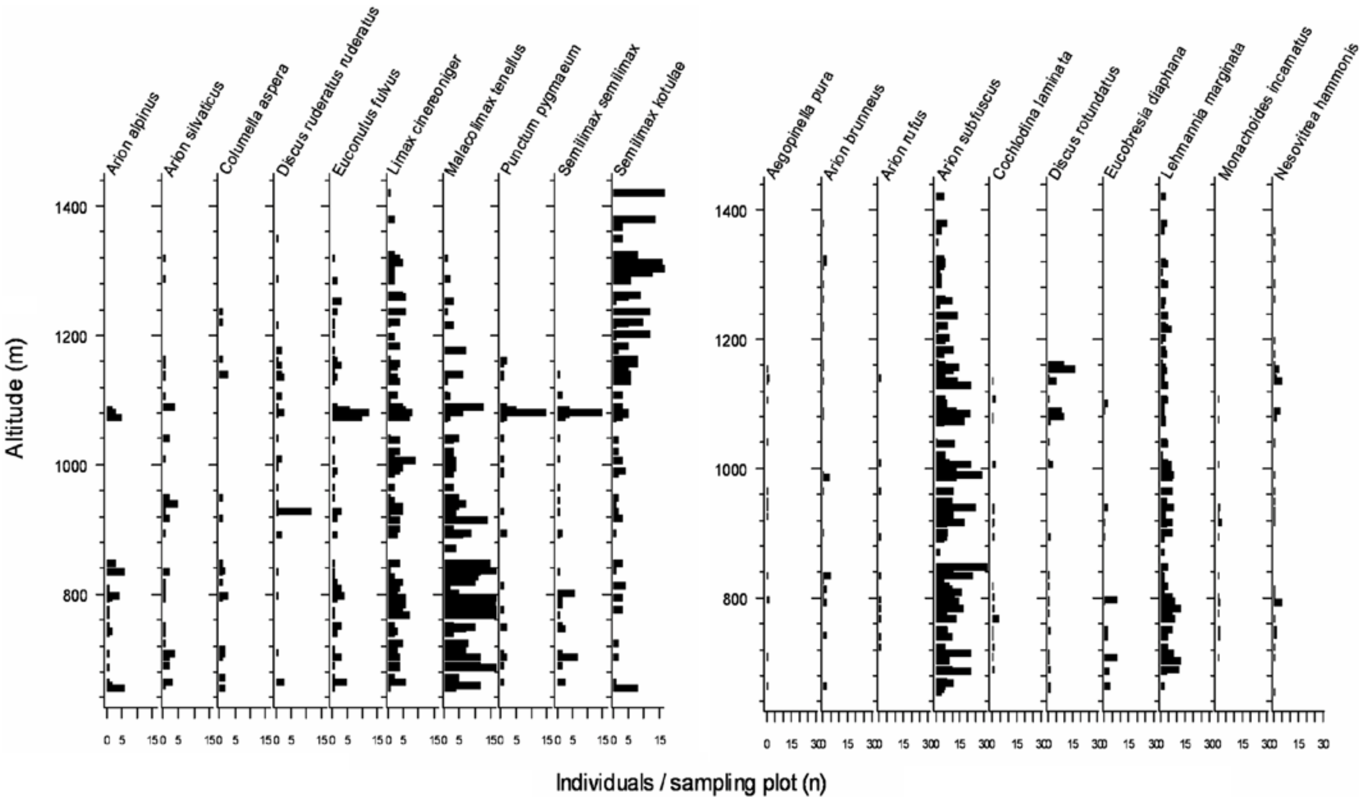


FIG. 2. Abundance of the species, occurring in at least ten sampling plots along altitudinal gradients within the Bavarian Forest National Park (each bar represents one of the 111 plots; see Fig. 1). The upper part shows species where we found at least a marginal significant relationship in spatial glm between abundance and temperature ($p < 0.1$) Otherwise, species are presented in alphabetical order (see also Table 2).

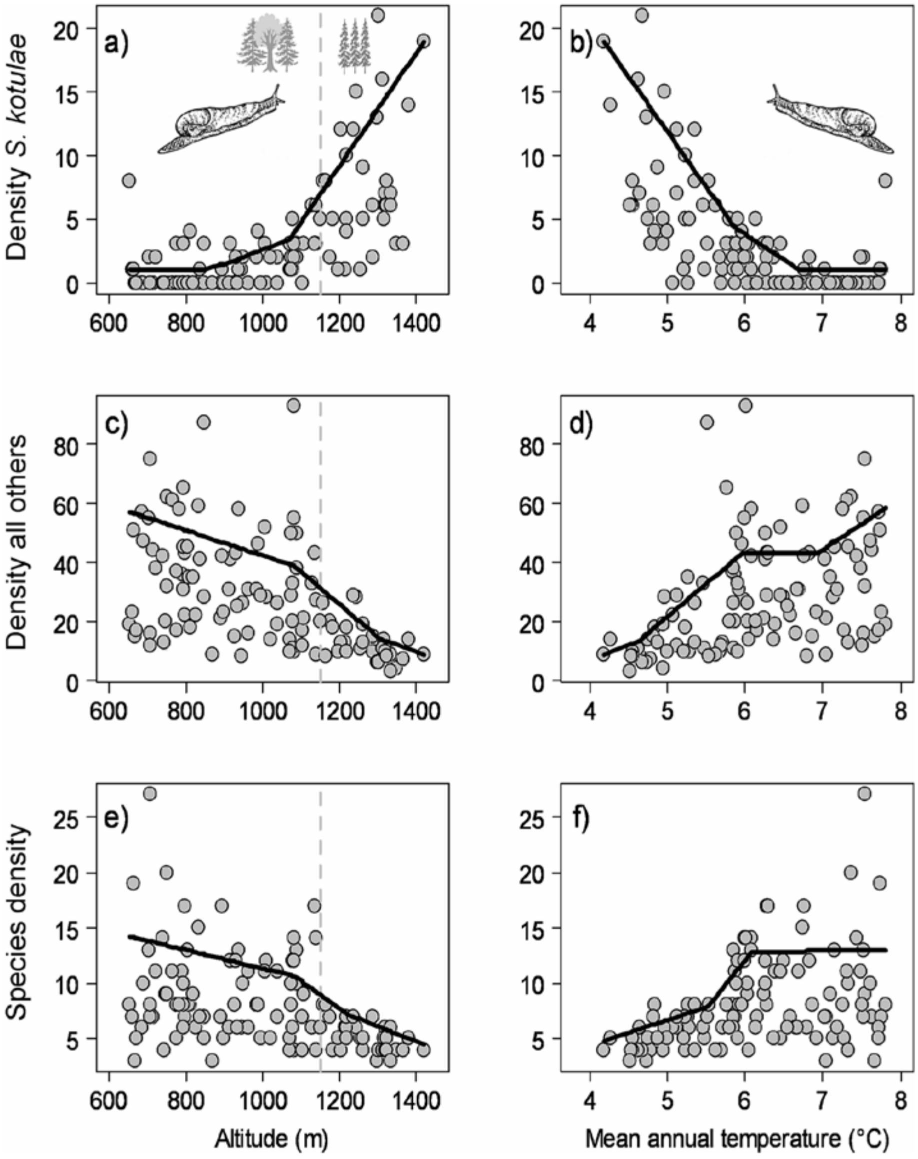


FIG. 3. Number of species, abundance of *Semilimax kotulae* as well as abundance for all species (with exception *S. kotulae*) versus altitude and temperature across 111 plots sampled within the Bavarian Forest National Park (Fig. 1). Lines are additive quantile regressions. The dashed line and the tree symbols indicate the altitude of the change between mixed montane (< 1,150 m) and high montane spruce forests (> 1,150 m).

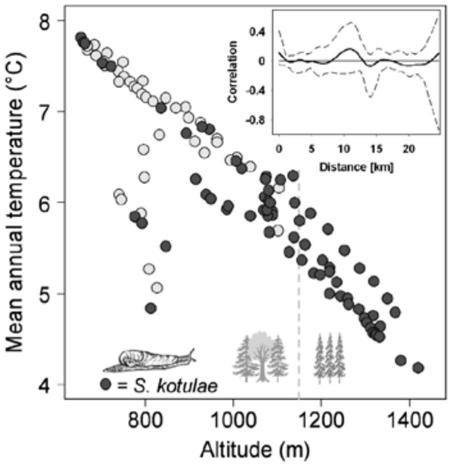


FIG. 4. Relation of mean annual temperature and altitude across the 111 sampling plots in the Bavarian Forest National Park. The outliers are typical sinks for cold air. Dark symbols indicate plots where we recorded *Semilimax kotulae*. Inset shows the spatial autocorrelation of the residuals of a glm with presence/absence data for *S. kotulae* and temperature as predictor. The dashed line indicates the altitude of the change between mixed montane and high montane spruce forests (1,150 m).

in the mean annual temperature of 1.8°K will already lead to a decrease of occurrences by about 50% at altitudes of 1,300 m (Fig. 5). Note that most mountains in the region are below this altitude. Nevertheless, within this optimistic scenario some sinks for cold air at lower altitudes may act as refuges for *S. kotulae* assuming that local circulation patterns of the air will not change with global warming. An increase in mean annual temperature of 4.0°K would probably lead to the extinction of *S. kotulae* in the national park. Modelling abundance produced even more pessimistic results (Fig. 5). Again taking 1,300 m as an example the model predicts abundances of ≈1 if mean annual temperature increases by 1.8°K and close to 0 for an increase of 4.0°K. Note that at present abundances are ≈ 7. These predictions do not change considering temperature and precipitation together.

DISCUSSION

Even though the decrease of diversity along altitudinal gradients has fascinated biologists since Darwin, the reasons are still unclear (Gaston, 2000). We found a non-linear decrease of species richness in molluscs. Aubry et al. (2005) studied richness of molluscs in

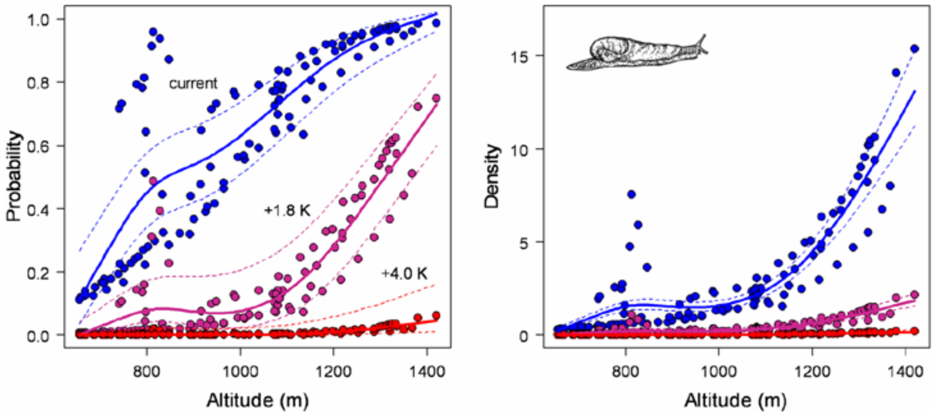


FIG. 5. The blue symbols indicate the predicted probability of occurrences (left) and abundance (right) of *Semilimax kotulae* across the 111 sampling plots versus altitude within the National Park "Bavarian Forest" using annual mean temperature. The blue curves are a local smoother (spline) with heuristic confidence bands (for details see Material and Methods). The other two groups of points and curves are predictions for *S. kotulae* using scenarios of global warming with an increase of the mean annual temperature by 1.8°K and 4.0°K.

calcareous mountains in southeastern France, where they found a plateau of species richness at elevations between 200 m and 1,000 m. Below and above this range they documented a decrease in species richness. Even though this study was undertaken in an area geologically and climatically very much different to our study area, the diversity patterns in our area are rather similar. We found a change in the slope of the decrease of species richness with altitude at around 1,150 m, the altitude where the switch from mixed montane to high montane forests occurs. Several studies have already stressed the close correlation between altitudinal zonation of molluscs and plant communities (e.g., Coppois, 1984).

Körner (2007) noted the difficulty of interpreting effects of non-climatic variables that are strongly correlated with elevation only within certain regions. Such variables can modify altitudinal patterns of diversity in such a way that climate seems to be unimportant (Lee et al., 2004). Nevertheless, Aubry et al. (2005) suggest that climate and the availability of microhabitats determines the number of species. Clearly, our results are consistent with this idea. Temperature, soil water balance, age of trees and plant species diversity are significantly and positively correlated with the densities of several species (Barker & Mayhill, 1999; Müller et al., 2005a; Horsák, 2006). Habitat suitability should be even of more importance in our study area than in the area studied by Aubrey et al. (2005). The sampled region is characterized by acidic soils whereas molluscs often prefer habitats with high pH values (Wäreborn, 1969; Waldén, 1981; Coney et al., 1982; Martin & Sommer, 2004; Horsák, 2006).

Tree age was of overwhelming importance in our models. Furthermore, abundance and number of species also increased with tree age. In forests, the age of the oldest tree in a stand is a surrogate of habitat continuity (Speight, 1989; Sverdrup-Thygeson & Lindenmeyer, 2003; Müller et al., 2005b). Continuity is an important factor for the distribution of molluscs on a regional scale. For example, the abundance of *Limax cinereoniger* and *Macrogastra plicatula plicatula* increases with stand age and therefore habitat continuity (Müller et al., 2005a; Bußler et al., 2007). The importance of continuity for molluscs has at least three components: Firstly, some species feed on the bark of old broadleaved trees and therefore require veterans. Such species are *Clausilia cruciata cruciata* or *Lehmannia marginata*, which at least in Bavaria occurs only in forests (Falkner, 1991; Hässlein, 1966). Secondly, several species need dead wood to obtain calcium, for example *Macrogastra badia crispulata*, *M. plicatula nana*, *Causa holosericea*, *Discus ruderatus ruderatus* (Kappes, 2005; Strätz & Müller, 2006). Thirdly, some mollusc species are consumers of wood-inhabiting or hypogeous fungi (*Arion alpinus*, *Malacolimax tenellus*), which are more common in old stands (Junninen & Angelstam, 2006). Old forests are not only important to molluscs with their low propensity for dispersal (Ant, 1963; Shikov, 1984; Rüetschi, 1999; Strätz, 2005), but also for lichens, wood-inhabiting fungi, saproxylic beetles, or birds (Stubbs, 1989; Bader et al., 1995; Nilsson et al., 1995; Ulikzka et al., 2000; Gustafsson et al., 2004). Our results once more underline the importance of strict forest reserves for conserving the biodiversity of a wide variety of organisms (Christensen et al., 2005).

Overall, we found an increase in number of species and species richness with temperature. This suggests that climate warming will lead to an increase of species richness of molluscs in the national park for two reasons (Grabherr et al., 1994). Firstly, low altitude species will be able to shift the upper distributional limits to higher altitudes. Secondly, new species will be able to invade the area (including such alien species as *Arion lusitanicus*). Therefore, viewed naively, climate warming will be a positive phenomenon if one considers only species richness. However, for species adapted to cool, montane habitats climate warming may lead to local or regional extinction, especially because the available area suitable to them is limited at low mountain ranges. Our example, *Semilimax kotulae*, quantifies this dramatic risk of climate warming.

Semilimax kotulae is endemic to the Alpine-Carpathian area and occurs at altitudes above 600 m. Populations between 500 and 600 m exist in sites where cold air emanates from blocky scree slopes (Hässlein, 1966), which is fully in line with our results. When we compared our data with data from whole Bavaria (Strätz, unpublished) or the East Carpathians (Sulikowska-Drozd & Horsák, 2007), we found a very similar pattern of altitudinal distribution of *S. kotulae*, which suggests that this species may be a suitable indicator for the fate of montane species affected by global warming in whole Central Europe (see also De Groot et al., 1995; Kappelle et al., 1999). As indicated by

our exercise presented in Figure 5, an increase in the mean annual temperature of more than 1.8°K will increase the risk of extinction for this species and, if one accepts that *S. kotulae* may be used as an indicator species, of other montane species. Under pessimistic scenarios of climate warming, *S. kotulae* will only survive in regions that provide sufficient habitats at higher altitudes (> 1,300 m; Alps). Note also that the cool plots which at present still harbour populations of *S. kotulae* will also loose their suitability for this species (Fig. 5). The negative response of *S. kotulae* to higher temperatures may have two reasons: for eggs and juveniles a constant humidity is necessary. Humidity decreases with increasing temperature (Uminski, 1975). A second reason may be competition. Even though the biology of *S. kotulae* is still not well known, this species is described as a weak competitor (Falkner, 1991). At lower elevations, four species with similar habitat requirements occur (*Vitrina pellucida*, *Semilimax semilimax*, *Eucobresia diaphana* and *Vitrionobrachium breve*, Falkner, 1991) which may outcompete *S. kotulae*.

During recent years studies have demonstrated that projections produced by alternative models are sometimes such variable that their usefulness for policy decisions is compromised (Araújo et al., 2006). For example, different models predict changes in the distribution from 92% loss to a 323% gain for a South African plant species (Pearson et al., 2006). Such problems call for the application of a combination of modelling techniques (Drake et al., 2006). We checked our results by including additionally precipitation into the model. However, this model produced very similar results. Furthermore, the very similar conclusions from models using presence/absence and abundance data suggest that our conclusion is fairly robust: *S. kotulae* may disappear in the near future from the national park (cf. Berg et al., 2004).

The upper altitudinal zones of the low mountain ranges in Central Europe are not species rich when compared to lowland forests. Nevertheless, several species are restricted to this zone. Most of them are recorded only once or a few times during the last decades (e.g., *Vertigo modesta arctica*, *Vertigo alpestris*), and therefore they are not suited as indicators. Nevertheless their present range of occurrence is between 1,100 m and 1,400 m a.s.l., and these species are faced with a similar risk as *S. kotulae*. Overall global warming constraints one of the major aims of the Bavarian Forest National Park: the conservation of species assemblages of the high montane zone.

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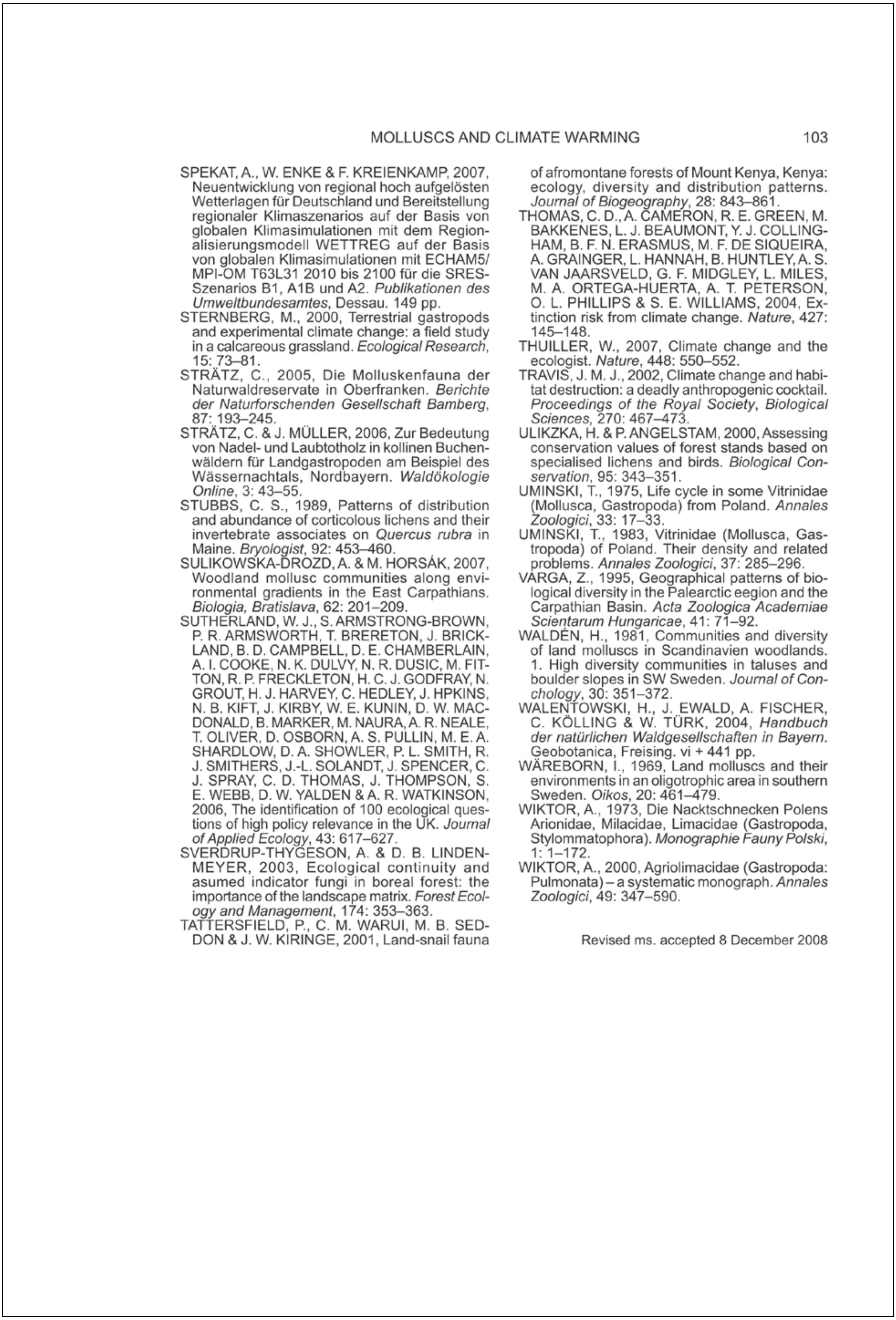

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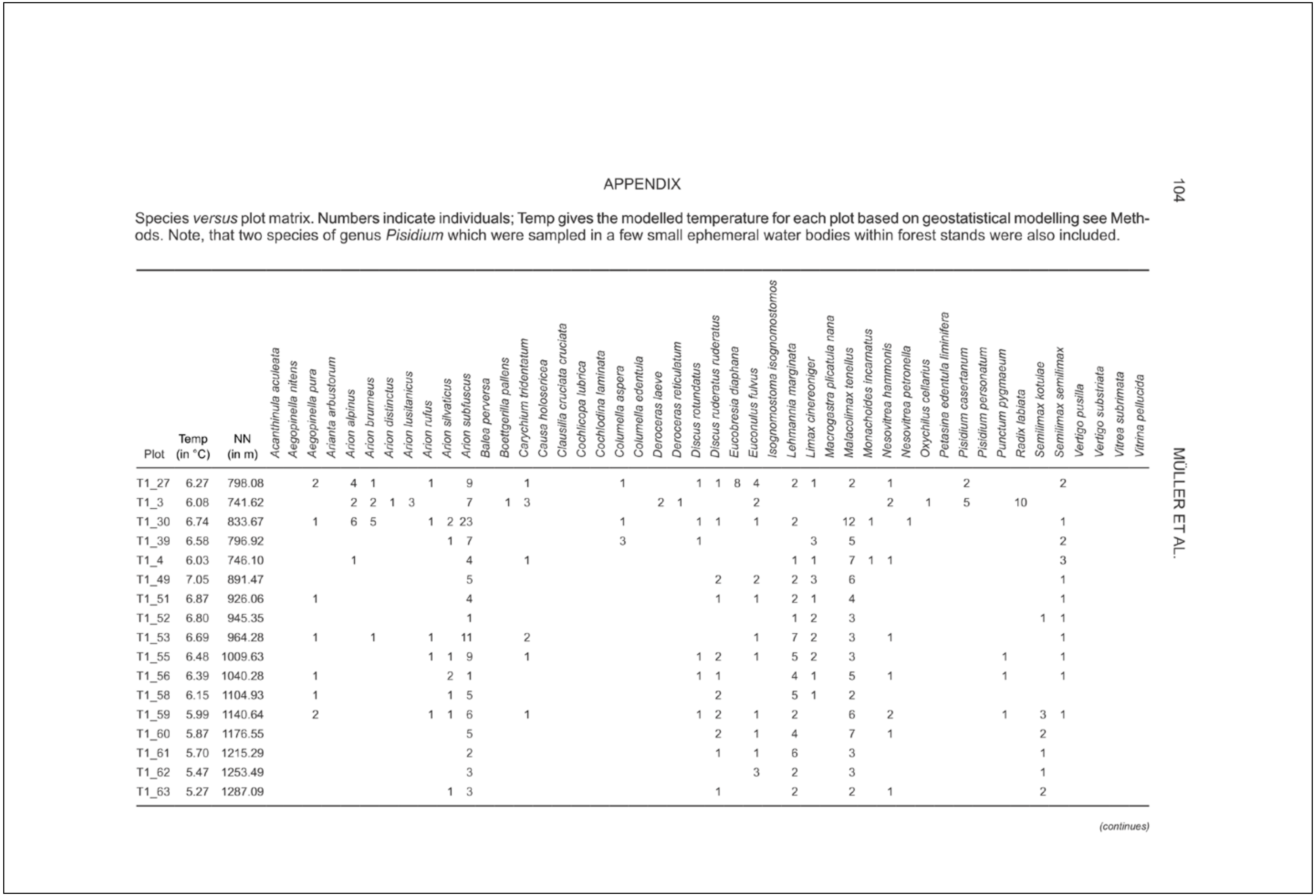

APPENDIX

Species *versus* plot matrix. Numbers indicate individuals; Temp gives the modelled temperature for each plot based on geostatistical modelling see Methods. Note, that two species of genus *Pisidium* which were sampled in a few small ephemeral water bodies within forest stands were also included.

Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T1_27	6.27	798.08			2		4	1			1		9			1					1				1	1	8	4		2	1		2		1				2					2				
T1_3	6.08	741.62					2	2	1	3			7		1	3							2	1				2							2		1		5			10						
T1_30	6.74	833.67			1		6	5			1	2	23								1				1	1		1		2			12	1		1								1				
T1_39	6.58	796.92										1	7								3				1						3		5											2				
T1_4	6.03	746.10					1						4			1														1	1		7	1	1									3				
T1_49	7.05	891.47											5													2		2		2	3		6											1				
T1_51	6.87	926.06			1								4													1		1		2	1		4											1				
T1_52	6.80	945.35											1																	1	2		3										1	1				
T1_53	6.69	964.28			1			1			1		11			2												1		7	2		3		1									1				
T1_55	6.48	1009.63									1	1	9			1									1	2		1		5	2		3								1			1				
T1_56	6.39	1040.28			1							2	1												1	1				4	1		5		1						1			1				
T1_58	6.15	1104.93			1							1	5													2				5	1		2															
T1_59	5.99	1140.64			2						1	1	6			1									1	2		1		2			6		2						1		3	1				
T1_60	5.87	1176.55											5													2		1		4			7		1								2					
T1_61	5.70	1215.29											2													1		1		6			3										1					
T1_62	5.47	1253.49											3															3		2			3										1					
T1_63	5.27	1287.09										1	3													1				2			2		1								2					

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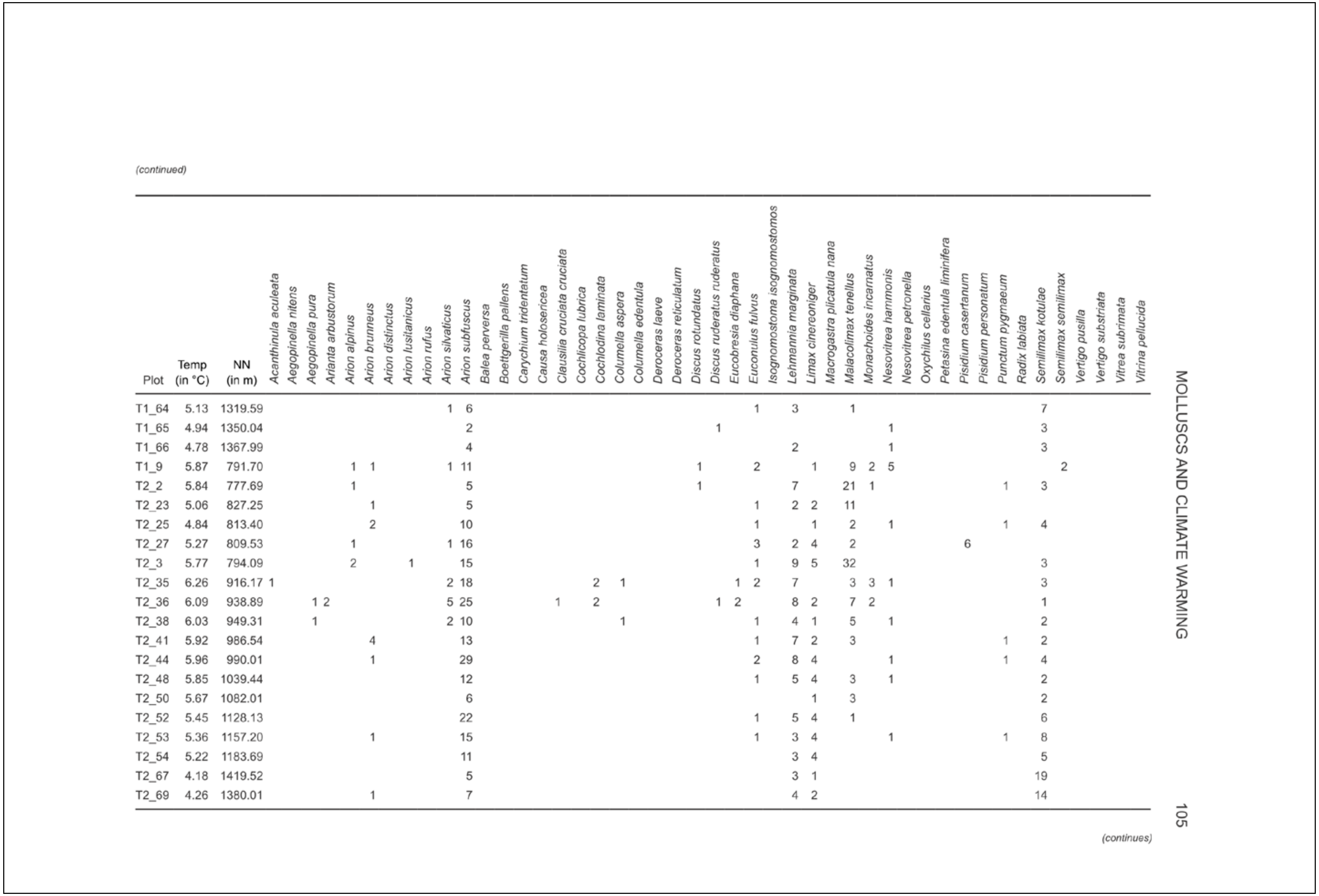

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Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T1_64	5.13	1319.59										1	6															1		3			1										7					
T1_65	4.94	1350.04											2													1									1								3					
T1_66	4.78	1367.99											4																	2					1								3					
T1_9	5.87	791.70					1	1				1	11												1			2			1		9	2	5									2				
T2_2	5.84	777.69					1						5												1					7			21	1							1		3					
T2_23	5.06	827.25						1					5															1		2	2		11															
T2_25	4.84	813.40						2					10															1			1		2		1						1		4					
T2_27	5.27	809.53					1					1	16															3		2	4		2						6									
T2_3	5.77	794.09					2			1			15															1		9	5		32										3					
T2_35	6.26	916.17	1									2	18							2	1						1	2		7			3	3	1								3					
T2_36	6.09	938.89			1	2						5	25					1		2						1	2			8	2		7	2									1					
T2_38	6.03	949.31			1							2	10								1							1		4	1		5		1								2					
T2_41	5.92	986.54						4					13															1		7	2		3								1		2					
T2_44	5.96	990.01						1					29															2		8	4				1						1		4					
T2_48	5.85	1039.44											12															1		5	4		3		1								2					
T2_50	5.67	1082.01											6																		1		3										2					
T2_52	5.45	1128.13											22															1		5	4		1										6					
T2_53	5.36	1157.20						1					15															1		3	4				1						1		8					
T2_54	5.22	1183.69											11																	3	4												5					
T2_67	4.18	1419.52											5																	3	1												19					
T2_69	4.26	1380.01						1					7																	4	2												14					

(continues)

(continued)

Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T2_73	4.76	1317.97						1					6																	5	2												5					
T2_75	4.83	1285.57						1					4															2		5	2				1								6					
T2_79	5.29	1218.65						1					2															1		5	1												5					
T2_81	5.36	1202.83											9															1		3													12					
T2_9	5.52	847.50					3						60															1		4	4		15										3					
T3_1	7.81	655.00					6						4								2							1			1		4		1								8					
T3_12	7.64	714.98											22								2				1			1		8	3		7															
T3_17	7.54	750.19										1	8									3			2		2			3	1		10								2							
T3_22	7.33	795.42											12								1				1		1	2		5	6		15	1	1													
T3_23	7.32	812.49											7																				1										1					
T3_25	7.14	846.87											8								1									5	4		10															
T3_26	7.04	870.08											3																	2			4															
T3_27	6.93	900.20						1					8																	7	4		3															
T3_28	6.83	929.44										1	11													12		3		3	5		4	1	1						1		2	1				
T3_29	6.65	964.35											2													1		1		7	2		3															
T3_3	7.75	660.02					2					1	5												2						1		12										1					
T3_30	6.46	994.48											13													1				6	5		4															
T3_31	6.37	1020.19											6																	1	4		3										2					
T3_33	6.06	1072.47											7																		5		2										3					
T3_34	5.89	1089.60										4	13												8	1		2		2	5		13								2		3					
T3_35	5.86	1090.18						1				2	10												3	1	1	2		1	2		10		4						1		2					

(continues)

(continued)

Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T3_36	5.85	1079.73						1					7																	1	1		1										1					
T3_37	5.91	1069.87											5																	3			1								1		1					
T3_45	5.69	1102.02											7														2			2	1																	
T3_48	5.62	1139.15											5								3										1												6					
T3_49	5.54	1163.20						1				1	2								1							1		1	1												8					
T3_52	5.24	1219.57						1					8								1							1		3	4												10					
T3_53	5.13	1236.23											14								1							2		5	6		1										12					
T3_57	4.94	1260.55											10																	3	6												5					
T3_9	7.73	686.59					1						22														3			4	4		23															
T4_14	7.67	668.72								1			11																				3															
T4_20	7.53	708.49			1								5					2			2									1	2		3															
T4_21	7.50	709.21		1	1								2					2		1						1				1			3															
T4_22	7.53	703.01										2	9					1			1				1			3	1	12	4		12								2		2	7				
T4_24	7.61	689.91										2	10							2					2			1		11	4		12								1			2				
T4_28	7.75	663.87			1	1	1	2				3	6									2			2	3	4	5		2	6		3					1	5		1		1	3				
T4_29	7.72	669.94											7								2							1			2		5															
T4_35	7.54	707.10					1			13		4	6		1	3		1		1		8		1			8	1		2	1	1	2	1	1	5		2	3		1			2	2	2	1	1
T4_36	7.50	722.71								2	1	1	6					7		2										5	5		8		1								2					
T4_37	7.44	739.53					1			3	1	1	10					5		1		4					2	2		5	2		3	2														
T4_38	7.37	751.68				1	1			7		1	7					3		1		4					2	3		7	2		3	2	2	1		1	10	2				2				
T4_39	7.32	766.85					1			2	1		13							4								1		9	7		21		1									1				

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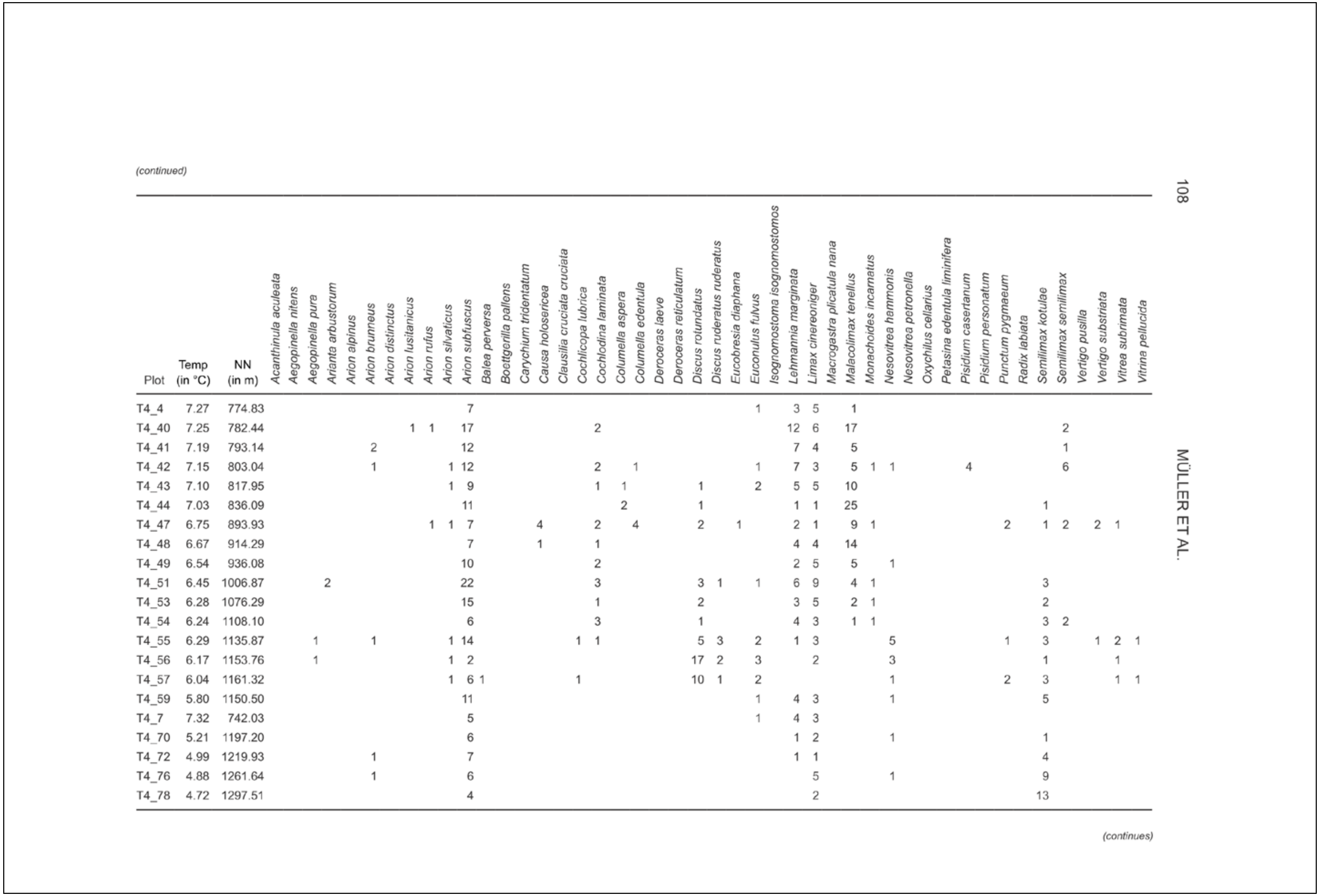

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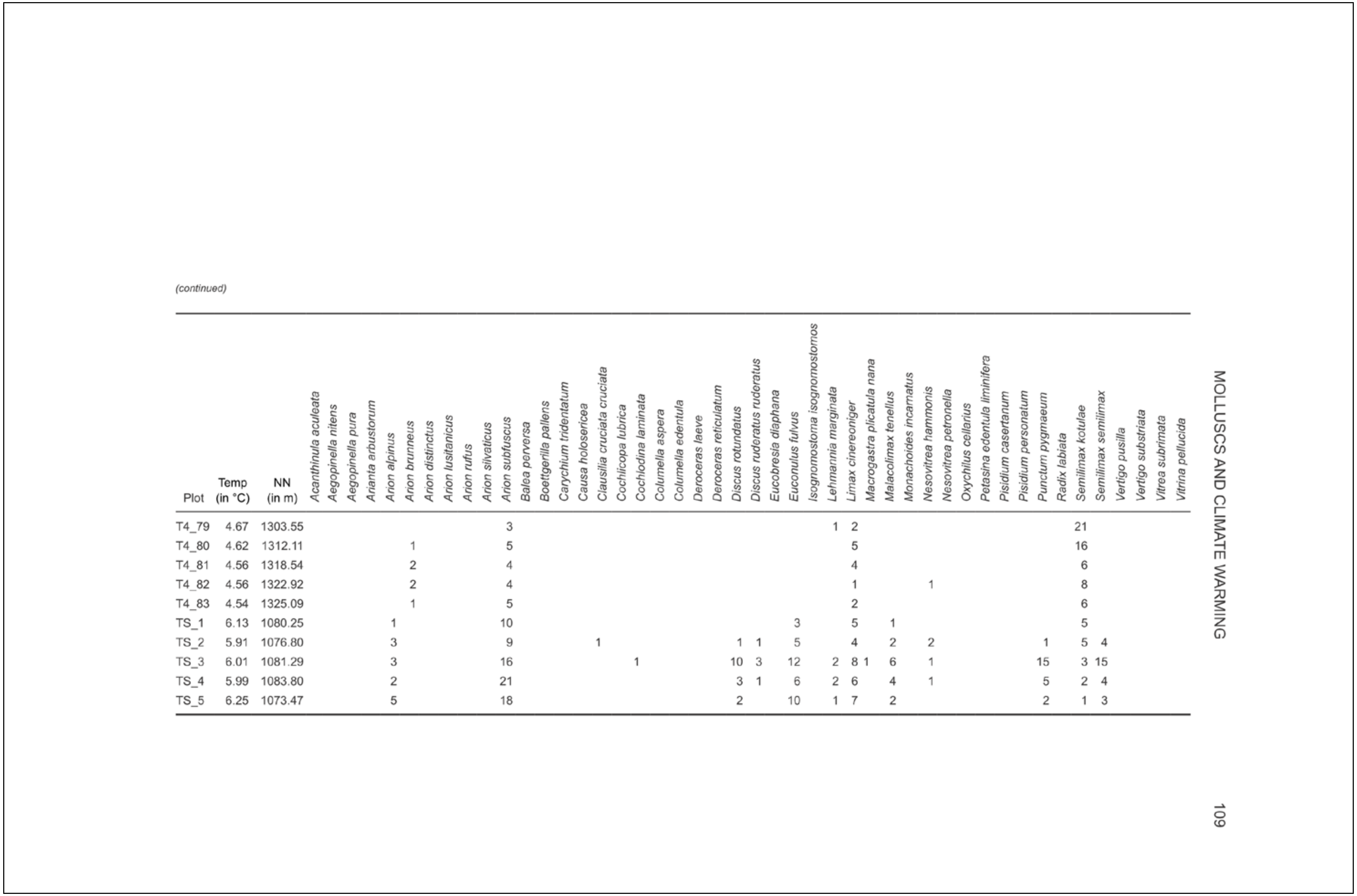
Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T4_4	7.27	774.83											7															1		3	5		1															
T4_40	7.25	782.44								1	1		17							2										12	6		17											2				
T4_41	7.19	793.14						2					12																	7	4		5											1				
T4_42	7.15	803.04						1				1	12							2		1						1		7	3		5	1	1				4					6				
T4_43	7.10	817.95										1	9							1	1				1			2		5	5		10															
T4_44	7.03	836.09											11								2				1					1	1		25										1					
T4_47	6.75	893.93									1	1	7				4			2		4			2		1			2	1		9	1							2		1	2		2	1	
T4_48	6.67	914.29											7				1			1										4	4		14															
T4_49	6.54	936.08											10							2										2	5		5		1													
T4_51	6.45	1006.87				2							22							3					3	1		1		6	9		4	1									3					
T4_53	6.28	1076.29											15							1					2					3	5		2	1									2					
T4_54	6.24	1108.10											6							3					1					4	3		1	1									3	2				
T4_55	6.29	1135.87			1			1				1	14						1	1					5	3		2		1	3				5						1		3			1	2	1
T4_56	6.17	1153.76			1							1	2												17	2		3			2				3								1				1	
T4_57	6.04	1161.32										1	6	1					1						10	1		2							1						2		3				1	1
T4_59	5.80	1150.50											11															1		4	3				1								5					
T4_7	7.32	742.03											5															1		4	3																	
T4_70	5.21	1197.20											6																	1	2				1								1					
T4_72	4.99	1219.93						1					7																	1	1												4					
T4_76	4.88	1261.64						1					6																		5				1								9					
T4_78	4.72	1297.51											4																		2												13					

(continues)



(continued)

Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T4_79	4.67	1303.55											3																	1	2												21					
T4_80	4.62	1312.11						1					5																		5												16					
T4_81	4.56	1318.54						2					4																		4												6					
T4_82	4.56	1322.92						2					4																		1				1								8					
T4_83	4.54	1325.09						1					5																		2												6					
TS_1	6.13	1080.25					1						10															3			5		1										5					
TS_2	5.91	1076.80					3						9					1							1	1		5			4		2		2						1		5	4				
TS_3	6.01	1081.29					3						16							1					10	3		12		2	8	1	6		1						15		3	15				
TS_4	5.99	1083.80					2						21												3	1		6		2	6		4		1						5		2	4				
TS_5	6.25	1073.47					5						18												2			10		1	7		2								2		1	3				

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Using airborne laser scanning to model potential abundance and assemblages of forest passerines

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Abstract

Modelling and forecasting of the distribution and abundance of organisms using environmental variables is a major focus of applied ecological research. High-resolution airborne laser scanning is a recently developed remote-sensing method that provides data that can be used as surrogates for the vertical structure of the vegetation. These data can be used for modelling the occurrence and abundance of species or species assemblages. Until now, few studies evaluated the potential of these data for use in such models, or compared the suitability of data obtained by airborne systems with data gained by alternative methods. To fill part of this gap, we used forest passerine bird species to evaluate airborne laser scanning data for statistical modelling of potential bird abundances and composition of assemblages. Birds were counted in a mixed montane forest, on 223 1-ha plots along four transects. In the same period, these areas were scanned using Light Detection And Ranging (LiDAR) to characterise canopy structure. Additionally, we used visual interpretations of aerial photographs and field measurements on the same plots to derive habitat variables for comparison. We found clear correlations between the LiDAR variables and the other two variable sets using canonical correlation analysis. With a few exceptions, predictive power of the LiDAR data set for modelling abundances of single species, with up to 40% explained variance, was superior to that of the other two data sets. Models agreed with existing ecological knowledge for these species. For modelling of species composition with redundancy analysis, LiDAR was also superior to the other two data sets with more than 20% unique contribution to the explained variance. Our results clearly showed that LiDAR provides valuable data for describing and modelling single species as well as assemblages of forest organisms.

Zusammenfassung

Die Modellierung und Vorhersage der Verbreitung und Abundanz von Organismen ist ein Schwerpunkt in der angewandten Ökologie. Neue entwickelte Anwendungen von Lasern aus Flugzeugen liefern Daten, die sich zur Charakterisierung der Vegetation eignen. Mit diesen Daten lassen sich Vorkommen und Häufigkeit von Arten in Wäldern modellieren. Bis heute haben aber nur wenige Arbeiten das Potential solcher Daten für den Gebrauch in Habitatmodellen geprüft oder die Eignung der Daten mit Parametern aus anderen Quellen verglichen. Um diese Lücke zumindest teilweise zu schließen, haben wir die Abundanz von Sperlingsvögeln und sowie die Artenzusammensetzungen verwendet, um die Eignung von solchen durch Fernerkundung gewonnene Charakterisierung der

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Vegetationsstruktur für statistische Modellierung zu evaluieren. In einem Bergmischwald wurden auf 223 Ein-Hektar Quadranten entlang von vier Transekten Vögel standardisiert erfasst. Parallel dazu wurde die Fläche mit Hilfe von Light Detection And Ranging (LiDAR) aus der Luft erfasst. Darüber hinaus wurden Luftbilder interpretiert und auch Strukturvariablen im Gelände erhoben. Kanonische Korrelationsanalysen Analysen zeigten eine klare Korrelation der drei verschiedenen Datensätze. Mit wenigen Ausnahmen zeigten die aus LiDAR abgeleiteten Umweltdaten die beste Vorhersagekraft bei der Modellierung der Abundanz einzelner Arten und erreichten eine Varianzerklärung von 40%. Darüber hinaus standen die Ergebnisse auch im Einklang mit dem bestehenden Wissen zur Ökologie der Vogelarten. Auch bei Modellierung der Artenzusammensetzung mit Hilfe einer Redundanzanalyse zeigten die aus LiDAR abgeleiteten Variablen mit 20% unabhängiger erklärter Varianz den größten unabhängigen Erklärungsbeitrag. Unsere Ergebnisse unterstreichen das Potential von LiDAR-Daten für die Modellierung von Arten und auch Artengemeinschaften in Wäldern.

Keywords: Aerial photography; Breeding birds; LiDAR; National park "Bavarian Forest"; Temperate montane forest; Species-abundance models

Introduction

As early as 1935 the term phyto-vertical distribution was introduced for the vertical occurrence of birds in plant communities (Dunlavy 1935). During the golden age of community ecology commencing in the 1950s and 1960s, ecologists recognised that vertical distributions differ between phylogenetically closely related species, e.g. within the genus *Dendroica* (MacArthur, 1958; see also Morrison, Ralph, Verner, & Jehl 1990; Shaw, Freeman, & Flick 2002) and that diversity increases with increasing complexity of vegetation structure (MacArthur & MacArthur 1961; Recher 1969). These patterns were interpreted as resulting from competitive interactions (Levine 1976). Although ecologists are nowadays reluctant to ascribe patterns of bird–vegetation relationships solely to competition (Hinsley, Hill, Gaveau, & Bellamy 2002; Shaw & Flick 1999), the analysis and understanding of these relationships is still important in predicting species responses to management (Stork, 2001). However, the measurement of vegetation structure is not without problems, particularly in forests: first, the direct measurement of vegetation characteristics is time consuming, leading to a trade-off between intensity and extent of sampling. Therefore many studies rely on point measurements in small areas. Second, for logistical reasons it is difficult to measure the crown structure, because methods such as canopy cranes provide only access to crowns within a restricted area (Nadkarni & Cushing 2002).

During the last decades the increasing sophistication of remote sensing offered the possibility of measuring vegetation structure of even large and remote areas (Mason et al. 2003). One example is the use of Light Detection And Ranging (LiDAR) data obtained by airborne laser scanning (Lefsky, Cohen, Parker, & Harding 2002; Vierling, Vierling, Gould, Martinuzzi, & Clawges 2008). LiDAR is a technology that offers the ability to measure vegetation height with a high vertical resolution across large areas and the resultant data fulfil the twin requirements of adequate resolution and sufficient area coverage required in statistical modelling of animal–vegetation relationships. Although other remote-sensing technologies also provide large-scale information, LiDAR seems to be particularly effective (Bradbury et al. 2005). Forest authorities already started to use this method to estimate timber production (Naesset 2004). During the last decade ecologists also recognised that LiDAR provides valuable information for modelling relationships between vegetation structure and birds, mammals and plants (Bongers 2001; Mason et al. 2003; Turner et al. 2003).

First studies using LiDAR were conducted on the habitat structure of breeding territories and breeding success of tit species in broadleaf forests (Broughton, Hinsley, Bellamy, Hill, & Rothery 2006; Hill, Hinsley, Gaveau, & Bellamy 2004; Hinsley, Hill, Bellamy, & Balzter 2006). In temperate forests LiDAR data have been used for predicting bird species richness of various functional groups (Clawges, Vierling, Vierling, & Rowell 2008; Goetz, Steinberg, Dubayah, & Blair 2007). However, few studies have evaluated the power of LiDAR in comparison to other methods that allow measurement of the vegetation structure for predicting density using general linear or general additive models and assemblages of forest species using canonical ordinations. Using forest birds as an example we show that LiDAR data provide a valuable basis for modelling the relationship of birds and vegetation within forests. We used not only standardised bird counts together with LiDAR data, but also aerial photos and field measurements to explore two questions:

1. Do canopy characteristics provided by LiDAR allow modelling habitat relationships of forest birds at the species and assemblage level?
2. Does LiDAR provide a database, which is more efficient for predicting densities of single species and assemblages than do aerial photography and field measurements?

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Material and methods

Study site and bird sampling

We estimated the densities of bird species across the montane zone of the Bavarian Forest National Park in southeast Germany using quantitative grid mapping (Moning & Müller 2008). This zone is dominated by mixed montane forests consisting of spruce (*Picea abies*), beech (*Fagus sylvatica*) and fir (*Abies alba*). Due to extensive infestation by bark beetles (mainly *Ips typographus*) in the southern part of the National Park, the structure of the canopy varies widely from open forests dominated by dead wood to more or less dense stands. We established four transects (see Moning & Müller 2008). Each transect was divided into plots of 100 m × 100 m, resulting in 223 plots.

Each plot was visited on five dates in 2007: end of March, in mid-April, at the beginning and at the end of May, and at the beginning of June. Observations were conducted from sunrise till 11 a.m. Each of 3–4 experts visited a section of around 3.0 km length at one morning, so that each observation campaign could be completed within 3 days. For 10 min in each plot, the locations of all bird individuals seen or heard were recorded with an accuracy of about 5 m on a field map. We restricted our analyses to passerines, because plot size was not sufficient for mapping non-passerines with territories much larger than 1 ha. The sum of all observations per plot and species was used as a surrogate for bird abundance. Our measure of abundance integrates across the migratory and breeding period. The importance of the migratory and breeding period for our abundance measure differs between bird species and it is not possible to compare densities among species (for further discussions see Moning & Müller 2008).

Environmental variables sets

Full waveform canopy data were gathered by digital airborne LiDAR using a Riegl LMS-Q560 scanner with a flight height of 400 m, as reviewed by Bradbury et al. (2005). After leaf flush in May 2007 data were collected with an average point density of 25 m^{-2}. On the basis of this data a digital surface model and a digital terrain model were calculated (for methods see Axelsson 2000). The digital crown model was then derived by subtracting the digital terrain model from the digital surface model. Finally, for each plot the mean canopy height (MeanCH), the standard deviation of MeanCH (SDCH), and the maximum height of canopy (MaxCH) were calculated.

MeanCH provides a measure of the vegetation height, but is also a strong surrogate for density (see Appendix A). SDCH is an index of vertical variation of canopy height (Table 1).

Table 1. Summary of the environmental variables extracted from LiDAR data, aerial photographs and field measurements.

Environmental variables	Mean	Min.	Max.	Skewness	Kurtosis
LiDAR					
Mean canopy height—MeanCH (m)	14.6	**1.75**	**28.6**	−0.336	−0.242
Standard deviation of canopy height—SDCH (m)	8.29	2.87	**12.4**	−0.286	−0.110
Maximum canopy height—MaxCH (m)	37.7	22.6	51.7	0.261	−0.0276
Penetration rate 5–1 m above ground—Pen5 (%)	71.3	35.1	93.5	−0.593	−0.508
Penetration rate 10–2 m above ground—Pen10 (%)	63.5	21.1	76.3	−0.367	−0.523
Aerial photographs					
Gaps without regeneration (m^2)	272	0.00	7376	5.48	36.1
Young broadleaf forest, height 0–6 m (m^2)	801	0.00	8799	2.59	6.18
Young coniferous forest, height 0–6 m (m^2)	446	0.00	9108	4.03	16.7
Middle aged broadleaf forest, height 6–12 m (m^2)	1114	0.00	8641	1.97	3.39
Mature broadleaf forest. height above 12 m (m^2)	2568	0.00	9620	0.751	−0.577
Mature coniferous forest. height above 12 m (m^2)	3051	0.00	10,000	0.824	−0.428
Edge length of patches (m)	568	0.00	1257	0.048	−0.381
Field measurements					
Number of tree species	2.71	1	6	0.855	2.23
Number of cavity trees	1.66	0	12	1.93	3.49
Volume of snags ($m^3\,ha^{-1}$)	37.6	0.00	411	2.86	9.03
Maximal diameter in breast height (cm)	57.6	8.00	130	0.57	1.08
Age of the oldest tree (years)	131	0	400	2.16	6.92

For LiDAR variables the abbreviations used throughout the paper are also given. The canopy surface models for the values in bold are shown in Appendix A.

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Plots with a uniform tree height exhibit a small SDCH, plots with a mixture of small and large trees a larger SDCH. MaxCH provides information about the occurrence of the tallest tree canopy within a single 1.0 ha plot. Additionally, we calculated penetration rates for two different lower canopy layers: first, we calculated the sum of all laser echoes below 2 m above ground divided by the sum of all laser echoes below 10 m above ground (= Pen10). Second, as an estimator for the shrub and regeneration layer we calculated the penetration ratio between 5 and 1 m above ground (= Pen5).

For comparison we used data from aerial photography and field measurements collected on the same plots (Table 1). We used the ERDAS stereo analyst to analyse infra-red aerial photographs from 2007, with a spatial resolution of 40 cm. The whole area of a plot was divided into conifers and broadleaf trees and height categories by visual 3D inspection. We measured edge length as the length in metres of the classified vegetation patches. For the field measurements, conducted in 2007, we selected characteristics that were often used in ornithological studies (Chambers, McComb, & Tappeiner 1999; Clawges et al. 2008; Goetz et al. 2007; Hinsley et al. 2006; James & Wamer 1982) and characteristics with the potential to explain the abundance of a wide array of forest species (Bradbury et al. 2005; James & Wamer 1982; Swallow, Gutierrez, & Howard 1986). The number of cavity trees was counted in all plots. The volume of snags per hectare and the diameter of the largest tree at breast height were measured in a 0.1 ha plot. At the centre of the plot, we recorded the number of tree species in all canopy layers, while the age of the oldest tree within each plot was taken from National Park field inventories (for more details see Appendix A).

Statistical analysis

To investigate the multivariate relationships between the data sets gained by LiDAR, aerial photography and field measurements, we used canonical correlation analysis provided by 'vegan' within R. Our bird data are counts and accordingly we used Poisson regression to analyse the relationships of the abundance of single bird species, occurring in 20 or more plots, with the five variables extracted from the LiDAR data (Everitt & Hothorn 2006; Quinn & Keough 2002). To obtain comparable estimators, all predictors were standardised. Due to our transect design we expected some spatial autocorrelation between. Therefore we used Bayesian semiparametric spatial generalised linear models, in which spatial autocorrelation is alleviated by including a spatial surface in the regression model. Assuming asymptotic normality of the estimated regression coefficients, confidence bands and p-values can be computed based on the standard deviations obtained from the expected Fisher information matrix as implemented in 'BayesX' (Brezger, Kneib & Lang 2005).

Preliminary detrended correspondence analysis indicated that linear ordination techniques were appropriate for summarising our bird data. Therefore we extracted the main patterns of bird assemblages, including bird species occurring in at least five plots, using partial principle component analysis (PCA) on the covariance matrix to consider space as a covariable with the terms X, Y, $X \times Y$. In an ordination using the covariance matrix the result is dominated by the common species. Therefore we used square root transformation to down-weight this influence. Subsequently, LiDAR data were fitted to the ordination and the significance of the relation between LiDAR data and plot scores tested with 1000 permutations.

As a simple metric for evaluating the predictive power for single species we used the mean-squared multiple regression coefficient R^2 calculated by cross-validation using 200 randomly selected training and test data sets. Training sets consisted of 123 plots; the remaining 100 plots were used to calculate R^2 by correlating observed versus predicted abundances. These simulations also permit the construction of confidence limits. We considered only species occurring in at least 20 plots and calculated for each species the predictive power for each of the three environmental data sets as well as space based on all plots. Furthermore, we calculated the unique contribution of each environmental data set x to the total predictive power across all three data sets x,y,z:

$$\text{Unique contribution of set } x = R^2_{x,y,z} - R^2_{y,z}$$

To compare the explanatory power of different environmental data sets for bird assemblages we used variance partitioning implemented in 'vegan', again with square root transformed density data. Bootstrapping was used to estimate the error of our variance components (Roff 2006).

Results

The canopy surface models used to extract forest stand characteristics with LiDAR exhibited rich patterns, sometimes with obvious differences between plots (see Appendix A). Compared with aerial photography and field measurements, the skewness and kurtosis of our variables extracted from LiDAR data indicated that the latter were often close to normal distributions (see Table 1). Canonical correlation analysis showed a clear relationship of the first roots extracted from LiDAR

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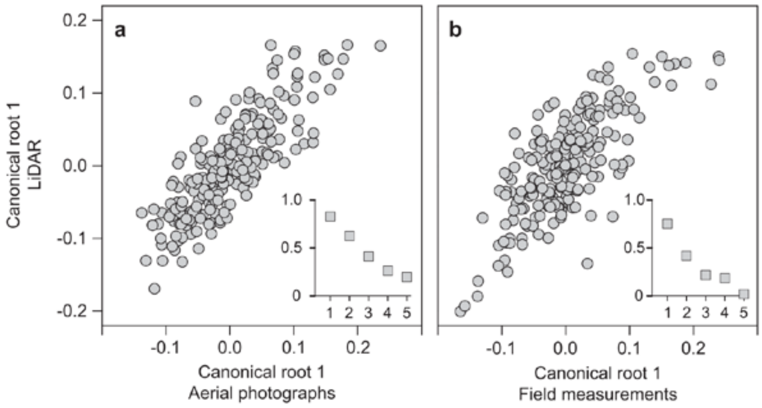

Fig. 1. Canonical correlations between the first roots extracted to maximise the correlation between the data sets using variables derived form LiDAR and aerial photographs (A) as well as from LiDAR and field measurements (B). The insets show the decrease of correlation coefficients for the first five roots of each pair of data sets.

Table 2. List of bird species occurring in at least 5 of 223 plots and results of spatial GLM for species occurring in at least 20 plots (rare species are indicated by #).

	Species	Frequ.	MeanCH	SDCH	MaxCH	Pen5	Pen10
#	Grey Wagtail *Montacilla cinerea*	7					
	Wren *Troglodytes troglodytes*	153	−0.37***	0.29***			
	Dunnock *Prunella modularis*	63	−1.13***	0.67***	−0.39*	−0.47*	
	European Robin *Erithacus rubecula*	198					
#	Redstart *Phoenicurus phoenicurus*	5					
	Blackbird *Turdus merula*	142	0.22*	0.17*			−0.28**
	Song Thrush *Turdus philomelos*	135	0.47*	0.19*	−0.27*	0.25*	−0.24*
	Mistle Thrush *Turdus viscivorus*	76					
	Blackcap *Sylvia atricapilla*	157	−0.37***	0.20*		−0.27*	
#	Wood Warbler *Phylloscopus sibilatrix*	19					
	Chiffchaff *Phylloscopus collybita*	98	−0.94***	0.48***		−0.42**	
	Willow Warbler *Phylloscopus trochilus*	36	−1.70***			−0.53*	
	Goldcrest *Regulus regulus*	143		0.19*			
	Firecrest *Regulus ignicapillus*	65	0.53*				−0.44*
#	Red-breasted Flycatcher *Ficedula parva*	6					
#	Long-tailed Tit *Aegitalos caudatus*	11					
	Marsh Tit *Parus palustris*	30					
#	Willow Tit *Parus montanus*	13					
	Crested Tit *Parus cristatus*	100					
	Coal Tit *Parus ater*	212	0.19**				
	Blue Tit *Parus caeruleus*	30					
	Great Tit *Parus major*	85					
	Nuthatch *Sitta europaea*	119	0.24*	−0.18*	0.40**	−0.40**	
	Common Treecreeper *Certhia familiaris*	115		0.36***			
	European Jay *Garrulus glandarius*	87					
#	Nutcracker *Nucifraga caryocatactes*	6					
	Chaffinch *Fringilla coelebs*	222	0.15***	0.09**			
	Eurasian Siskin *Carduelis spinus*	127	−0.27**	0.37***			
	Common Crossbill *Loxia curvirostra*	132	−0.80***	0.16*			
	Northern Bullfinch *Pyrrhula pyrrhula*	38					
#	Hawfinch *Coccothraustes coccothraustes*	9					

We show only significant estimators and in order to compare estimators, the independent variables were zero mean—unit variance standardised. Species are listed in taxonomical order. Significance levels: *$p<0.05$, **$p<0.01$, ***$p<0.001$.

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with those from aerial photographs (Fig. 1A). The canonical correlations between LiDAR and field measurements were also compelling, but with a lower canonical correlation coefficient (Fig. 1B inset). Thus, there were similarities between the structural variables extracted by all three methods, although the correlation coefficients between pairs of variables from two data sets were always less than 0.5.

Forest birds and LiDAR

Twenty three passerine species were found in at least 20 plots, and 31 in at least five (Table 2; for a list of all species see Moning & Müller 2008). Spatial general linear models using density of individual bird species as the independent variable and the five LiDAR variables as predictors detected a significant influence of at least one predictor for 15 of the 23 species (Table 2). The most frequent significant variable (for explanation of abbreviations see Table 1) was MeanCH (13), followed by the SDCH (12), the Pen5 (6), the Pen10 (3) and the MaxCH (3).

The first two axes of a partial PCA with space as a covariable explained 20% of total variance (Fig. 2). After fitting the LiDAR data to this ordination the first axis can be interpreted as a gradient from open to dense stands (Table 3, Fig. 2). The second axis was correlated with MaxCH and SDCH and therefore represents a gradient from homogenous to highly structured forest stands.

Predictive power of LiDAR data

Predictive power of the best single species-abundance model reached values of almost 40% for LiDAR and aerial photography (Fig. 3A). The predictive power of the aerial photographs was in most cases close to the lower boundary of the 95% confidence intervals constructed for the predictive power of LiDAR data, although aerial photographs had seven variables compared with five in the LiDAR data set. In more than 50% of our analysed species LiDAR had the highest unique contribution to the predictive power (Fig. 3B).

The three environmental data sets together with space explained in total slightly more than 20% of the variation in the bird assemblage, much more than expected by randomising bird densities across plots (Fig. 4). Setting the total explained variance to 100%, the unique contribution of LiDAR to the predictive power of the environmental variable sets and space was

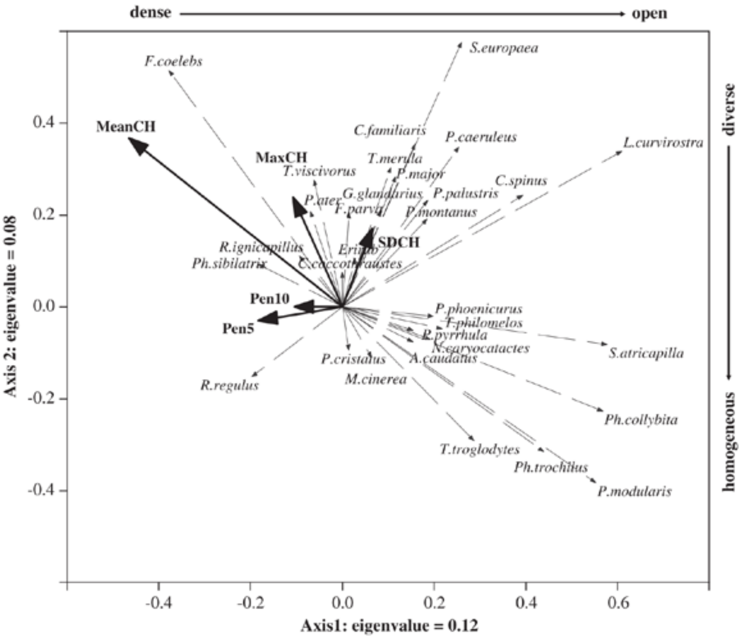

Fig. 2. Partial PCA ordination, considering space as covariable, of the square root abundance of 31 passerine bird species occurring in at least 5 plots. LiDAR variables were fitted on the ordination space. For statistical tests see Table 3. Sum of all eigenvalues standardised to one. Therefore eigenvalues present the percentage of explained variance.

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Table 3. Individual correlations of LiDAR variables with the plot scores of the first two ordination axes extracted by partial PCA with space as covariate.

LiDAR variables		PC 1	PC 2	R^2	p
Mean canopy height	MeanCH	−0.46	0.37	0.35	**<0.001**
Standard deviation of canopy height	SDCH	0.068	0.17	0.033	**0.018**
Maximum canopy height	MaxCH	−0.11	0.24	0.069	**0.001**
Penetration rate from 5 to 1 m above ground	Pen5	−0.18	−0.031	0.034	**0.028**
Penetration rate from 10 to 2 m above ground	Pen10	−0.10	−0.0027	0.011	>0.3

R^2 measures the correlation with both axes (sum of the squared values of the correlation coefficients in PC1 and PC2), p-value for this coefficient was estimated with 1000 permutations.

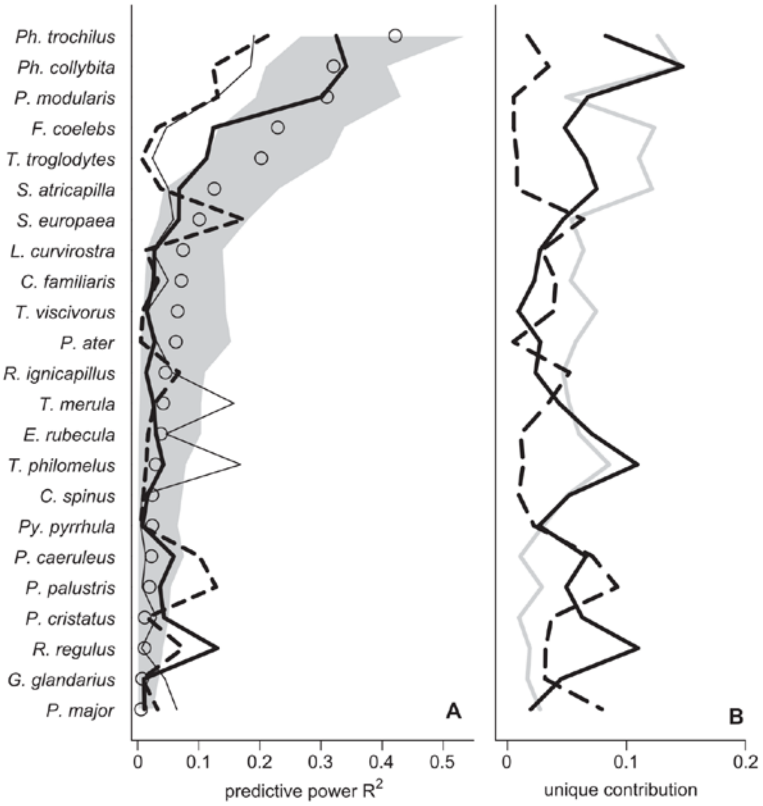

Fig. 3. (A) Predictive power expressed by the squared multiple correlation coefficients (R^2) between abundance of 23 species as dependent variable and three sets of environmental variables and space as independent variables. Species are ranked by decreasing R^2 of LiDAR (open circles). The gray area gives the approximate 95% confidence band for these circles. The other three variable sets are plotted without symbols: black line—aerial photography; dashed line—field measurements; hairline—space). (B) Unique contribution of the three environmental data sets (gray line—LiDAR data; black line—aerial photographs; dashed line—field measurements).

21% (95% CF 16.7–25.5%). The respective values for the other sets are only between 5% (95% CF 2.1–8.5%) and 16% (95% CF 11.7–19.8%). Note that the joint effect of LiDAR and aerial photographs (unique contribution 14%, 95% confidence limits 9.9–17.5%) is almost 15% (Fig. 4).

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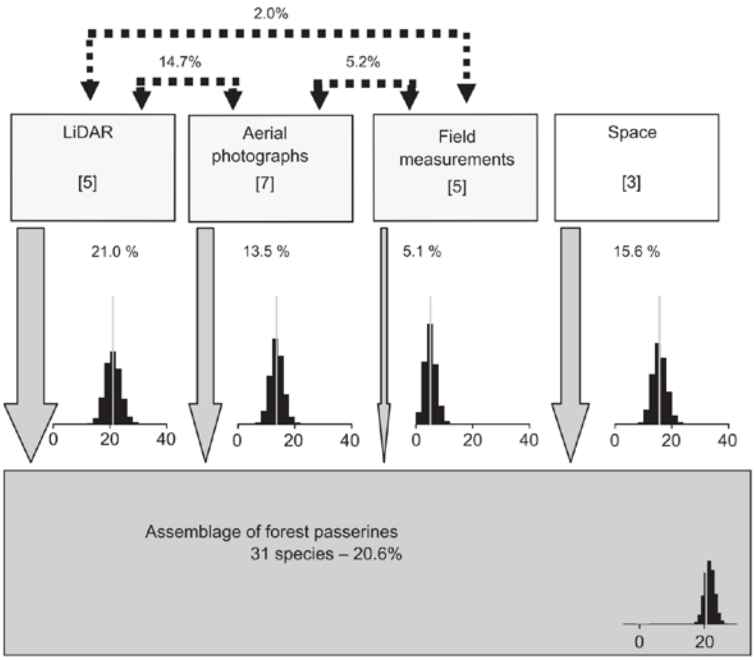

Fig. 4. Percentages of explained variances of breeding bird assemblages (abundances of 31 species across 223 plots) by three environmental sets and space using redundancy analysis. Abundance values of species are the combined counts from five sampling campaigns (see also Material and Methods). These data were square-root transformed to down weight the influence of common species. The number of variables in each data set is given in brackets. The histograms give the distribution of the bootstrap values with the mean indicated by gray lines. The variance partitions were standardised by setting the total explained variance to 100%. Note that for clarity not all joint effects are given. The plot with the two histograms gives the distribution of bootstrap values of the total explained variance as well as the explained variance for communities, generated by randomising species across plots (histogram around zero).

Discussion

Our results showed that LiDAR is a useful method for reducing the complexity of the canopy structure to a few ecologically meaningful variables. Furthermore, these LiDAR variables allowed the construction of statistical models of the abundance of species, which were often more powerful than the models derived from the aerial photography or field measurements used in this study.

Measuring forest canopy structure

Of course, one can always achieve a high predictive power of statistical models by increasing the number of independent variables. To achieve high predictive ability the aim is to use as few independent variables as possible with the incorporation of habitat variables that reflect the habitat selection of the species. Habitat selection is, however, a complex behavioural process and only time-consuming experimental methods for a small number of species can reveal the decision chains of animals in habitat selection (e.g. Thaler, 1986). However, our aim was to compare variable sets consisting of variables with some implication for as many bird species as possible, although the direct ecological process linking each variable to the abundance of a species is far from obvious. From the conservation perspective, statistical species-abundance models for many species are needed to predict changes in biodiversity resulting from habitat change (Turner et al. 2003). Such applications are also possible with models based on phenomenological relationships, particularly at larger spatial scales. Field measurements are often too time consuming, but the array of available remote-sensing methods offers alternatives to derive surrogates (Bradbury et al. 2005; Goetz et al. 2007; Hinsley et al. 2006; Lefsky et al. 2002; Turner et al. 2003).

Although more expensive than aerial photography (for costs see Appendix A), the main advantage of LiDAR is that it allows sampling habitat characteristics

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across large areas, including underlying canopy layers, with a high resolution even in remote regions with rough terrain or otherwise restricted access. Finally, the variables derived from the LiDAR data are statistically well behaved (e.g. symmetric distribution, few outliers) compared with variables obtained by the other methods, which is an important advantage for statistical modelling (for more details see Appendix A).

Modelling abundance of forest species

The main objectives of our study were not only to show that LiDAR is a cost-effective method of characterising complex habitat structures like forest canopies in large areas, but also to show that the variables extracted from LiDAR data are to a certain extent ecologically meaningful. For this purpose, we used birds as an example. Especially in Central Europe, the ecology of birds is well understood, which allows checking of our statistical models against generally accepted knowledge. For example, the most common and widely distributed bird in the sampled area, the chaffinch, is positively correlated with MeanCH (Table 2) and has an extreme position on the left-hand side along the first axis of our ordination space. This indicates that this species prefers dense, mature high forests. Of course the chaffinch occurred almost everywhere along the transects, but its abundance varied considerably. In contrast, the dunnock is negatively correlated with MeanCH, with an extreme position on the right side of the first axis, indicating high abundance in open forests. In one of the many handbooks dealing with birds one finds “chaffinches maybe found breeding … where ever there are trees or bushes. The densest population occur in major broadleaf woodlands.” (Sharrock 1976). For the Dunnock the habitat is described as “choosing glades and edges away from tall trees and among scrub coniferous growth, dwarf heath, alder *Alnus* or willow *Salix* bushes” (Cramp, Simmons, & Perrins 1977–1994). Clearly, the statistical models derived from LiDAR data match these descriptions.

However, habitat variables derived from LiDAR are not always successful in predicting the abundance of certain species (Fig. 3). This may have several mutually non-exclusive reasons. First, some species have no clear habitat preference. Second, the habitat variables may not include the important habitat characteristics for the species. Third, estimated densities may not be reliable. The breadth of the habitat niche of a species can vary considerably (Brändle & Brandl 2001). For example, the great tit may be considered to have a broad habitat niche, as this species occurs in considerable densities in all types of habitats with at least some shrubs or trees. Therefore, we were not surprised that we failed to find significant relationships between density and our LiDAR variables (and even the other variable sets) for this species. Our LiDAR variable set also had a low predictive power for the goldcrest. This species illustrates the second condition. The goldcrest is adapted to and prefers conifers in habitat choice experiments (Thaler 1986). In contrast to our variables extracted from the aerial photographs, the LiDAR data do not directly estimate occurrence of particular tree species in a plot. Consequently, the predictive power derived from the aerial photographs was higher than for LiDAR. Note that the goldcrest showed a significant relation to SDCH, a LiDAR variable, which is partly influenced by tree species composition (see discussion above). Finally, low predictive power of species density models may be the result of a low precision of the abundance data. Density cannot be reliably estimated for all species during only a few short visits, leading to considerable statistical noise in the data (Boulinier, Nichols, Sauer, Hines, & Pollock 1998). Furthermore, some species show considerable variation in density between years, influenced by weather conditions and/or mast years of beech or spruce (Scherzinger 2006).

Conclusions

Using birds as an example, we have shown that LiDAR has the potential to provide habitat data with considerable predictive power for modelling potential abundances of single species as well as assemblages. Predictive power was similar to that of aerial photography and superior to that of field measurements. Thus for large areas it seems to be the method of choice in measuring habitat characteristics. As already recommended by Bradbury et al. (2005), LiDAR data should increasingly be integrated into ecological projects. We only want to mention two applications for LiDAR data in conservation ecology. First, LiDAR data may create new opportunities for deriving key structures for species under conservation focus (e.g. the capercaillie: Graf, Mathys, & Bollmann 2009). Second, forest science has developed high-quality models for tree and stand growth for evaluation of management strategies in forests, allowing connection of tree growth models with LiDAR data. In the long run this offers the possibility of modelling distribution and abundance of forest species in relation to management strategies.

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Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2009.03.004.

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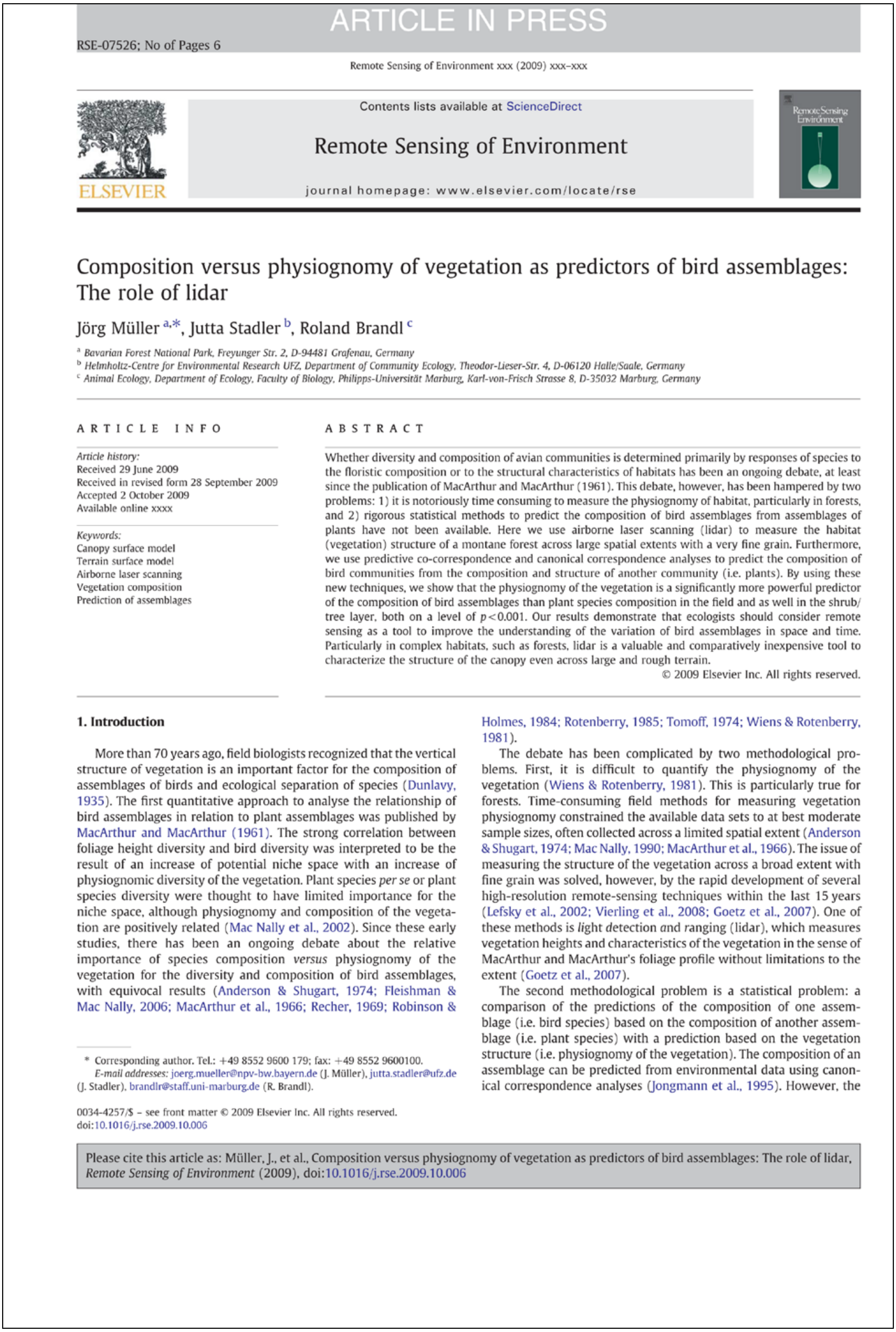

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Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar

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ABSTRACT

Whether diversity and composition of avian communities is determined primarily by responses of species to the floristic composition or to the structural characteristics of habitats has been an ongoing debate, at least since the publication of MacArthur and MacArthur (1961). This debate, however, has been hampered by two problems: 1) it is notoriously time consuming to measure the physiognomy of habitat, particularly in forests, and 2) rigorous statistical methods to predict the composition of bird assemblages from assemblages of plants have not been available. Here we use airborne laser scanning (lidar) to measure the habitat (vegetation) structure of a montane forest across large spatial extents with a very fine grain. Furthermore, we use predictive co-correspondence and canonical correspondence analyses to predict the composition of bird communities from the composition and structure of another community (i.e. plants). By using these new techniques, we show that the physiognomy of the vegetation is a significantly more powerful predictor of the composition of bird assemblages than plant species composition in the field and as well in the shrub/tree layer, both on a level of $p < 0.001$. Our results demonstrate that ecologists should consider remote sensing as a tool to improve the understanding of the variation of bird assemblages in space and time. Particularly in complex habitats, such as forests, lidar is a valuable and comparatively inexpensive tool to characterize the structure of the canopy even across large and rough terrain.

1. Introduction

More than 70 years ago, field biologists recognized that the vertical structure of vegetation is an important factor for the composition of assemblages of birds and ecological separation of species (Dunlavy, 1935). The first quantitative approach to analyse the relationship of bird assemblages in relation to plant assemblages was published by MacArthur and MacArthur (1961). The strong correlation between foliage height diversity and bird diversity was interpreted to be the result of an increase of potential niche space with an increase of physiognomic diversity of the vegetation. Plant species *per se* or plant species diversity were thought to have limited importance for the niche space, although physiognomy and composition of the vegetation are positively related (Mac Nally et al., 2002). Since these early studies, there has been an ongoing debate about the relative importance of species composition *versus* physiognomy of the vegetation for the diversity and composition of bird assemblages, with equivocal results (Anderson & Shugart, 1974; Fleishman & Mac Nally, 2006; MacArthur et al., 1966; Recher, 1969; Robinson & Holmes, 1984; Rotenberry, 1985; Tomoff, 1974; Wiens & Rotenberry, 1981).

The debate has been complicated by two methodological problems. First, it is difficult to quantify the physiognomy of the vegetation (Wiens & Rotenberry, 1981). This is particularly true for forests. Time-consuming field methods for measuring vegetation physiognomy constrained the available data sets to at best moderate sample sizes, often collected across a limited spatial extent (Anderson & Shugart, 1974; Mac Nally, 1990; MacArthur et al., 1966). The issue of measuring the structure of the vegetation across a broad extent with fine grain was solved, however, by the rapid development of several high-resolution remote-sensing techniques within the last 15 years (Lefsky et al., 2002; Vierling et al., 2008; Goetz et al., 2007). One of these methods is *l*ight *d*etection *a*nd *r*anging (lidar), which measures vegetation heights and characteristics of the vegetation in the sense of MacArthur and MacArthur's foliage profile without limitations to the extent (Goetz et al., 2007).

The second methodological problem is a statistical problem: a comparison of the predictions of the composition of one assemblage (i.e. bird species) based on the composition of another assemblage (i.e. plant species) with a prediction based on the vegetation structure (i.e. physiognomy of the vegetation). The composition of an assemblage can be predicted from environmental data using canonical correspondence analyses (Jongmann et al., 1995). However, the

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problem of predicting one community matrix from another was only recently solved by Ter Braak and Schaffers (2004) by developing a procedure called co-correspondence analysis. The number of relevant axes for comparing the predictions can be selected by using the number of axes providing the best cross-validatory fit or by using the significant axes for each of two ordinations. In earlier studies, the problem regarding the relationship between bird assemblages and vegetation was bypassed either by using certain surrogates representing characteristics of the two communities [i.e. species richness, diversity; e.g. MacArthur and MacArthurs (1961)], by using Procrustes superimposition of independent ordinations of the two matrices, or by using matrix correlation (Mac Nally, 1990). Reducing the composition of an assemblage to a vector, i.e. species richness, reduces much of the information in the community composition to single numbers. When Procrustes superimposition is used, the same number of axes of the ordination of bird and plant data must be used to evaluate the similarity in the configurations (Ter Braak & Schaffers, 2004); this selection of the number of axes is often arbitrary, and the relevant axis of each ordination may not capture the essentials of the joint information. Matrix correlations require the input of a similarity index between bird assemblages and the vegetation, and these are plotted against each other (for a comparison of matrix correlation and Procrustes superimposition, see Peres-Neto & Jackson, 2001). The plethora of similarity and dissimilarity coefficients leads to arbitrary decisions in the selection of appropriate coefficients. Matrix correlations as well as Procrustes rotations are by definition correlative rather than predictive.

The combination of variables derived from high-resolution lidar data with predictive statistical methods now provides the methodological basis for a rigorous test of the differences in the power of plant species composition *versus* structure of the vegetation to predict the composition of bird assemblages, i.e. the relative abundance of each species.

2. Methods

2.1. Study area

We sampled the composition of bird and plant assemblages in the Bavarian Forest National Park in southeast Germany along four transects (Bässler et al., 2008; Müller et al., 2009a,b). These transects are part of a long-term monitoring project of biodiversity and climate changes (for a map and further discussion about spatial effects see Bässler et al., 2008; Müller et al., 2009a; Müller & Brandl, 2009). The elevation ranges from 650 to 1420 m above sea level and is dominated by mixed montane forests consisting of spruce (*Picea abies*), beech (*Fagus sylvatica*), and fir (*Abies alba*). At higher elevations, spruce is the dominant tree species. Owing to natural disturbances during the last decades (wind throw, bark beetle attack; Müller et al., 2008), the canopy structure within all transects varies from open to closed, independent of altitude. Owing to the acidic soil, the field layer at higher elevations with an open canopy is dominated by *Vaccinium* sp., and the field layer in the beech-dominated stands is species poor. In open stands, grass species, in particular *Calamagrostis villosa*, dominate the vegetation (for an illustration, see Appendix Fig. S1).

2.2. Bird and vegetation data

Along each transect, plots were arranged in 100 m intervals. We counted birds within 100 m × 100 m grids around each plot centre for 10 min during five visits at the end of March, in mid-April, at the beginning and at the end of May, and at the beginning of June in 2007. The sum of all registrations of a species was used as a surrogate for the abundance of this species within the plot and was arranged in a matrix of bird composition by site ([B]). Our measure of abundance integrates across the migratory and breeding season. Although the probabilities of registering migratory and breeding species differ, this measure is nevertheless a fair representation of the usage of a plot by the bird assemblage from spring to autumn (for more details and discussion of methods, see Moning & Müller, 2008; Müller et al., 2009b).

The plant species composition was mapped by rélevees (excluding mosses and lichens) covering 0.5 ha in the centre of each plot. Cover-abundance of species was noted for four strata following Braun-Blanquet (1964): herb layer, shrub layer up to 5 m, tree layer 1 from > 5 to 20 m, and tree layer 2 from > 20 m. From these raw data, we generated two matrices characterizing the composition of the plant assemblages as well as cover-abundance of each species (for an example, see Appendix material Tables S1, S2): First, we summarized the cover-abundance of species among the shrub and tree layers ([T]). Second, we formed a similar matrix only for the plant species recorded in the field layer ([F]).

2.3. Airborne laser scanning (lidar)

Canopy data were gathered by digital airborne lidar using a Riegl LMS-Q560 scanner installed on a helicopter at a flight height of 400 m. The pulse at half maximum lasted 4 ns and the laser wavelength was 1550 nm. Full waveform data were collected in May 2007 after leaf flush, with an average point density of 25 m^{-2} and a vertical error of 15 cm, on an approximately 400 m wide strip along the transects. The lidar points were derived from the full waveform data, with one to 11 discrete points generated per laser shot. On the basis of these data, a digital surface model and a digital terrain model were calculated. To calculate the digital surface model, the raw data points were sorted into a rectangular array of cells (0.25 m × 0.25 m). When sorting these data into the grid, some cells may contain more than one value. From these points, only the cell with the highest elevation value was used. The cells not covered by laser data points were filled by bilinear interpolation.

The digital terrain model was developed in three steps according to the method described by Axelsson (2000). First, during the automatic classification, where the appropriate suitable estimation area of 60 m × 60 m was defined step-wise, the lowest data points were located, classified as ground points, and connected by a triangulated irregular network. This network was then refined by an iterative addition of lidar points and therewith new triangles, until no further points could be found. Second, the automatically classified digital terrain model was checked visually, and incorrectly classified points (<1 % of all points) were manually assigned to the correct classes. Third, the raster digital terrain model was created by interpolation of the height values generated by the previous steps to obtain values for the centres of the digital terrain model cells with a spatial resolution of 1.0 m (Axelsson, 2000). The digital crown model was then derived by subtracting the digital terrain model from the digital surface model, providing a canopy model with a spatial resolution of 0.25 m.

Finally, for each 100 m × 100 m plot, we calculated six parameters characterizing the canopy structure (after MacArthur & MacArthur, 1961). The mean canopy height, the standard deviation of mean canopy height, and the maximum height of canopy were calculated from the digital crown model. Mean canopy height provides a measure of the vegetation height. The standard deviation of vegetation height is an index of vertical variation of canopy height: plots with a uniform tree height exhibit a small standard deviation, and plots with a mixture of small and large trees exhibit a larger standard deviation. The maximum height of canopy provides information about the occurrence of the tallest tree canopy within a single 1.0 ha plot. To characterize the openness of the canopy, we calculated the penetration ratio at 2 m above ground, dividing the sum of all laser echoes below 2 m by the sum of all laser echoes below 50 m, and the penetration ratio at two different lower canopy layers.

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The sum of all laser echoes below 2 m above ground divided by the sum of all laser echoes below 10 m above ground (including those of below 2 m) represents an estimate of the proportion of intermediate trees (mid-storey) of the forest stands in our region, with a regular height up to 30–40 m. The ratio of the sum of echoes below 1 m above ground divided by the sum of all laser echoes below 5 m in the same way is an estimator particularly for the shrub and regeneration layer, with high values in plots having a low density of shrubs and regeneration (for further discussion of the ecological interpretation of these parameters, see Müller et al., 2009b). Overall, we characterized the structure (physiognomy) of the vegetation by a matrix of six variables derived from lidar across sites ([P]). We deliberately did not derive topographic parameters from the terrain model in this application because the aim of this study was to compare only the predictive power of physiognomy and plant species composition on bird species assemblages. However, the elevation gradient has some influence on both the physiognomy and the plant species composition (see above). Furthermore, none of our species under focus was restricted by elevation *per se*. A quantification of the influence of altitude in predictive power can be found in Müller and Brandl (2009) and Müller et al. (2009b).

2.4. Statistical methods

The trees at some sites were too densely grown for any plants to occur in the herb layers on the plots; other sites were open plots lacking tree or shrub species after bark beetle infestation (see Appendix Fig. S1). For these latter plots, the column sums in [T] and [F] were zero. Therefore, for all statistical analyses, we used only plots with at least one record in [T] and [F]. Overall, 254 plots passed these two criteria. To test the correlation of bird composition [B], floristic composition ([T], [F]), and vegetation characteristics [P], we used matrix correlation (Mantel test) with a Bray–Curtis distance for all matrices with bird and plant species ([B], [T], [F]) and Euclidian distance for structural characteristics [P]. These two indices are widely used in ecology for that purpose (e.g. Magurran, 2004; Wolda, 1981). The significance of the matrix correlation was evaluated by 999 permutations in the first matrix. To test for differences between two matrix correlations, we compared the difference between two matrix correlations with the differences calculated during the permutations using a two-sided test.

To predict the composition of the bird assemblages from the structural characteristics, we used a predictive version of canonical correspondence analysis (CCA); to predict [B] from [T] and [F], we used the recently developed (predictive) co-correspondence (CoCA) analysis, which allows the prediction of an assemblage by a second highly complex assemblage. In the analyses, we included only bird and plant species that occurred in at least five plots. To reduce the effect of very abundant bird species, the counts were square-root transformed. To determine the number of relevant axes, we used "leave-one-out" cross-validation (see Ter Braak & Schaffers, 2004). The number of relevant axes is the number of axes that minimizes the squared prediction error. We followed the method of Ter Braak and Schaffers (2004) and reported the cross-validatory fit:

$$\text{Cross}-\text{validatory fit} = 100\left(\frac{1-\text{ssp}_n}{\text{ssp}_0}\right),$$

where ssp_n is the sum of squared prediction error using *n* axes, and spp_0 is the sum of the squared prediction errors if rows and columns of the response matrix are independent. The cross-validatory fit may even become negative ($\text{spp}_0 > \text{ssp}_n$), which indicates that the prediction using the mean abundance of species is already better than the statistical models. We also report the significance of axes determined by permutations using functions available in the add-on package *vegan* for CCA analyses (Oksanen et al., 2006) and *cocoresp* for CoCA (Ter Braak & Schaffers, 2004). Finally, the significance of pair-wise differences in the cross-validatory fit was tested by a randomization test suggested by van der Voet (1994). This test randomizes the residuals of the predictions between the two prediction methods and therefore can cope with a different number of relevant axes selected for the two methods. All analyses were conducted in R 2.8.1 (R Core Development Team, 2008).

3. Results

Our final data set comprised 35 bird species in [B], 83 plant species in [F], and 6 plant species in [T]. In our analyses, the use of presence/absence of species in [F] and [T] produced consistently better relationships to [B] irrespective of whether we used matrix correlation or ordination methods. Furthermore, the matrix correlation analyses as well as the predictive co-correspondence and canonical correspondence analyses agreed very well (Table 1); we will only discuss the results of the latter two methods in detail. Cross-validatory fit was more than 10% for [P] and almost 8% for [F] (Fig. 1, Table 1). Although the shrub/tree layer provides the main habitat for most of our forest birds, [T] showed only a weak power for predicting bird assemblages (<2.5%). Permutation tests showed that only the first and third axes of [F] and only the first axis of [T] were significant, while the first four axes of [P] were significant. A two-sided permutation test indicated that the difference between [P] and [F] as well as between [P] and [T] was highly significant. Therefore, [P], the physiognomy of the vegetation, is the most appropriate predictor of [B], the quantitative composition of the bird assemblages.

4. Discussion

4.1. Footprint size, full wave form and lidar-derived variables

For many current ecological applications, particularly in Europe, only discrete return, small footprint lidar data are available for analysis. In our study, we used a lidar density of about 25 shots m^{-2} and a footprint size of 25 cm, which is a high spatial sampling density even for small footprint laser data. Other discrete return small footprint lidar applications to studies of birds used lower shot densities of 1–4 shots m^{-2} (i.e. Clawges et al., 2008; Hill et al., 2004), but were also able to model bird and physiognomy relationships with sufficient accuracy and ecologically meaningful results. In addition, Goetz et al. (2007) were able to predict bird species richness in forests using full waveform lidar data collected at a footprint size of nominally 12 m in diameter. In our study, however, we collected a high density of shots m^{-2} for a number of reasons. First, such a high information density is required for the detection of single trees,

Table 1
Comparison of matrix correlations with the maximum cross-validatory fits (number of axes given in parentheses) between the different matrices of bird species composition, physiognomy, and plant species composition in the field and shrub/tree layers.

Independent matrix	Dependent matrix	Mantel correlation	*P*	Cross-validatory fit (number of axes)
Physiognomy [P]	Field layer [F]	0.27	<0.001	6.80 (5)
Physiognomy [P]	Shrub/tree layer [T]	0.28	<0.001	10.7 (5)
Field layer [F]	Shrub/tree layer [T]	0.14	<0.001	3.64 (5)
Physiognomy [P]	Birds [B]	0.44^b	<0.001	10.3^b (5)
Field layer [F]	Birds [B]	0.11^b	<0.001	7.83^a (5)
Shrub/tree layer [T]	Birds [B]	0.16^b	<0.001	1.91^a (1)

For the matrix correlations, we used the Bray-Curtis distance for species × site matrices using presence/absence information and Euclidian distance for structure × sites matrices. Significant differences between the three matrix correlations and between the three cross-validatory fits are coded by letters.

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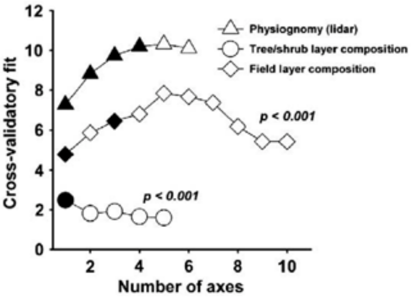

Fig. 1. Cross-validatory fit of the avian community composition. The cross-validatory fit is plotted against the number of ordination axes for the three sets of predictor variables: canopy structure and physiognomy of the vegetation, plants species composition of the shrub/tree layer, and plant species composition of the field layer. The filled symbols indicate significant axes using permutation tests. To test for differences in the cross-validatory fit between two data sets, we permuted residuals between data sets (see van der Voet, 1994) using the number of axes with the maximum of predictive power (five for physiognomy and field layer composition; one for the tree/shrub layer). The significance of axis is shown as additional information. The p values for the comparison of physiognomy and each of the two plant composition matrices are indicated; the difference in the predictive power between field and tree/shrub layer composition was not significant ($p = 0.43$).

particularly of smaller trees. Second, we wanted to capture characteristics also of the understory, which is difficult to measure with lower resolution lidar data in broadleaf stands during the growing season, because understory vegetation provides important habitat for birds as well as for other groups of organisms. Indeed, in our study area we have previously shown that variables describing the understory can be important in characterizing the bird community (Müller et al., 2009b).

Our aim to collect small footprint, discrete return lidar data at a very fine spatial resolution to characterize the vegetation canopy is consistent with studies that have utilized larger footprint full waveform lidar data. In contrast to first-last pulse and even to multiple-return, full waveform data records substantial amounts of energy as returned from throughout the vertical profile of the canopy (including more reflections in the tree crowns, which can be critically in bird habitat modelling (Graf et al., 2009)) and allows one to derive a broad set of habitat variables (Goetz et al., 2007). By using small footprint, discrete return data collected at a high density and averaging the returns over a larger area (i.e., similar in size of a large footprint system), it is possible to derive "simulated" waveforms to characterize vegetation structure (e.g. Falkowski et al., 2009) that may assist our future data analyses.

However, the question remains if a density 25 of shots m^{-2} is necessary. In this respect, we also tested our ability to model the relationships of organisms with a much smaller body size than birds, i.e. beetles (see Müller & Brandl, 2009), with the expectation that we would find greater importance particularly of fine scale information as the organisms decrease in size. In general, the question of resolution decreases in importance with increasing plot size. Our recent study on the predictability of beetle assemblages as a typical small-body-sized species group showed a higher predictive power of lidar variables when we integrated the data across 1.0 ha around the trap stations than when we integrated the data across 0.1 ha (Müller & Brandl, 2009). Considering these results, we expect that even lidar data with a lower shot density in small footprint data or much lower resolution of Satellite-borne large footprint waveform lidar data, when more broadly available in the future, have enormous potential for modelling assemblages of birds or other organisms and remove spatial restrictions. A rigorous investigation of the required resolutions and spatial scales is urgently needed in order to assess the appropriate scales at which similar relationships can be modeled. We need to compare the relationships of habitat variables derived by remote sensing and ecological data using environmental data of different resolution and ecological data of organisms differing in body size and dispersal propensity. Only a few steps have been taken in this direction (e.g. for skylark, Mason et al., 2003).

The first applications of lidar used only the canopy height as parameter in modeling forest bird response (Hinsley et al., 2006). The rapid increase of applications in the last three years resulted in a wide set of different variables derived, which evokes the question, of whether the use of other variables could have improved our results. We attempted to quantify the cover of the typical layers in temperate forests, which may be useful in characterizing habitats for bird species according to the literature (Glutz von Blotzheim & Bauer, 1991). We aimed to measure important variables which can be directly interpreted. Nevertheless, the usefulness of such variables may differ between species as well as habitats. Clawges et al. (2008) derived not the same but similar variables capturing different vegetation layers as well as the diversity of layers. Furthermore they combined the information with multispectral data which clearly will improve the information beyond physiognomy if tree species can be identified and taken into account. However, this was not the aim of our study, as we restricted the information to physiognomy only following the idea of MacArthur and MacArthur (but see also previous analysis in our study using aerial photography; Müller et al., 2009b). Goetz et al. (2007) successfully developed an index of the vertical distribution of the vegetation independent from height using full waveform data. We included only the standard deviation of height as a measurement of vertical distribution, but we have to be aware that many of the different variables are clearly correlated. Therefore we would not expect a much better result using different parameters in our analysis. At present there is no standard set of variables derived from lidar to characterize the physiognomy of the vegetation (i.e. for birds see Bradbury et al., 2005; Clawges et al., 2008; Goetz et al., 2007; Vierling et al., 2008). A systematic evaluation of the different possible ways to measure single habitat characteristics with lidar in bird studies and their ecological interpretation across organisms and ecosystems would be helpful.

4.2. Statistical methods

Beyond the availability of meaningful physiognomic data, the development of co-correspondence analyses and the first applications of this technique by Schaffers et al. (2008) paved the road for studies comparing the predictive power of the vegetation structure and of the plant species composition for the community composition of birds and other organisms. Such a predictive approach seems to be more powerful and rigorous than the comparison of matrix correlations (Legendre et al., 2005; Ter Braak & Schaffers, 2004). In the ecological literature, one finds some discussion about the conceptual differences between the two approaches (Pélissier et al., 2008; Tuomisto & Ruokolainen, 2006). Nevertheless, in our study (Table 1), the matrix correlations between the data sets did not statistically differ, whereas the predictive power showed clear significant differences. Beyond the advanced possibilities of testing predictive ordinations, these methods also maintain information about species identity. This may turn into a disadvantage, however, when data with very different species compositions are used. A further advantage of co-correspondence analyses and canonical correspondence analysis is the visual inspection of the relationship of species or variables in the dependent and independent matrices (for an example, see Appendix Figs. S2, S3), which is also possible for Procrustes superimpositions (Peres-Neto & Jackson, 2001; see also Müller et al., 2009b).

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4.3. Physiognomy versus plant species composition

The main aim of MacArthur and MacArthur's classic 1961 study, and of our study, was to compare the predictive power of plant species composition and physiognomy for forest bird assemblages. In an analysis of insect assemblages along road verges, Schaffers et al. (2008) demonstrated that plant species composition had more predictive power than the physiognomy of the vegetation. This result was attributed to the integrative character of the plant assemblages for characterizing the environmental condition, which in turn determines the occurrence of insects. Our results for bird assemblages contrast with this recent finding for insect assemblages. In our study, the structure of the vegetation was a significantly more powerful predictor for birds than plant species composition. Even if the majority of the bird species in our study have mostly shrubs and trees as habitat (for the species list, see Appendix Table S3), the species composition of the field layer had more predictive power than the species composition of the shrub/tree layer (see Table 1). The density and cover of the shrub layer influences foraging and resting behaviour. Nevertheless, the structure of the shrub/tree layer, like the canopy in general, also determines the composition of the field layer, which leads to a positive matrix correlation and cross-validatory fit of physiognomy and field layer (Table 1): below an open canopy, plant species composition differs between open and closed habitats. Our results suggest that for birds the lidar-derived variables characterize the physiognomy of the shrub/tree layer in a more meaningful way than the plant species composition of the field layer.

A number of published studies using matrix correlations have shown that plant species composition is more closely correlated to bird species composition than a similarity matrix constructed from physiognomic data (Mac Nally, 1990; Wiens & Rotenberry, 1981). This was not the case in our study, where the correlation coefficients were higher between physiognomy and community composition of birds than between plant composition and birds (Table 1). Furthermore, matrix correlation and the new statistical methods generated almost similar results, which indicate that the difference in the conclusions between our study and previous studies is not due to different statistical methods. We argue that the different results are a matter of spatial scale (Mac Nally, 1990). Studies favouring the importance of physiognomy use sites spread across a larger geographical range and with a greater diversity of habitat types than in our study. In contrast, studies favouring the composition of the plant community use fewer and less diverse sites (Mac Nally, 1990).

4.4. Remote sensing opens new doors for ecology

As demonstrated, lidar-derived variables provide elegant possibilities to test the long-standing hypothesis about the relationship between vegetation and assemblages of organisms. Clearly, remote-sensing techniques allow the collection of data of the vegetation across large spatial extents and with a small grain. In the extremes, lidar can identify single trees (Popescu et al., 2003) and can also provide information across continents. Although several review articles on the potential of lidar for habitat modelling have appeared, the number of applications that approach basic ecological questions is still small (for an overview, see Bradbury et al., 2005; Clawges et al., 2008; Vierling et al., 2008). As Turner et al. (2003) point out, this probably stems from the persistent false impression among scientists that there is a mismatch between the supposed coarse resolution of remote sensing *versus* the fine scale of environmental response of small organisms (e.g. arthropods). If an expanding number of biodiversity studies can show that there is a strong correlation with a causal link between environmental parameters derived with remote sensing and the distribution of an organism (e.g. Lassau et al., 2005a,b; Müller & Brandl, 2009), the remote-sensing revolution could be the key to obtain wide spatial coverage of biodiversity estimators, without sacrificing data resolution. Even in aquatic habitats, there are several ecological applications of lidar for modelling fish diversity in coral reefs (Kuffner et al., 2007) or salmon nesting patterns in rivers (McKean et al., 2008).

5. Conclusions

Our study shows that airborne laser scanning (lidar), a comparatively inexpensive remote-sensing technique, provides statistically well-behaved data on plant physiognomy in a complex habitat, i.e., forest. This technique enabled us to better test the long-standing hypothesis on the relationship between vegetation structure and assemblages of birds. The physiognomy of the vegetation was clearly a better predictor than plant species composition. The initial sampling of detailed information on the vegetation structure, even across large areas, allows the application of powerful statistical methods, such as co-correspondence analysis. Therefore, ecologists should consider lidar as an important remote-sensing tool to test ecological theories and to improve the understanding of the variation of assemblages in space and time, even across large areas and rough terrain.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rse.2009.10.006.

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Artikel 10: Umsetzung Ökologischer Schwellenwerte in betriebliche Naturschutzkonzepte in Bergmischwäldern

Status: Eingereicht bei Naturschutz und Landschaftsplanung, 2009.

Umsetzung ökologischer Schwellenwerte in betriebliche Naturschutzkonzepte in Bergmischwäldern

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Zusammenfassung

Das Fehlen harter Richtlinien für Naturschutzkonzepte in Bergmischwäldern war Grundlage zur Initiierung des DBU Projektes „Waldökologische Schlüsselwerte in Bergmischwäldern als Grundlage für eine ökologisch nachhaltige Forstwirtschaft“, das im Nationalpark Bayerischer Wald zwischen 2007 und 2010 durchgeführt wurde. Die wesentlichen Produkte des Projektes sind Empfehlungen für Maßnahmen auf Bestandsebene sowie auf der übergeordneten Planungsebene ökologische Schwellenwerte und deren Umsetzung in betriebliche Naturschutzkonzepte. Dieser Artikel skizziert die Grundlagen und Abläufe des letzten Punktes. Auf Grundlage der Forstinventurdaten wurden die aus dem Projekt resultierenden ökologischen Schwellenwerte in ein naturschutzfachliches Konzept umgewandelt. Dazu mussten die Inventur-Punktdaten interpoliert werden, um flächige Informationen zu ökologischen Schlüsselwerten zu erhalten. Darauf basierend wurden die errechneten Schwellenwerte genutzt, um die flächigen Daten zu klassifizieren. Auf Grundlage dieser Klassifikation konnten naturschutzfachliche Handlungsempfehlungen auf betrieblicher Ebene abgeleitet werden. Der Ansatz zeigt, wie man selbst in Betrieben mit sehr hohem naturschutzfachlichen Potenzial über die Schwellenwerte zu einer flächendifferenzierten Naturschutzplanung kommen kann.

1 Einleitung

Trotz der großen naturschutzfachlichen Bedeutung, die Bergmischwälder in Mitteleuropa haben, existieren wenige harte Richtlinien zu Naturschutzbelangen für diesen Lebensraum. Mittlerweile stehen jedoch statistische Methoden zur Verfügung, um aus einer Fülle von

Umwelt- und Bestandsdaten die wichtigsten Schlüssel- und Schwellenwerte für das Vorkommen naturschutzfachlich relevanter Arten und Artengruppen zu errechnen (LAUSEN & SCHUMACHER 1992, HOTHORN & LAUSEN 2003, HOTHORN et al. 2006, HOTHORN & ZEILEIS 2008). Diese können Förstern in Wirtschaftswäldern belastbare Zielgrößen liefern (z.B. BÜTLER et al. 2004, MÜLLER & HOTHORN 2004, MÜLLER & BUSSLER 2008, MONING et al. 2009a, b).

Fehlende Schlüssel- und Schwellenwerte sind generell ein großes Defizit bei der Erstellung von Naturschutzkonzepten. Wo immer sie aber bisher eingesetzt wurden, haben sie sich als erfolgreiches Planungsinstrument erwiesen (VILLARD & JONSSON 2009). Bisher existiert kein überregionales, die Naturschutzziele integrierendes Bewirtschaftungskonzept für Bergmischwälder. Der Hauptgrund liegt darin, dass von naturschutzfachlicher Seite konkrete Vorstellungen über Mindestanforderungen in der Regel nicht vorhanden sind. Dabei sind in der Zone der Bergmischwälder großflächig Schutzgebiete (Natura 2000) ausgewiesenen, in denen größtenteils weiterhin eine Bewirtschaftung allerdings mit besonderem Augenmerk auf die Naturschutzbelange stattfindet (AMMER 1992, MÜLLER-KRÖHLING 2004, NEFT 2006).

Um diese Wissenslücke zu schließen, wurde das durch die Deutsche Bundesstiftung Umwelt (DBU) geförderte Projekt „Waldökologische Schlüsselwerte in Bergmischwäldern als Grundlage für eine ökologisch nachhaltige Forstwirtschaft“ im Nationalpark Bayerischer Wald initiiert (im folgenden kurz als „DBU-Bergmischwaldprojekt“ bezeichnet). Dieses Projekt liefert Beiträge zum Naturschutz in bewirtschafteten Bergmischwäldern auf der Ebene der übergeordneten Forstbetriebsplanung und Empfehlungen für die Berücksichtigung bei der waldbaulichen Behandlung von Beständen (Abbildung 1).

[[Abbildung 1]]

****************************Infobox**

Schlüsselwerte und Schwellenwerte

Diese Begriffe stehen im Zentrum dieser Publikation und sind wie folgt zu verstehen:

Ein **Schlüsselwert** definiert eine Umweltvariable, die in einer bestimmten Ausprägung vorhanden sein muss, damit naturschutzfachlich bedeutsame Arten oder Artengruppe vorkommen können. Dies kann beispielsweise Totholz für gefährdete Holzkäfer oder das Waldalter für den Zwergschnäpper sein.

Ein **Schwellenwert** bezeichnet hingegen einen Übergangsbereich entlang eines Gradienten einer Umweltvariable, ab dem eine bestimmte Artengruppe oder Art statistisch signifikant häufiger oder seltener auftritt. So erhöht sich die Zahl der in Baumhöhlen brütenden Vogelarten ab fünf Höhlenbäumen je Hektar signifikant.

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2 Schwellenwerte als Naturschutzziele

Ein Großteil der aus Naturschutzsicht bedeutenden waldbewohnenden Arten, hängt von einer jeweils spezifischen Ausprägung bestimmter Waldstrukturen ab (BERG et al. 1994). Daraus ergibt sich, dass die Beschreibung und Quantifizierung dieser Strukturen bei jeglichen Zielsetzungsprozessen berücksichtigt werden müssen (BÜTLER et al. 2004, PENTTILÄ et al. 2004). Dies führte dazu, dass Schwellenwerte während der letzten zehn Jahre auch international zu einem wirksamen Schutzinstrument wurden (VILLARD 2009). Ihre Naturschutz-bezogene Anwendung birgt jedoch einige Probleme. Schutzziele, die für einzelne Arten oder Artengruppen definiert werden, müssen nicht zwangsläufig sinnvoll für die gesamte Naturschutz-bedeutsame Artengemeinschaft eines Systems sein. Indem man Schwellenwerte aus verschiedenen Untersuchungsgebieten und zu verschiedenen Arten und Artengruppen eines Schlüsselwertes, wie beispielsweise Totholzmengen, sammelt, lässt sich demonstrieren ob ein bestimmter Schwellenwert nur für ein spezifisches Gebiet oder eine Art gültig ist, oder verallgemeinert werden kann (MÜLLER & BÜTLER in Vorbereitung).

Auch der Charakter eines plötzlichen Abundanzwechsels der Zielarten oder -artengruppe entlang eines Umweltgradienten muss um einen Schwellenwert herum gegeben sein, um Schwellenwerte sinnvoll anwenden zu können. Zwar lassen sich auch Schwellenwerte berechnen, die auf graduellen also linearen Zusammenhängen basieren, jedoch spiegeln sie keine wirklich ökologisch wirksame Schwelle wider (MURADIAN 2001, GUENETTE & VILLARD 2005, LINDENMAYER et al. 2005, RANIUS & FAHRIG 2006). Mit der Berechnung von Konfidenzintervallen zu den Schwellenwerten kann man dieser Problematik ein Stück weit begegnen, da man mit ihnen den Charakter der Schwellenwerte beschreibt.

Die Identifikation von Schwellenwerte soll das lokale oder regionale Aussterben von Arten verhindern. Ist der Schwellenwert unterschritten, steht der entsprechende Schlüsselwert nicht mehr in ausreichender Ausprägung zur Verfügung, die entsprechende Art stirbt mit immer größerer Wahrscheinlichkeit aus. Schwellenwerte markieren also die unakzeptable Schwelle der Habitatbeeinträchtigung, sie sollten nicht als maximal akzeptierbare Niveaus der Habitat-Degradation verstanden werden (LINDENMAYER & LUCK 2005, RADFORD et al. 2005, RANIUS & FAHRIG 2006). In mitteleuropäischen Wirtschaftswäldern liegen Schlüsselwerte wie Totholzmengen und Waldalter fast immer unter den kritischen Schwellenwerten die sich für Zielarten im Waldnaturschutz ermitteln lassen. Schwellenwerte liefern hier einen Richtwert, den es auf möglichst großer Fläche zu überschreiten gilt. Grundsätzlich sollte man Schwellenwerte nicht als fixe Naturgesetzte, sondern als den derzeitigen Stand des Wissens interpretieren.

3 Herleitung und Definition der Schwellenwerte für den Bergmischwald

Grundlage der Analysen des DBU-Bergmischwald-Projektes waren 293 Probeflächen, die im Nationalpark Bayerischer Wald eingerichtet wurden (BÄSSLER et al. 2008). Auf den Probeflächen wurden möglichst viele (n=24) und möglichst vollständige Artengruppen untersucht (BÄSSLER et al. 2008, MONING & MÜLLER 2008, MONING & MÜLLER 2009, MONING et al. 2009b). Daneben wurden zeitgleich und auf den gleichen Flächen zahlreiche Umweltparameter (n=28) wie Höhenlage, Klimaparameter, Waldstruktur und Bodeneigenschaften erhoben, gemessen oder modelliert, so dass sich das Auftreten der untersuchten Arten und Artengruppen mit den entscheidenden Umweltvariablen korrelieren ließ (BÄSSLER et al. 2008). Daraus resultierte eine Reihe von ökologischer Schlüsselwerte und Schwellenwerte, die durch Werte aus der Literatur ergänzt werden konnten. Die wichtigsten Schwellenwerte sind nach den Schlüsselwerten gegliedert in Tabelle 1 dargestellt.

[[Tabelle 1]]

3.1 Repräsentativität und Übertragbarkeit der Ergebnisse

Der Nationalpark Bayerischer Wald bietet für die Forschung an Schlüssel- und Schwellenwerten in Bergmischwäldern günstige Rahmenbedingungen, denn

1. Er ist ein repräsentativer Ausschnitt des Bergmischwaldes in Mitteleuropa (240 km²) entlang eines langen Höhengradienten von 800 m (von 655 m bis 1420 mNN) und in

verschiedensten Ausprägungen (Bodentypen, Borkenkäferbefall unterschiedlicher Intensität, usw.).

2. Auch seit Jahrhunderten ungenutzte Bestände stehen für Untersuchungen zur Verfügung.
3. Das Gebiet ist groß genug, um räumlich unabhängige und somit statistisch belastbare und auf größere Regionen übertragbare Ergebnisse zu erzielen.

Bei dem Versuchsdesign wurde besonders darauf geachtet, dass sich die weiten Umweltgradienten statistisch repräsentativ in der Flächenauswahl wiederfinden. Dies gilt auch für komplexe Einflussgrößen wie die Nutzungsintensität. So lagen zwei der Transekte im Altpark und zwei im Erweiterungsgebiet des Nationalparks. Während die Forschungsflächen im Altpark der unbeeinflussten Entwicklung unterliegen, findet im Erweiterungsgebiet auf Teilen der untersuchten Flächen noch ein Borkenkäfermanagement statt, so dass die Probeflächen sowohl noch beeinflusste als auch seit Jahrhunderten kaum beeinflusste Bestände umfassen (BÄSSLER et al. 2008). Diese Bestände sind in Alterstruktur und Totholzausstattung den angrenzenden Wirtschaftswäldern der Bayerischen Staatsforsten voll vergleichbar.

Reine Wirtschaftswälder sind für Untersuchung unserer Fragestellung wenig geeignet, da in ihnen die vollständigen Gradienten (Totholzmengen wenige bis hunderte Festmeter je ha, Waldalter >300 Jahre, usw.) nur sehr kleinräumig vorhanden sind und somit einige kritische Schwellenwerte nur auf kleiner Fläche überschritten werden. Für bestimmte Schlüsselwerte wie hohe Totholzmengen fehlen in Wirtschaftswäldern die für statistische Analysen ausreichende Anzahl an Probeflächen.

Die in diesem Projekt realisierte Untersuchung möglichst vieler Artengruppen sichert eine Art Kreuzvalidierung der ermittelten Schwellenwerte, die möglichst belastbar für das ganze Ökosystem Bergmischwald gelten sollen.

In den meisten Fällen ist es nicht ausreichend, für einen Schlüsselwert nur einen Schwellenwert für weitere Konzepte zugrunde zu legen. Totholzmengenschwellenwerte (Abbildung 2) sind ein typisches Beispiel für die Streuung der Werte, wenn verschiedene Artengruppen und Regionen betrachtet werden.

[[Abbildung 2]]

Der einzelne Wert allein gibt keine verlässliche Richtgröße für Naturschutzziele, wenn man ganze Artengemeinschaften oder Ökosysteme im Visier hat. Die Werte der Totholzmengen kulminieren in einem Bereich zwischen 30 und 60 m³/ha. Zwar lassen sich auch Werte finden, die deutlich höher liegen (beispielsweise für Flechten), jedoch bietet der Bereich 30-60 m³/ha eine solide Grundlage für eine für viele Artengruppen wirksame Zielgröße in der Forstwirtschaft. Als Grundlage für ein Naturschutzkonzept für bewirtschaftete Bergmischwälder wurden die Schwellenwerte in dem vorliegenden Projekt deshalb aus der Perspektive möglichst verschiedener Artengruppen und möglichst vieler Bergmischwaldregionen (Literatur) definiert (Tabelle 1).

4 Umsetzung der Schwellenwerte in ein betriebliches Naturschutzkonzept

Viele der aus dem Projekt resultierenden Schwellenwerte liegen weit über dem Flächendurchschnitt der meisten Betriebe im Bergmischwalbereich. Diese auf ganzer Fläche in einem ökonomisch orientierten Forstbetrieb zu überschreiten, kommt als Ziel demnach nicht in Frage. Die Schwellenwerte lassen sich vielmehr zur Identifikation der naturschutzfachlichen „Hotspots" sowie weiterer Flächen in denen vorrangig Naturschutzziele verfolgt werden sollen, innerhalb der Gesamtbetriebsfläche verwenden.

Forstinventurdaten bieten hier eine hervorragende Grundlage, um Schwellenwerte in flächige Naturschutzkonzepte umzusetzen. Sie sind überregional flächig verfügbar, wurden bislang jedoch erst wenig für naturschutzfachliche Anwendungen genutzt (z.B. MÜLLER et al. 2009). Obwohl Forstinventurdaten aus einem groben Raster bestehen (die Entfernung zwischen den Stichprobepunkten beträgt 100-200 m) können sie für betriebliche Gesamtkonzeptionen (Durchschnitt Betriebsfläche Bayerische Staatsforsten (reine Waldfläche): 17.500 ha) eine ausreichend genaue Übersicht liefern.

In dem DBU-Bergmischwaldprojekt wurden die Schwellenwerte (Tabelle 1) auf Basis der Inventurdaten in ein Naturschutzkonzept für bergmischwald-dominierte Betriebe exemplarisch umgesetzt (Tabelle 3). Dazu musste in einem ersten Schritt aus den Inventurpunkt-Daten eine flächige Information erstellt werden. Zu diesem Zweck wurde das so genannte Kriging-Verfahren angewendet, bei dem Inventur-Punktdaten auf die Fläche interpoliert werden (siehe Infobox).

****************************Infobox***************************************

Das Kriging Verfahren

Unter Kriging (oder auch: Krigen) versteht man ein geostatistisches Verfahren, mit dem man Werte an Orten, für die keine Probe vorliegt, durch umliegende Messwerte interpolieren oder auch annähern kann. Das Verfahren wurde von dem südafrikanischen Geostatistiker DANIEL KRIGE (1951) entwickelt und später nach ihm benannt. Der wesentliche Vorteil gegenüber einfacheren Methoden ist die Berücksichtigung der räumlichen Varianz. Für einen gesuchten Wert werden dabei die Gewichte der in die Berechnung einfließenden Messwerte so bestimmt, dass die Schätzfehlervarianz möglichst gering ist.

Bei einfacheren Interpolationsverfahren können bei Häufung der Messpunkte Probleme auftreten. Dies wird beim Kriging durch die Berücksichtigung der statistischen Abstände zwischen der in die Berechnung eines Punktes einfließenden Nachbarn vermieden. Kriging beruht auf effizienten und erwartungstreuen Schätzern. Tritt an einer Stelle eine Klumpung auf, werden die Gewichte der Punkte innerhalb dieses Clusters gesenkt.

Für das vorliegende Verfahren wurde die Ausgabe-Zellengröße wurde mit maximal 100 angegeben. Als Anzahl der zur Interpolation zu nutzenden umliegenden Punkte wurde acht festgelegt. Auf diese Weise werden alle Punkte, die einen Punkt umgeben in die Interpolation einbezogen. Bei 12 Punkten, wie es in dem Kriging-Menü voreingestellt ist, greift die Interpolation weiter, Maximalwerte nivellieren sich stärker. Für die Suchkulisse im Bergmischwald macht die Einbeziehung jeweils nur der Nachbarpunkte mehr Sinn. Insbesondere, da das Inventurraster eher weit und von Haus aus eher größerskalig angelegt ist.

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Das Kriging-Verfahren liefert für die einzelnen Schlüsselwerte flächige und stufenlose Daten. Diese wurden dann gemäß den Schwellenwerten klassifiziert (Tabelle 2), so dass sich folgende Flächenkategorien abbilden lassen (Tabelle 3):

1. Flächen, in denen die Schwellenwerte überschritten sind.
2. Flächen, in denen nur Teile der Schwellenwerte überschritten sind.
3. Flächen, in denen keiner der Schwellenwerte überschritten ist.

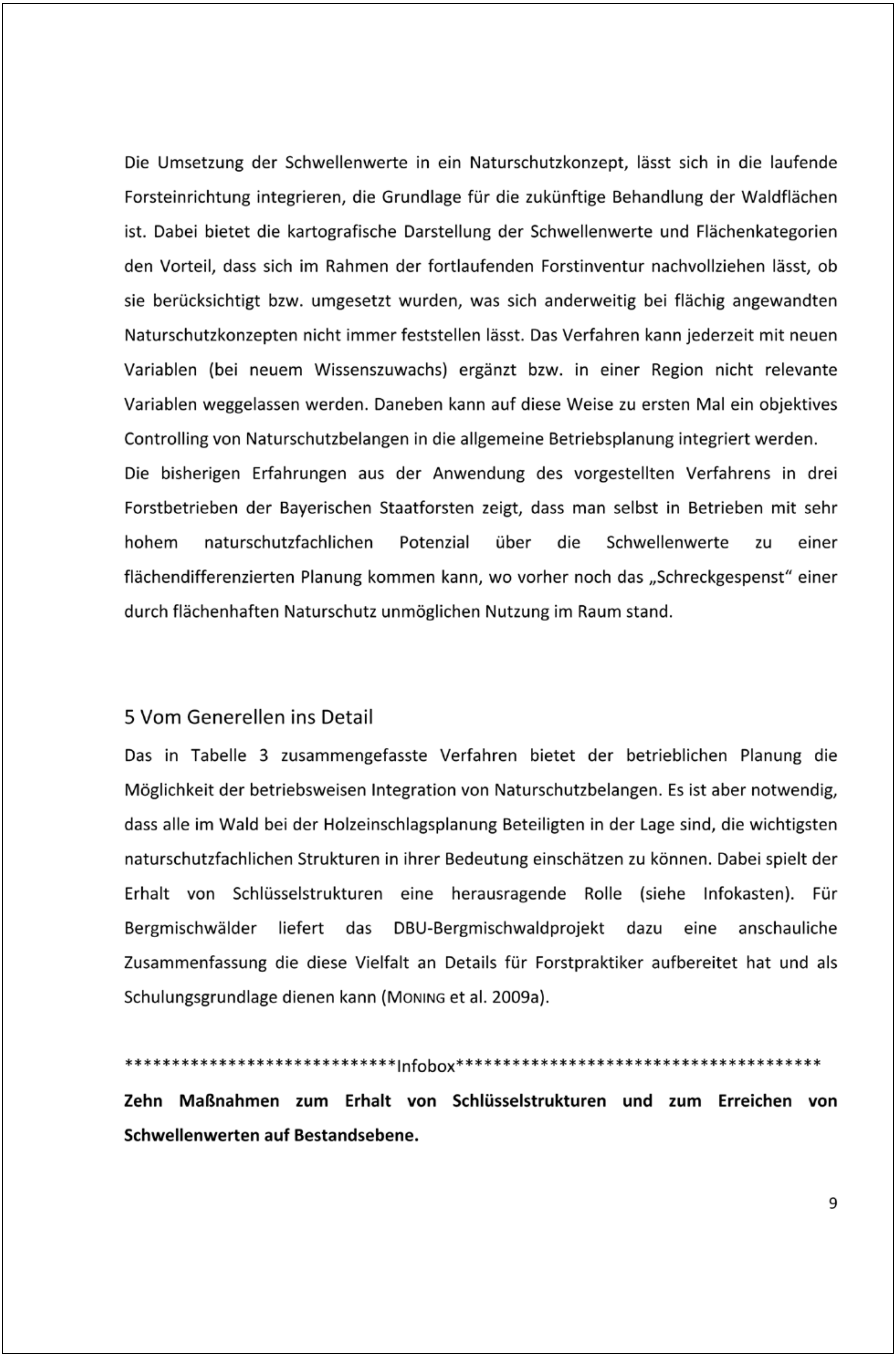
[[Tabelle 2]]

[[Tabelle 3]]

Auf diesen Flächenkategorien basierend konnten Handlungsempfehlungen abgeleitet werden (Schritt 3, Tabelle 3). Flächen der Kategorie 1 sind naturschutzfachliche Kernflächen. In ihnen steht der Erhalt der Qualität der vorliegenden Schwellenwerte im Vordergrund. Flächen der Kategorie 2 sind Entwicklungsflächen. In ihnen wird das Überschreiten der Schwellenwerte angestrebt. Dabei sollte insbesondere in Beständen mit einem verhältnismäßig hohen Bestandsalter ab rund 140 Jahren angestrebt werden, mindestens 30 m³ Totholz je ha zu erreichen. Diese Bestände bieten eine große Nischenvielfalt, die durch die alten Bäume entsteht. Im Zusammenhang mit hohen Totholzmengen können sie Lebensraum gerade für hoch spezialisierte Tier- und Pflanzengruppen bieten.

Flächen der Kategorie 3 sind schließlich ökonomische Vorrangflächen. Dies soll nicht bedeuten, dass dort langfristig nicht auf naturnähere Waldbestände hingearbeitet werden soll (z.B. Laubholzeinbringung in Fichtenreinbeständen, Entwicklung von Biotopbäumen, Erhalt und Markierung von Höhlenbäumen). Der Gesamtablauf des skizzierten Verfahrens ist in Tabelle 3 schematisch dargestellt.

Auf Basis der naturschutzfachlichen Kernflächen und der Entwicklungsflächen können auch Empfehlungen für die Etablierung von Habitatkorridoren abgeleitet werden, denn wenn naturschutzfachlich wertvolle Flächen von anspruchsvollen Arten besiedelt werden sollen, müssen sie durch Korridore vernetzt sein. Dazu bieten sich vor allem die Flächen der Kategorie 2 an, soweit diese zwischen Flächen der Kategorie 1 vorhanden sind. Neben dem Anstreben der Schwellenwerte lässt sich die Vernetzung auch durch weitere Einzelmaßnahmen verbessern, z.B. den Erhalt oder die Schaffung von Biotopbäumen, oder den Erhalt und die Verbesserung bachbegleitender Baumbestände, die meist baumarten- und totholzreicher als die Durchschnittsbestände sind.



Die Umsetzung der Schwellenwerte in ein Naturschutzkonzept, lässt sich in die laufende Forsteinrichtung integrieren, die Grundlage für die zukünftige Behandlung der Waldflächen ist. Dabei bietet die kartografische Darstellung der Schwellenwerte und Flächenkategorien den Vorteil, dass sich im Rahmen der fortlaufenden Forstinventur nachvollziehen lässt, ob sie berücksichtigt bzw. umgesetzt wurden, was sich anderweitig bei flächig angewandten Naturschutzkonzepten nicht immer feststellen lässt. Das Verfahren kann jederzeit mit neuen Variablen (bei neuem Wissenszuwachs) ergänzt bzw. in einer Region nicht relevante Variablen weggelassen werden. Daneben kann auf diese Weise zu ersten Mal ein objektives Controlling von Naturschutzbelangen in die allgemeine Betriebsplanung integriert werden.

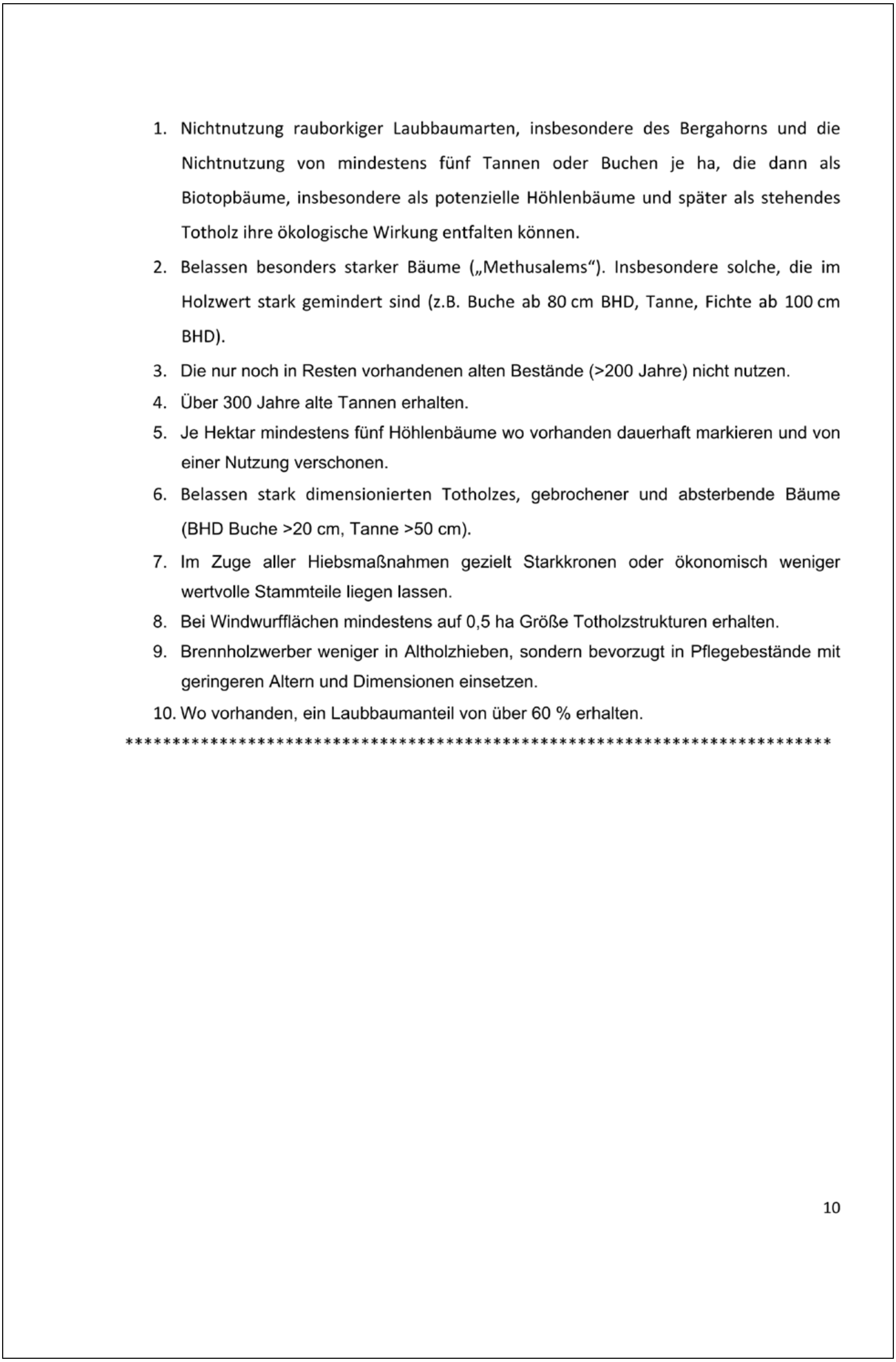
Die bisherigen Erfahrungen aus der Anwendung des vorgestellten Verfahrens in drei Forstbetrieben der Bayerischen Staatforsten zeigt, dass man selbst in Betrieben mit sehr hohem naturschutzfachlichen Potenzial über die Schwellenwerte zu einer flächendifferenzierten Planung kommen kann, wo vorher noch das „Schreckgespenst“ einer durch flächenhaften Naturschutz unmöglichen Nutzung im Raum stand.

5 Vom Generellen ins Detail

Das in Tabelle 3 zusammengefasste Verfahren bietet der betrieblichen Planung die Möglichkeit der betriebsweisen Integration von Naturschutzbelangen. Es ist aber notwendig, dass alle im Wald bei der Holzeinschlagsplanung Beteiligten in der Lage sind, die wichtigsten naturschutzfachlichen Strukturen in ihrer Bedeutung einschätzen zu können. Dabei spielt der Erhalt von Schlüsselstrukturen eine herausragende Rolle (siehe Infokasten). Für Bergmischwälder liefert das DBU-Bergmischwaldprojekt dazu eine anschauliche Zusammenfassung die diese Vielfalt an Details für Forstpraktiker aufbereitet hat und als Schulungsgrundlage dienen kann (Moning et al. 2009a).

****************************Infobox***

Zehn Maßnahmen zum Erhalt von Schlüsselstrukturen und zum Erreichen von Schwellenwerten auf Bestandsebene.



1. Nichtnutzung rauborkiger Laubbaumarten, insbesondere des Bergahorns und die Nichtnutzung von mindestens fünf Tannen oder Buchen je ha, die dann als Biotopbäume, insbesondere als potenzielle Höhlenbäume und später als stehendes Totholz ihre ökologische Wirkung entfalten können.
2. Belassen besonders starker Bäume („Methusalems“). Insbesondere solche, die im Holzwert stark gemindert sind (z.B. Buche ab 80 cm BHD, Tanne, Fichte ab 100 cm BHD).
3. Die nur noch in Resten vorhandenen alten Bestände (>200 Jahre) nicht nutzen.
4. Über 300 Jahre alte Tannen erhalten.
5. Je Hektar mindestens fünf Höhlenbäume wo vorhanden dauerhaft markieren und von einer Nutzung verschonen.
6. Belassen stark dimensionierten Totholzes, gebrochener und absterbende Bäume (BHD Buche >20 cm, Tanne >50 cm).
7. Im Zuge aller Hiebsmaßnahmen gezielt Starkkronen oder ökonomisch weniger wertvolle Stammteile liegen lassen.
8. Bei Windwurfflächen mindestens auf 0,5 ha Größe Totholzstrukturen erhalten.
9. Brennholzwerber weniger in Altholzhieben, sondern bevorzugt in Pflegebestände mit geringeren Altern und Dimensionen einsetzen.
10. Wo vorhanden, ein Laubbaumanteil von über 60 % erhalten.

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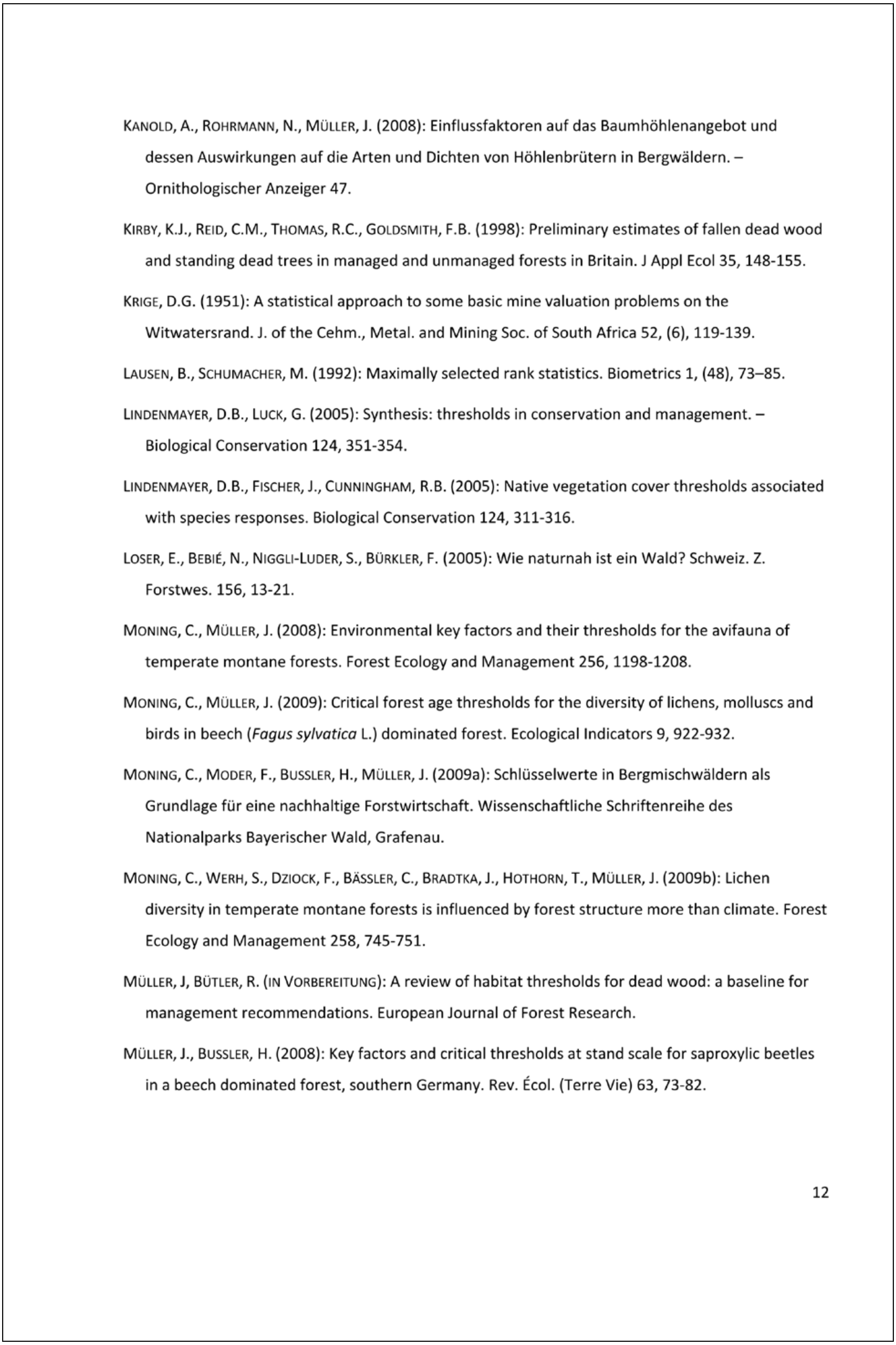

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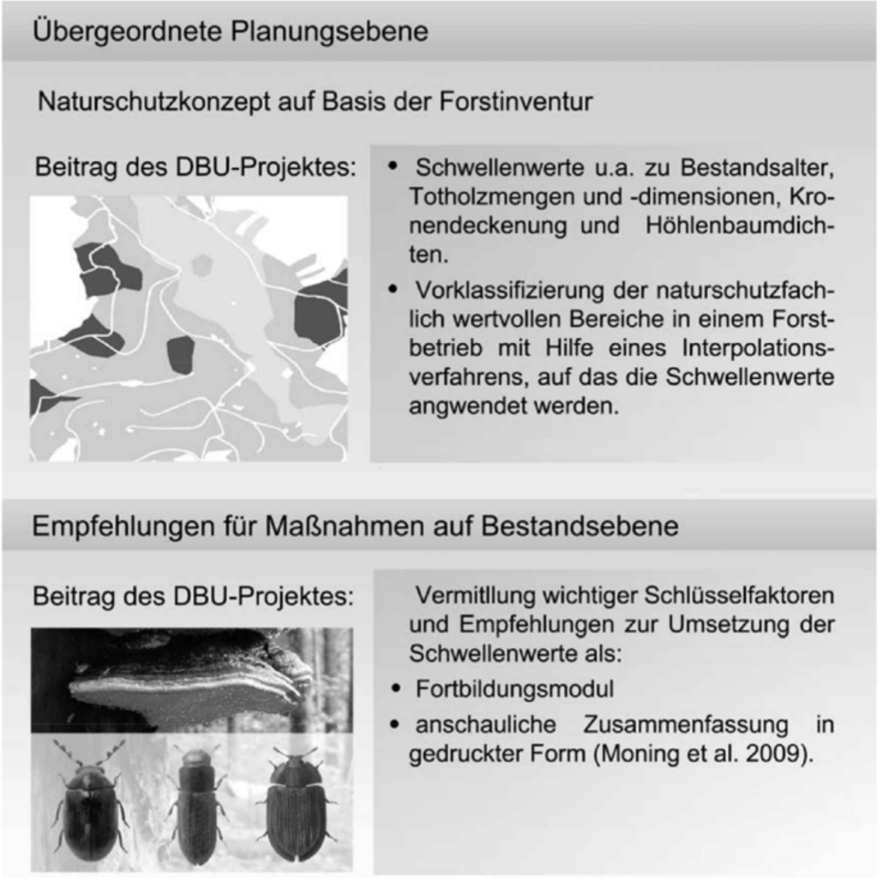


Übergeordnete Planungsebene

Naturschutzkonzept auf Basis der Forstinventur

Beitrag des DBU-Projektes:

- Schwellenwerte u.a. zu Bestandsalter, Totholzmengen und -dimensionen, Kronendeckenung und Höhlenbaumdichten.
- Vorklassifizierung der naturschutzfachlich wertvollen Bereiche in einem Forstbetrieb mit Hilfe eines Interpolationsverfahrens, auf das die Schwellenwerte angwendet werden.

Empfehlungen für Maßnahmen auf Bestandsebene

Beitrag des DBU-Projektes:

Vermitllung wichtiger Schlüsselfaktoren und Empfehlungen zur Umsetzung der Schwellenwerte als:

- Fortbildungsmodul
- anschauliche Zusammenfassung in gedruckter Form (Moning et al. 2009).

Abbildung 1: Das DBU-Bergmischwaldprojekt liefert auf zwei Ebenen naturschutzfachliche Instrumente und Handlungsempfehlungen.

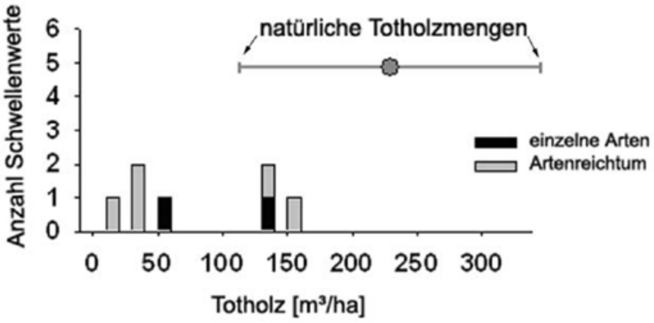
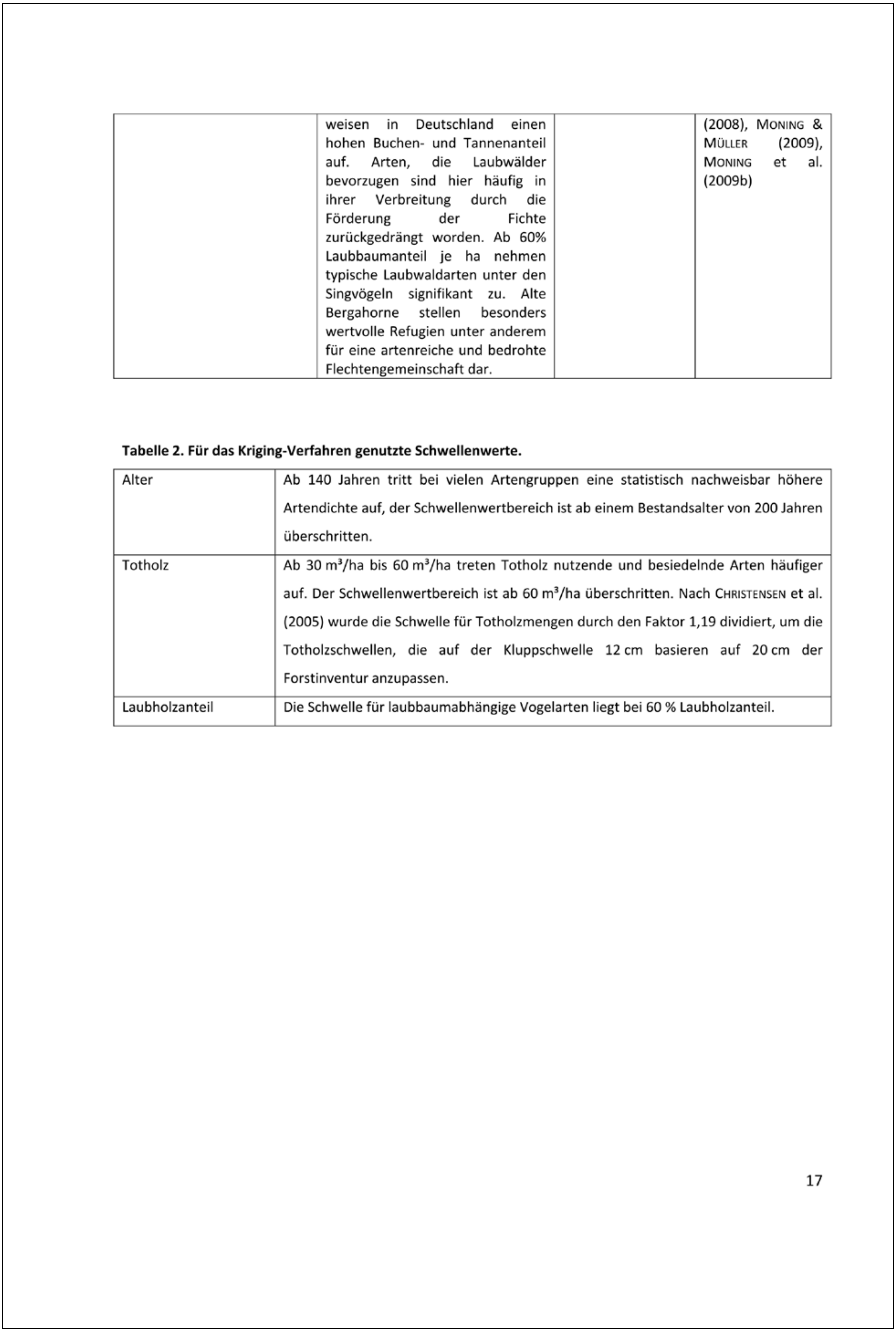


Abbildung 2. Histogramm von sieben Schwellenwerten für das Auftreten einzelner Arten oder Artenreichtum in Abhängigkeit zur Totholzmenge [m³/ha] in Bergmischwäldern. Die waagerechte Linie zeigt die Spannweite natürlicher Totholzmengen in alten Naturwaldreservaten. Bei den Werten aus der Literatur wurden nur die Mittelwerte verwendet. Aus MÜLLER & BÜTLER (in Vorb.).

Tabelle 1. Ökologische Schlüsselwerte und Schwellenwerte in Bergmischwäldern. Projektergebnisse Nationalpark Bayerischer Wald und Literatur.

Schlüsselwert	Schwellenwert	Untersuchte Artengruppen	Quellen
Totholzmenge	Totholz besiedelnde Artengruppen und insbesondere bedrohte Arten unter den Totholzbesiedlern profitieren ab Totholzmengen von rund 30 m³/ha. Ab 60 m³/ha ist eine für den Erhalt vieler Artengruppen nachhaltige Totholzmenge erreicht (siehe auch Abbildung 2).	Flechten, Moose, Pilze, holzbewohnende Insekten insbesondere Käfer, Vögel	Ammer (1991), Bütler et al. (2004), Erdmann & Wilke (1997), Frank (2002), Kirby et al. (1998), Loser et al. (2005), Moning & Müller (2008), Moning et al. (2009a), Müller & Bütler (in Vorb.), Roberge et al. (2008), Utschick (1991)
Waldbestandsalter	Ab einem Bestandsalter von rund 200 Jahren (gemessen am ältesten Baum im Probekreis) erreicht die Artendichte bei verschiedenen Artengruppen wie Flechten, Mollusken und Vögeln ein statistisch signifikant höheres Niveau. Der ansteigende Trend beginnt im Bergmischwald bei einem Bestandsalter von rund 140 Jahren.	Flechten, Mollusken, Vögel	Moning & Müller (2008), Moning & Müller (2009)
Waldlücken	Unter den kühlen klimatischen Bedingungen von Bergwäldern treten lichtbedürftige Arten erst ab Lückengrößen von mindestens 0,5 ha signifikant zahlreicher auf. Einige Artengruppen wie Flechten und holzbewohnende Käfer treten in diesen Waldlücken erst bei ausreichendem Substrat- also Totholzangebot auf. Ein breiter Gradient der Kronendachöffnung zwischen 15 % und 50 % über eine größere Fläche bewirkt, dass alle ökologischen Nischen bei den Strauchbewohnern unter den Vögeln bedient werden und somit eine hohe Artenvielfalt erzeugt wird.	Flechten, pflanzenfressende Wanzen, Spinnen, holzbewohnende und Pflanzenfressende Käfer	Moning & Müller (2008), Moning et al. (in Vorb.), Müller et al. (2007)
Baumhöhlen	Mindestens fünf Höhlenbäume je Hektar gewährleisten signifikant hohe Niveaus bei Arten und Individuen bei den höhlenbrütenden Vögeln.	höhlenbrütende Vögel	Kanold et al. (2008)
Baumartenzusammensetzung	Natürliche Bergmischwälder	Flechten, Vögel	Moning & Müller



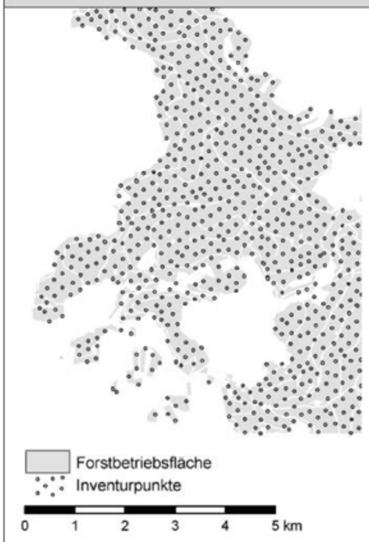
	weisen in Deutschland einen hohen Buchen- und Tannenanteil auf. Arten, die Laubwälder bevorzugen sind hier häufig in ihrer Verbreitung durch die Förderung der Fichte zurückgedrängt worden. Ab 60% Laubbaumanteil je ha nehmen typische Laubwaldarten unter den Singvögeln signifikant zu. Alte Bergahorne stellen besonders wertvolle Refugien unter anderem für eine artenreiche und bedrohte Flechtengemeinschaft dar.		(2008), MONING & MÜLLER (2009), MONING et al. (2009b)

Tabelle 2. Für das Kriging-Verfahren genutzte Schwellenwerte.

Alter	Ab 140 Jahren tritt bei vielen Artengruppen eine statistisch nachweisbar höhere Artendichte auf, der Schwellenwertbereich ist ab einem Bestandsalter von 200 Jahren überschritten.
Totholz	Ab 30 m³/ha bis 60 m³/ha treten Totholz nutzende und besiedelnde Arten häufiger auf. Der Schwellenwertbereich ist ab 60 m³/ha überschritten. Nach CHRISTENSEN et al. (2005) wurde die Schwelle für Totholzmengen durch den Faktor 1,19 dividiert, um die Totholzschwellen, die auf der Kluppschwelle 12 cm basieren auf 20 cm der Forstinventur anzupassen.
Laubholzanteil	Die Schwelle für laubbaumabhängige Vogelarten liegt bei 60 % Laubholzanteil.

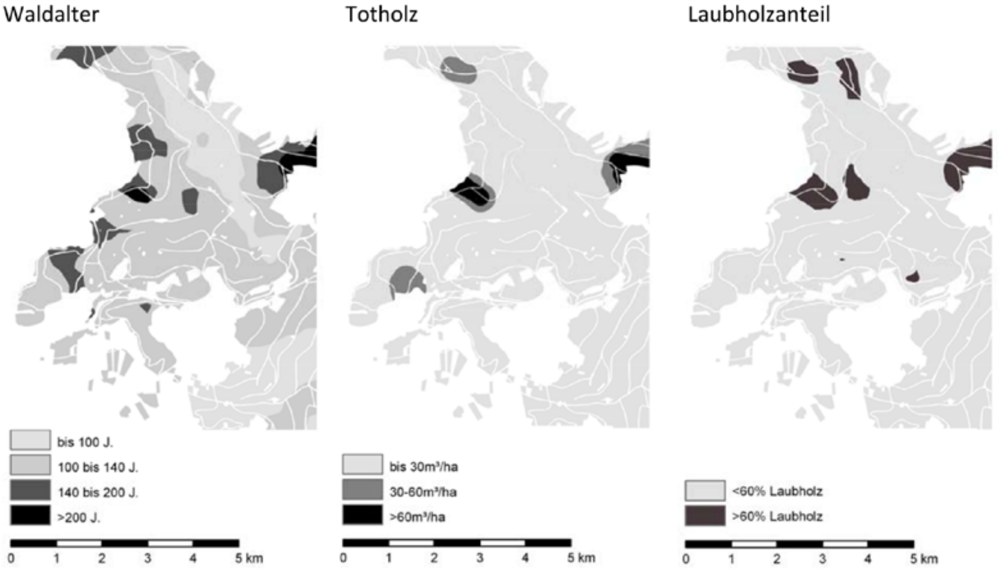
Tabelle 3. Ablaufschema des Bewertungsverfahrens: Von den Inventurpunkten bis zu den Handlungsempfehlungen. Dargestellt ist ein Ausschnitt eines bayerischen Bergmischwald-dominierten Betriebes.

Schritt 1: Forstinventur

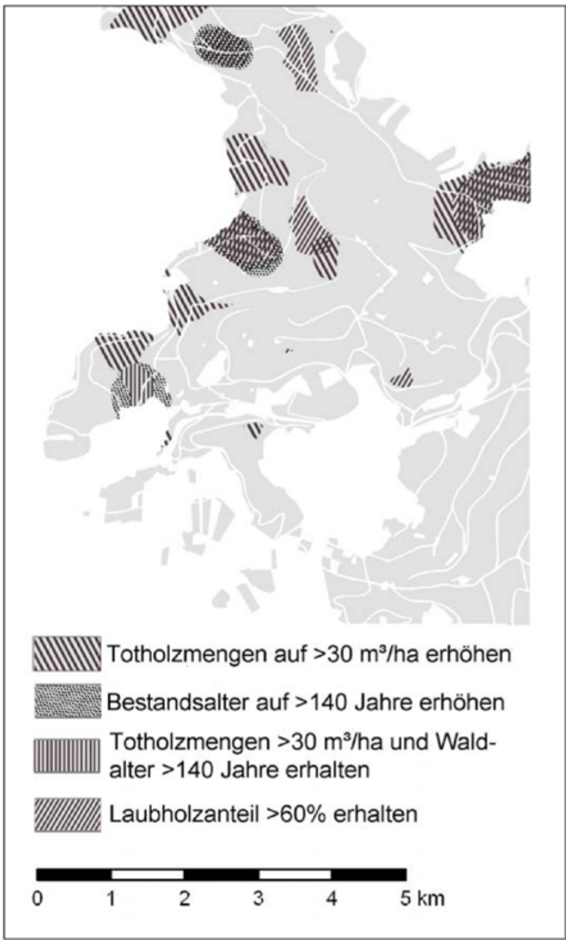


Die Forstinventurpunkte geben die Grundinformationen vor. In einem Raster von 100 m (bzw. 200 m in Montanlagen) Probepunktabstand werden auf konzentrischen Probekreisen (0,05 ha) Daten wie Baumarten, Altersstrukturen, Wachstums- und Holzvorräte erfasst.

Schritt 2: Die Darstellung der Schwellenwerte mit Hilfe des Kriging Verfahrens (Schwellenwertanalyse)



Schritt 3: Handlungsempfehlungen aus der Verschneidung der Schwellenwertanalyse



In der Synthese der überlagerten Flächen aus der Schwellenwertanalyse werden Managementempfehlungen abgeleitet. In Bereichen, die den Alters-Schwellenwertbereich von 140 Jahren erreichen, wird eine Totholzanreicherung auf über 30 m³/ha empfohlen. In Bereichen mit hohen Totholzsummen von über 30 m³/ha wird ein Belassen des überschirmenden Bestandes bis in ein Waldalter von über 140 Jahren empfohlen. In Bereichen, die bereits einen Laubholzanteil von über 60 % aufweisen wird empfohlen, den hohen Laubbaumanteil zu erhalten.

Exkursionsführer für das Fortbildungsmodul

Exkursionsführer
-
Drei Beispielbestände zur Umsetzung von Naturschutzsdandards in Bergmischwäldern im Forstbetrieb Neureichenau

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Fortbildung DBU-Projekt

„Ökologische Schlüsselwerte in Bergmischwäldern als Grundlage für eine nachhaltige Forstwirtschaft“

DBU
Deutsche Bundesstiftung Umwelt

BAYERISCHE STAATSFORSTEN
Nachhaltig Wirtschaften.

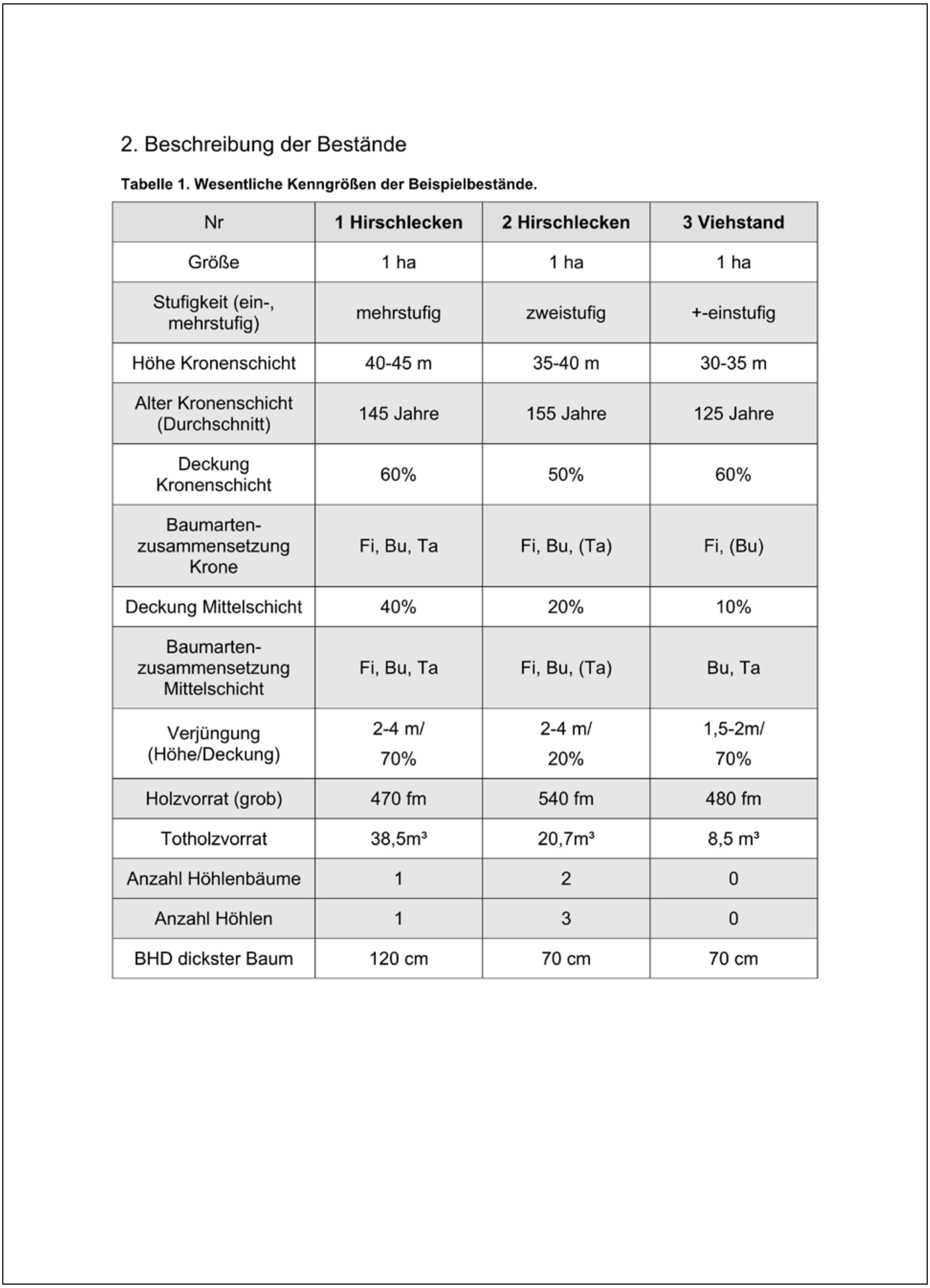
1. Lage der Bestände

Abbildung 1. Lage der Beispielbestände.

1. Hirschlecken

2. Hirschlecken

3. Viehstand



2. Beschreibung der Bestände

Tabelle 1. Wesentliche Kenngrößen der Beispielbestände.

Nr	**1 Hirschlecken**	**2 Hirschlecken**	**3 Viehstand**
Größe	1 ha	1 ha	1 ha
Stufigkeit (ein-, mehrstufig)	mehrstufig	zweistufig	+-einstufig
Höhe Kronenschicht	40-45 m	35-40 m	30-35 m
Alter Kronenschicht (Durchschnitt)	145 Jahre	155 Jahre	125 Jahre
Deckung Kronenschicht	60%	50%	60%
Baumarten-zusammensetzung Krone	Fi, Bu, Ta	Fi, Bu, (Ta)	Fi, (Bu)
Deckung Mittelschicht	40%	20%	10%
Baumarten-zusammensetzung Mittelschicht	Fi, Bu, Ta	Fi, Bu, (Ta)	Bu, Ta
Verjüngung (Höhe/Deckung)	2-4 m/ 70%	2-4 m/ 20%	1,5-2m/ 70%
Holzvorrat (grob)	470 fm	540 fm	480 fm
Totholzvorrat	38,5m^3	20,7m^3	8,5 m^3
Anzahl Höhlenbäume	1	2	0
Anzahl Höhlen	1	3	0
BHD dickster Baum	120 cm	70 cm	70 cm

Tabelle 2. Spezifikation Totholzwerte.

Nr	1 Hirschlecken	2 Hirschlecken	3 Viehstand
Totholzvorrat	38,5m^3	20,7m^3	8,5 m^3
davon Wurzelstöcke	11,3m^3	8,7m^3	6,3 m^3
Totholz Fichte	30,8 m^3	7,2 m^3	7,5 m^3
Totholz Buche	5,1 m^3	9,0 m^3	0,2 m^3
Totholz Tanne	2,6 m^3	4,5 m^3	0,8 m^3
Zersetzungsgrad 1	0,03 m^3	1,1 m^3	0 m^3
Zersetzungsgr. 1-3	29,4 m^3	15,1 m^3	6,4 m^3
Zersetzungsgrad 4	9,0 m^3	4,5 m^3	2,1 m^3

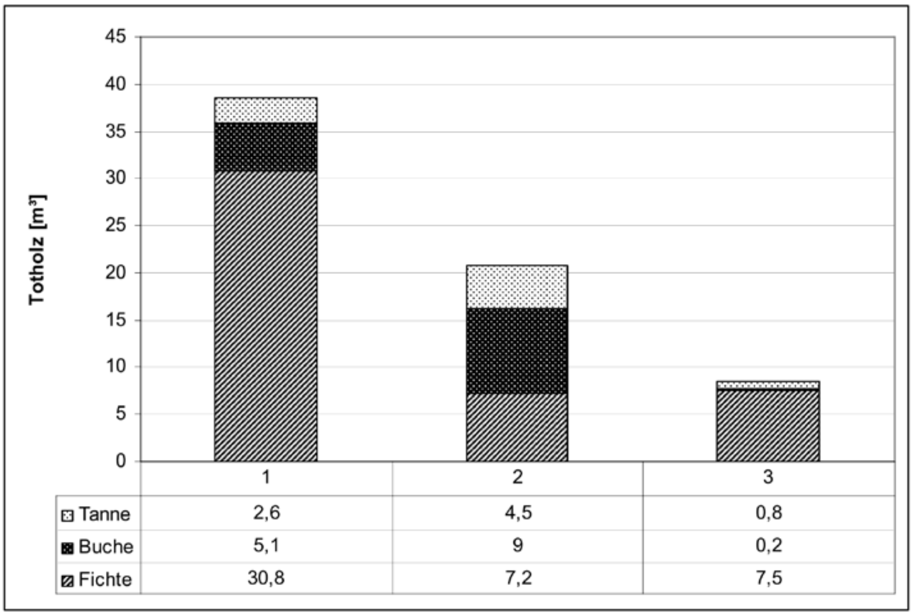
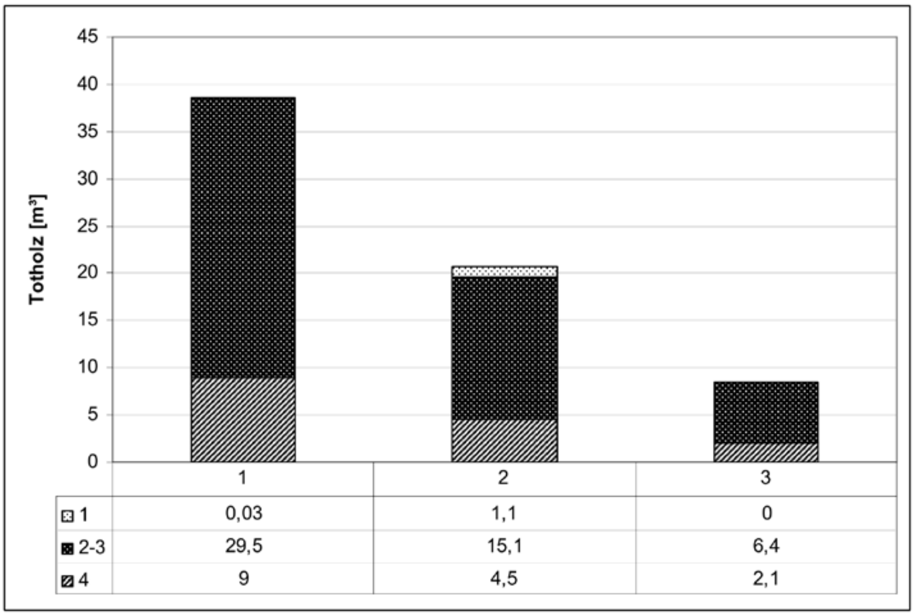


Abbildung 3. Totholz [m³] nach Baumarten.



	1	2	3
⚄ 1	0,03	1,1	0
▩ 2-3	29,5	15,1	6,4
▨ 4	9	4,5	2,1

Abbildung 4. Totholz [m³] nach Zersetzungsgrad.

Standardisierung Zersetzungsgrade

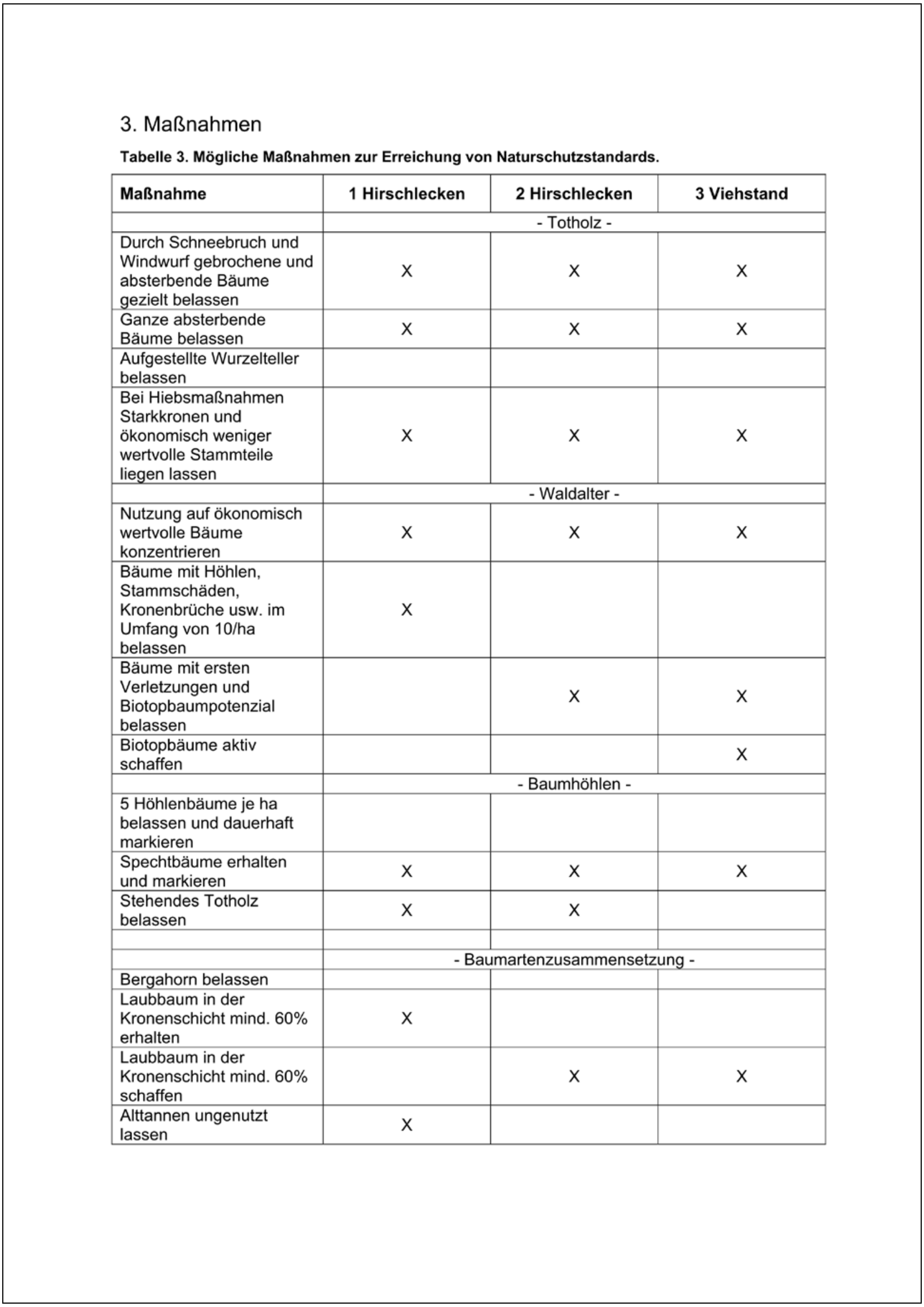
Zersetzungsgrade und -verlauf (Müller-Using 2005)

Zersetzungsgrad 1	Frisch abgestorben. Kambium noch grün.
Zersetzungsgrad 2	Rinde lose. Meist feine Trockenrisse im Holz in Längsrichtung.
Zersetzungsgrad 3	Ausweitung der Risse durch Zersetzung. Entstehung von Furchen.
Zersetzungsgrad 4	Stammform aufgelöst. Holz lässt sich leicht brechen.

Abbaugeschwindigkeit und Durchlaufzeiten in Jahren:

Gesamt: 33,8 Jahre

Z°1: 3,6 J. **Z°2: 5,4 J.** **Z°3: 9,1 J.** **Z°4: 15,7 J.**



3. Maßnahmen

Tabelle 3. Mögliche Maßnahmen zur Erreichung von Naturschutzstandards.

Maßnahme	**1 Hirschlecken**	**2 Hirschlecken**	**3 Viehstand**
		- Totholz -	
Durch Schneebruch und Windwurf gebrochene und absterbende Bäume gezielt belassen	X	X	X
Ganze absterbende Bäume belassen	X	X	X
Aufgestellte Wurzelteller belassen			
Bei Hiebsmaßnahmen Starkkronen und ökonomisch weniger wertvolle Stammteile liegen lassen	X	X	X
		- Waldalter -	
Nutzung auf ökonomisch wertvolle Bäume konzentrieren	X	X	X
Bäume mit Höhlen, Stammschäden, Kronenbrüche usw. im Umfang von 10/ha belassen	X		
Bäume mit ersten Verletzungen und Biotopbaumpotenzial belassen		X	X
Biotopbäume aktiv schaffen			X
		- Baumhöhlen -	
5 Höhlenbäume je ha belassen und dauerhaft markieren			
Spechtbäume erhalten und markieren	X	X	X
Stehendes Totholz belassen	X	X	
		- Baumartenzusammensetzung -	
Bergahorn belassen			
Laubbaum in der Kronenschicht mind. 60% erhalten	X		
Laubbaum in der Kronenschicht mind. 60% schaffen		X	X
Alttannen ungenutzt lassen	X		