

Climate Change and Biodiversity in Temperate Montane Forests - Patterns, Processes and Predictions

vorgelegt von
Diplom-Umweltwissenschaftler
Claus Bässler
aus Hohenau

Von der Fakultät VI - Planen Bauen Umwelt
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Promotionsausschuss:

Vorsitzender: Prof. Dr. Joachim Erber
Berichter: Prof. Dr. Frank Dziock
Berichter: Prof. Dr. Ingo Kowarik

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Preface

In 2007 the Intergovernmental Panel on Climate Change (IPCC) published its fourth Assessment Report summarizing the current scientific understanding of impacts of climate change on natural, managed and human systems, the capacity of these systems to adapt and their vulnerability (Ipcc 2007a). According to this report, observational evidence from all continents and most oceans shows that many natural systems are being affected by regional climate changes, particularly temperature increases. The resilience of many ecosystems is likely to be overpowered this century by an unprecedented combination of climate change, associated disturbances (e.g., flooding, drought, wildfire, insects, ocean acidification), and other drivers of global change (e.g. land use change, pollution, overexploitation of resources) (Sala et al. 2000, Travis 2002, Hooper et al. 2005). Approximately 20-30% of plant and animal species assessed so far are likely to be at greater risk of extinction if increases in global average temperature exceed 1.5-2.5 °C. For increases in global average temperature exceeding 1.5-2.5°C and for concomitant atmospheric carbon dioxide concentrations, major changes are projected to occur in ecosystem structure and function as well as species' ecological interactions and geographic ranges, with predominantly negative consequences for biodiversity (Ipcc 2007a). 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) (Loreau et al. 2001, Sutherland et al. 2006). It is difficult to measure the impacts of increasing air temperature on biodiversity. But ecological changes in the phenology and distribution of plants and animals are occurring in all well studied marine, freshwater, and terrestrial groups. These observed changes are heavily biased in the directions predicted for global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research (Walther et al. 2002, Parmesan 2006) but the potential effect on complex communities is little understood. 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 must 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.

Despite much discussion and a high level of research activity in various disciplines on assessing the impact of global change caused by temperature increase on biodiversity and natural systems, there is still a major lack of knowledge at relevant temporal and spatial scales (Sutherland et al. 2006). Currently, the most relevant physical and temporal scale of ecological investigations is a local one (Walther et al. 2002). As a response to mainly the expected increase in temperature, a powerful effect on biological systems is very likely and the most significant effects of climate change will occur on regional scales in the next 50 years. Current climate change predictions for the study area at a regional scale show increasing temperatures until the end of the 21st century (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 this study is to contribute to the knowledge of expected effects of climate change on these low mountain range forest ecosystems in Central Europe. The thesis is based on six manuscripts. The first concerns the magnitude of the physical change (air temperature) related to the study area and discusses the necessity of climate change research efforts. Building on this, the second manuscript relates the climate change research framework to the regional scale, thus creating a broad basis for analyses. The third paper deals with the dependency of vascular plants on altitude and examines the character of changes (continuous/discrete), in order to reveal unknown species distribution patterns in low mountain ranges and identify climate sensitive zones for future climate change monitoring. The confounding environmental effects occurring along the altitudinal gradient for forest structure dependent species (wood inhabiting fungi and molluscs) are examined in the fourth and six papers, by revealing the effect of climate under consideration of forest structure factors, both co-varying along the altitudinal gradient. The fifth paper determines the extinction risk for high montane species, expected to be very vulnerable to climate change, and their suitability for use as indicators and cross-taxon indicators in further monitoring.

Abstract

Globally detected temperature change varies strongly on a regional scale; sometimes trend values are negative. Thus, the first aim of this study is to analyse the trend of air temperature for the study area based on data from selected meteorological stations and to reveal regional patterns of climate change. Mean air temperature; mean daily minimum and maximum temperatures were considered. After data preparation, checking of data by time series analysis (trend and cutpoint analysis) and examination of spatial and time representation was carried out. To investigate orographic differences, data from two meteorological stations representative for hillside or valley locations were analysed for the time frame 1948-2002. Predominantly positive trends were noticeable for the period under consideration. The highest trend of mean air temperature change was calculated for May (0.04 K a^{-1} for hillside locations and 0.03 K for valley locations) and August (0.02 K a^{-1} for hillside locations and 0.03 K for valley locations). Thus, there was a trend of 0.02 K a^{-1} (hillside) and 0.01 K a^{-1} (valley) increase for the growing season (May-August). More distinct were the trends of the mean monthly minimum temperature, where almost all trends were positive. In contrast, the mean maximum temperature showed a much more moderate reaction. There is a common cutpoint for the mean annual air temperature time series under study (1948-2002) in 1988. Hence, the detected overall trend is mostly a result of the increasing temperature since this point in time. To summarize: climate change is taking place in our low mountain range study area in a similar way to change at the global scale. Thus, consequences are expected for biological systems on a regional scale.

After identifying signs of warming for the study area, the expectation of continued future increase in temperatures as revealed by downscaled climate change scenarios led to development of a climate research programme which was initiated in the National Park Bavarian Forest. The BIOKLIM Project (Biodiversity and Climate Change- Project) is intended to fill gaps in our knowledge on the impacts of climate change on montane and high montane forest biodiversity of Central European low mountain ranges on a regional scale. This is one of the most threatened mixed montane ecosystems worldwide. The Bavarian Forest National Park is characterised by its altitudinal range of ca. 800m 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. We set up 293 sampling plots along four main straight transects following the altitudinal gradient. All abiotic and stand structure data regarded as relevant, resulting from geographical information systems as well as from

recording and measurement in the field, 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. Worldwide, only a few multidisciplinary biodiversity and climate change 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.

We attempted to obtain deeper insights on the meaning of the complex factor altitude and its influence on distribution patterns. To this end, vascular plant community compositions were studied, to assess the influence of altitude among other habitat predictors as well as the character of revealed changes. The ordination confirms that altitude is the best explanatory variable, even when other habitat predictors are considered. The identification of a threshold at 1142m a.s.l. using maximally selected rank statistics indicates discrete changes in vascular plant community composition along the altitudinal gradient. Due to the strong correlation of altitude and temperature, this elevation is considered to represent a climate sensitive zone. It is an ecological threshold which separates the montane from the high montane zone. Weaker signals of change could be detected at 1047 and 1225m a.s.l. These altitudinal zones will be affected most if temperature increase continues and monitoring of climate change should thus be concentrated there.

To solve the problem of strong co-variation of abiotic and structural factors along the altitudinal gradient and to reveal the contribution of these confounding effects, a further objective is to determine the relative influence of climate, forest structure and habitat continuity on composition of wood-inhabiting fungi communities, species density, number of species records and number of threatened species. The combined effect of forest structure variables was clearly more important than the set of climate variables in its effect on community composition, species density and species records. Only for threatened species was habitat continuity shown to be an important factor. It is concluded that wood-inhabiting fungi are mostly affected by management activity which alters forest structure. Changes in microclimate driven by global warming are not expected to directly influence wood-inhabiting fungi in the future. Rather, global warming could trigger changes in forest structure that might affect wood-inhabiting fungi indirectly, such as alterations in tree species composition. With a similar intention, we also assessed the influence of the regional temperature gradient with altitude on species density and density of single species of molluscs. An additional objective here was to test the influence of site-specific habitat factors by considering several habitat variables ranging from stand age to plant species richness.

Based on 3437 individuals and 46 species, we found that density of individuals and species decreased non-linearly with altitude. The slope of this decrease changed between 1100 and 1200 m a.s.l.. Contrastingly, the density of *Semilimax kotulae*, an Alpine-Carpathian endemic montane mollusc, increased with altitude, but again with a change in the slope between 1100 and 1200 m a.s.l. Spatial generalized linear models showed that especially habitat age is an important predictor for the density of many species, but that global warming should lead to an overall increase in species density.

To assess the regional risk of extinction and to identify appropriate indicators for climate change monitoring, the final immediate objective is to model the occurrence, under two global warming scenarios, of six high montane species selected a priori from the literature to represent ferns, vascular plants, wood inhabiting fungi, molluscs, saproxylic beetles and breeding birds. The suitability of the selected high montane species for climate change monitoring as cross-taxon indicators is then evaluated. Temperature was revealed as the main predictor for all selected high montane species, for which our statistical model predicts a considerable risk of extinction within the Bavarian Forest National Park as a result of global warming. The similar species-environmental relationships shared by many high montane species lead to the conclusion, that their cross-taxon suitability as indicators of early signs of global warming is high where the model discrimination is of high quality. The choice of which indicator to use should be determined mainly by the type of monitoring systems which are already employed in a region. As a rough assessment and prospect for the future, from 1.5 - 23.4 % of the target taxa may become extinct in the study area as a result of climate change. Red listed species are disproportionally sensitive, with an extinction risk of 3.3 % - 75.0%.

One main conclusion is that the regionally different effects of climate change make it necessary to intensify research on indications of change, indicators for these and extinction risk. To achieve this, continued and expanded climate change research and monitoring are necessary.

To summarize: Altitude was revealed as the main driver, with similar patterns of occurrence along the gradient for different taxonomic groups, distributed non-linearly and changing abruptly at approximately 1100-1200m a.s.l. However, it was revealed that not all taxonomic groups affected by altitude are primarily driven by climate. Sensitivity to climate change and usefulness for indication of climate sensitive zones was detected for vascular plant community compositions, which are expected to be affected directly by global warming. Mapping repeated in a few years could reveal displaced thresholds. Further studies are also necessary which will prove shifts in distribution at the species level (where do species reach

their lower and upper limits) in the detected climate sensitive zones. As clear indicators, the high montane species here studied (with one exception) seem to be well suited for monitoring of climate change, and possess cross-taxon capability. Their use in monitoring should be implemented as soon as possible, to achieve rapid and unequivocal proof of effects of climate change in the Central European montane zones.

Zusammenfassung

Der durch den Klimawandel sich ergebende globale Lebensraum- und Biodiversitätsverlust macht es erforderlich, den gegenwärtigen Status der Ökosysteme zu analysieren sowie den Zusammenhang zwischen den Arten und ihrer Umwelt zu erforschen.

Der global festgestellte Trend variiert regional sehr stark, teilweise kehrt sich der Trendbetrag sogar um. Deshalb gilt als erstes Ziel, den Trend der Lufttemperatur auf der Grundlage ausgewählter Klimastationen im Untersuchungsgebiet zu berechnen, um Muster des lokalen Klimawandels aufzudecken. Es wurden die mittleren Lufttemperaturen sowie die mittleren Tagesminimum- und Tagesmaximumtemperaturen berücksichtigt. Im Anschluss an die Homogenisierung der Datensätze wurden Zeitreihenanalysen (Trend- und Bruchpunktanalysen) durchgeführt. Weiterhin wurde die zeitliche- und räumliche Repräsentanz bewertet. Um orographischen Unterschieden gerecht zu werden, wurden zwei repräsentative Klimastationen, einmal für die Hanglagen und einmal für die Tallagen, gewählt und die Analysen für eine Zeitreihe von 1948-2002 durchgeführt. Für die mittleren Lufttemperaturen konnten überwiegend positive Trends für die berücksichtigte Zeitreihe ermittelt werden. Der deutlichste Trend konnte für Mai (Hanglage 0.04 K a^{-1} und Tallage 0.03 K a^{-1}) und August (Hanglage 0.02 K a^{-1} und Tallage 0.03 K a^{-1}) errechnet werden. Demzufolge beläuft sich der Trend für die Vegetationsperiode (Mai-August) auf 0.02 K a^{-1} (Hanglage) bzw. 0.01 K a^{-1} (Tallage). Stärkere Trends konnten für die mittleren Minimumtemperaturen errechnet werden, nahezu alle Monate zeigen einen positiven Trend. Im Gegensatz dazu zeigen sich die Trends der mittleren Maximumtemperaturen eher moderat. Ein gemeinsamer Bruchpunkt für die untersuchten Zeitreihen konnte für das Jahr 1988 festgestellt werden. Demzufolge ist der errechnete Trend ein Ergebnis zunehmender Erwärmung seit diesem Zeitpunkt. Zusammenfassend lässt sich feststellen, dass der Klimawandel im Untersuchungsgebiet wirksam wird und dessen Ausmaß sehr wahrscheinlich zu einschneidenden Veränderungen in biologischen Systemen (Biodiversität) führt.

Nachdem ein deutliches Erwärmungssignal festgestellt werden konnte und, wie regionale Szenarien zeigen, von einer weiteren Zunahme der Temperaturen auch zukünftig ausgegangen werden kann, wurde ein Forschungskonzept zum Klimawandel erarbeitet und im Nationalpark Bayerischer Wald eingerichtet. Ziel des BIOKLIM-Projektes (Biodiversitäts- und Klima-Projekt) ist es, Wissenslücken im Zusammenhang mit den Auswirkungen des Klimawandels auf montane und hochmontane Wälder Europas auf regionaler Ebene zu schließen. Diese Wälder gehören weltweit zu den gefährdeten Bergmischwaldsystemen. Der Nationalpark Bayerischer Wald ist durch einen Höhengradienten von 800m und einem starken

Waldstrukturgradient geprägt. Relikte alter Wälder mit Habitattradition (alte Naturschutzgebiete und Naturwaldreservate) und durch Borkenkäferentwicklung abgestorbene Bestände gehen einher mit einer breiten Variation von Todholz und unterschiedlichen Belichtungs(wärme)verhältnissen. Es wurden 293 Probekreise in Form von vier Transekten entlang des Höhengradienten eingerichtet. Alle als wesentlich erachteten abiotischen und Bestandesstruktur-Parameter wurden aus dem Geographischen Informationssystem (GIS) extrahiert oder im Feld erhoben und gemessen. Diese Parameter stehen für jeden Probekreis zur Verfügung. Gefäßpflanzen, Holzpilze und Vögel wurden auf allen 293 Probekreisen kartiert. Für die restlichen 22 untersuchten Artengruppen wurde, den Untersuchungsmethoden entsprechend, das Untersuchungsdesign stratifiziert. Weltweit gibt es gegenwärtig nur wenige interdisziplinäre Untersuchungen zu Biodiversität und Klima entlang von Höhengradienten. Jedoch ist in den meisten Fällen die Untersuchungstechnik dieselbe, sodass Vergleiche der Ergebnisse zwischen den Kontinenten möglich werden.

Zweites Ziel ist das Herausarbeiten der Bedeutung des Faktors Höhe unter den Steuerfaktoren sowie das Auflösen von Verteilungsmustern für Gefäßpflanzen- und Farngemeinschaften entlang des Mittelgebirgsgradienten. Mit Hilfe der Korrespondenzanalyse konnte der Faktor Höhe als wichtigstes Steuerelement identifiziert werden. Die Bruchpunktanalyse detektiert bei 1142m üNN eine deutliche Veränderung in der Zusammensetzung der Artengemeinschaften. Der enge Zusammenhang zwischen der Höhe und der Temperatur qualifizieren diese Höhenstufe als klimasensitive Zone. Dieser Bruchpunkt differenziert die Bergmischwaldzone von der Hochlagenzone. Weitere Bruchpunkte konnten für die Höhenlagen 1047m üNN und 1225m üNN abgeleitet werden. Es kann davon ausgegangen werden, dass Veränderungen von Gefäßpflanzen- und Farnstrukturen durch zunehmende Erwärmung in den ermittelten Höhenzonen als erstes auftreten. Demzufolge sollte sich ein klimaorientiertes Monitoring in erster Linie auf diese Höhenzonen erstrecken.

Drittes Ziel ist die Erarbeitung der relativen Einflüsse von Klima, Waldstrukturen und Habitattradition auf strukturgebundene Artengruppen am Beispiel holzbewohnender Pilze zur Auflösung komplexer Effekte des Höhengradienten. Zielgruppen sind Artengemeinschaften, Artendichten, Zahl der Registrierungen und Vorkommen bedrohter Arten. Wichtigste Steuergrößen für die Artengemeinschaften, Artendichte und Anzahl der Registrierungen sind die Faktoren, welche unter der Variablengruppe der Waldstrukturen subsummiert sind. Diese überlagern den Einfluss der Klimavariablen deutlich. Habitattradition ist nur entscheidend für die Zielgruppe der bedrohten Arten. Demzufolge werden holzbewohnende Pilze gegenwärtig am stärksten durch anthropogenes Waldmanagement beeinflusst, welches die Waldstrukturen

unmittelbar verändert (Todholzangebot, Beschirmungsgrad etc.). Demnach werden zukünftig holzbewohnende Pilze durch Veränderungen des Mikroklimas infolge globaler Erwärmung nur indirekt beeinflusst. Allerdings ist zu erwarten, dass die globale Erwärmung langfristig Waldstrukturen verändern wird, wie zum Beispiel die Baumartenzusammensetzung, weshalb hier ein langfristiger Einfluss auf holzbewohnende Organismen zu vermuten ist. Weiterhin wurde der Einfluss des regionalen Temperaturgradienten entlang der Höhe auf die Molluskenartendichte und die Dichte einzelner Mollusken bewertet. Ebenso wurde der Einfluss standortspezifischer Habitatfaktoren auf diese Zielgruppen getestet. Auf der Grundlage von 3437 Individuen und 46 Arten konnte nachgewiesen werden, dass die Zielgrößen mit zunehmender Höhe nicht linear abnehmen. Der Bruch dieser Veränderung findet in der Höhenstufe 1100-1200m üNN statt. Demgegenüber nimmt die Dichte von *Semilimax kotulae*, als alpin-carpatisch und endemisch eingestuft, entlang des Höhengradienten zu, ebenfalls mit einem klaren steilen Anstieg in der Höhenzone 1100-1200m üNN. Das Alter der Habitate ist der überragende Faktor, welcher die Dichte vieler Arten beeinflusst. Allerdings kann ebenfalls festgestellt werden, dass die globale Erwärmung zu einem Anstieg der Artendichte führen wird.

Viertes Ziel ist die Modellierung von 6 Hochlagenarten, repräsentiert durch die taxonomischen Gruppen Farne, Gefäßpflanzen, holzbewohnende Pilze und Käfer, Mollusken und Vögel auf der Basis von zwei Klimaszenarien zur Abschätzung des Extinktionsrisikos. Weiterhin soll überprüft werden, in wie weit sich die ausgewählten Arten als Indikatoren eignen und sich für ein Klimawandelmonitoring gegenseitig ersetzen lassen. Der Faktor Temperatur konnte als überragende Steuergröße für alle Arten errechnet werden. Ebenso wird auf der Basis der statistischen Modelle ein erhöhtes Aussterberisiko der Zielarten für den Nationalpark Bayerischer Wald vorhergesagt, wenn es zur weiteren Erwärmung kommt.

Durch ähnliche Arten-Umweltbeziehungen besteht für die ausgewählten Arten eine sehr gute artenübergreifende Indikatoreignung zur Feststellung frühzeitiger Veränderungen durch globale Erwärmung, wenn die Modellgütewerte (Diskriminanz) eine vergleichbar hohe Qualität zeigen. Die Wahl der Indikatoren kann deshalb an bestehendem Monitoring orientiert werden. Eine grobe Abschätzung, orientiert am Anteil der Hochlagenarten von den Gesamtarten der untersuchten Taxa, welche für das Untersuchungsgebiet nachgewiesen sind, zeigt Aussterberaten von 1.5 - 23.4%. Rote Liste Arten sind nach dieser Abschätzung überproportional betroffen (Extinktionsrisiko von 3.3 - 75%).

Zusammenfassend lässt sich sagen, dass der Klimawandel im Untersuchungsgebiet wirkt und aus diesem Grund Indikatoren erarbeitet sowie Extinktionsrisiken abgeschätzt werden

müssen. Hierfür ist Klimaforschung und Monitoring dringend notwendig. Der Faktor Höhe konnte als überragender Steuerfaktor für verschiedene taxonomische Gruppen bestätigt werden. Es bestehen vergleichbare Muster entlang des Gradienten, geprägt durch eine nicht-lineare Verteilung mit einem gemeinsamen Bruch in der Höhenstufe 1100-1200 m üNN. Es konnte gezeigt werden, dass nicht alle taxonomischen Gruppen, geprägt durch den Höhengradienten, primär durch den Faktor Klima gesteuert werden.

Gefäßpflanzengemeinschaften sind klimasensitiv und hieraus ist ein direkter Einfluss durch die globale Erwärmung zu erwarten. Der Bruch in der Artengemeinschaft bei 1142m üNN macht diese Höhenstufe zur klimasensitiven Zone. Wiederholungskartierungen in einigen Jahren fördern demnach vermutlich neue Schwellenwerte zu Tage. Aber weitere Studien auf der Ebene von Einzelarten, welche in dieser Zone ihre untere oder obere Verbreitungsgrenze besitzen, sind dringend erforderlich, um Arealverschiebungen nachzuweisen. Die untersuchten hochmontanen Arten sind sehr gute Indikatoren und auch geeignet, sich im Rahmen eines Monitoring gegenseitig zu ersetzen. Diese Indikatoren eignen sich sehr gut für eine schnelle und vertrauenswürdige Beurteilung vom Effekt des Klimawandels auf die Areale von Arten.

Part A: Synthesis

1. Aims of the Study

1.1 Postulates

Even although distribution patterns along altitudinal gradients have fascinated biologists and biogeographers ever since Darwin, the reason for these patterns on a broad spatial scale are still disputed (Gaston 2000). However, one of the most important factors for life is undoubtedly the gradient in air temperature (Körner 2007). At the same time, the response of many species to large scale climate change will be modified by factors operating at a smaller scale (Ellis et al. 2007). For deeper insights into the impacts of climate change on a regional scale along altitudinal gradients, it is first essential to reveal the contribution of climate as a driving factor for the occurrence of species by distinguishing the confounding effects of habitat predictors.

- Postulate 1: The magnitude of increasing temperature revealed on a global scale as part of climate change may not necessarily apply to our low mountain range and can vary strongly according to local topography.
- Postulate 2: Variation of species distribution in low mountain ranges is best explained by altitude.
- Postulate 3: Changes of distribution patterns along altitudinal gradients are non-linear.
- Postulate 4: Changes of distribution patterns along altitudinal gradients can be traced back to the continuous change of climate along the altitudinal gradient.
- Postulate 5: High montane species from European low mountain ranges are extremely sensitive and vulnerable, to the point of being threatened with extinction caused by global warming. They thus represent suitable indicators for use in climate change monitoring.

1.2 Specific objectives

- Paper I: to test whether there is a significant trend in the mean air temperatures and mean daily minimum and maximum temperatures for the study area during the last decades.

- Paper II: 1) to present the objectives, structure and study design of the BIOKLIM Project.
2) to present the proxy factor altitude as driver of overwhelming importance for community compositions in several taxa.
3) to compare our study design with those of other climate change projects worldwide.
- Paper III: 1) to test whether the altitudinal climate gradient is the best explanation for the variation of vascular plant and fern community compositions in the montane forest.
2) to test whether it is possible to identify climate sensitive zones for vascular plant and fern assemblages along the altitudinal gradient.
- Paper IV: to reveal whether climate gradients are indeed important in shaping community structure, density, species records and occurrence of threatened species in taxa such as wood-inhabiting fungi dependent on forest structure, when other causes of variance such as forest structure and habitat continuity factors are accounted for.
- Paper V: 1) to assess the regional influence of the temperature gradient with altitude on mollusc species density and density of single species.
2) to test the influence of site-specific habitat factors.
3) to describe the differences in the extinction risk of a high montane mollusc species caused by different levels of global warming.
- Paper VI: 1) to test for high montane species (defined a priori) of a low mountain range, whether temperature is still the dominating predictor even under consideration of a broad set of environmental factors.
2) to test whether the extinction risks of species studied are similar under two climate change scenarios.
3) to test whether six high montane species in six taxonomic groups are suitable cross-taxon indicators for climate change monitoring.

2. Material and Methods

2.1 Study sites

The National Park “Bavarian Forest”, the first to be established in Germany in 1970, is located in the south-eastern corner of Bavaria, at the border to the Czech Republic. The Park covers approximately 24000 ha at elevations from 650 m to 1430 m a.s.l. Total annual precipitation is between 1200 mm and 1800 mm depending on altitude. Mean annual temperature (1972-2001) varies between 3.8°C and 5.8°C (Bässler 2004). Geologically, the Bavarian Forest is the south-western part of the Bohemian Massif, consisting of granite and gneiss and therefore containing acidic soils. Above about 1100 m to 1200 m a.s.l. the stands are dominated by spruce *Picea abies*, with a low proportion of beech *Fagus sylvatica* and mountain ash *Sorbus aucuparia* (high montane forest). Below this, the stands are dominated by spruce, beech and fir *Abies alba* (mixed montane forest) (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.

2.2 Methods used to test the postulates

Dealing with spatial autocorrelation

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. 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 implementation. A further approach to evaluation of autocorrelation is the use of semiparametric spatial generalised linear models, where it 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 and Fahrmeir 2006).

Postulate 1:

After tests of homogeneity of all temperature time series (Craddock 1979, Paesler 1983, Alexanderson 1986) some series were statistically extrapolated so that they could be compared with the trend values. Goodness of fit was calculated by applying the Theil disparity coefficient (Andres and Spiwoks 2000). Linear regression models (Zar 1999) were used as a basis for time series analyses. To test the significance of the detected trends we used the Mann-Kendall approach (Rapp 2000). Changes within the time series were detected using Pettitt cutpoint analysis following Mann-Whitney (WMO 2003). To assess time representation we calculated the regressive trend. Spatial representation was tested using correlation coefficients (Schönwiese 2000).

Postulate 2:

To assess patterns of plant assemblage variation as well as environmental and physical factors affecting these, direct and indirect gradient analyses were applied (Hill 1973, Jongmann et al. 1995). Variables were selected by the forward selection procedure. Using PCA (Goodall 1954) environmental variables were ordinated to assess the variability and pattern within the sample plots and to exclude multicollinearity. Significance of the relationships between species and the set of environmental variables, as well as the significance of the eigenvalues, were tested using the Monte Carlo Test (999 permutations).

Postulate 3:

To derive thresholds of assemblage change on the basis of the sample scores calculated by the correspondence analysis (CA), we applied maximally selected rank statistics (Lausen and Schumacher 1992, Hothorn and Lausen 2003, Müller and Hothorn 2004), which allow for 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 some independent variable and the response. By contrast, classification and regression trees rely on cross-validation techniques for determining tree sizes, without a formal hypothesis test.

The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics, and their validity is judged by multiple test procedures. The key results are those where the difference between high and low values of the dependent variable is

largest. The approach can be applied to a single or to multiple environmental variables. After the data set is divided into two subsets by the threshold with highest explanatory power, the subsets are searched for additional thresholds. The methodology provides a decision tree with p-values for one or more critical thresholds. On the basis of 1000 bootstrap samples the confidence interval (95%) was calculated on the function of density.

Finally we used additive quantile regression smoothing (Koenker et al. 1994) where $\tau = 0.8$ to characterize distribution patterns along the altitudinal gradient.

Postulate 4:

Using partial CCA (Ter Braak and Smilauer 2002), we partitioned variance (Økland 2003) for community composition into three sets of explanatory variables (climate[C], forest structure[S] and habitat continuity [T]). To assess spatial correlation one additional set was formed to include geographical coordinates [G]. Hierarchical portioning (Chevan and Sutherland 1991) was undertaken for species density, species records and threatened species. This technique calculates the goodness-of-fit values for the entire hierarchy of models using all combinations of N independent variables. It takes the list of goodness-of-fit values and, using the partition function, applies the hierarchical partitioning algorithm of (Chevan and Sutherland 1991) to return a simple table listing each variable and its independent contribution. The independent effects of the environmental variables were assigned to the sets: climate[C], forest structure[S] and habitat continuity [T]).

Postulate 5:

To estimate the influence of climate change on the altitudinal distribution of the selected high montane species (see above), we first built logistic regression models (generalized linear models with an assumed binomial error distribution) using “BayesX” to predict the occurrence of each species in our sampling plots. To avoid multicollinearity, a Spearman two-sided rank correlation test was applied on the selected set of predictor variables whilst setting a limit for considering both correlated variables of $r_s=|0.7|$ (Fielding and Haworth 1995). Since the results of the spatial GLM were specific to the locations where the data were collected, they are not suitable for a general predictive approach. To obtain the desired generalized model, we fitted a GLM using the estimated current mean annual temperature and other significant variables resulting from the first spatial GLM, whilst excluding the spatial effects, and used this to predict the probability of occurrence of the selected species for each plot.

The two main performance criteria of a habitat model are calibration and discrimination (Pearce and Ferrier 2000, Reineking and Schröder 2003). We used Nagelkerke (R^2_N) to evaluate the calibration of our model and to measure the amount of explained variation (Nagelkerke 1991). The discrimination of our model was tested by calculating the AUC-value (area under the receiver operation characteristics) which is based on the ROC (receiver operation characteristics: a threshold independent criterion for model discrimination) (Fielding and Bell 1997, Harrell 2001). Furthermore, a 'Presence/Absence histogram' was created and some further criteria examined using a confusion matrix. Included were: Cohen's kappa, correct classification rate, sensitivity (true positive rate) and specificity (true negative rate) using a cut-off value $P_{crit}=0.5$ (Cohen 1960, Pontius 2000). The fact that estimates of performance criteria are over-optimistic when they are calculated only on the training data, means that these must be validated. Because no external data were available in this study, an internal validation, using a conventional bootstrap resampling technique (Verbyla and Litvaitis 1989, Efron and R.J. 1993) with 1000 iterations, has been used to validate our performance criteria (Schröder and Reineking 2004, Araújo et al. 2005).

In a final step we used two official scenarios (Ipcc 2007c) to predict the occurrence of the selected species on the sample plots after global warming. Accordingly, 1.8 K and 4 K were added to the estimated mean annual temperature and the occurrence of the selected species predicted using the model generated with the current annual temperature. Predictions for the three temperature scenarios were plotted against altitude and the general trend described using a spline fit as a local smoother. To visualize the uncertainty of the general trend heuristic confidence bands were constructed using pointwise 95% prediction intervals calculated from the standard error of the predictions. The upper and lower limits were again calculated using smoothing splines. Finally, we used the models generated for each species to predict the occurrence of species from other taxonomical groups, in order to assess suitability as cross-taxon indicators. To validate the suitability we used the AUC-value, as explained above. The differences between the species models and the occurrence of the remaining species (predictors) were tested with an analysis of variance (ANOVA) (Zar 1999) using the AUC-values.

3. Trend of air temperature for the Bavarian Forest

In the 20th century, global air temperature has increased by 0.74 K (0.007 K a^{-1}). The global trend is confirmed by rapid atmospheric warming in the last decades. However, the trend revealed on a global scale can vary strongly at regional and local scales (Ipcc 2007b).

Accordingly, the analysis of the trend in air temperatures is based on data from selected meteorological stations in the study region. Mean air temperature, mean daily minimum and maximum temperature were considered. To allow for orographic differences, data from two representative meteorological stations (Waldhäuser for hillside locations, 1948-2002, extended with data from the station Hohenpeißenberg 1781-2003; Zwieselberg for valley locations, 1948-2002) were analysed.

Predominantly positive trends were noticeable for the period under consideration (Tab 3). The highest trend in mean air temperature was calculated for May (0.04 K a⁻¹ for hillside locations and 0.03 K for valley locations) and August (0.02 K a⁻¹ for hillside locations and 0.03 K for valley locations). Thus, there was a trend of 0.02 K a⁻¹ (hillside) and 0.01 K a⁻¹ (valley) for the growing season (May-August). Trend of the mean annual air temperature is about 0.01 K a⁻¹ uniformly from valley to mountain top for the study area. More distinct were the trends in the mean monthly minimum temperature, which were almost all positive. In contrast, the mean maximum temperature showed a much more moderate behaviour.

Tab.3: Trendvalues (T) in K a⁻¹ and significance according to Mann-Kendall Test (MK) for the meteorological stations Waldhäuser (hillside) and Zwieselberg (valley side), P >95% in bold (Paper I).

	T _{mit}				T _{min}				T _{max}			
	Zwieselberg		Waldhäuser		Zwieselberg		Waldhäuser		Zwieselberg		Waldhäuser	
	T	MK	T	MK	T	MK	T	MK	T	MK	T	MK
January	0,02	74,9	0,03	86,4	0,03	86,0	0,04	97,9	0,02	59,3	0,04	94,6
February	0,03	55,9	0,03	64,7	0,04	83,2	0,04	84,3	0,03	74	0,02	61,2
March	0,02	83,5	0,01	51	0,05	99,7	0,03	85,9	0	26,7	-0,004	6,4
April	-0,01	55	-0,01	21,2	0,01	40,9	0	9,8	-0,02	67,3	-0,02	38,9
May	0,03	97,7	0,04	99,8	0,03	99,4	0,03	99,1	0,03	98,3	0,03	98,6
June	-0,002	12,1	0,004	17,3	0,02	97,9	0,01	81,4	-0,01	35,3	0,001	2,9
July	0,01	25,1	0,01	42,4	0,02	96,2	0,02	83,9	0	3,5	0,01	30
August	0,03	99,7	0,02	98,8	0,04	>99,9	0,04	97,6	0,02	90,4	0,02	94,6
September	-0,01	63,6	-0,02	86,9	0,02	89,9	-0,004	36,3	-0,03	89,8	-0,03	92
October	0,01	76,1	0,001	9,8	0,04	99,8	0,02	78	-0,01	72,7	-0,01	25,1
November	-0,01	49,1	-0,01	65,9	0,004	21,2	-0,004	31	-0,01	77,2	-0,01	69,1
December	0,01	30	-0,01	46,3	0,03	74,3	0,01	47,7	-0,001	16,7	-0,005	42,4
Year	0,01	90,6	0,01	89,6	0,03	>99,9	0,02	99,6	0,001	38,9	0,004	44,3
Growing Season (May- Aug.)	0,01	96,6	0,02	98,9	0,03	>99,9	0,03	>99,9	0,01	89,8	0,02	94,9
Spring (March - May)	0,01	90,1	0,02	84,7	0,03	>99,9	0,02	97	0,004	39,4	0,01	39,9
Summer (June - Aug.)	0,01	88,2	0,01	92,6	0,03	>99,9	0,02	99,6	0,004	64	0,01	91,3
Autumn (Sept. - Nov.)	-0,001	39,4	-0,01	82,8	0,02	99,3	0,003	23,4	-0,02	93,7	-0,02	92,6
Winter (Dec. - Feb.)	0,02	89,3	0,02	64	0,03	97,3	0,03	96,8	0,02	76,1	0,02	73,6

It is concluded that the revealed trend can be expected to affect the ecosystems in the study area strongly, because the highest trend values occur during the growing season. For altitudinal thermal gradient analysis to be biologically meaningful, the temperatures need to be considered which can act physiologically, i.e. occur during the growing season (Körner 2007).

4. Conceptual Framework of Climate Change Research

There are several reasons why alpine and montane ecosystems should be used preferentially for indicating climate change. Being exposed to low temperature conditions, montane systems are generally considered particularly sensitive to climate warming. Their ecological complexity is also comparatively low and abiotic factors are more important than biotic factors (Grabherr et al. 2000). Furthermore, altitudinal sequences of thermal life zones on high mountains are, compared with latitudinal ones, more compressed with small ecotones. Environmental gradients therefore occur along short distances. Distribution of many species is limited by altitude, as an expression of climate parameters or limitation of resources (Grabherr et al. 1994b, Theurillat and Guisan 2001). The steep altitudinal gradient recommends the chosen study area for research work on the impacts of climate change.

After detecting the principal determinants in the system as a whole, it is possible to answer specific questions on the impacts of climate change on taxonomic groups or species.

Well-documented samples and standardized sampling methods form a solid foundation for long term monitoring to detect environmental change and its impacts on a broad spectrum of forest inhabitants.

4.1 Study Design

We set up a total of 288 plots (Fig. 1) along four straight transects following the altitudinal gradient. Five additional plots were installed adjacent to the main transects to compensate for the lack of old growth forest samples at higher altitudes. The plots thus comprise various altitudinal ranges and forest structures.

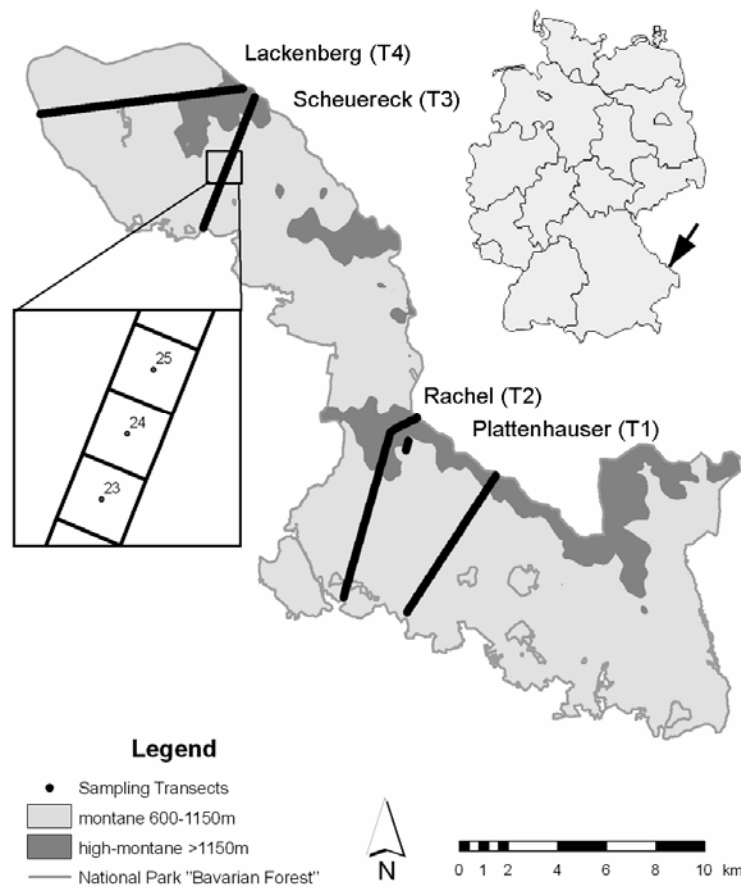


Fig. 1: Study area and study design of the sampling transects with indication of the boundaries of the montane and high montane zone (Paper II).

The four transects were selected using a stratified random scheme. First imperative was to include within the straight transects the entire vertical gradient of the study area from valleys to mountain tops. 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. The number of plots to be investigated was decided as a result of the estimation of the expected range of environmental variables (Guisan and Zimmermann 2000, Steyerberg et al. 2001). 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. 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 utilization and management were abandoned several decades ago. The other two transects were set up in areas still subject to management. The plots represent fairly well the main plant communities of the National Park (Fig.2).

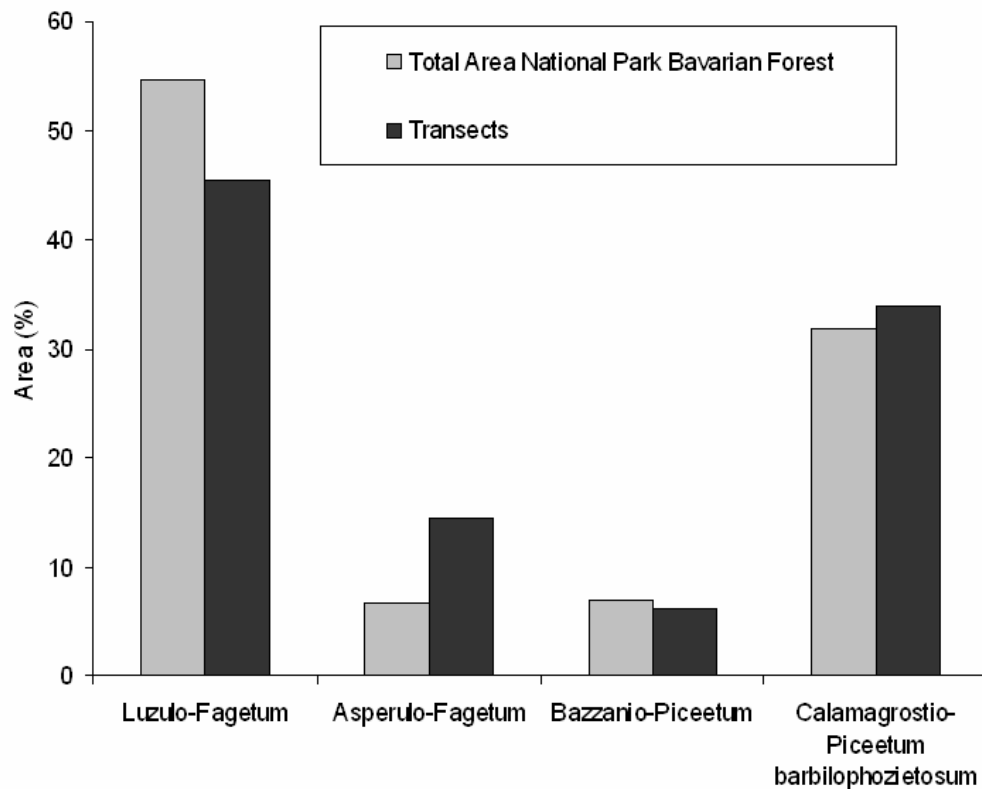


Fig. 2: Vegetation type represented by our study plots and their frequency throughout the whole area of the National Park (Paper II).

4.2 Environmental data

Much knowledge of species distributions results from observational data and surveys. These data are often of little value because they yield only a description of current conditions (Juilliard et al. 2003). Specific biological targets (e.g. community composition, species, species density) must be linked to quantitative environmental predictors to assess the response along the predictor's gradient and to quantify the contribution of climate variables to variance in occurrence when other explanatory variables are accounted for (Stenseth et al. 2002). We considered the explanatory variables listed in Tab.1 to be strong determinants for the taxonomic groups under study.

Tab. 1: Environmental factors (general information, climate parameters, forest stand structure variables and soil variables): definitions, spatial distribution and measurement (Paper II).

Variables	Definition	Plot	point	0.02 ha	0.1 ha	1.0 ha	50 ha	Measurement
Geographical co-ordinates	Co-ordinates (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/m ²)	x						
Temperature	Yearly mean (1980-2006) in °C	x						GIS Model (ArcEgmo)
Precipitation	Yearly mean (1980-2006) in °C	x						
Global Radiation	Yearly mean (1980-2007) in kwh/m ²	x						
Canopy Cover	Sample area shaded by horizontal projection of tree layer (upper L., middle L., under L.) separated for 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 diameter	DBH at 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	x	Airborne Laserscanner
Canopy mean height			x	x	x	x	x	
Canopy standard deviation			x	x	x	x	x	
Woody debris (CWD)	CWD-Fractions, decay level, length and diameter				x			Measurement, visual estimation
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					
Humus forms	4 humus-layer samples, classification following AK Standortskartierung (1996)		x					Visual estimation
Podsol grade	4 samples up to 30cm, 4 categories following AK Standortskartierung (1996)		x					
Exchangable nutrient elements	separately for 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	separately for litter and topsoil (µeq/g and %)		x					
Cation exchange capacity (CEC)	CEC separately for litter and topsoil (µeq/g)		x					
C/N ratio	Carbon (%) / Nitrogen (%) ratio		x					

4.3 Biological data

We sampled the taxonomic groups under focus in this study as part of a more comprehensive program to characterise spatial variation of biodiversity across the National Park. All mapped and sampled taxonomic groups, methods and numbers of sampled plots (replications) are presented in Tab. 2. 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 interception 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.

Tab. 2: Number of samples and sampling methods for the taxonomic groups considered in the BIOKLIM Project (Paper II).

Taxonomic 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			
Neuroptera		x			
Syrphidae		x			
Symphyta		x			
Aculeata		x			180 pitfall traps
Fomicidae		x			
Araneae		x			
Opiliones		x			
Chilopoda		x			
Diplopoda		x			
Collembola		x			
Isopoda		x			
Mecoptera		x			36 Malaise traps

4.4 World wide climate change research - a comparison

A comparable approach to studying biodiversity with respect to climate change along an altitudinal gradient is being made in Queensland, Australia. The IBISCA Queensland Project is a major international collaborative effort to survey different taxonomic groups in south-east 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. Despite similar project aims, the chosen designs represent different approaches. 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.

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.

The BIOKLIM design with its relatively high number of plots compares favourably with both these approaches and should ensure adequate representation of the variability in environmental and structural conditions within the sampling plots, with a minimum risk of spatial autocorrelation and avoidance of pseudo-replication (Hurlbert 1984).

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. 1994a, 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 been 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.

5. The surrogate factor altitude and its influence on community composition

As mentioned, distribution of taxonomic assemblages is shaped by altitude, as an expression of climate parameters and limitation of resources (Theurillat and Guisan 2001). Altitude is therefore a surrogate gradient representing many climate factors which affect species directly as well as being correlated with resources and regulators of species development (Austin 1980, Lomolino 2001, Körner 2007). The many components of climate, including for example temperature, precipitation and seasonality, vary in a non-random fashion along most elevation gradients (Lomolino 2001). Climate can be adequately described using topographical surrogates like altitude when the extent of the study area is relatively small, climate is fairly uniform throughout the area and the lapse rate of temperature with increasing elevation is constant within the area (Austin 2002, Sergio and Pedrini 2007). All three conditions were fulfilled in this study. The decrease of temperature along our altitudinal

gradient is generally very stable (Noack 1979, Elling et al. 1987), as can also be seen in Fig.3. The outliers are typical sinks for cold air.

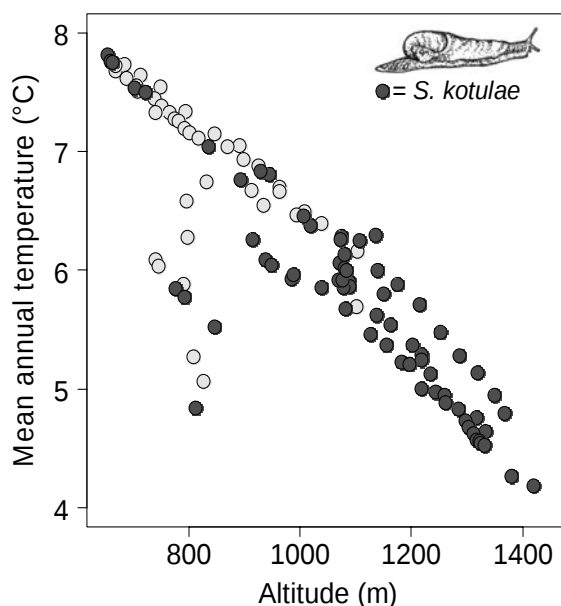


Fig. 3: Relation of mean annual temperature to altitude across 111 sampling plots in the National Park “Bavarian Forest”. The outliers are typical sinks for cold air. Dark symbols indicate plots where we recorded *Semilimax kotulae*, as an example of a typical montane species (Paper V).

There is only a weak dependency of global radiation (W m^{-2}) and potential sum of radiation (kwh m^{-2}) on altitude (Noack 1979, Elling et al. 1987). Further, there is only a weak decrease of sum of sunshine (hours) and relative humidity (%) with altitude. Wind speed varies very widely and depends primarily on surface conditions (Baumgartner 1960, 1964). 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 and Šrůtek 2002, Walentowski et al. 2004, Lee et al. 2005). Additionally, forest structures have mostly been heavily influenced by human activity in the past, such as logging (Spehn et al. 2006). A major challenge to the BIOKLIM Project is to establish the importance of the hidden, directly (physiologically) operating factors within the proxy altitude and to deal with confounding environmental effects.

Preliminary unconstrained ordination (CA) of data for six taxonomic groups (carabids, breeding birds, wood-inhabiting fungi, molluscs, plants and spiders) reveals the altitudinal gradient as the main driver for the compositions of the communities studied: this follows the

first axis (Fig.4). 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.

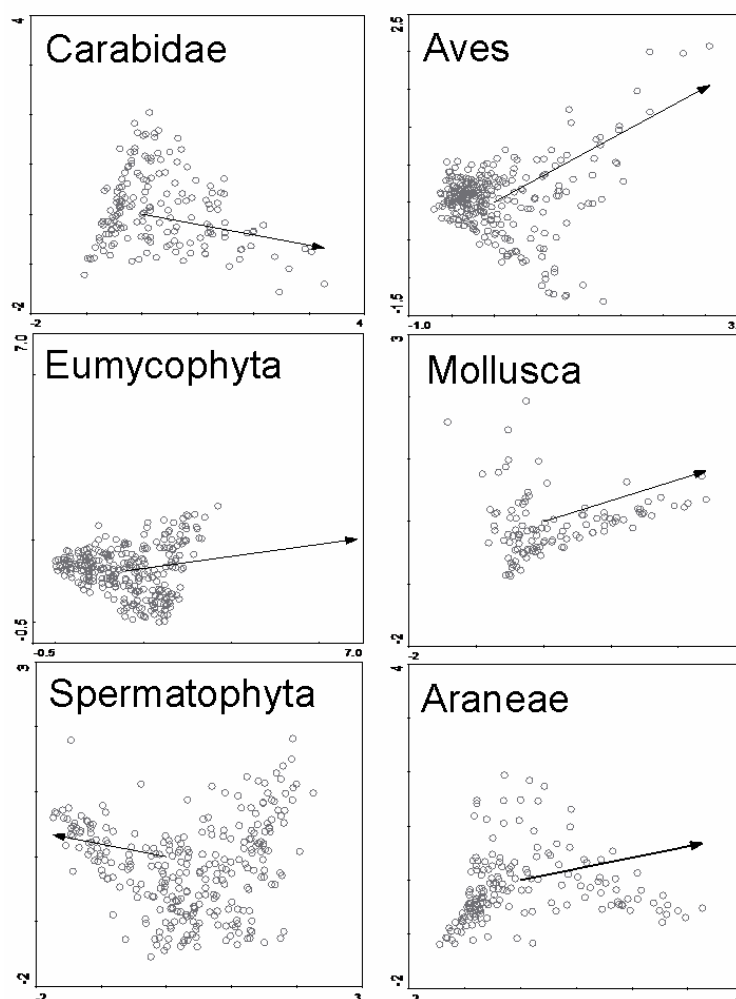


Fig. 4: Wood-inhabiting fungi, vascular plant, bird, mollusc, spider and carabid communities and their dependence on the altitudinal gradient. Results based on unconstrained correspondence analysis (CA). The circles represent the community compositions; the vector (arrow) represents the factor altitude (Paper II).

6. Distribution patterns along the altitudinal gradient

After identifying altitude as the main driver for community compositions (Fig.4 and see paper III), the patterns of distributions were studied by applying maximally selected rank statistics. There is a clear decrease in the sample scores of the first ordination axis with altitude (Fig. 5). The decrease was non-linear, indicating a discrete change of community compositions along the altitudinal gradient. Cutpoint and confidence interval are quite similar for both vascular plant and wood-inhabiting fungi community compositions, with the zone of greatest change

identified by maximally selected rank statistics as occurring at the transition between montane and high montane assemblages. The consistent importance of this transition zone as an ecological threshold was confirmed by the narrow confidence interval indicating its altitudinal width as approximately 30 m.

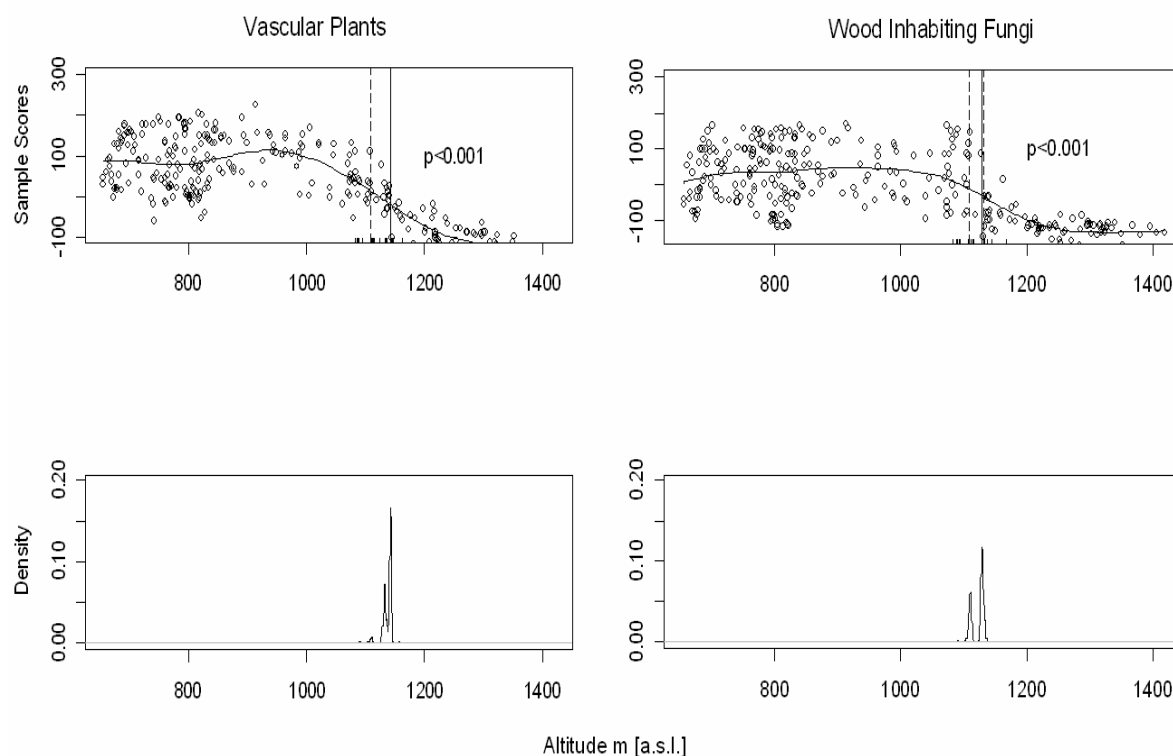


Fig. 5: Sample scores from the ordination axis 1 for vascular plants and wood-inhabiting fungi versus altitude across 290 sampled plots (above). Smooth lines result from generalized additive models (GAM), vertical lines indicate the cutpoint (with p - values) revealed by maximally selected rank statistics and the dashed lines indicate the 95% confidence intervals from bootstrapping (5000 runs). Density plots are presented (below) resulting from bootstrapping for the two taxonomic groups.

The same pattern as described for species assemblages was also revealed for species density and single species. This is illustrated using mollusc data as an example (Fig. 6).

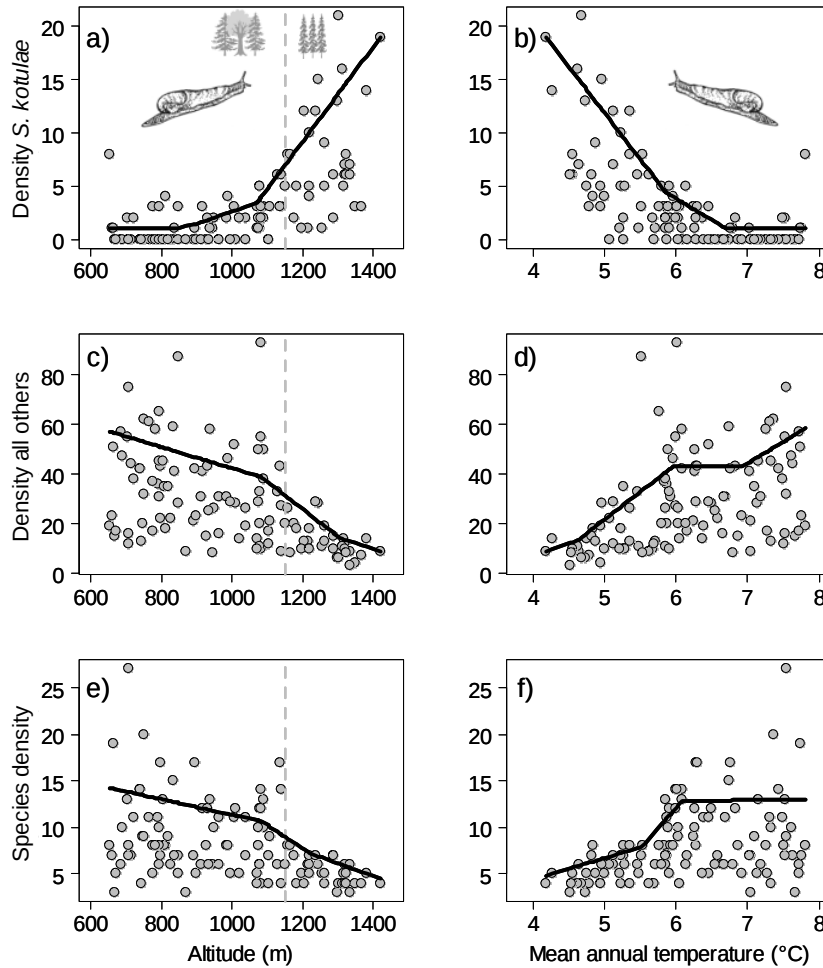


Fig. 6: Species density: density of *Semilimax kotulae* as an example of a montane species as well as density for all species (with exception *S. kotulae*) versus altitude and temperature across 111 plots sampled. Lines are additive quantile regressions. The dashed line indicates the altitude of the change between mixed montane and high montane spruce forests at 1150 m (Paper V).

7. Effects of climate and other factors along the altitudinal gradient

Understanding patterns in species composition along altitudinal (environmental) gradients is of primary interest in climate change research, although establishing causal relationships between communities and gradients is a difficult task. Few multivariate methods enable testing of specific hypotheses on relationships between communities and environmental gradients (Økland and Eilertsen 1994). One technique is based on CCA for partitioning of the variation in a species-sample data matrix into different sets of explanatory variables. This not only allows statistical testing, but also provides a quantification of the variation explained by

the different sets of variables (for more detail see paper IV). We used this method to test and quantify the relative influence of climate and other habitat predictors (forest structure factors). First step is to perform a DCA (Detrended Correspondence Analysis) to reveal the main gradient structure of the data sets. Using partial CCA, variance partitioning was calculated for vascular plant and wood inhabiting fungi community compositions, as an example, using two sets of explanatory variables (climate and forest structures) (Fig.7). The communities in the example are characterized by different ecological responses (see paper III, IV). Apart from climate factors, vascular plants are primarily driven by soil attributes, whereas wood inhabiting fungi depend more on woody debris attributes. Fig.7 illustrates the different response to climate of the two taxa. Thus the independent effect of climate dominates all other factors driving occurrence of vascular plants, but for woody debris organisms such as wood-inhabiting fungi, forest structure variables clearly overlay climate variables.

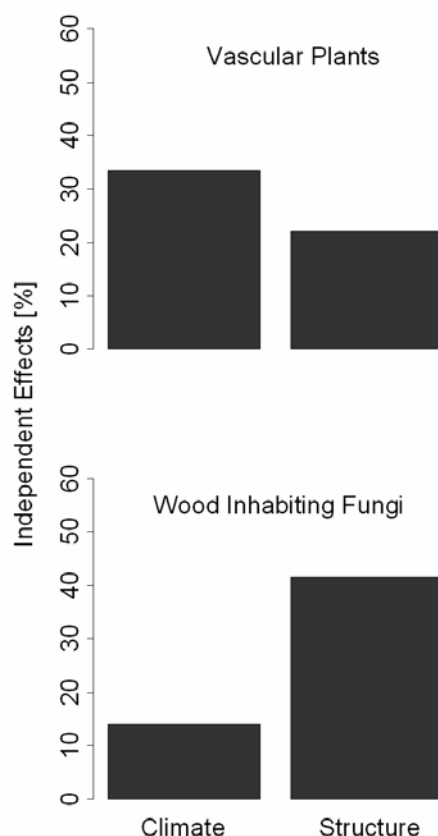


Fig. 7: Explained variance (%) for vascular plant and wood-inhabiting fungi community composition according to variance partitioning by partial CCA in relation to the environmental set of variables divided into climate and forest structure. Note that bars for geographical and unexplained variance are lacking (Paper IV).

It follows that vascular plants are more appropriate indicators of climate change, because the effect of climate is revealed as direct. On the other hand, wood-inhabiting fungi are more affected by management activity (e.g. logging) and only changes in forest structure (e.g. upward shift of European beech) triggered by global warming will affect them on a longer time scale.

8. High montane species as climate change indicators

As described in Chapter 4, montane ecosystems should be preferred for use in research on climate change because of their sensitivity to climate. Distribution of many species is limited by altitude, as an expression of climate parameters or limitation of resources (Grabherr et al. 1994b). Species limited to higher altitudes are thus disproportionally sensitive and vulnerable to global warming (Thuiller et al. 2005, Parmesan 2006, Pauli et al. 2007). It follows that there are some obvious cases of species, such as those of mountain tops, which should lose parts of their range because of climate change. Using these species as indicators seems to be reasonable. In order to be able to detect responses of individual species to climate change, to assess “critical levels” and to develop anticipating measures, better information on climate sensitivity of species is essential. There is also a need to find appropriate indicators for the identification of the effects of climate change, to verify results from modelling and to prove the response of species (Kappelle et al. 1999, Sutherland et al. 2006) with special attributes (DeGroot et al. 1995). Ecological indicators are identified by establishing a strong relationship with some characteristic of their environment (Kitching et al. 2000). One essential criterion of suitability as an indicator for global warming is sensitivity to temperature (DeGroot et al. 1995). The adaptation to low temperatures in the high montane zone characterizes the majority of montane species as belonging to a group of specialists, which are in general more sensitive than generalists (Juilliard et al. 2003). Species vulnerability must be linked to quantitative predictors to assess the response along the predictor’s gradient (Stenseth et al. 2002). This makes it necessary to focus more on species-environmental relationship analysis to answer the question of what makes some species more vulnerable, and thus more suitable as indicators, than others.

We tested the suitability of high montane species selected a priori from different taxonomic groups as indicators for global warming, to reveal whether strong temperature dependency exists even where other environmental variables play a role. This led to the conclusion that fairly simple species-environmental relationships exist for high montane species across different taxonomical groups, determined particularly by low temperature conditions (Tab. 4)

to which all high montane are species necessarily adapted. Sensitivity of these species to increasing temperature, with future modification of the distribution pattern as a consequence, could be expected. The selected species are hence good indicators at a regional scale, suitable for long term monitoring aimed at proving responses of species caused by climate change.

Tab. 4: Significant environmental variables identified with spatial GLM. Black triangles indicate significant influence (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), up means positive estimator, down negative estimator. Independent effect values (%) determined by hierarchical partitioning under the triangles (Paper V).

Environmental variable	<i>Athyrium distentifolium</i>	<i>Trientalis europaea</i>	<i>Hymenochaete fuliginosa</i>	<i>Semilimax kotulae</i>	<i>Ampedus auripes</i>	<i>Turdus torquatus</i>
Temperature	▼** 57.6	▼*** 100	▼** 100	▼** 100	▼*** 97.1	▼*** 82.7
Radiation	▼* 25.0					
Canopy Cover	▼* 17.4					
Opening of canopy layer						▲** 17.3
Spruce woody debris (middle decay stage)					▲* 2.8	
Spruce woody debris (advanced decay stage)					▲* 0.1	

9. Extinction risk

Topographically isolated mountain ranges with a high rate of endemism are severely threatened worldwide by climate change (Williams et al. 2003, Thuiller et al. 2005, Rull and Vegas-Vilarrúbia 2006). Broad consensus has been reached that work on models to elucidate the correlation between climate and biophysical processes should be undertaken (Ipcc 2007a). Furthermore, there is a clear need to increase our ability to predict the consequences of

environmental change (Sutherland 2006). Especially needed are considerably improved models for evaluation of the effects of climate change on distribution of species and their habitats (Sutherland et al. 2006). It is essential to develop models that link the distribution of species to alternative scenarios of climate change (Lawler et al. 2006).

Our low mountain range ecosystem underwent dramatic historical changes and is thus in general poor in species, particularly as a result of the alternating extremes of conditions in glacial and interglacial periods (Pleistocene) and probably also the warm conditions of postglacial periods (Quaternary) (Chapin and Körner 1994). This has led to high extinction rates and the presence of some rare endemic relicts. The magnitude of the current warming in a very short time frame on a global scale is unique in climate history and will certainly drive some species to extinction (Ipcc 2007a).

Projected rates of extinction for different taxa and regions of the world range from 9 - 52 %, depending on the chosen climate change scenario as well as dispersal capacity (Thomas et al. 2004). On a European scale the loss of plant species from mountains, described as disproportionally sensitive to climate change, is projected until the end of the 21st century as reaching 60% (Thuiller et al. 2005). A study from the Australian tropical rainforest predicts that even a 1 K increase will cause significant declines in range size in almost every species of regionally endemic vertebrate (Williams et al. 2003). Preliminary estimates for the neotropical Guyana Highlands, based on representative endemic vascular plants, show that roughly 10-30% would lose their habitat with a 2-4 K temperature increase (Rull and Vegas-Vilarrúbia 2006). This agrees fully with our findings for Central Europe. We modelled the extinction risk for six species selected a priori from different taxonomical groups (see Chapter 8), using two official climate change scenarios (Ipcc 2007b). According to our models, even an increase in the mean annual temperature of 1.8 K will lead to a decrease in the occupancy for almost all species included in our study by about 25 % at altitudes of 1400 m. (Fig. 8). Nevertheless, within this optimistic scenario some sinks for cold air may act only for *Semilimax kotulae* as refuges at lower altitudes, if one assumes that local air circulation patterns will not change with global warming. An increase in mean annual temperature of 4.0 K would probably lead to the extinction of all selected species in the area covered by the National Park. This effect will be strengthened by the disproportional decrease in available area with altitude, which limits how species may alter their ranges in response to increasing temperature.

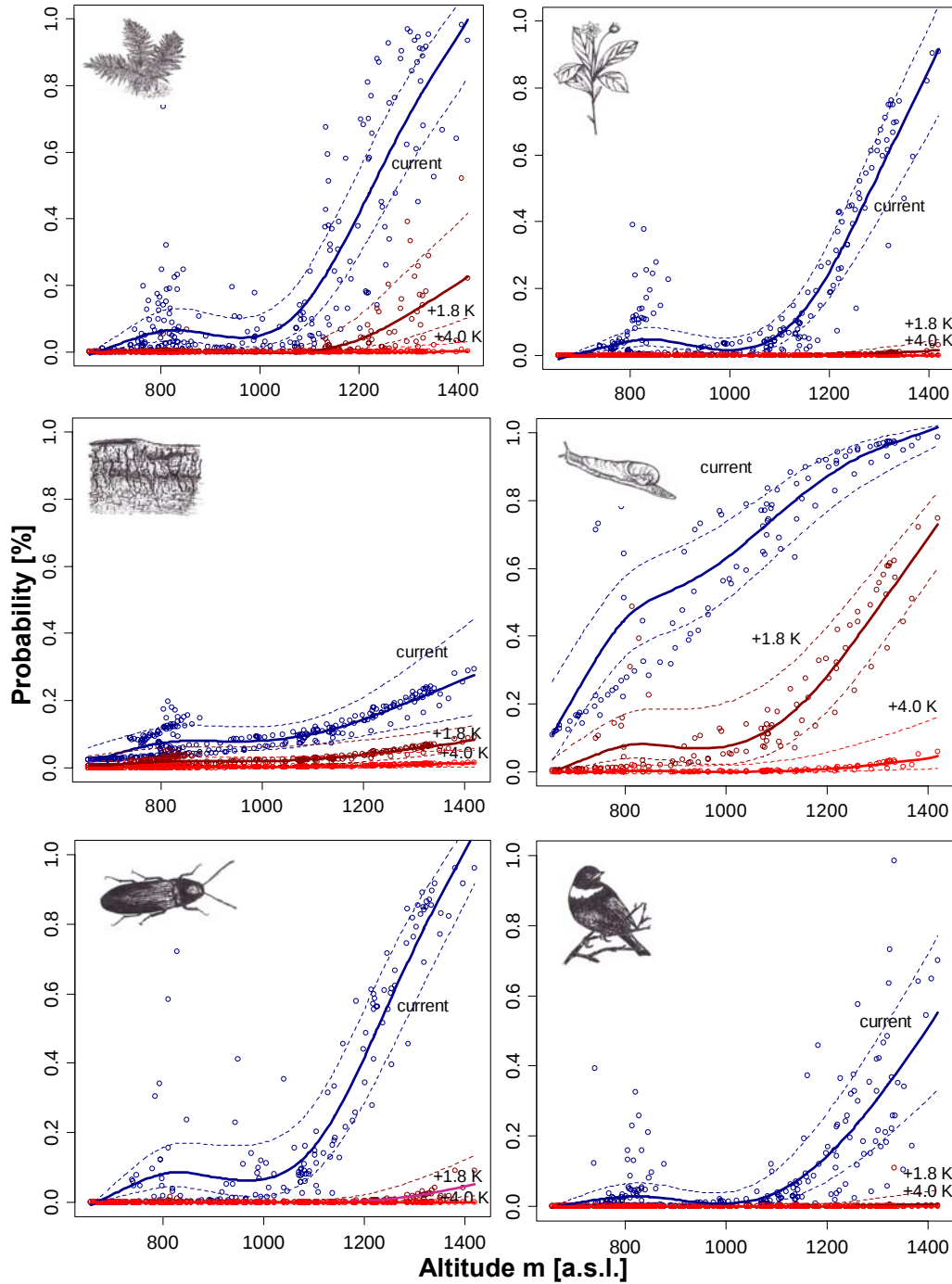


Fig. 8: The blue points represent the predicted probability of occurrences of *Athyrium distentifolium*, *Trientalis europaea*, *Hymenochaete fuliginosa*, *Semilimax kotulae* (Müller et al. 2008), *Ampedus auripes* and *Turdus torquatus* using annual mean temperatures from 2000 and 2004 for the sampling plots versus altitude of these plots within the National Park “Bavarian Forest”. The curves are locally smoothed (splined), with heuristic confidence bands (for details of calculating these intervals see text). The other two groups of points and curves are predicted probability of occurrences under scenarios of global warming where the mean annual temperature increases by 1.8 K and 4.0 K (Paper VI).

From the reference species lists for the study area we calculated for each taxonomic group the proportion of species restricted to the high montane zone as well as the proportion of the red listed high montane species and assessed the rough potential for extinction caused by climate change. According to this, from 1.5 - 23.4 % of the target taxa assessed may become extinct in the study area. Red listed species are disproportionally sensitive, with an extinction risk of up to 75.0%. The reason for the particularly severe effect on red listed species can almost be explained alone by their existing restriction to montane-alpine zones and consequent rarity, often involving a degree of endemism. In the case of molluscs, 15 of 18 high montane species are included as threatened species in the red data book. The predicted extinction rates are mainly based on assumptions where pessimistic SRES scenarios are adopted (Ipcc 2007b, Spekat et al. 2007)

10. Conclusions and recommendations for monitoring of climate change

Climate change is clearly taking place in the study area, as shown by a trend analysis of air temperatures which detected clear warming signals during the last decades. Studying the impacts of climate change on a regional scale necessitates the setting up of a suitable study design which as well as considering biological data, also includes appropriate environmental variables which can overcome confounding environmental effects along altitudinal gradients. Observational data and surveys on their own are insufficient to answer questions about the impacts of climate change or to identify suitable indicators. A first step is therefore to reveal the effects of climate on biological targets (species, community composition, species density etc.) whilst considering effects of other environmental predictors, necessary because of the different responses of individual taxonomic groups to climate shown in this study. Consideration of a broad set of biological and environmental data unfortunately increases the research and monitoring effort enormously. We required two years to map and sample 25 taxonomic groups and record environmental factors based on 293 replications. As examples from our study, we surveyed 9300 fungi, determined 27000 beetles from 180 flight interception traps and collected 3400 individuals of molluscs. Repetition of such a large program is to be realized only within a period of about ten years. However, to prove only the effect of climate change, monitoring of the indicators here revealed is sufficient. This could be realized within shorter time frames, such as regularly every 5 years.

This study considered only a few taxa and different biological targets (e.g community composition, species density, and species) sampled within a relatively short period. For vascular plant community compositions the overall effect of temperature as main driver was

revealed by a clear, discrete change at 1142m asl (climate sensitive zone), resulting from a smooth and continuous climate gradient. Repeated recording using the same methods in five or ten years may indicate displaced thresholds and thus highlight the effects of climate change. But further studies should focus on where species of this zone reach their lower and upper limits, which are both expected to shift upwards. However, climate is not the most important overall factor for all taxonomic groups studied. At least on a regional scale, structure-dependent organisms like wood inhabiting fungi are more strongly influenced by their specific structural requirements than by larger scale climate. Thus it has to be concluded, that for some taxa the effects of global climate change are clearly overlaid by the influence of forest structure and that climate change will have only an indirect, long-term effect resulting from the change in these structures.

A rapid and reliable method of proving the effects of climate change would be the use of the indicators revealed in this study. These represent the key attributes of the ecological properties that are regarded as important. Good co-variation exists between the high montane species of different taxa because of a similar predictor response common to cold-adapted organisms. It can be concluded that it little matters which of the selected species is used as an indicator, as long as the models show a similarly high quality of discrimination. The choice made in our study of indicators in different taxa should make it easy to combine the inventory of some of these indicators with other biodiversity surveys or fieldwork through the seasons, thus reducing the sampling effort. Most of our indicators are detectable throughout the year with the same reliability, and are readily identified, mapped or sampled. It can be stated in conclusion, that the easiest and most efficient method of monitoring is to map in a standardized way species such as *Athyrium distentifolium* or *Trientalis europaeus* which occur regularly in the study area, are really easy to identify and are found during the entire growing season. Also recommended is the mapping of *Turdus torquatus*, which could be effectively undertaken in spring. For *Semilimax kotulae* a standardized hand sampling strategy in early autumn (peak of activity) could also reduce the effort and make it suitable as a target species. Highest effort is to be expected for sampling *Ampedus auripes*, caused by the time involved in identifying and sorting the very large numbers of insect individuals caught in flight interception traps. In such cases we should develop cheaper sampling methods, particularly for taxa having a large number of species, such as beetles. *Hymenochaete fuliginosa* is the only species which should not be considered as an indicator, because of its poor discrimination. This species is poorly predicted by the other models and its own model underestimates the occurrence of the other selected species. In general, it must be borne in

mind that studies on the performance of biodiversity indicators show that the exclusive use of indicator species in monitoring is likely to result in an undetected loss of species. Therefore, a complete inventory of biodiversity is necessary if the goal is to maintain all species in the landscape. The selected species do not necessarily represent the overall biodiversity in the high montane zone, but our results show similar response patterns for the selected species. The simple and similar species-environmental relationships in the high montane zone resulting from cold-adaptation lead us to expect similar responses for almost all species in this zone.

In accordance with the objectives of the BIOKLIM Project (see paper II), we are continuing to gather data for long-term comparison, with the goal of improving our understanding of different taxonomic groups and the climate-change driven forces operating on complex biological systems. The real impacts of climate change caused by complex interactions and interspecies relationships will be evident only with the passing of time and only detectable through fieldwork. Use of bio-monitoring will therefore be essential for future research and formulation of policy.

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Part B: Research Papers

Klimawandel – Trend der Lufttemperatur im Inneren Bayerischen Wald (Böhmerwald)

Climate Change – Trend of air temperature in the Innerer Bayerischer Wald (Bohemian Forest)

Claus Bäessler

*Nationalparkverwaltung Bayerischer Wald, Freyunger Strasse 2, D-94481 Grafenau,
Deutschland, claus.baessler@npv-bw.bayern.de*

Abstract

The trend of the air temperatures on the basis of selected meteorological stations of the Innerer Bayerischer Wald (German side of the Bohemian Forest) has been analysed. Mean air temperature, mean daily minimum and maximum temperature were considered. After data preparation and data check time series analysis (trend and cutpoint analysis) and examination of spatial and time representation was carried out. To consider orographic differences, two representative meteorological stations (Waldhäuser for hillside locations, 1948-2002 and extended with data from the station Hohenpeißenberg 1781-2003; Zwieselberg for valley locations, 1948-2002) were analysed.

Predominantly positive trends were noticeable for the period under consideration. The highest trend of mean air temperature was calculated for May ($0,04 \text{ K a}^{-1}$ for hillside locations and $0,03 \text{ K}$ for valley locations) and august ($0,02 \text{ K a}^{-1}$ for hillside locations and $0,03 \text{ K}$ for valley locations). Thus, there was a trend of $0,02 \text{ K a}^{-1}$ (hillside) respectively $0,01 \text{ K a}^{-1}$ (valley) for the growing season (may-august). On the other hand there was neither a significant trend considering the annual average values, nor the climatological seasons, especially winter. More distinct were the trends of the mean monthly minimum temperature, almost all trends were positive. In contrast the mean maximum temperature showed a much more moderate reaction. There is a common cutpoint in 1988 for the meteorological stations Waldhäuser, Zwieselberg and the reference station Hohenpeißenberg. Hence, the detected overall trend is mostly a result of the increasing temperature since this point in time.

Key words: air temperature, trend analysis, climate change

EINLEITUNG

Meteorologische Messungen zeigen entscheidende Änderungen des globalen Klimas im 20. Jahrhundert. Demnach geben klimabestimmte Parameter eindeutige Hinweise auf eine weltweite, aber regional durchaus sehr unterschiedliche Erwärmung. Seit Beginn der instrumentellen Messungen (z.B. in Bayern seit 1781) waren die bodennahen Durchschnittstemperaturen der Erde noch nie so hoch wie in den letzten Jahrzehnten (IPCC a 2007). Allerdings bestehen regional sehr unterschiedliche Trends signale (KLIWA 2006,

DEUTSCHER WETTERDIENST 2001). Die folgende Analyse hat zum Ziel, konkrete Trendwerte anhand ausgewählter Klimastationen des Untersuchungsgebietes zu Tage zu fördern. Neben natürlichen Faktoren für die Veränderung des globalen Klimas treten zunehmend anthropogene Einflüsse auf, die in Form der Immission von Treibhausgasen im 21. Jahrhundert aller Voraussicht nach deutlich hervortreten werden (BAYERISCHER KLIMAFORSCHUNGSVERBUND 1999, IPCC a 2007). Für die Absicherung von Prognosen werden Klimamodelle eingesetzt. Aktuelle Klimaprojektionen ergeben eine Erhöhung der globalen Mitteltemperatur, abhängig vom gewählten Emissionsszenario von 1,8 (1,1 – 2,9 K) – 4,0 K (2,4 - 6,4 K), (2090-99 im Vergleich zu 1980-1999). Szenariobeeinflussende Faktoren sind z.B. die Entwicklung der Weltbevölkerung, zukünftiger Energieverbrauch und eingesetzte Energieträger (CUBASCH 2004). Aktuelle Prognosen, basierend auf den SRES-Szenarien (IPCC a 2007) für ganz Deutschland, zeigen einen Anstiegstrend, der eine Erwärmung um bis zu 3 Grad zum Ende des 21. Jahrhunderts nahe legt (SPEKAT 2007). Zahlreiche Studien belegen den Zusammenhang zwischen der Zunahme der globalen Kohlendioxidkonzentration und der deutlichen Erwärmung der letzten Jahrzehnte einerseits sowie einem Wandel der Ökosysteme andererseits (KASANG 2004, IPCC a 2007).

Die vorliegende Untersuchung soll einer ersten Einschätzung dienen, in wie weit sich die auf globaler, deutschland- und süddeutschlandweiter Ebene beobachteten Trends im Zusammenhang mit der Lufttemperatur ebenfalls auf lokaler Ebene (Böhmerwald, v.a. Nationalpark Bayerischer Wald) wieder finden. Die Analyse soll wesentliche Veränderungen bezüglich der mittleren Lufttemperaturen und Extremtemperaturen detektieren. Im Anschluss an die erste Einschätzung sollen in weiteren Studien die Auswirkungen des Klimawandels auf Ökosysteme untersucht werden. Hierfür soll ein Bioindikationssystem entwickelt werden, anhand dessen ein Wandel langfristig nachgewiesen werden kann.

MATERIAL und METHODEN

Untersuchungsgebiet und verwendete Klimastationen

In Tab.1 sind die für die Analyse herangezogenen Klimastationen sowie die entsprechenden Höhenangaben aufgeführt. Hauptziel soll die klimatologische Betrachtung des Nationalparks und seines Umfeldes sein, um lokale Aussagen über Entwicklungen treffen zu können (Abb.1). Der ARBEITSKREIS STANDORTSKARTIERUNG (1985) ordnet den untersuchten Naturraum des Böhmerwaldes in die Wuchsbezirkskategorie „Innerer Bayerischer Wald“ ein.

Tab. 1: Zur Analyse herangezogene Klimastationen, vorliegende Daten und Höhenlage der Klimastationen (m üNN).

Tab.1: Meteorological stations used for the analyses, available data and elevation of the meteorological stations (m a.s.l.).

Stationsname	Erfassungszeitraum	Höhe ü. NN
Waldhäuser	1972 - 2003	945
Grosser Arber	1983 - 2003	1.437
Grosser Falkenstein	1947 - 1981	1.307
Klingenbrunn Bahnhof	1981 - 2004	756
Mauth/Finsterau	1942 - 1956	1.004
Hausstein	1936 - 1944, 1947 - 1952	648
Buchenau	1900 - 1929	750
Zwieselberg	1948 - 2002	590
Grainet/Rehberg	1958 - 2000	645
Taferlruck	1980 - 2004	771
Fichtelberg	1949 - 2004	1.213
Hohenpeißenberg	1781 - 2004	977

Die Stationen Fichtelberg und Hohenpeißenberg dienen als Referenz im Zusammenhang mit Datenprüfungen (Homogenitätsanalyse). Die Station Hohenpeißenberg findet weithin für Reduktionen zum Verlängern von Zeitreihen Verwendung, da ihre instrumentelle Messlänge seit 1781 für Bayern einmalig ist. Der Fichtelberg ist naturräumlich dem Erzgebirge zuzuordnen und befindet sich ca. 200 km nord-westlich vom Untersuchungsgebiet. Es handelt sich ebenfalls um ein Mittelgebirge mit kontinentaler Prägung und starker vertikaler Gliederung und ist somit mit dem Klimaraum des Böhmerwaldes vergleichbar. Die Station Hohenpeißenberg befindet sich im Alpenvorland (Wuchsbezirk Oberbayerische Jungmoräne und Molassevorberge) und ist ca. 250 km Luftlinie vom Untersuchungsgebiet entfernt.

Datengrundlage

Als Datengrundlage dienen insbesondere Messreihen des Deutschen Wetterdienstes. Ein Teil der Daten stammt von Klimastationen des Nationalparks Bayerischer Wald, die z.T. im Rahmen bestimmter Forschungsvorhaben eingerichtet wurden (z.B. Station Taferlruck, Forschungsprojekt „Große Ohe“) oder als Privatstation geführt werden (z.B. Klingenbrunn Bahnhof). Die genannten Daten liegen nahezu alle in Tagesauflösung vor. Entsprechend fanden zur Aggregation der Mittelwerte für die untersuchten Klimaparameter die Tageswerte Verwendung.

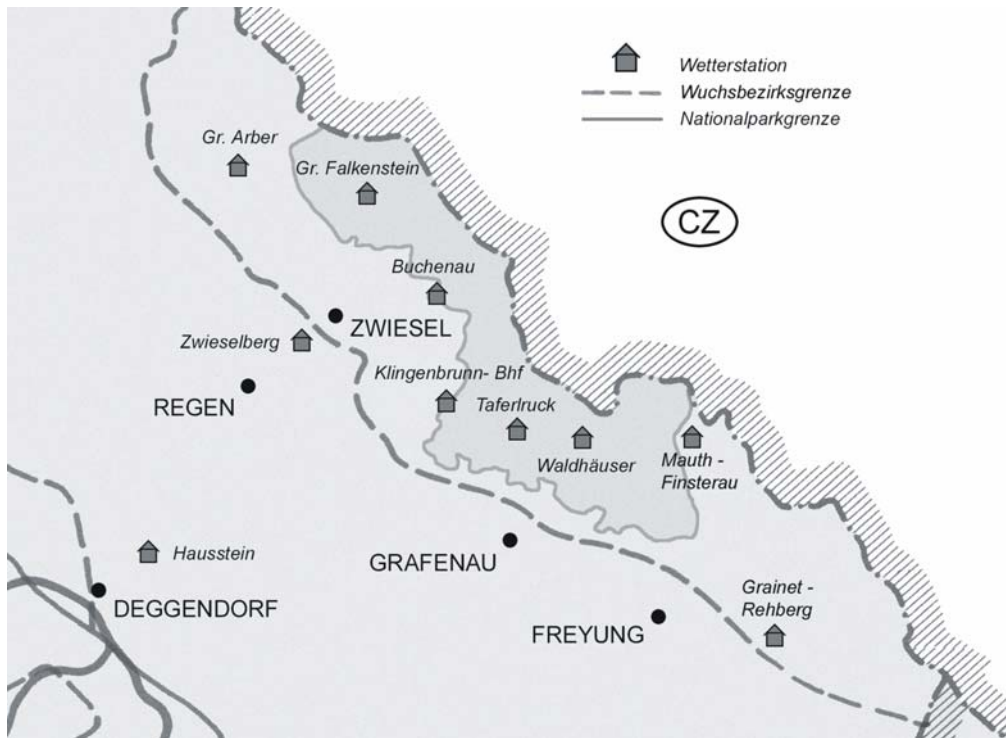


Abb.1: Übersicht über das Untersuchungsgebiet mit den Standorten der verwendeten Klimastationen (ohne Station Fichtelberg und Hohenpeißenberg).

Fig.1: Study area and sites of the meteorological stations (without the stations Fichtelberg and Hohenpeißenberg).

Datenaufbereitung, Prüfung der Datenvoraussetzung als Grundlage statistischer Tests und Basisanalysen

Für den einfacheren Umgang mit den Daten wurden einheitliche Tabellen erstellt. Im Falle lückenhafter Messreihen erfolgte eine Datenergänzung mit Hilfe von Regressionsbeziehungen zu vorhandenen Messreihen benachbarter Stationen. Zweifelhafte oder z.T. unvollständige Reihen wurden aus Sicherheitsgründen entfernt.

Zu Beginn der Analyse wurden alle Zeitreihen einem Homogenitätstest unterzogen. Die Prüfung sollte Inhomogenitäten bzw. Instationarität aufdecken (SCHÖNWIESE 2000, RAPP 2000). Es wurden sowohl absolute als auch relative Homogenitätsprüfungen angewendet. Als absoluter Homogenitätstest wurde das ABBEsche Homogenitätskriterium (PAESLER 1983) verwendet. Dieser Test lässt sich allerdings nur unter Vorbehalt anwenden, da mit Hilfe der zu prüfenden Datenreihe Inhomogenitäten ausschließlich indirekt aufgedeckt werden können. Dieses Verfahren bewertet auch solche Reihen als inhomogen, die relativ ausgeprägte langfristige Schwankungsanteile beinhalten, die durchaus auch natürlich verursacht sein können (SCHÖNWIESE 2000). Aus diesem Grund wurden zusätzlich relative Homogenitätstests durchgeführt. Hierfür sind nachweislich homogene Zeitreihen als Referenz verwendet

worden. Für diese Prüfung wurde der relative Test nach CRADDOCK (1979) angewandt (Test der kumulativen Abweichung), sie wurde rein graphisch ausgewertet. Die verwendeten Terme folgen der World Meteorological Organization (2003). Um die mit Hilfe des Craddock-Tests detektierten Inhomogenitäten quantifizieren zu können, wurde zusätzlich der Test nach Alexanderson angewendet. Vergleichstests ergaben weitgehende Übereinstimmung, wenngleich dieser Test insbesondere für Niederschlagsdaten entwickelt wurde (ALEXANDERSON 1986). Es fand weiterhin eine graphische Prüfung in Form des Vergleichs der zu prüfenden Zeitreihe mit entsprechenden Referenzreihen statt. Hierfür wurden die Daten gefiltert (Gauß'scher Tiefpassfilter), um Abweichungen leichter aufzeigbar zu machen. Zuletzt wurden noch die Differenzen der Jahresmittel zwischen Referenzdaten und Prüfdaten gebildet, um langfristig gerichtete Veränderungen zu detektieren.

Als Voraussetzung des Craddock-Tests gilt das Vorliegen normalverteilter Daten. Aus diesem Grund wurden alle verwendeten Zeitreihen auf Normalverteilung (NV) getestet und mit dem Kolmogoroff-Smirnoff-Test geprüft. Nach SCHÖNWIESE (2000) ist der Kolmogoroff-Smirnoff-Anpassungstest verlässlicher als der ebenfalls häufig verwendete χ^2 -Anpassungstest, da dieser anfälliger gegenüber relativ unwichtigen Verteilungsabweichungen im Bereich relativ geringer Häufigkeiten (bei eingipfeligen Verteilungen wie der NV im Bereich der „Verteilungsränder“) ist. Dies kann eine Fehlentscheidung hinsichtlich zu schlechter Anpassung hervorrufen, die unter Umständen nicht gerechtfertigt ist. Voraussetzung für den Test ist ein Stichprobenmindestumfang von $n > 35$, nach SACHS (1997) erzielt man mit $n > 50$ verlässlichere Ergebnisse; dies entspricht einer Mindestklassenzahl von $K = 6$ nach der Sturges-Formel. Diese Bedingungen werden erfüllt. Neben dem Datensatz wurden ebenfalls die Residuen auf Normalverteilung getestet (nach RAPP 2000 Voraussetzungen zur Anwendung des linearen Regressionsmodells).

Die verwendeten Tests zur Feststellung von Trends sind parameterfrei.

Die mathematische Statistik setzt bei der Anwendung ihrer Methoden voraus, dass die Daten der betrachteten Kollektive voneinander unabhängig sind. Allerdings ist diese Voraussetzung in der Regel für meteorologische Zeitreihen nicht erfüllt. Um diese Daten dennoch statistisch auswerten zu können, sind bestimmte Bedingungen einzuhalten (WERNER 2002). Demzufolge wurde die Persistenz (Erhaltungsneigung) der Daten über die Autokorrelationsprüfung getestet (WERNER 2000). Es sollte festgestellt werden, in wie weit die Werte nicht signifikant (auf dem 95% bzw. 99% - Niveau) von den vorangehenden abweichen. Zur Prüfung und zur quantitativen Kennzeichnung wurde der Autokorrelationskoeffizient berechnet (SCHÖNWIESE 2000).

Als maximale Zeitverschiebung M empfiehlt Schönwiese (2000) als empirischen Richtwert: $M \max. n/2$ oder $n/3$, mit $n \geq 30$ oder besser $n \geq 100$. Die Prüfung der Daten wurde mit M 30% von n durchgeführt. Für die Autokorrelationsfunktion wurde ein Mutungsbereich auf dem 99% - Niveau ($\alpha = 0,01$) und zum Vergleich auf dem 95% - Niveau ($\alpha = 0,05$) berechnet.

Um für eine bestimmte Station eine Zeitreihe von gewünschter Länge für die Analyse zu erhalten, wurde diese auf der Grundlage vorhandener, insbesondere benachbarter Stationen verlängert. Dies erfolgte für die Klimastationen innerhalb des Nationalparks mit dem von BÄSSLER (2004) errechneten vertikalen Temperaturgradient, der aufgrund von innerjährlichen Schwankungen für jeden Monat identifiziert ist. Die Eignung des Gradienten bzw. der Ausgangsdaten für die jeweilige Reduktion wurde mit Hilfe des PEARSON-Korrelationskoeffizienten getestet (SCHÖNWIESE 2000). Da der Korrelationskoeffizient als Gütemaß nicht ausreichend ist, wurde weiterhin die Qualität der Anpassung mit Hilfe eines Prognosegütemaßes geprüft. Hierfür fand der Theil'sche Ungleichheitskoeffizient (ANDRES & SPIWOKS 2000) Verwendung. Der Theil'sche Ungleichheitskoeffizient U nimmt Werte zwischen Null (vollständige Übereinstimmung) und Eins (vollständige Unabhängigkeit) an und kann in relative Fehlerkomponenten zerlegt werden. MF dient der systematischen Fehleinschätzung des Niveaus (Mittelwertfehler), VF dient der systematischen Fehlschätzung der Schwankungen (Varianzfehler) und der ZF ist die zufällige, nichtsystematische Fehlerkomponente (Zufallsfehler).

Grundlage der Zeitreihenanalyse ist die Berechnung des Trends. Dieser setzt sich aus einer Richtung (Vorzeichen), einem Betrag sowie der statistischen Signifikanz zusammen (RAPP 2000). Die Berechnung basiert auf der Annahme eines linearen Trends der jeweilig betrachteten Zeitreihe, entsprechend wurde das lineare Regressionsmodell verwendet. Beim linearen Trend wird durch die Zeitreihe y_n der Länge N eine Regressionsgerade ($y_n = b \cdot x_n + a$) nach dem Kriterium der kleinsten Quadrate gelegt. Der lineare Trend ergibt sich aus der Differenz der Ordinatenwerte am Anfang und Ende der Regressionsgeraden, welche durch die Zeitreihenwerte führt (SCHÖNWIESE 2000).

Als Trendtest diente das Verfahren nach Mann-Kendall. Dieser ist nach RAPP (2000) ein geeignetes Verfahren zur Abschätzung der Signifikanz, ohne dass eine Normalverteilung der Daten oder die Linearität des Trends vorausgesetzt wird (nicht parametrischer Test).

Zur Charakterisierung der Zeitreihe diente die Bruchpunktanalyse nach Mann-Whitney (Pettitt-Test, WORLD METEOROLOGICAL ORGANIZATION 2003). Diese Analyse stellt einen verteilungsfreien Homogenitätstest für die Zeitreihe dar. Sie liefert als Information den

wahrscheinlichsten Zeitpunkt innerhalb einer Zeitreihe, an der mit einer definierten Wahrscheinlichkeit eine Änderung vorliegt. Somit geht die Bedeutung über die Funktion eines Homogenitätstests hinaus, da der Bruchpunkt ein Charaktermerkmal des Zeitreihenverlaufs darstellt. Die Bruchpunktanalyse erfolgt über die in KLIWA (2003) dargestellten Terme.

Der wahrscheinlichste Bruchpunkt liegt bei dem Zeitschritt k , für den die Prüfgröße K_n ein Maximum darstellt. Die Wahrscheinlichkeit des Bruchpunkts kann somit geschätzt werden. Der errechnete und benannte Zeitpunkt über die Bruchpunktanalyse ist das erste Jahr nach dem Wechsel

Zur Abschätzung der zeitlichen Stabilität des Trends wurde der rückschreitende Trend (zeitliche Repräsentanz) berechnet. Unter der zeitlichen Repräsentanz ist die Veränderlichkeit des Trendwertes zu verstehen, falls der Analysezeitraum sukzessiv variiert (RAPP 2000). Diese Prüfung berücksichtigt, ob bestimmte Entwicklungen auch zeitlich stabil verlaufen.

Über den rückschreitenden Trend kann für eine Zeitreihe beurteilt werden, wie sich das Trendverhalten bei konstantem Zeitreihenende als Funktion der Beobachtungslänge verändert. Es ergibt sich die Trendsteigung in Abhängigkeit der Beobachtungslänge als Ganglinie. Als minimale Zeitreihenlänge wurde $n = 20$ Jahre festgelegt (KLIWA 2003). Für den rückschreitenden Trend wurde die Signifikanz berechnet.

Mit der räumlichen Repräsentanz sollte geprüft werden, inwieweit sich die zeitliche Schwankungsstruktur, einschließlich der Trends, auch in der Umgebung der Station widerspiegelt (BÄSSLER 2004). Die räumliche Repräsentanz wurde mit dem zweidimensionalen linearen Produkt-Moment-Korrelationskoeffizienten nach PEARSON (r) geprüft (z.B. SCHÖNWIESE 2000). Dieser beschreibt die Ähnlichkeit von Zeitreihen zweier Stationen (RAPP 2000). Das Bestimmtheitsmaß r^2 ist der Betrag der gemeinsamen Varianz der beiden Zeitreihen und in Prozent angegeben (SACHS 1993, SCHÖNWIESE 2000).

Als Mindestkriterium nennen SCHÖNWIESE et al. (1990) einen Koeffizient von $r = 0,7$ (gemeinsame Varianz von r^2 ca. 50 %) für eine befriedigend hohe Repräsentanz. Allerdings erlaubt die geringe räumliche Variabilität der monatlichen Temperaturmittel mit Koeffizienten von $r = 0,8$ oder sogar $r = 0,9$ ein anspruchsvolleres Kriterium (RAPP 2000).

ERGEBNISSE

Ergebnis der Datenprüfung und Datenaufbereitung

Es wurden alle Klimastationen für die Parameter T_{mit} (mittlere Lufttemperatur) T_{min} (mittlere Minimumtemperatur) und T_{max} (mittlere Maximumtemperatur) auf Inhomogenität getestet.

Das absolute Homogenitätskriterium nach ABBE wurde für die genannten Parameter und Klimastationen angewendet. Hierbei konnte festgestellt werden, dass für keine Reihe Homogenität gegeben war. Auch der Test an der nachweisbar homogenen Zeitreihe Fichtelberg (DEUTSCHER WETTERDIENST 2005) ergab nach ABBE Inhomogenität. Dieses Ergebnis unterstreicht den Hinweis von SCHÖNWIESE (2000), dass absolute Homogenitätstests nur unter Vorbehalt anzuwenden sind. Es ist festzustellen, dass diese Prüfung für die folgende Analyse unbrauchbar ist, da selbst klimatologische Trends als Inhomogenität detektiert werden. Die relativen Tests zeigten insbesondere verlässliche Zeitreihen an. Für die folgenden Analysen wurden nur Zeitreihen verwendet, welche auf der Basis der genannten Kriterien homogen sind. Der KOLMOGOROFF-SMIRNOFF-Test bestätigt für alle Stationen Normalverteilung auf dem 95%-Niveau. Es wurden alle Jahresmittel sowie die einzelnen Monate berücksichtigt.

Für alle Stationen wurden für die mittleren Luft- und Extremtemperaturen Autokorrelationsfunktionen errechnet. Alle berechneten Funktionen zeigen kaum zyklische oder periodische Varianz. Die Kurven variieren i.d.R. insignifikant um Null. Es konnten keine starken Ausreißer beobachtet werden. Das Ergebnis der Prüfung aller herangezogenen Stationen wurde zur Sicherheit mit bereits analysierten Stationen (vorangegangene Untersuchungen) verglichen, um ein quantitatives Vertrauensmaß zu erhalten. Auffällig ist ein einheitliches Muster der Persistenz. So besitzen die geprüften Stationen ein ähnliches Bild wie die bereits häufig herangezogene Station Hohenpeißenberg (z.B. RAPP 2000).

Zum Schluss wurden die Residuen graphisch ausgewertet. Die Residuen schwanken zufällig um den Mittelwert. Somit sind die Voraussetzungen für die Anwendung des linearen Regressionsmodells erfüllt.

Mit Hilfe des vertikalen Temperaturgradienten (BÄSSLER 2004) wurde die Zeitreihe der Klimastation Waldhäuser (1972-2003) auf der Basis der Station Großer Falkenstein (1947-1980) reduziert. Die gemeinsame Zeitreihe von 1972-1980 wurde zur Prüfung der Anpassung verwendet. Die Berechnungen fanden auf der Ebene der Tages- und Monatsmittel statt. Dabei lag r^2 bis auf wenige Ausnahmen bei $>90\%$. Für eine differenziertere Aussage stehen die Ergebnisse der Prüfung nach dem THEILschen Ungleichheitskoeffizient zur Verfügung.

Hierbei trat zutage, dass für T_{mit} , T_{min} und T_{max} U bei allen Monaten nahe Null liegt. Zusammenfassend lässt sich feststellen, dass die Anpassung aufgrund der hohen Korrelationskoeffizienten sowie den günstigen U -Werten akzeptabel ist. THEIL (1961 in ANDRES & SPIWOKS 2000) schätzt, dass U für eine brauchbare Prognose nicht höher liegen darf als 0,3 – 0,4. Die Berechnungen ergaben für November (T_{min}) als ungünstigsten Monat eine Güte von $U = 0,22$.

Da für das Untersuchungsgebiet Zeitreihen bis in das 19. Jhd. nicht zur Verfügung stehen, der Analysezeitraum aber eine Mindestlänge aufweisen muss um eine Einschätzung der Klimavariabilität des Untersuchungsraumes vornehmen zu können, wurde die Zeitreihe Hohenpeißenberg (1781-2004) auf ihre Eignung geprüft, in wie weit die Werte, entsprechend dem Gradient, auf die Gegend des Böhmerwaldes übertragbar sind. Das Ergebnis für die Jahresmittel und die einzelnen Monate ist sehr differenziert. Bis auf Januar ($r^2 = 78\%$) zeigen alle Monate ein Bestimmtheitsmaß $> 80\%$. Die Werte für U liegen alle nahe Null. Alle Fehlerkomponenten liegen im akzeptablen Rahmen ($ZF > 0,8$). Eine Ausnahme bildet Februar, der eine Varianzschwäche von 0,29 aufweist. Hieraus wird deutlich, dass der Gradient für die angegebene Distanz zwischen Hohenpeißenberg und Waldhäuser für die mittleren Lufttemperaturen sehr stabil ist. RAPP (2000) geben als Maß für die Repräsentanz der Lufttemperatur (Jahresmittelwerte) ca. 1000 km an. Die Entfernung zwischen Waldhäuser und Hohenpeißenberg liegt Luftlinie unter 250 km. Um Sicherheit über den Zeitraum der Verlängerung zu erhalten, wurden zusätzlich die berechneten Werte mit lückenhaft vorhandenen Klimadokumentationen aus Archivaufzeichnungen des Untersuchungsgebietes verglichen. Hierfür dienten Angaben aus Buchenau und Mauth/Finsterau für den Zeitraum von 1900-1927 und 1942-1947. Die Prüfung der Temperaturverläufe zeigt ein einheitliches Bild, die Temperaturdifferenzen sind erklärbar. Somit kann der wahrscheinliche Verlauf auf der Reduktionsgrundlage Hohenpeißenberg akzeptiert werden. Dieser Vergleich bestätigt den vermutlichen Temperaturverlauf mit eher normalen Temperaturverhältnissen zwischen 1900 und 1950 mit einer wärmeren Periode gegen Ende der 40er Jahre.

Trendanalyse

Gegenstand der Trendanalyse sind die Stationen Waldhäuser und Zwieselberg für die gemeinsame Zeitreihe 1948-2002. Beide Stationen besitzen die längste Zeitreihe. Die Station Waldhäuser repräsentiert die für den Naturraum typischen „warmen Hanglagen“, die Station Zwieselberg repräsentiert die ebenfalls für den Raum typischen Inversionsstandorte. Ein Vergleich (Korrelationsvergleich) der Stationen Großer Arber (1437 m ü NN) und Fichtelberg

(1213 m ü NN) mit Waldhäuser bestätigen die Annahme, dass das Trendverhalten der Hochlagen dem der Hanglagen entspricht (Tab.2). Die Analysen aller anderen Stationen bestätigen den analogen Trendverlauf. Somit ist der beobachtete Naturraum durch die verwendeten Stationen Waldhäuser und Zwieselberg sehr gut repräsentiert (vgl. Räumliche Repräsentanz).

Tab.2: Korrelation der mittleren Lufttemperatur nach PEARSON zur Prüfung der räumlichen Repräsentanz und zur Prüfung der Voraussetzung für den Homogenitätstest anhand von Fichtelberg und Hohenpeißenberg.

Tab.2: Correlation coefficients of mean air temperature according PEARSON to assess spatial representation and suitability of the time series of Fichtelberg and Hohenpeißenberg as basis for the tests of homogeneity.

Stationskombination	Korrelationskoeffizient (PEARSON)												
	Jan.	Febr.	Mrz.	Apr.	Mai	Jun.	Jul.	Aug.	Sep.	Okt.	Nov.	Dez.	Mittel
Waldhäuser-Zwieselberg	0,8	0,9	1,0	1,0	1,0	1,0	1,0	1,0	0,9	0,9	0,8	0,7	0,9
Waldhäuser-Fichtelberg	0,9	1,0	1,0	1,0	1,0	1,0	1,0	0,9	1,0	0,9	0,9	0,9	1,0
Waldhäuser-Hohenpeißenberg	0,9	1,0	1,0	0,9	1,0	0,9	1,0	0,9	0,9	0,9	0,9	0,9	0,9
Waldhäuser-Greinet	0,9	0,9	1,0	1,0	1,0	1,0	1,0	1,0	1,0	0,9	0,9	0,9	0,9
Waldhäuser-Klingenbrunn Bhf.	0,9	1,0	1,0	0,9	1,0	1,0	1,0	1,0	1,0	0,9	0,9	0,8	1,0
Waldhäuser-Taferlruck	0,8	0,9	0,9	0,6	0,9	0,9	0,9	0,8	0,9	0,8	0,8	0,6	0,6
Waldhäuser-Großer Arber	0,9	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	0,9	1,0
Zwieselberg-Hohenpeißenberg	0,8	0,9	1,0	0,9	0,9	0,9	0,9	0,9	0,9	0,9	0,8	0,8	0,9
Zwieselberg-Fichtelberg	0,8	0,9	0,9	0,9	1,0	0,9	1,0	0,9	0,9	0,8	0,7	0,8	0,9
Zwieselberg-Greinet	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0
Zwieselberg-Klingenbrunn Bhf.	1,0	1,0	1,0	0,9	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0
Zwieselberg-Taferlruck	0,8	1,0	0,9	0,6	0,9	0,9	0,9	0,7	0,9	0,8	0,8	0,7	0,7
Zwieselberg-Großer Arber	0,6	0,9	1,0	0,9	1,0	1,0	1,0	1,0	0,9	0,9	0,8	0,5	0,9
Fichtelberg-Hohenpeißenberg	0,9	1,0	0,9	0,9	0,9	0,8	0,9	0,8	0,9	0,9	0,9	0,9	0,9
Fichtelberg-Greinet	0,8	0,9	1,0	1,0	1,0	0,9	1,0	0,9	1,0	0,8	0,8	0,9	0,9
Fichtelberg-Klingenbrunn Bhf.	0,8	0,9	1,0	0,8	1,0	1,0	1,0	0,9	0,9	0,8	0,8	0,6	0,9
Fichtelberg-Taferlruck	0,7	0,8	0,8	0,5	0,9	0,9	0,9	0,7	0,9	0,8	0,7	0,4	0,6
Fichtelberg-Großer Arber	0,9	1,0	1,0	1,0	1,0	1,0	1,0	0,9	1,0	1,0	1,0	0,9	1,0
Hohenpeißenberg-Greinet	0,8	0,9	1,0	0,9	1,0	0,9	0,9	0,9	0,9	0,9	0,8	0,9	0,9
Hohenpeißenberg-Klingenbrunn Bhf.	0,9	0,9	1,0	0,8	1,0	0,9	0,9	0,9	0,9	0,8	0,9	0,7	1,0
Hohenpeißenberg-Taferlruck	0,8	0,9	0,8	0,5	0,8	0,8	0,8	0,7	0,8	0,7	0,7	0,6	0,6
Hohenpeißenberg-Großer Arber	0,8	0,9	1,0	0,9	1,0	0,9	1,0	0,9	0,9	0,9	1,0	0,8	0,9
Greinet-Klingenbrunn Bhf.	1,0	1,0	1,0	0,9	1,0	1,0	1,0	1,0	1,0	0,9	1,0	0,9	1,0
Greinet-Taferlruck	0,8	0,9	0,9	0,6	0,9	0,9	0,9	0,8	0,9	0,8	0,8	0,7	0,7
Greinet-Großer Arber	0,7	0,9	1,0	1,0	1,0	1,0	1,0	0,9	1,0	0,8	0,8	0,5	0,9
Klingenbrunn Bhf-Taferlruck	0,8	1,0	0,9	0,7	0,9	0,9	0,9	0,7	0,9	0,8	0,8	0,7	0,7
Klingenbrunn Bhf.-Großer Arber	0,6	0,9	0,9	0,8	1,0	1,0	1,0	1,0	0,9	0,8	0,8	0,4	0,9
Taferlruck-Großer Arber	0,6	0,8	0,9	0,4	0,9	0,9	0,9	0,8	0,9	0,8	0,7	0,3	0,7

Generell lässt sich feststellen, dass unabhängig von Lage und Klimaparameter insbesondere positive Trends für die Zeitreihen bestehen (Tab. 3). Keines der negativen Trendsignale ist signifikant. Das deutlichste Anstiegssignal ist für die mittleren Minimumtemperaturen der Tallagenstandorte zu verzeichnen. Für alle Prüfparameter und Standorte sind die Jahresmittel mit positiven Trends belegt. Allerdings bestehen nur für die mittleren Minimumtemperaturen signifikante Signale von $0,03 \text{ K a}^{-1}$ (Tallage) bzw. $0,02 \text{ K a}^{-1}$ (Hang- und Hochlage). Die von Mai bis August aggregierten Werte als Maß für die Vegetationsperiode zeigen starke Trends für die mittleren Temperaturen und die mittleren Minimumtemperaturen bis $0,03 \text{ K a}^{-1}$. Jahreszeitliche Trends finden sich ausschließlich bei den mittleren Minimumtemperaturen, die bis auf den Herbst der Hang- und Hochlagen durchwegs signifikant sind bis $0,03 \text{ K a}^{-1}$ betragen. Diese Auffälligkeiten spiegeln sich bei Betrachtung der Einzelmonate wider.

Tab. 3: Trendwerte (T) und Signifikanz (Si) über Mann-Kendall Test für Zwieselberg und Waldhäuser (1948-2002), Si >95% fettgedruckt

Tab.3: Trendvalues (T) and significance (Si) according to Mann-Kendall Test for the meteorological stations Waldhäuser and Zwieselberg, Si >95% in bold.

	T _{mit}				T _{min}				T _{max}			
	Zwieselberg		Waldhäuser		Zwieselberg		Waldhäuser		Zwieselberg		Waldhäuser	
	T	Si	T	Si	T	Si	T	Si	T	Si	T	Si
Januar	0,02	74,9	0,03	86,4	0,03	86,0	0,04	97,9	0,02	59,3	0,04	94,6
Februar	0,03	55,9	0,03	64,7	0,04	83,2	0,04	84,3	0,03	74,0	0,02	61,2
März	0,02	83,5	0,01	51,0	0,05	99,7	0,03	85,9	0	26,7	-0,004	6,4
April	-0,01	55,0	-0,01	21,2	0,01	40,9	0	9,8	-0,02	67,3	-0,02	38,9
Mai	0,03	97,7	0,04	99,8	0,03	99,4	0,03	99,1	0,03	98,3	0,03	98,6
Juni	-0,002	12,1	0,004	17,3	0,02	97,9	0,01	81,4	-0,01	35,3	0,001	2,9
Juli	0,01	25,1	0,01	42,4	0,02	96,2	0,02	83,9	0	3,5	0,01	30,0
August	0,03	99,7	0,02	98,8	0,04	>99,9	0,04	97,6	0,02	90,4	0,02	94,6
September	-0,01	63,6	-0,02	86,9	0,02	89,9	-0,004	36,3	-0,03	89,8	-0,03	92,0
Oktober	0,01	76,1	0,001	9,8	0,04	99,8	0,02	78,0	-0,01	72,7	-0,01	25,1
November	-0,01	49,1	-0,01	65,9	0,004	21,2	-0,004	31,0	-0,01	77,2	-0,01	69,1
Dezember	0,01	30,0	-0,01	46,3	0,03	74,3	0,01	47,7	-0,001	16,7	-0,005	42,4
Jahr	0,01	90,6	0,01	89,6	0,03	>99,9	0,02	99,6	0,001	38,9	0,004	44,3
Vegetationsperiode (Mai - Aug.)	0,01	96,6	0,02	98,9	0,03	>99,9	0,03	>99,9	0,01	89,8	0,02	94,9
Frühling (März - Mai)	0,01	90,1	0,02	84,7	0,03	>99,9	0,02	97,0	0,004	39,4	0,01	39,9
Sommer (Juni - Aug.)	0,01	88,2	0,01	92,6	0,03	>99,9	0,02	99,6	0,004	64,0	0,01	91,3
Herbst (Sept. - Nov.)	-0,001	39,4	-0,01	82,8	0,02	99,3	0,003	23,4	-0,02	93,7	-0,02	92,6
Winter (Dez. - Febr.)	0,02	89,3	0,02	64,0	0,03	97,3	0,03	96,8	0,02	76,1	0,02	73,6

Demnach sind offensichtlich Mai und August für das signifikante Signal der Vegetationsperiode verantwortlich. Für Mai liegen alle Trends (alle Parameter und Lagen) zwischen $0,03 \text{ K a}^{-1}$ und $0,04 \text{ K a}^{-1}$. Ein ähnliches Bild zeigt August, allerdings liegen hier die Werte bei den mittleren Maximumtemperaturen nur knapp unter dem Signifikanzniveau. Die Unterschiede zwischen den Tallagen und den Hang- und Hochlagen sind für die mittleren

Minimumtemperaturen am deutlichsten. Demnach zeigt Januar in den Hang- und Hochlagen ein signifikantes Anstiegssignal von $0,04 \text{ K a}^{-1}$, welches in der Tallage nicht zu erkennen ist. Weiterhin lassen sich für die Tallagen für März ($0,05 \text{ K a}^{-1}$), für die Sommermonate Juni und Juli ($0,04 \text{ K a}^{-1}$) sowie für Oktober ($0,04 \text{ K a}^{-1}$) signifikante Trends finden. Somit findet sich das stärkste Anstiegssignal in den Tallagen für die mittleren Minimumtemperaturen.

Zusammenfassend lässt sich feststellen, dass beide Höhenstufen ein ähnliches Bild im Trendverhalten zeigen. Dies zeigt sich insbesondere bei Monaten mit einem starken Trend (Mai und August). Die Tallagenstandorte grenzen sich deutlich durch stärkere Trends im Sommer und Herbst gegenüber den Hang- und Hochlagen bei den mittleren Minimumtemperaturen ab.

Bruchpunktanalyse (Mann-Whitney):

Die für die Zeitreihen der Klimastationen des Inneren Bayerischen Waldes durchgeführte Bruchpunktanalyse wurde durch die Analyse der Zeitreihe von Hohenpeißenberg ergänzt, um näheres über Unterschiede bzw. die räumliche Repräsentanz (spezifischer räumlicher Charakter) in Bezug auf Trendveränderungen zu erfahren. Für die folgende Analyse wurde ausschließlich die Zeitreihe T_{mit} (mittlere Lufttemperatur) herangezogen.

In Tab. 4 sind die errechneten Bruchpunkte sowie deren Signifikanz der einzelnen Monate und der Jahresmittel für die Stationen Waldhäuser, Zwieselberg und Hohenpeißenberg dargestellt (1948-2002). Hieraus lässt sich für die Jahresmittel ein gemeinsamer signifikanter Bruchpunkt im Jahr 1988 detektieren. Eine weitgehende Übereinstimmung der Bruchpunkte ist für die Monate Januar und Februar sowie April bis Juli feststellbar (± 2 Jahre). Für März und August besteht in so weit Ähnlichkeit, da bei Berücksichtigung der sekundären Maxima (die Maxima der Funktion identifizieren die wahrscheinlichen Bruchpunkte) ebenfalls gute Übereinstimmung besteht. Ab September besteht für keinen der festgestellten Bruchpunkte Signifikanz. Die erfolgte Bruchpunktanalyse bestätigt die graphische Einschätzung des steilen Anstiegs der mittleren Lufttemperatur am Ende der 80er Jahre, der bis heute sichtbar anhält (Fig.3).

Die Monate mit den stärksten und sichersten Trends zeigen ebenfalls signifikante Bruchpunkte. Demnach liegt der Bruchpunkt im Mai bei den herangezogenen Stationen im Jahr 1985 ($> 95\%$). Für August liegen die Bruchpunkte bei vergleichbarer Sicherheit ($> 95\%$) in Waldhäuser im Jahr 1990, in Zwieselberg in 1982 und am Hohenpeißenberg in 1980. Jedoch rücken die Jahre, wie oben beschrieben, bei Berücksichtigung der sekundären Bruchpunkte sehr nahe zusammen. Erwähnenswert ist weiterhin April, welcher für alle

Stationen einen Bruchpunkt um das Jahr 1968 aufweist. Bei graphischer Betrachtung der Zeitreihe fällt auf, dass bis ca. 1968 ein deutlicher negativer Trend besteht und sich der Trend danach deutlich positiv entwickelt. Der gegenläufige Trend dieser Zeitabschnitte steigert das Rauschen der Gesamtzeitreihe, sodass hierfür kein Trend festzustellen ist (vgl. Trendanalyse).

Tab. 4: Bruchpunkte nach Mann-Whitney und Signifikanz (Si) für Waldhäuser, Zwieselberg und Hohenpeißenberg (1948-2002), Si >95% fettgedruckt.

Tab. 4: Cutpoints according Mann-Whitney and significance (Si) for the meteorological stations Waldhäuser and Zwieselberg, Si >95% in bold.

Monat	Waldhäuser		Zwieselberg		Hohenpeißenberg	
	Jahr	Si (%)	Jahr	Si (%)	Jahr	Si (%)
1	1988	95,0	1988	86,6	1988	96,0
2	1987	71,4	1988	72,2	1989	90,9
3	1972	67,9	1989	85,9	1989	86,8
4	1969	69,9	1967	84,4	1969	68,3
5	1985	99,7	1985	99,0	1985	99,1
6	1992	69,1	1992	62,3	1992	77,8
7	1982	70,6	1982	73,6	1982	89,5
8	1990	99,3	1982	99,7	1980	99,8
9	1971	70,2	1970	52,0	1993	48,1
10	1970	46,6	1976	84,1	1976	58,7
11	1971	69,5	1965	57,8	1955	21,7
12	1960	77,1	1977	52,0	1971	79,6
Jahr	1988	97,0	1988	98,8	1988	99,5

Räumliche Repräsentanz

Alle Stationen mit durchgehend vergleichbaren Zeitreihen wurden gegeneinander mit Hilfe des Korrelationskoeffizienten nach PEARSON getestet (Monate und Jahresmittel für T_{mit})(Tab.2). Zusammenfassend lässt sich sagen, dass in fast allen Fällen die Kriterien für eine ausreichend hohe Repräsentanz vorliegen. Insbesondere bei Beteiligung der Klimastation Taferlruck konnten ungünstige Koeffizienten ermittelt werden. Da die Homogenitätsanalyse für Taferlruck positiv ausfiel, sind die klimatologischen Differenzen in der Inversionsprägung zu suchen. Dieser Sachverhalt wird durch weitere Korrelationsschwächen im Zusammenhang von Hang- und Hochlagenstandorten mit Kaltluftstaustandorten gestützt. Das Korrelationsbild der Kaltluftstaustandorte untereinander ist wiederum günstig. Das gleiche Muster kann innerhalb der Hang- bzw. Hochlagenstandorte beobachtet werden. Hier liegen die Korrelationskoeffizienten häufig bei 1,0. Durch dieses Ergebnis wird ebenfalls deutlich, dass eine Trennung der Analyse zwischen der Hang- bzw. Hochlage und Tallage sinnvoll ist.

Ein weiteres Maß für die Qualität der räumlichen Repräsentanz ist die Richtung und der Betrag des Trends. Die Betrachtung gemeinsamer Perioden macht deutlich, dass für alle

Stationen, getrennt nach Hang- bzw. Hochlage und Tallage ein einheitliches Trendmuster besteht. Somit lässt sich feststellen, dass die Übertragbarkeit der Ergebnisse von Waldhäuser und Zwieselberg auf das Untersuchungsgebiet voll gegeben ist.

Rückschreitender Trend (Zeitliche Repräsentanz)

Der rückschreitende Trend wurde für Waldhäuser und Zwieselberg für die gemeinsame Zeitreihe 1948-2002 berechnet (Abb. 2). An beiden Standorten ist der Ganglinienverlauf sehr ähnlich. Auffällig ist der nahezu konstant größer werdende Trend ($K a^{-1}$) seit Beginn der Messungen auf sehr hohem Signifikanzniveau. Die sehr starke Zunahme des Trends bei sukzessiver Verschiebung des Beobachtungsrahmens zum Ende der Periode bestätigt bisherige Beobachtungen, die den Gesamttrend insbesondere auf den Anstieg der letzten Jahrzehnte zurückführen. Demnach ist der Gesamttrend von $0,01 K a^{-1}$ für beide Standorte eher instabil.

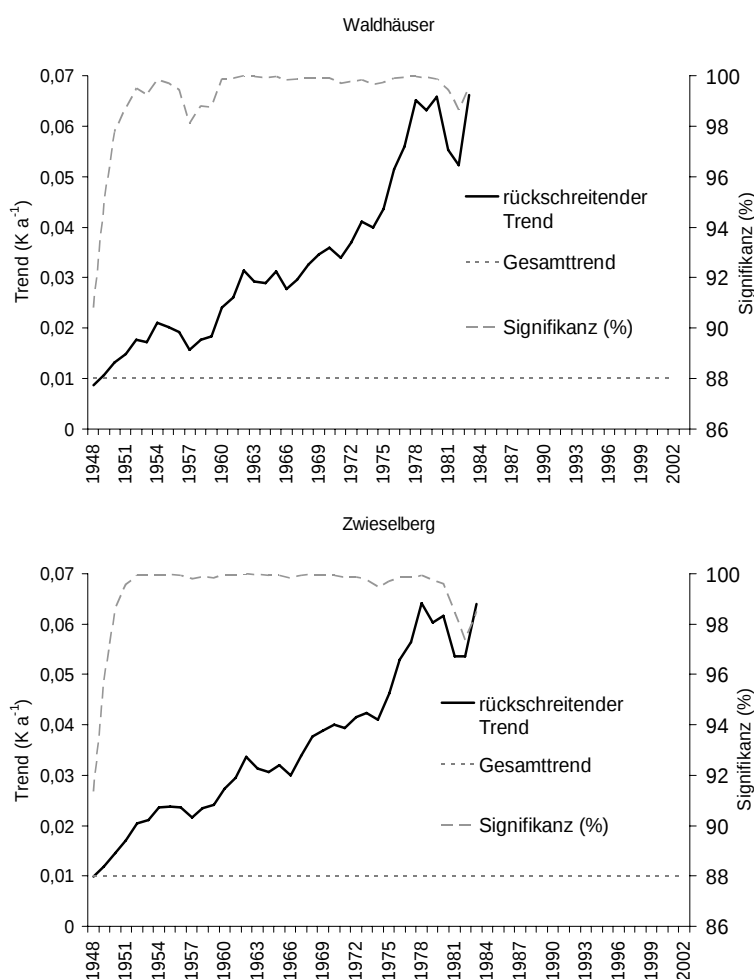


Abb. 2: Rückschreitender Trend und Signifikanz für Waldhäuser und Zwieselberg (1948-2002).

Fig. 2: Regressive trend and significance for the meteorological station Waldhäuser and Zwieselberg (1948-2002).

Die mittlere Lufttemperatur im Inneren Bayerischen Wald seit 1781

Die verlängerte Zeitreihe von Waldhäuser auf der Datengrundlage der Station Hohenpeißenberg ermöglicht es, zumindest annäherungsweise, die mittlere Temperaturentwicklung seit 1781 zu analysieren.

Bei Betrachtung der gesamten Periode fällt ein zweigeteilter Temperaturverlauf auf (Abb. 3). Seit Beginn der Aufzeichnungen bis ca. 1890 können tendenziell sinkende mittlere Temperaturen beobachtet werden. In ähnlichem Maß, wie die Temperaturen bis zum Zeitpunkt 1890 sanken, stiegen sie im weiteren Verlauf mit einem vergleichbaren Betrag wieder an. Dies wird durch die Berechnung der Regressionen deutlich. Weiterhin lässt sich dieses Bild bei Betrachtung der 20-jährig tiefpassgefilterten Werte bestätigen.

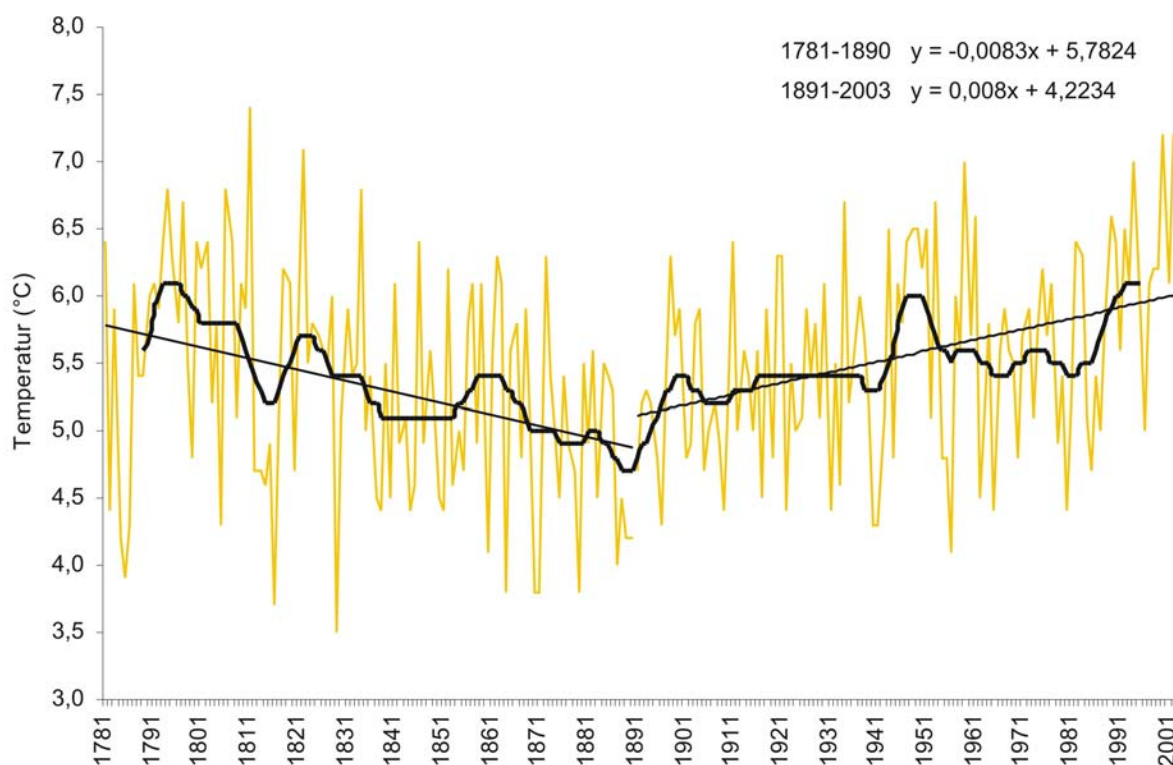


Abb. 3: Jahresmitteltemperatur (20-jährig tiefpassgefiltert nach Gauß) und Trendgeraden für die Teilintervalle 1781-1890 und 1891-2003 für Waldhäuser.

Fig. 3: Mean air temperature (20-year low pass filter according to Gauß) and trend lines for the time series 1781-1890 and 1891-2003 for Waldhäuser.

Der Trend ist für die gesamte Periode bei einer Signifikanz $<95\%$ sehr schwach ($0,002 \text{ K a}^{-1}$ bzw. $0,4 \text{ K}$ für den gesamten Zeitraum). Für das Teilintervall 1781 bis 1890 beträgt der Trend $-0,01 \text{ K a}^{-1}$ und für das Teilintervall 1891 bis 2003 $0,01 \text{ K a}^{-1}$, die Signifikanz nach Mann-Kendall überschreitet hierbei jeweils $99,9\%$. Dies wird ebenfalls durch die Berechnung des

rückschreitenden Trends deutlich (Abb. 4). Für die gesamte Reihe besteht ein sehr schwacher, nicht signifikanter Trend. Ausschlaggebend für den positiven Trend scheint die Zeit ab ca. 1945, da der Temperaturverlauf ab diesem Zeitpunkt sehr stark ansteigt. Bestätigt wird dieser Zeitpunkt durch das Ergebnis der Bruchpunktanalyse, welche als wahrscheinlichsten Veränderungszeitpunkt das Jahr 1943 (Si 99,8%) detektiert. Es lässt sich aussagen, dass der Gesamttrend nicht stabil ist, sondern die Zeitreihe ab dem Bruchpunkt im Jahr 1943 einen sehr steilen Trendanstieg erfährt. Hierdurch wird der Trend erst ab dem Jahr 1811 signifikant ($Si > 95\%$). Der Signifikanzeinbruch ab dem Jahr 1942 bis 1948 findet seine Erklärung in der relativ kalten Phase zwischen 1960 und 1980.

Das letzte Jahrzehnt des 20. Jahrhunderts gilt als das wärmste seit 1781. Jedoch ist auch das letzte Jahrzehnt des 18. Jahrhunderts erwähnenswert, da hier die mittleren Lufttemperaturen nur um ein zehntel Grad unter den 1990er Jahren liegt. Weiterhin kann festgestellt werden, dass die mittleren Dezenniumstemperaturen seit 1941, mit Ausnahme der 60er Jahre, immer über dem Gesamtdurchschnitt der Lufttemperatur liegen.

Das langjährige Mittel beträgt $5,4 (\pm 0,8) ^\circ\text{C}$. Das kälteste Jahresmittel betrug $3,5^\circ\text{C}$ (1829), das wärmste $7,4^\circ\text{C}$ (1811). Demnach liegt das Maximum der Jahresmittel nicht am Ende des 20., bzw. am Beginn des 21. Jahrhunderts (2002 mit $7,2^\circ\text{C}$).

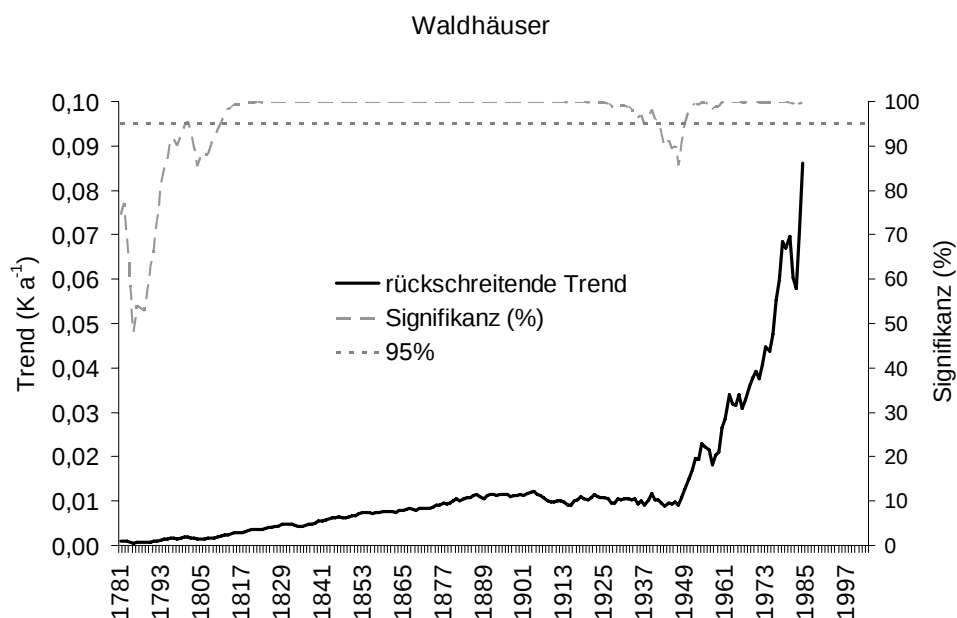


Abb. 4: Rückschreitender Trend und Signifikanz für Waldhäuser (1781-2003).

Fig. 4: Regressive trend and significance for the meteorological station Waldhäuser (1781-2003).

DISKUSSION

Grundproblem bei der statistischen Analyse langjähriger Zeitreihen zur Detektion von Trends sind Inhomogenitäten, z.B. entstanden durch allmähliche Veränderungen der Stationsumgebung (RAPP 2000). Die hierdurch verursachten Trends sind sehr schwer von Klimaveränderungen zu unterscheiden. Aus diesem Grund wurde auf eine sorgfältige Aufbereitung der Daten mit Homogenitätsanalysen Wert gelegt. Die Station Waldhäuser, Kernstück der Analyse, wird seit Beginn der Messungen von der Nationalparkverwaltung betreut. Eine detaillierte Dokumentation bestätigt konstante Verhältnisse der Stationsumgebung sowie der Messvorgänge.

Zur Einordnung der Ergebnisse für den Inneren Bayerischen Wald sollen diese mit unterschiedlich skaligen Untersuchungen verglichen werden. Hierfür fand die Zeitreihe von Waldhäuser, als repräsentativer Standort der Hang- und Hochlagen der ostbayerischen Mittelgebirge, Verwendung.

Einordnung der Ergebnisse in globale Muster

Für das 20. Jahrhundert (1900-2000) kann eine signifikante Zunahme (Si 90-99%) der mittleren globalen Temperatur von 0,6 K ($\pm 0,2$) beobachtet werden (IPCC 2001). Die Temperaturzunahme für Waldhäuser im gleichen Beobachtungszeitraum beträgt 0,7 K (Si > 99%). RAPP (2000) kommt zu dem Resultat, dass die Lufttemperatur in Europa für den genannten Zeitraum in den meisten Regionen um 0,5 bis 1 K angestiegen ist, eine Erwärmung, die in Deutschland signifikant ist. Weiterhin gilt das letzte Dezennium des 20. Jahrhunderts als das wärmste des Jahrtausends (IPCC 2001, DEUTSCHER WETTERDIENST 2001). Da die berechnete Zeitreihe nur bis in das 18. Jahrhundert zurückreicht, kann hierfür kein Vergleich angestellt werden. Allerdings kann das letzte Jahrzehnt des Jahrhunderts als das wärmste seit 1781 bestätigt werden. Der DEUTSCHE WETTERDIENST (2001) stellt weiterhin fest, dass neun Jahre des letzten Jahrzehntes im Mittel (Gebietsmittel Deutschland) wärmer waren, als das Mittel aus der Normalperiode 1961-1990, bzw. fünf der zehn wärmsten Jahre überhaupt in diese Phase fallen. Dieses Faktum ist ebenfalls für Waldhäuser zu bestätigen, allerdings fallen hier nur drei der zehn wärmsten Jahre in die Vergleichsperiode. Bei Betrachtung des klimatologischen Sommers (Juni bis August) stellt der DEUTSCHE WETTERDIENST (2001) auf Deutschlandebene einen statistisch signifikanten Anstieg von ca. 0,7 K fest. Diese Entwicklung ist v.a. auf die Zeit seit 1955 zurückzuführen. Drei der zehn wärmsten Sommer findet man demnach im letzten Jahrzehnt (1994, 1992 und 1997). Der statistisch signifikante Anstieg kann für Waldhäuser bestätigt werden (0,8 K, Si > 98%). Hier

waren die Jahre 1992 und 1994 die wärmsten, die jemals gemessen wurden. Das klimatologische Frühjahr (März bis Mai) zeigt weder auf Deutschlandebene noch auf der Ebene des Inneren Bayerischen Waldes ein besonderes Trendverhalten. Der in Deutschland markant statistische Anstieg im Herbst, welcher auf die rasche Erwärmung in den 20er Jahren zurückzuführen ist, kann für Waldhäuser nicht bestätigt werden (DEUTSCHER WETTERDIENST 2001).

Zusammenfassend lässt sich sagen, dass die Trendbeträge zwar sehr nahe beieinander liegen, es sich hierbei allerdings um Zufall handeln kann. Entscheidend bei der vorgenommenen Einordnung ist die Feststellung der gemeinsamen Richtung der Trends.

Einordnung der Ergebnisse in Süddeutsche und Regionale Muster

Im Rahmen des Projektes Klimaveränderungen und Konsequenzen für die Wasserwirtschaft (KLIWA 2004) analysierte der Deutsche Wetterdienst das Langzeitverhalten der Lufttemperatur. Da sich das Projekt auf Süddeutschland bezieht, wurden 354 Klimastationen des Deutschen Wetterdienstes im Raum Baden-Württemberg und Bayern für die Periode 1931 bis 2000 untersucht. Hierbei wurden zwar Stationsdaten als Ausgangsmaterial verwendet, diese wurden allerdings auf ein $7 \times 7 \text{ km}^2$ Gitternetz eines digitalen Höhenmodells mit einem geostatistischen Ansatz regionalisiert. Aus diesen wurden Gebietsmittel gebildet, um den Einfluss einzelner Stationen auf den Trend zu minimieren. Auf dieser Basis erfolgte die Trendanalyse. Nach diesen Untersuchungen erfuhr der süddeutschen Raum (alle Gebietsmittel) eine Temperaturzunahme von 0,5 bis 1,2 K (Si 99%). Der Schwerpunkt der Erwärmung für Süddeutschland liegt im Winterhalbjahr (Oktober bis März), hier vor allem Dezember bis März. Stärkere Trends können in dieser Zeit für Waldhäuser bestätigt werden, allerdings besteht hierfür keine Signifikanz. Der stärkste Trend (Si 99%) konnte für Süddeutschland im Dezember nachgewiesen werden (1,8 – 2,7 K). Für das Sommerhalbjahr sind die Veränderungen in Süddeutschland nicht so deutlich. Auffällig zeigt sich nur August mit hochsignifikanten Zunahmen von 0,8 bis 1,7 K (KLIWA 2004). Das von uns gewählte Untersuchungsgebiet fällt in die Kliwa - Region D15, welches von der Donau bis zur deutsch-tschechischen Landesgrenze reicht. In das D15-Gebietsmittel gingen 7 Stationen ein. Der Trend beträgt für den Zeitraum 1931-2000 1,2 K. Im gleichen Zeitraum ist für Waldhäuser eine signifikante Zunahme von 0,6 K (Si 94,4%) zu beobachten. Dieser Unterschied lässt sich mit dem Einfluss von tiefer gelegenen Stationen in diesem Kliwa - Gebiet erklären. Hierin liegt ebenfalls der Grund, dass die deutlichen Trends für August (1,4K) und Dezember (2,0K) für die Gesamtregion nicht in diesem Maß von Waldhäuser erreicht werden (August 0,7K,

Dezember 1,4 K). Allerdings besteht für Mai ein ähnlich hohes Trendsignal für Waldhäuser (1,1 K) im Vergleich zur Kliwa - Region D15 (1,2 K). Das für den Inneren Bayerischen Wald herausgearbeitete klimatologische Muster deckt sich sehr gut mit Ergebnissen aus dem westlichen Teil (tschechische Seite) des Böhmerwaldes (Čertovo See). In dieser Studie wurde das Langzeitverhalten der mittleren Lufttemperatur modelliert und es konnten ebenfalls Mai und August detektiert werden, welche in den letzten Jahrzehnten einen stärkeren positiven Trend erfuhren (KETTLE et al. 2003).

Mit Hilfe der Bruchpunktanalyse (1988) für Waldhäuser kann ebenfalls bestätigt werden, dass insbesondere das letzte Dezennium für den Trend verantwortlich ist. Diese Beobachtung ist für ganz Deutschland zutreffend (DEUTSCHER WETTERDIENST 2001). Nach den Untersuchungen durch den DEUTSCHEN WETTERDIENST (2001) waren die 30er und 40er Jahre ebenfalls schon überdurchschnittlich warm. Dieses Ergebnis kann für die 40er Jahre auf den Inneren Bayerischen Wald übertragen werden. Allerdings waren die 30er Jahre im Vergleich eher kalt.

Zusammenfassende Bewertung des Skalenvergleichs

Es konnte gezeigt werden, dass sich deutschlandweite, süddeutsche oder auch regionale Trends nicht unbedingt in lokalen Trends wieder finden müssen. Der Grund liegt in der Bildung von Gebietsmittel durch Regionalisierung. So können beispielsweise die Unterschiede zwischen der Kliwa-Region D15 und der Station Waldhäuser mit dem Einfluss tiefer gelegener Stationen erklärt werden, da hier Stationen bis zur Donau Berücksichtigung finden.

Einfluss des Klimawandels auf Ökosysteme – Erfordernisse

In dieser Studie konnte belegt werden, dass ein deutliches Erwärmungssignal für das Untersuchungsgebiet besteht. Abschätzungen für den Inneren Bayerischen Wald prognostizieren eine zunehmende Erwärmung (1,7 - 2,1 K) bis zum Ende des Jahrhunderts (SPEKAT et.al 2007). Der enge Zusammenhang zwischen den Temperaturen und ökosystemaren Prozessen ist belegt (WILLDENOW 1805, LOMOLINO 2001), sodass in naher Zukunft mit einschneidenden Veränderungen zu rechnen ist. Beobachtungen in verschiedenen Ländern beweisen bedeutsame Veränderungen natürlicher Systeme, insbesondere durch Temperaturzunahme, aber auch durch andere physikalische Parameter wie Niederschlag und Wind (IPCC b 2007). Abschätzungen der Auswirkungen durch veränderte physikalische Parameter auf die Wälder fallen schwer, da verschiedene Wirkungskomplexe und

Rückkopplungen bestehen. Dennoch ist davon auszugehen, dass im Laufe dieses Jahrhunderts die Belastbarkeit vieler Ökosysteme durch den globalen Wandel (insbes. Treibhausgasemissionen und Landnutzung) und damit verbundenen Störungen (Überflutung, Trockenheit, Feuer, Insekten etc.) überschritten wird (z.B. OVERBECK 2005, WALTHER et al. 2002, IPCC b 2007). Diese Störungen entscheiden über das zukünftige Vorkommen, Verteilung, Vitalität oder auch Massensterben von Individuen (VILLALBA & VEBLEN 2002, PARMESAN et. al. 2000, BRESHEARS et al. 2005). Insbesondere Wälder (Boreale Wälder und Bergwälder) sind sehr sensibel gegenüber dem Klimawandel (KIRSCHBAUM & FISCHLIN 1996). Schäden sind bei Überschreitung kritischer Schwellenwerte, verursacht durch Trockenheit, Insekten und Feuer zu erwarten (GITAY et al. 2001), verbunden mit dem Verlust von Leistungen der Waldökosysteme (Schutzwald, Wasserretention etc.). Nach Modellrechnungen ist mit einem Aussterberisiko aufgrund des Klimawandels für Mitteleuropa von 10 - 30% des derzeitigen Artbestandes, zumindest regional, zu rechnen. 32% der Pflanzenarten werden bis 2050 aus ihren jetzigen Arealen verschwinden und auf 44% der Fläche Europas wird der Verlust an Arten 32% und mehr betragen (BAKKENES et al. 2002, THOMAS et al. 2004). In Deutschland könnten zwischen 5 - 30% der derzeitigen Tier- und Pflanzenarten betroffen sein (LEUSCHNER u. SCHIPKA 2004). Nach SCHRÖTER et al. (2005) liegt der Schwerpunkt der Veränderung in den Regionen Iberische Halbinsel, Skandinavien und Mitteleuropa. Diese Studie prognostiziert für Schutzgebiete eine Artenextinktionsrate von 6-12% in den nächsten Jahren aufgrund klimatischer Veränderungen. Starke Veränderungen sind in alpinen und montanen Gebieten zu erwarten (GRABHERR 1994, PAULI 2007).

Zusammenfassend lässt sich feststellen, dass die zu erwartenden Auswirkungen des Klimawandels auf die Waldökosysteme sehr komplex sind und dies interdisziplinäre Forschungsansätze notwendig macht, um seriöse Abschätzungen treffen zu können. Die vielschichtige und sehr komplexe Thematik kann hier nur angerissen werden (mehr Details in IPCC 2007 b). Stärkere Veränderungen werden aber auf regionaler Ebene stattfinden, weshalb regionale Forschungsansätze und Monitoring intensiviert werden müssen.

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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. 800m 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.

Key words: 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. 800m) 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 (Transekten) 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 and 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 and 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 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; 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 occurrence 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 is possible to answer special questions such as the impacts of climate change on taxonomical or functional groups. The ultimate aim of the study is 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 1.420 m a.s.l.). Slopes in the National Park have mainly a southwest exposition. Long-term phases of weathering and erosion have led to rounded, elevated landforms. Typical geomorphological elements below 900m a.s.l. are foothills, flat hillsides and valleys, with steep hillsides between 900 und 1100 m a.s.l. and flat ridges dominated by summits between 1100 und 1400m a.s.l.

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 podsoles), 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* L. H.Karst (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.

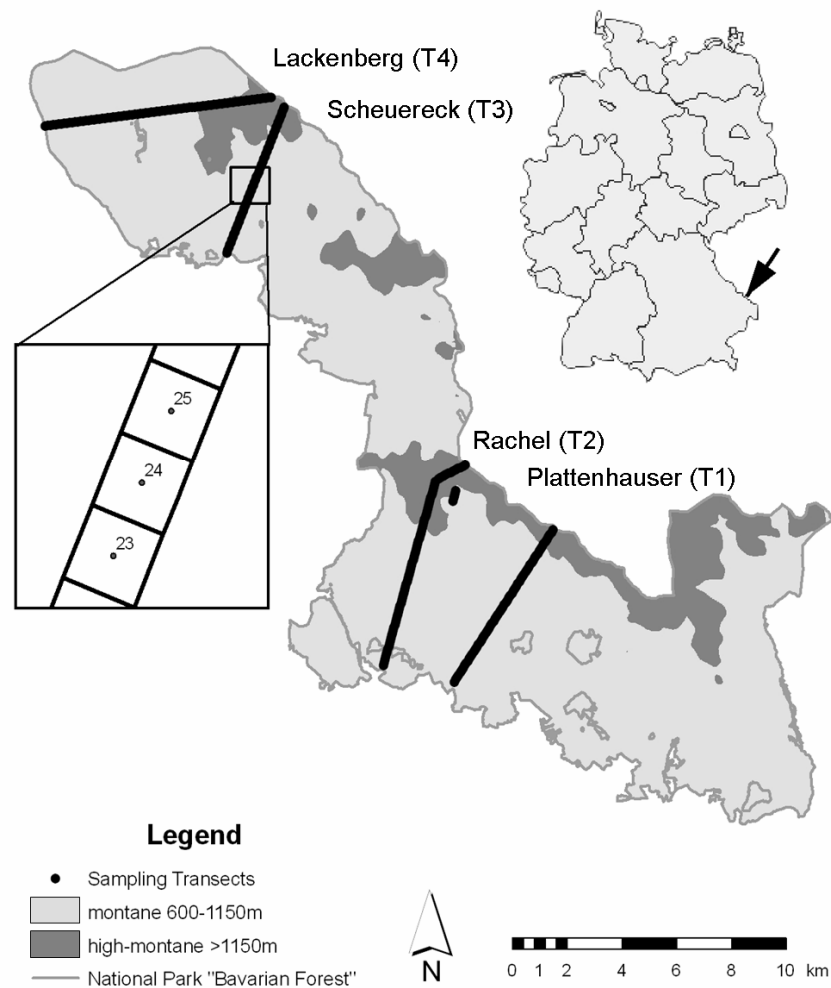


Fig. 1: Study area and study design of the sampling transects with indication of the boundaries of the montane and high montane zone.

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).

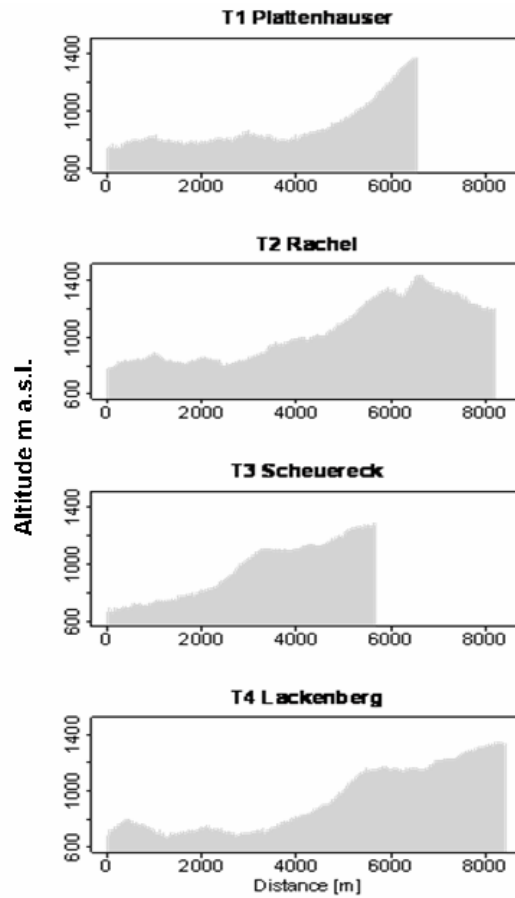


Fig. 2: Vertical profiles of the four transects, from airborne laser scanner data.

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, 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).

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

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. The transects were marked permanently, to reduce the need for repeated measurement and sampling. The distance between the plots is 100 m (Fig.1). The plots represent fairly well the main plant communities of the National Park (Fig.3).

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

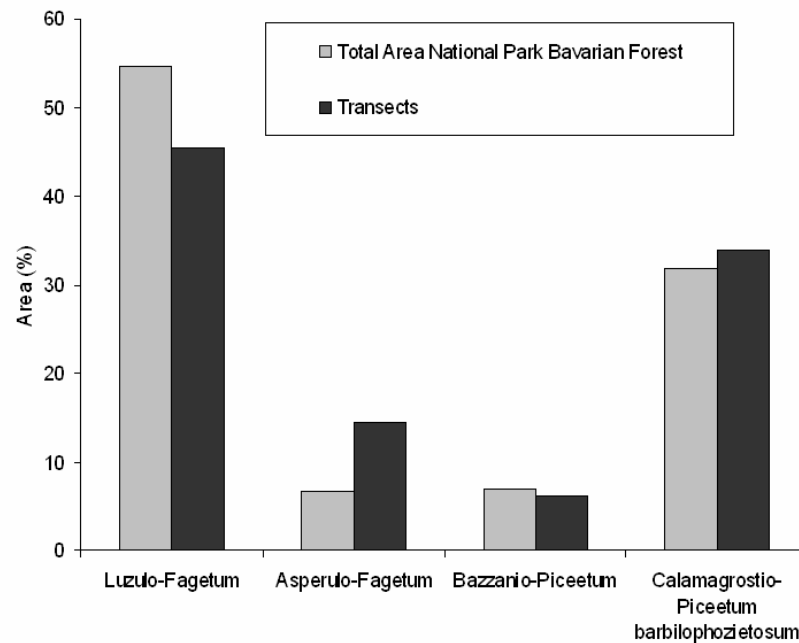


Fig. 3: Vegetation type represented by our study plots and their frequency throughout the whole area of the National Park.

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 for example: 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 of stand structure were recorded by measuring and estimation on 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 30cm 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 HNO₃ 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 NH₄Cl for 2 hours on a rotation shaker (BUNDESMINISTERIUM FÜR ERNÄHRUNG, LANDWIRTSCHAFT UND FORSTEN 1990, LUEHR and 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).

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
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/m ²)	x						
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/m ²	x						
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	x	Airborne Laserscanner
Canopy mean height			x	x	x	x	x	
Canopy standard deviation			x	x	x	x	x	
Woody debris (CWD)	CWD-Fractions, decay level, length and diameter				x			Measurement, visuel estimation
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					
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					
Exchangable nutrient elements	Separated 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	Separated into 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					

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 interception 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.

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

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).

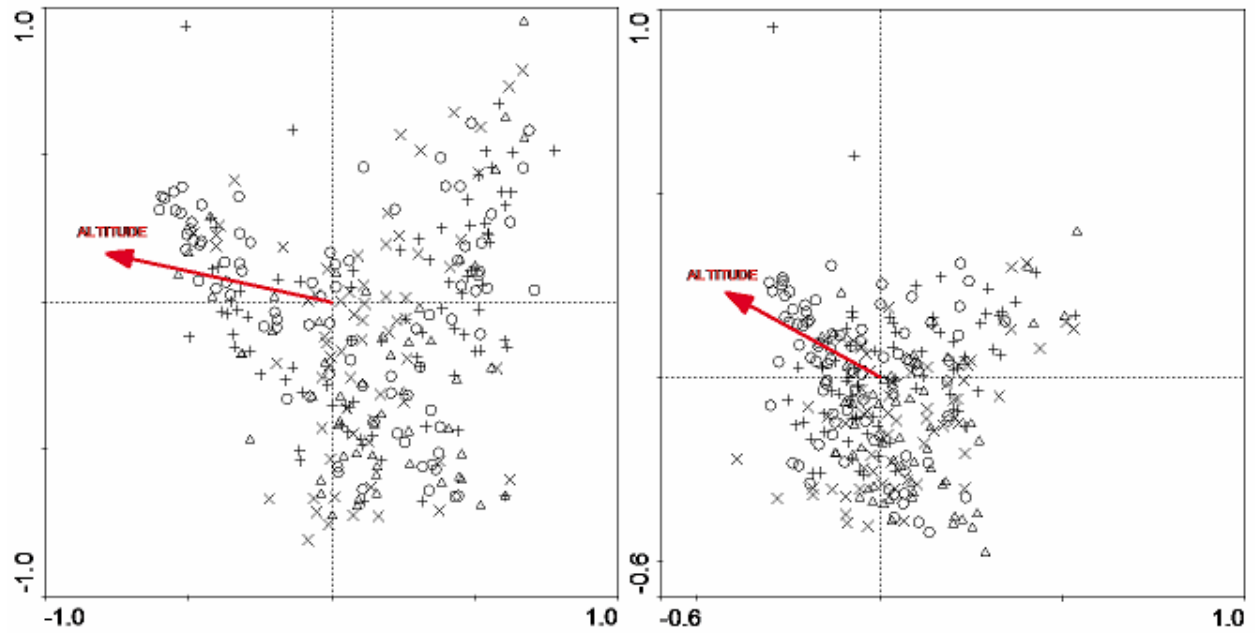


Fig. 4: Correspondence Analysis (CA) of vascular plant communities with (right) and without (left) consideration of geographical coordinates as co-variables. Same symbols represent plots from the same transect.

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 implementation. 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). 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 & GUISAN 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).

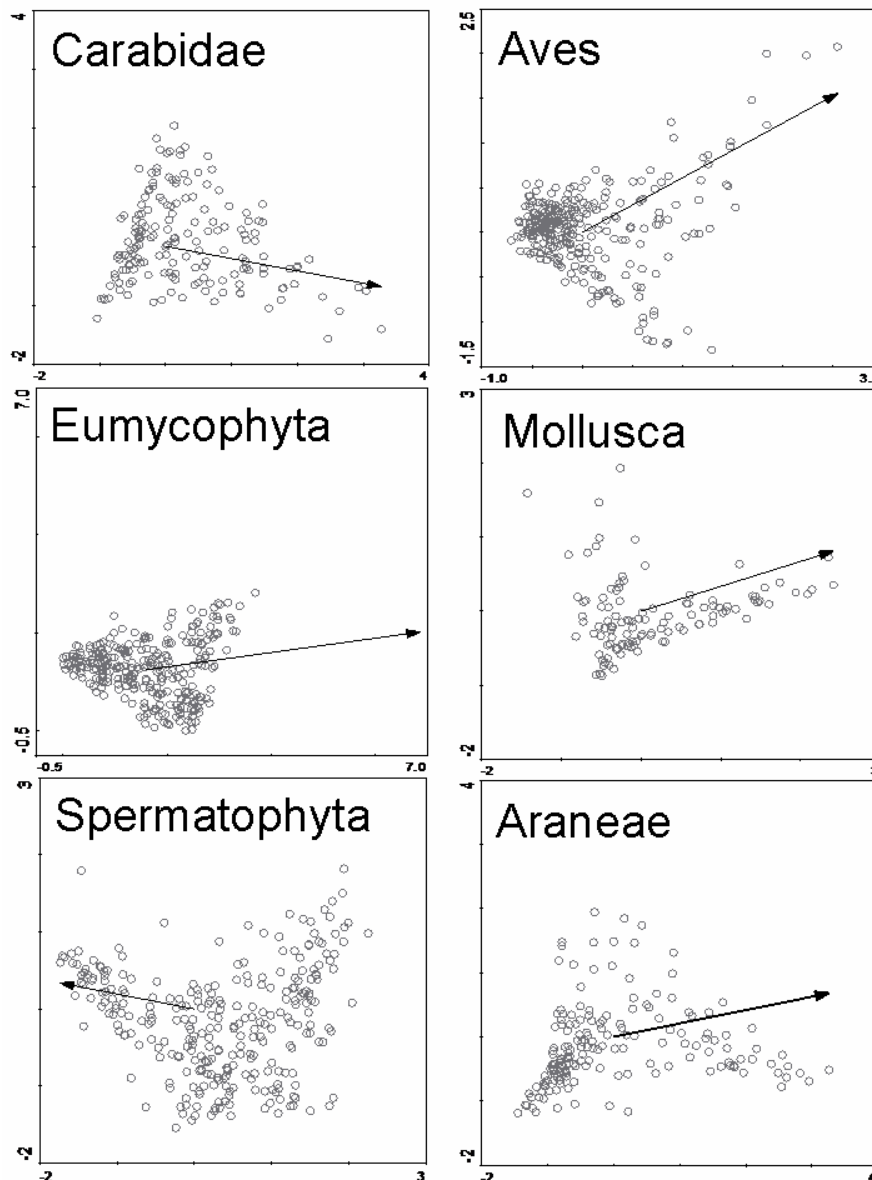


Fig. 5: Wood inhabiting fungi, vascular plant, bird, mollusc, spider and carabid communities and their dependence on the altitudinal gradient. Results based on unconstrained correspondence analysis (CA). The circles represent the assemblages, the vector (arrow) represents the factor altitude.

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 south-east 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 1300m 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 been 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.

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Identification of climate sensitive zones for plants in montane forests

Claus Bässler^{1*}, Jörg Müller^{1,2} and Frank Dziock³

¹Bavarian Forest National Park, Freyunger Str. 2, D-94481 Grafenau, Germany; ²email: joerg.mueller@npv-bw.bayern.de; ³Department of Biodiversity Dynamics, Technische Universität Berlin, Sekr. AB1, Rothenburgstr. 12, D-12165 Berlin, Germany; ³e-mail: frank.dziock@tu-berlin.de; * Corresponding author; email: claus.baessler@npv-bw.bayern.de

Abstract

Question: Aim of this study is to detect changes in vascular plant and fern assemblages along an altitudinal gradient in montane forests and to identify these climate sensitive zones.

Location: Bavaria in South East Germany

Methods: Canonical correspondence analysis was used to determine the factors governing the composition of plant and fern assemblages. In a second step cutpoints of altitude were identified using maximally selected two-sample statistics to indicate discontinuities in the vascular plant and fern assemblage.

Results: The ordination confirms that altitude is the best explanatory variable. First cutpoint is at 1142m a.s.l., differentiating the montane zone from the high montane zone. Weaker signals of change could be detected at 1047 and 1225m a.s.l., identifying climate sensitive zones.

Conclusions: The indicated altitudinal zones will be affected first if temperature increase continues. Monitoring of climate change should be concentrated around these altitudes.

Key words: climate change, montane forest, vegetation, cutpoints, species turnover

Introduction

In the 20th century, global air temperature has increased by 0.74K. The global trend is indicated by rapid atmospheric warming in the last decades (Ipcc 2007b). Latest scenarios predict further warming until the end of the 21st century; the most likely value for the highest increase is 4.0K (2.4 - 6.4K) (Ipcc 2007b).

It is difficult to assess the probable impacts of increasing air temperature on biodiversity. Nevertheless, there is broad evidence that anthropogenic climate change will lead to massive species extinction (Ipcc 2007a). One of the hot spots of change will be Central Europe (Schröter et al. 2005). In the whole of Europe, projected late 21st century distribution for 1350 plant species shows that more than a half of those studied could be vulnerable or threatened by 2080 (Thuiller et al. 2005). It is improbable that entire biological assemblages, vegetation types or habitats will shift with increasing temperature. The potential effect on complex assemblages is less well known (Harrington et al. 1999; Ipcc 2001; Sutherland et al. 2006). It is assumed that species will react individually (Parmesan et al. 1999; Pimm 2001; Thomas et al. 2001) and that assemblages will therefore be disrupted (Walther et al. 2002). Most immediately, the effects are shifts in species' geographical range, prompted by shifts in the normal patterns of temperature and humidity that generally delimit species boundaries (Thuiller 2007). It is to be expected that increasing temperatures will lead to upward migration of species in montane systems. Species located at the lower limit of their altitudinal range are decreasing, whereas thermophile species are increasing, as previous studies have shown (Carraro et al. 1999; Walther & Grundmann 2001). However, these studies also show that changes are not so pronounced that the structure of plant assemblages is disrupted. The trend of upward movement detected for alpine systems has not lead to extinction; nearly all species could be confirmed after repeated survey (Burga et al. 2004). Broad consensus has been reached that work on models to elucidate the correlation between climate and biophysical processes should be undertaken (Ipcc 2007a). There is a need for considerably improved models to evaluate the effects of climate change on distribution of species and their habitats (Sutherland et al. 2006). Additionally, there is a need to find appropriate indicators for the identification of the effects of climate change on natural assemblages. Analyses concerning sensitivity of species or assemblages are often experimental–manipulative, but ignore the effects of interactions in the ecosystems (Henry & Molau 1997; Marion et al. 1997; Shaver et al. 2000). On this basis it is thus difficult to assess long-term impacts of climate change. An alternative is the possibility of using long-term bio-monitoring to evaluate the effects of climate change under natural conditions (Doran et al. 2003; Grabherr et al. 1994;

Harrison et al. 2001; Pauli et al. 2007). However, there is a lack of knowledge about climate change sensitivity at the level of species assemblages, on systematic identification of appropriate climate change indicators, and the practical implementation of long-term bio-monitoring (Leuschner & Schipka 2004). To obtain this knowledge it is first necessary to assess the dependency of taxa on climate parameters and to discriminate these from other environmental factors in order to evaluate the suitability of taxa as indicators of climate change.

In this study we obtained concrete values for zones along the altitudinal gradient and applied an ecological threshold approach to changes of plant assemblages induced by climate (Muradin 2001). The ecological thresholds in our study are defined as sudden changes in plant species assemblages resulting from a smooth and continuous climatological change along the altitudinal gradient. Thresholds thus imply existence of critical values of the independent variable around which the system flips from one stable state to another. These climate-induced ecological thresholds represented by defined altitudinal zones are regarded as climate sensitive zones. The monitoring of these zones allows for early quantification of climate change effects because changes take place here first as warming proceeds. Climate sensitive zones are in this sense equivalent to climate-induced discontinuity patterns, or transition / species turnover zones (Doležal & Šrůtek 2002; Doran et al. 2003; Kazakis et al. 2007; Pauli et al. 2007; Thuiller et al. 2005). Identification of these climate sensitive zones through vegetation survey is urgently required to permit future bio-monitoring with respect to climate change (Sutherland et al. 2006). Regions with steep altitudinal gradients are well suited for this type of research because change is expected to occur within small distances. Geographical variation in plant 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). Therefore, abiotic changes along altitudinal gradients may lead to discontinuity changes as generally confirmed for forest communities (Lee et al. 2005; Walentowski et al. 2004). Altitude is consequently a surrogate gradient representing many climate factors which affect species directly and is thus correlated with resources and regulators of plant growth (Austin 1980). Climate can be adequately evaluated using topographical surrogates such as altitude, if geographical and climatological prerequisites for the study area are fulfilled (Austin 2002; Sergio & Pedrini 2007). Furthermore, it is well known that altitudinal components vary in a non-random fashion along most altitudinal gradients (Lomolino 2001).

Pronounced change is to be expected especially in climate sensitive zones if the temperature rise predicted until the end of the 21st century takes place (Ipcc 2007b). The objective of the present study is the identification of such zones by detecting nonlinear changes (thresholds) in plant assemblages along an altitudinal gradient in a Central European area of montane forest.

Two main questions are addressed:

1. Is the altitudinal climate gradient the best explanation for the variation of vascular plant and fern assemblages in the montane forest?
2. Is it possible to identify climate sensitive zones for vascular plant and fern assemblages along the altitudinal gradient?

In attempting to answer these questions we made two assumptions founded on previous research. Firstly, that the altitudinal gradient is mainly determined by the effect of temperature, because of an even vertical temperature decrease with altitude (Noack 1979). Of all environmental factors, temperature should play the dominant role in affecting most plant assemblages. Secondly, it is assumed that the distributional pattern of plant assemblages has a discrete character, as already confirmed for various communities, not only those of the forest (e.g. (Doran et al. 2003; Walentowski et al. 2004). Furthermore, we expect that climate sensitive zones are specific to macroclimatic zones; the general validity of individual climate sensitive zones throughout biomes is unlikely.

Material and Methods

Study area

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

The National Park (242 km²) is located in the middle of the Inner Bavarian Forest, with about 98% of the area covered by forest (Elling et al. 1987). It is characterized by montane and high montane areas within a vertical range of approximately 800m. Slopes in the National Park have mainly a southwest exposition. Long-term phases of weathering and erosion have led to rounded, elevated landforms. Typical geomorphological elements below 900m a.s.l. are foothills, gently-sloping hillsides and valleys, with steep hillsides between 900 und 1100 m a.s.l. and flat ridges dominated by summits between 1100 und 1400m a.s.l.

The Bavarian Forest is the south-western part of the Bohemian Massif (variszic basement) and consists essentially of granite and gneiss. Accordingly, soils are acidic, with sandy and loamy soils dominating (particularly brown earths and podsoles), 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. Sum of precipitation is between 1200 und 1800mm per year dependent on altitude. 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 (Bässler 2004; Noack 1979).

Study design and botanical survey

We set up a total of 293 plots along four main straight transects (Meyer et al. 2001; Traxler 1997) following the altitudinal gradient. The transects were selected using a stratified random scheme in order to avoid autocorrelation with forest structure. For example, we ensured that specific stand attributes such as age were distributed continuously along the altitudinal gradient. Vascular plants and ferns were recorded in a 200 square metre circular plot. The distance between the plot centres is 100m. The plots represent almost all plant associations occurring in the National Park (Bässler et al. 2008 submitted). The lowest is at 655m a.s.l. and the highest at 1420m a.s.l. The following analysis deals with the herb layer (understorey vegetation) up to 1 metre high. Data were obtained in July and August 2006 in a single survey. Due to the short growing season, it was possible to record the complete flora including spring species within this time frame. The cover of vascular plants and ferns in the understorey was estimated visually and recorded for all plant species using the scale proposed by (Londo 1976). Mean cover was used as the basis for analysis. Finally, 288 plots were analysed (dominance >0%, ≤1m height).

Environmental variables

The general information comprises altitude (m a.s.l.) and potential sum of radiation (sum during the growing season in kwh m⁻²), obtained by use of geographical information systems (GIS). Basis of calculation was a Digital Terrain Modell (DTM 25, Bayerische Vermessungsverwaltung) with a cell size of 50 m. Global radiation (mean 1980 - 2004 in J m⁻²d) was calculated by geostatistical modelling using ArcEGMO (Becker et al. 2002; Pfützner 2002), made available for the study area by (Klöcking et al. 2005). Canopy cover is expressed as the percentage of sample area shaded by horizontal projection of the tree layer (> 15m

height) and was estimated for each plot. Additional information on the richness of the tree layer is included. Ages of stands are taken from forest inventory data based on core samples. Four soil samples were collected on each plot and combined as two mixed samples of humus layer and mineral soil up to 30cm depth. The pH was measured in 1 M KCl, using a Hamilton glass electrode. Visual assessment was also made of characteristics of the humus layer (e.g. humus type) and the mineral soil (e.g. soil texture) up to 30cm depth. On the basis of these records, a soil water balance index was calculated for each plot (Ewald et al. 2000). Precipitation is thus integrated in the soil water balance index and was therefore not considered separately in the following analysis.

Statistical Methods

To assess patterns of plant assemblage variation as well as environmental and physical factors affecting these, direct and indirect gradient analyses were applied. Understorey cover was first normalized by square root transformation. Variables were selected by the forward selection procedure in CANOCO. Using PCA (Goodall 1954) environmental variables were ordinated to assess the variability and pattern within the sample plots and to exclude multicollinearity. All explanatory variables were standardized by adjustment to standard deviation (Leyer & Wesche 2006; McCune & Mefford 1999). In a second step species data for mean cover per plot were ordinated (CA) using correspondence analysis (Hill 1973; Jongmann et al. 1995). A detrended correspondence analysis of the plant frequency-plot matrix revealed a length of gradient of 3.795, indicating unimodal behaviour of the plant assemblages (Leps & Smilauer 2003), thus suggesting the application of a direct gradient analysis with unimodal response type (CCA). Using a CCA, the patterns in the plant assemblage were correlated directly with final environmental factors to obtain the single contribution of each factor to the linear combination for all axes, thus explaining the variation in the dataset. In each case the first three axes were calculated to assess the decline of eigenvalues. Occurrence of the same patterns under constrained and unconstrained ordination indicates environmental factors responsible for the variability of assemblages (Ter Braak & Smilauer 2002). Significance of the relation between the species and the set of environmental variables as well as the significance of the eigenvalues were tested using the Monte Carlo Test (999 permutations). Correspondence analysis may be applied to evaluate spatial dependencies of the plots of a transect at every level of ordination. Descriptive assessment reveals no plot dependencies on a transect. Here we also considered the role of geographical coordinates as co-variables (plus interaction term) in the ordination by comparing the general pattern with

and without their implementation. According to this analysis, the importance of the main driver is not obscured by spatial dependency. For more detail concerning methods of dealing with spatial correlation see (Bässler et al. 2008 submitted). Calculations were carried out using PC Ord (McCune & Mefford 1999) and Canoco 4.5 (Ter Braak & Smilauer 2002).

To derive thresholds of assemblage change on the basis of the sample scores calculated by the correspondence analysis (CA), we applied maximally selected rank statistics (Hothorn & Lausen 2003; Lausen & Schumacher 1992; Müller & Hothorn 2004). Maximally selected rank statistics allow for 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 some independent variable and the response. In contrast, classification and regression trees rely on cross-validation techniques for determining tree sizes without a formal hypothesis test.

The thresholds are derived from estimates of break points by means of maximally selected two-sample statistics, and their validity is judged by multiple test procedures. The key results are those where the difference between high and low values of the dependent variable is largest. The approach can be applied to a single or to multiple environmental variables. After the data set is divided into two subsets by the threshold with highest explanatory power, the subsets are searched for additional thresholds. The methodology provides a decision tree with p-values for one or more critical thresholds. On the basis of 1000 bootstrap samples the confidence interval (95%) was calculated on the function of density. These calculations were performed using the statistical software R 2.6.0 (RDevelopmentCoreTeam 2006) in combination with the package “party” (Hothorn et al. 2006).

Results

Environmental variables determining the plant and fern assemblages

The ordination of the species data using CA, with the supplementary second matrix plotted as overlaid vectors, yields environmental variables for all axes. The factors revealed are altitude, potential sum of radiation, canopy cover of the tree layer, pH value of the humus layer and type of humus. According to the vector plot, altitude represents the main factor among all environmental variables, correlating significantly with axis one (eigenvalue 0.499, 72.7%, $p < 0.001$).

The final ordination using CCA (Fig.1) reveals a similar pattern to CA, confirming that all environmental factors responsible for the variation of the assemblages were considered. The species / environmental correlation along the first axis (eigenvalue 0.438, $p < 0.001$) is about

93.7%. CCA explains altitude as accounting for 84.1% ($p < 0.001$) of variation on the first axis and indicates this as the main driver for the variation of the plant assemblages. Canopy cover as the second most important factor correlates with 62.4% ($p < 0.001$) on the first axis and is followed by the potential sum of radiation with 30.4% ($p < 0.001$). Most important factor on the second axis is the pH-value of the humus layer: eigenvalue 0.186, correlation 65.2% ($p < 0.001$). Finally, the humus form correlates with 48.1% ($p = 0.003$) on this axis.

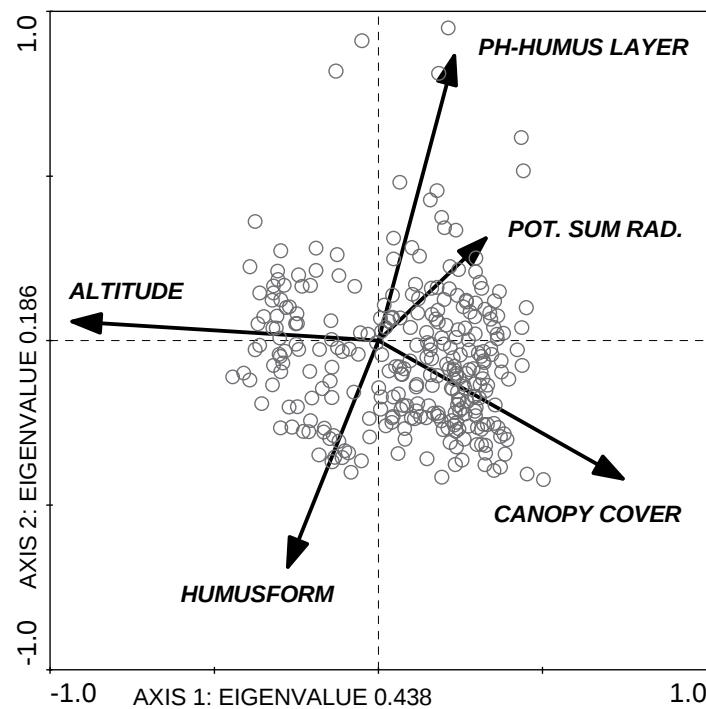


Fig. 1: CCA of final variables controlling vascular plant and fern assemblage, on the square root transformed species matrix. Monte Carlo Test (999 permutationen) was applied for the first three axes and the species environmental correlation revealing p -value < 0.01 .

Altitudinal change of assemblages

Maximally selected rank statistics split the assemblages on the first level (Fig. 2) at 1142m a.s.l. (95% C.I. 1108-1142). Hence there is less than 5% likelihood of a threshold in assemblage change above 1142m a.s.l. as assessed with a 95% confidence interval using the bootstrap density plot. Two more thresholds could be detected at the second level (Fig. 2). These changes in plant assemblages take place at 1047m a.s.l. ($p < 0.001$, 95% C.I. 994-1084) and 1225m a.s.l. ($p < 0.001$, 95% C.I. 1159, 1304).

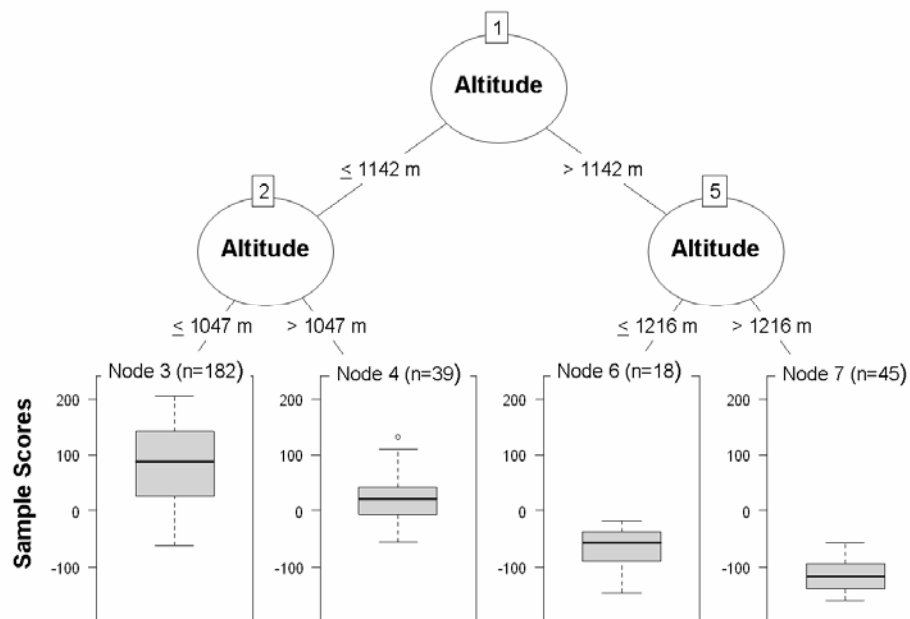


Fig. 2: Critical cutpoints of altitude (m a.s.l.) for the sample scores of the first axis (eigenvalue 0.499) resulting from CA. Boxplots display medians and quartiles; median is shown as a bold line. One outlier ($>1.5 \times \text{IQR}$) shown as a circle. All cutpoints are highly significant ($p < 0.001$).

Discussion

Altitude as an expression of temperature change and as main factor influencing the plant assemblages

Our results revealed altitude as the main factor affecting vascular plant assemblages. Most studies along altitudinal gradients deal with the distribution patterns of diversity and richness and not with the structure of assemblages e.g. (Bhattarai et al. 2004; Grytnes 2003; Grytnes et al. 2006). Only a few studies deal with the turn-over of plant assemblages along an altitudinal gradient (Doležal & Šrůtek 2002; Doran et al. 2003; Hokkanen 2006).

Altitude is a gradient which is only indirectly correlated with resources and regulators affecting vegetation growth and is thus a surrogate factor (Kazakis et al. 2007). Climate can be adequately described using topographical surrogates like altitude when the extent of the study area is relatively small, climate is fairly uniform throughout the area and the lapse rate of temperature with increasing elevation is constant within the area (Austin 2002; Sergio & Pedrini 2007). All three conditions were fulfilled in this study. The decrease of temperature along the altitudinal gradient is generally very stable (Elling et al. 1987; Noack 1979). The overriding influence of decreasing temperature with altitude is further corroborated by

discrimination of the effect of precipitation by its inclusion in the soil water balance index, which proved to be of negligible importance. There is no dependency of global radiation (W m^{-2}) and potential sum of radiation (kWh m^{-2}) on altitude (Elling et al. 1987; Noack 1979). Further, there is only a weak decrease of sum of sunshine (hours) and relative humidity (%) with altitude. Wind speed varies very widely and depends primarily on surface conditions (Baumgartner 1960, 1964). Thus we interpret the variation of the vascular plant assemblages as being mainly driven by the direct effect of temperature and assume that altitude is a valid proxy for this.

Identification of climate sensitive zones

Identification of climate sensitive zones was achieved by detecting sudden changes in the plant assemblages along the altitudinal gradient, which for the purposes of this study can be regarded as representing a temperature gradient. These zones were revealed to be ecological thresholds by maximally selected rank statistics. Climate sensitive zones can also be described in terms of species turnover when this is caused by temperature changes (Doležal & Šrůtek 2002; Doran et al. 2003; Kazakis et al. 2007; Pauli et al. 2007; Thuiller et al. 2005).

The most conspicuous climate sensitive zone identified by maximally selected rank statistics occurs at the transition between montane and high montane assemblages at 1142m a.s.l. The consistent importance of this ecological threshold was confirmed by the narrow confidence interval indicating an altitudinal width of 34m for this transition zone. The calculated thresholds reveal pattern of change as discontinuity along the entire gradient, because there is no threshold between 655m a.s.l. and the first detected threshold at 1047m a.s.l. The distributional pattern of plant assemblages has also been investigated in other studies. Similar patterns were found in Tasmania by setting up a comparable design with an altitudinal gradient of 1230m (70m - 1300m a.s.l.) from lowland wet forests through scrubby subalpine woodlands to alpine heaths. Vegetation was also found to be distributed discontinuously (Doran et al. 2003). Change of the assemblage structure along altitudinal gradients was assessed by applying species turnover e.g. calculating dissimilarity indices or gain and loss of species between altitudes. A further study on the Lefka Ori Massif (Crete) detected the change between the montane- mediterranean and alpine zones on the basis of species turnover. Within this subalpine zone turnover is attributable to the loss of montane-mediterranean species and the gain in alpine species. These zones of species turnover were also identified as climate sensitive and as potentially prone to future shifts resulting from climate change (Kazakis et al. 2007). According to a case study in Slovakia (Mt Velký Gápel, Western

Carpathians) analysing the composition and structure of plant communities along an altitudinal transect (1150 - 1750m a.s.l.) from montane forests to woody shrub and alpine meadow communities, two coincident aggregations of boundaries identifying discrete ecotones were found, caused by the altitudinal gradient and related factors (soil depth). Results of this study were supported by a TWINSpan floristic classification. Despite this, none of the altitudinal zones could be shown to contain a significant aggregation of species limits (Doležal & Šrůtek 2002). The conclusion was therefore reached that a continuous variation of vegetation along the gradient exists, with individual species overlapping in transition zones delimited by dominant taxa. Further studies confirm the existence of continuous distributional patterns along elevation gradients for tropical montane forests (Vasquez G. & Givnish 1998) as well as for temperate areas (Auerbach & Shmida 1993; Whittaker 1956, 1960), all supporting the hypothesis of individualistic community organization, which posits that the distribution of each species is determined by its own ability to survive, compete and reproduce successfully in different environments, resulting in each species having its own distinctive distribution and in community composition changing more or less continuously along ecological gradients. However, other studies continued to report discrete vegetation boundaries (Ashton 2003; Fernandez-Palacios & de Nikolas 1995; Hemp 2005; Martin et al. 2007).

To summarize: similar patterns of discrete change in vegetation could be identified in many different biomes, but with different degrees of clarity probably arising from differing study designs and methods. To be robust, quantitative studies of plant assemblage distributions require highly replicated, fine scale sampling. However, such studies are rare, primarily because of the large sampling area needed for species recording. It is nevertheless remarkable that in our study the strongest threshold, i.e. the most clearly differentiated zone of species turnover, closely resembles those found in other studies of species altitudinal limits, although the causal mechanism remains hidden.

Conclusions

Changes in the structure of plant assemblages in response to climate change will take place first in climate sensitive zones, as defined in this study. For efficient monitoring it is important to know the localities of largest expected impact and the objects (species, assemblages, etc.) which will be most affected. At the assemblage level, repeated recording could within a few years indicate displaced thresholds and thus highlight the effects of climate change. However, it is assumed that species will react individually to increasing temperature

(Parmesan et al. 1999; Pimm 2001; Thomas et al. 2001). Most species occurring on the altitudinal gradient studied here reach their limit in the climate sensitive zones. Hence it is very important to focus further studies on species and their limits, modelling different climate scenarios and verifying these by repeating survey work every few years. To obtain information about direction, dynamics and size of the impacts of climate change, a systematic selection and intensive observation of indicators in climate sensitive zones is necessary (Sutherland et al. 2006). It is to be expected that thermophilous species at present reaching their upper limit in the montane zone will migrate upwards during a period of increasing warmth (Walther & Grundmann 2001). New assemblage structures will thus develop and modified thresholds may appear. The methodology used in this study revealed every change at different levels of climate sensitivity along the entire altitudinal gradient. This highlights the importance of considering in future species oriented studies the other climate sensitive zones which were indicated by a weaker signal (1047m a.s.l. and 1216m a.s.l.). Furthermore, vegetation represents a lower trophic level on which, for example, assemblages of phytophages depend (Brändle & Brandl 2001). Hence, vegetation is a key factor in the context of trophic changes caused by climate change.

Besides identifying climate sensitive zones in this study, we are continuing to gather data for long-term comparison, with the objective of improving our understanding of vegetation and the climate-change driven forces operating on complex biological systems. The real impacts of climate change caused by complex interactions and interspecies relationships will be evident only with the passing of time and only detectable through fieldwork. Use of bio-monitoring will therefore be essential for future research and formulation of policy.

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Effects of climate, forest structure and habitat continuity on wood-inhabiting fungi in low mountain range forests

Claus Bässler^{1*}, Jörg Müller¹ and Frank Dziock²

* Corresponding author: claus.baessler@npv-bw.bayern.de

¹ Bavarian Forest National Park, Freyunger Str. 2, D-94481 Grafenau, Germany, Telephone: ++49-8552-9600-179, Fax: ++49-8552-9600100

² Department of Biodiversity Dynamics, Technische Universität Berlin, Sekr. AB1, Rothenburgstr. 12, D-12165 Berlin, Germany, e-mail: frank.dziock@tu-berlin.de

Abstract

Global loss of habitats and the rapid rate of reduction in biodiversity due to global change make it necessary to analyse and evaluate the present state of ecosystems and to explore environmental relationships of species. Aim of this study in a Central European low mountain range is to determine the relative influence of climate, forest structure and habitat continuity on composition of wood-inhabiting fungi communities using variance partitioning by partial CCA. Hierarchical variance partitioning was then used to examine species density, number of species records and number of threatened species. The combined effect of forest structure variables was clearly more important than the set of climate variables in its effect on community composition, species density and species records. Only for threatened species was habitat continuity revealed to be an important factor. It is concluded that wood-inhabiting fungi are mostly affected by management activity which alters forest structure.

Changes in microclimate driven by global warming are not expected to directly influence wood-inhabiting fungi in the future. Rather, global warming could trigger changes in forest structure that might affect wood-inhabiting fungi indirectly, such as alterations in tree species composition.

Key words: wood-inhabiting fungi, climate change, forest structure, habitat continuity, variance partitioning, hierarchical partitioning

1. Introduction

Loss of habitat and living space has accelerated enormously during the last few decades, caused by global change (Sala et al. 2000). As a result of this rapid rate of change there is an urgent need to analyse and evaluate the present state of ecosystems, to explore relationships of species to their environment and to use this information for assessing and predicting changes caused by climate change (Sutherland et al. 2006).

There are several reasons why alpine and montane ecosystems should be used for monitoring climate change. These ecosystems are disproportionally sensitive to climate change (Thuiller 2007). Furthermore, altitudinal sequences of thermal life zones on high mountains are more compressed, with smaller ecotones, than latitudinal sequences, and environmental gradients in

mountains occur along short distances (Theurillat and Guisan 2001). Distribution of many species is limited by altitude, as an expression of climate parameters or limitation of resources (Grabherr et al. 1994).

Central European montane mixed forest is one of the most threatened natural systems worldwide (Hannah et al. 1995). More than half of Central Europe is covered by mountain areas, of which low, forested ranges form the major part (CIPRA 2007). Spatial variation in the environment is accentuated in mountainous regions.

Environmental conditions vary in a non-random manner along most altitudinal gradients (Lomolino 2001). The altitudinal pattern is a response to the same environmental factors throughout the altitudinal gradient, i.e. spatial clines in climate and energy (Willdenow 1805). Alterations in tree species composition correlated with altitude are obvious in forests both of high and low mountain ranges (Walentowski et al. 2004). Species richness co-varies strongly with climate, and this effect is very similar in different parts of the globe, even though the evolutionary histories of different regions may differ greatly (H-Acevedo and Currie 2003). But even on a small spatial scale along Low Mountain or alpine altitudinal gradients, climate has been revealed as the main driver for vascular plants (Bässler et al. 2008).

The occurrence of various types of woody debris is a key factor for biodiversity in forest ecosystems (Bader et al. 1995). Thus the importance of dead wood is widely acknowledged (Siitonen 2001) and large numbers of organisms depend on decaying wood for nutrients or as a habitat (McComb and Lindenmayer 1999). Various types of decaying wood constitute the most important habitats for threatened cryptogams and invertebrates (Berg et al. 1994).

Wood-inhabiting fungi comprise a major part of forest biodiversity and are one of the main groups responsible for decomposing wood on dead or living trees worldwide (Dix and Webster 1995). They are thus of special ecological significance (Junninen et al. 2006).

As a result of their species richness and key ecological position, fungi are highly suitable indicators for changes in forest ecosystem structure (Müller et al. 2007). Many of the polypores considered in this study are especially sensitive to environmental changes and specialized in their substrate requirements, thus indicating continuity in both forest canopy cover and availability of woody debris (Sippola et al. 2004).

Our knowledge of habitat preferences for wood-inhabiting fungi in the European deciduous forest zone is still rather fragmentary. Several studies focus on effects of logging intensities on wood inhabiting fungi diversity (Bader et al. 1995, Sippola and Renvall 1999, Sippola et al. 2004) or on wood inhabiting fungi assemblages (Müller et al. 2007). Studies on comparisons of fungal assemblages in old-growth and managed forests have clearly revealed

differences in species composition and richness due to continuity in both the forest canopy and presence of woody debris, which emphasizes the importance of habitat continuity (Jonsson and Jonsell 1999, Lindblad 1998, Penttilä et al. 2004). Others focus on the importance of fine and coarse woody debris, revealing the significance of different types of substrate (Heilmann-Clausen and Christensen 2004, Norden et al. 2004).

This study aims to explain general patterns in the occurrence of wood-inhabiting fungi caused by components of climate and forest structure and to enable further interpretation of the impacts caused by climate change. Even though the causes of distribution patterns on a broad spatial scale are still disputed (Gaston 2000), one of the most important factors for life is undoubtedly the gradient in air temperature (Körner 2007). However, the response of many species to large scale climate will be modified by factors operating at a smaller scale (Ellis et al. 2007). Until now, no study has been made on the joint effects of forest structure and climate variables on wood-inhabiting fungi. A specific objective of this study was therefore to resolve the confounding effects of climate and forest structure on these organisms. To obtain deeper insights on this, we analysed separately the community composition of wood-inhabiting fungi (plot assemblage), species density (number of species per sampling plot), species records (number of fungi records per plot) and threatened species (number of threatened species per plot). An overview of the effects of climate on the target groups prepares the way for further interpretative studies on their response to the impacts of climate change, as well as identifying indicators suitable for further monitoring. Threatened species are considered separately in the analyses because these are expected to be very vulnerable to climate change (Thomas et al. 2004).

We test the hypothesis that climate gradients on a regional scale are important in shaping wood-inhabiting fungi communities, species density, species records and occurrence of threatened species when other causes of variance such as forest structure and habitat continuity are accounted for. If this were so, then climate change could be expected to have the most important influence on wood-inhabiting fungi by overlaying the effects of direct human activity, such as the supply of woody debris and specific forest structures caused by altered spatial and temporal logging intensity.

2. Material and Methods

2.1 Study area

The National Park “Bavarian Forest”, the oldest national park in Germany, is located in the south-eastern corner of Bavaria, at the border of the Czech Republic. It covers approximately

24 000 ha at elevations from 650 m to 1430 m a.s.l. Total annual precipitation is between 1200 mm and 1800 mm depending on altitude. Mean annual temperature (1972-2001) 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 containing acidic soils. Above about 1100 m to 1200 m a.s.l. the high montane forest is dominated by spruce *Picea abies*, with a low proportion of beech *Fagus sylvatica* and mountain ash *Sorbus aucuparia*(; below this the mixed montane forest is dominated by spruce, beech and fir *Abies alba* (Walentowski et al. 2004). Infestation by bark beetles, mainly *Ips typographus*, has caused dieback of large areas of forest. The resulting structure varies widely from stands with an open canopy, dominated by dead wood, to dense, closed stands.

2.2 Study design, fungi survey and explanatory variables

We set up a total of 290 plots along four main straight transects following the altitudinal gradient (Bässler et al. 2008). The plots also represent a gradient of logging history ranging from 17 years up to more than one hundred years. Relicts of old-growth forest and wilding stands, partly killed by bark beetle (*Ips typographus* L.), allow investigation of a broad range of woody debris and light conditions. 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 harvesting and silvicultural management were abandoned about two decades ago. Two transects were set up in areas under continuous management.

Wood-inhabiting fungi were recorded on 290 circular plots with a plot size of 0.1 ha. The plots are situated along the four altitudinal transects, with a distance between plots of 100m. Almost all forest associations occurring in the National Park are represented (Bässler et al. 2008). The lowest plot is at 655m a.s.l and the highest at 1420m a.s.l. Data were obtained from August to October 2006. We chose standardized time as the sampling method, limited to one hour per plot. Wood-inhabiting fungi are here defined as all fungi with fruit bodies on decaying wood (macromycetes except fully resupinate corticioide basidiomycetes). Nomenclature follows the standard list of the German Mycological Society (DGfM 2000). The status of threatened species follows the red data book for Germany (DGfM and NABU 1992). Fruiting bodies of the same species on one piece of wood were regarded as one record (Junninen et al. 2006, Müller et al. 2007). In most previous studies and in this study, fungi were identified by the presence of their fruit bodies. It is to be expected that fungi were also present as mycelia on woody debris but that they did not fructify during the survey period.

Some species were probably therefore overlooked. Fruit body inventory is presently the main method used in larger field surveys and should provide data suitable for comparison between studies, e.g. Heilmann-Clausen and Christensen (2005), Junninen et al. (2006), Müller et al. (2007), Norden et al. (2004).

Selection of explanatory variables

We selected 14 explanatory variables (Table 1) which we expect, according to the literature, to strongly influence wood-inhabiting fungi and their diversity.

Main climate gradients in the study area are temperature and precipitation (Bässler 2004). Subordinate to temperature, the sum of radiation during the growing season is physiologically effective (Austin 1980). We therefore chose temperature, potential sum of radiation and precipitation as climate variables. At the stand scale the major determinant of fungal populations is the amount of woody debris (Edmann et al. 2006, Sippola et al. 2004).

Tab.1: Environmental predictor variables used in the analyses. Class attribution as used for variance partitioning and hierarchical partitioning; climate [C], forest structure variables [S], habitat continuity [T] and spatial variables [G].

Class	Variable	Explanation	Source	Range total
C	TEMP	Mean annual temperature 2000-2004 (°C)	ArcEcmo modelling	4.0 - 7.8 °C
	PRECIP	Mean sum of precipitation 2000-2004(mm)	ArcEcmo modelling	1395 - 1848 mm
	RADIATION	Sum of potential radiation for the growing season (kwh m ⁻²)	Surface terrain model	178 - 252 kwh m ⁻²
S	CWD AMOUNT	Total volume of woody debris (m ³ ha ⁻¹)	Inventory of plots/measurement 2006	0 - 709 m ³ ha ⁻¹
	TREE RICH	Tree richness within woody debris on 0.1 ha plot	Inventory of plots 2006	0 - 4 species
	CWD FRACTION	Richness of fractions within woody debris	Inventory of plots 2006	1 - 7 pieces
	EXPOSURE SUN	Proportion exposure woody debris to sunlight (%)	Inventory of plots/estimation 2006	0 - 86.8 %
	DECAY VAR	Variance of decomposition stages	Inventory of plots 2006	0 - 4 categories
	DIAMETER	Mean Diameter of woody debris	Inventory of plots/measurement 2006	0 - 71.5 cm
T	DBH	Maximum of diameter breast height (cm)	Inventory of plots/measurement 2006	0 - 130 cm
	AGE STAND	Age of the forest stand (years)	Forest inventory 2002	10 - 400 years
G	X	Longitude	Surface terrain model	
	Y	Latitude	Surface terrain model	
	X*Y	Longitude*Latitude	Surface terrain model	

However, not only the amount, but also the heterogeneity and quality of coarse woody debris are important factors, as revealed by several previous studies (Heilmann-Clausen and Christensen 2004, Sippola and Renvall 1999). Expression of heterogeneity involves the availability of different woody debris fractions and tree species representation within woody debris, which combine to cause specific fungus-tree species relations (Krieglsteiner 2000, Luschka 1993). The importance of the stage of decay on fungi community composition and diversity has been confirmed by several studies (Lindhe et al. 2004, Müller et al. 2007, Sippola and Renvall 1999). We therefore considered the decay stage of the woody debris objects. Mean diameter of woody debris is well known to be very important for fungal biodiversity (Bader et al. 1995, Heilmann-Clausen and Christensen 2004, Sippola and Renvall 1999). Exposure of woody debris to sunlight was included, because fungal decay processes are governed by the effect of this variable on wood moisture and temperatures (Rayner and Boddy 1988). Some of the study plots are characterized by dense understorey vegetation which shades the object, despite an open canopy. Exposure to sunlight is thus a more significant factor than canopy cover.

Finally, we considered the age of the stand and the maximum diameter at breast height (DBH). These variables are surrogates of habitat continuity in forests and have been shown to be strongly correlated with old growth forests and thus suitable for representing habitat continuity (Müller et al. 2005).

Source of explanatory variables

All environmental data are related to the sample plots of 0.1 ha size. Table 1 lists the categories of environmental data used for analyses, together with their definition and source. Topographical and geographical information were generated using Geographical Information Systems (GIS). Basis of the GIS calculations was the Digital Terrain Model (DTM 25) with a cell size of 50 m. To obtain reliable local data for temperature, in 2006 we set up 30 data loggers on representative sites across our altitudinal gradients. Additionally, data from five meteorological stations running in the region since 2000 were used to extrapolate averages for 2000-2007 from the data collected in 2006 and 2007. These were used to calculate the mean annual temperature for each sampled plot. We then developed a statistical model to predict for each plot the temperature, using independent variables extracted from the digital terrain model ArcEGMO (Becker et al. 2002). Data for the precipitation model are from 20 rain gauges in the study area. From these we calculated the mean sum of precipitation for the available time series 1980 - 2004 and developed a statistical model, like that described for temperature, to

predict the mean annual sum of precipitation for each sampled plot. Because data for precipitation are available only as a time series up to 2004, mean annual temperature and mean annual sum of precipitation from the common measurement period 2000 - 2004 were used for further analyses. The potential sum of radiation (kWh m^{-2}) was calculated from the digital terrain model and aggregated for the growing season (May-September). Variables of stand structure and dead wood availability were all recorded in 2006 in the field within 0.1 ha of every sample plot.

All explanatory variables were grouped in four sets; [C] = climate variables, [S] = woody debris structure variables, [T] = habitat continuity variables, [G] = geographical variables (see Table 1) for further statistical analysis. To avoid multicollinearity, we applied a two-sided rank-correlation-test after Spearman on the set of predictor variables, setting a limit for considering both correlated variables of $r_s=|0.7|$ (Fielding and Haworth 1995).

2.3 Statistical Methods

We performed correspondence analyses as unconstrained ordinations (DCA) to reveal the main gradient structure of the data set (Jongmann et al. 1995). DCA was applied because of the occurrence of an arch effect in ordinary correspondence analysis (Økland 1990). The length of gradient produced by DCA (Fig.1) indicates unimodal behaviour of the species and confirms the suitability of this technique as greater than PCA (Leps and Smilauer 2003). Correlation coefficients (Pearson) between environmental variables and DCA axes and their significance at a Bonferroni-corrected overall significance level $p=0.01$ were calculated. All explanatory variables were transformed and standardized by standard deviation adjustment (McCune and Mefford 1999). Using partial CCA (Ter Braak and Smilauer 2002), we partitioned variance (Økland 2003) for wood-inhabiting fungi community composition into three sets of explanatory variables (climate[C], forest structure[S] and habitat continuity [T]). One additional set containing geographical coordinates [G] was created to assess spatial correlation (Table 1). Tests of significance were carried out as Monte Carlo tests with 999 permutations. Calculations were made with Canoco 4.5 (Ter Braak and Smilauer 2002). Numbers of variables in our variable sets differ. We believe that this should not adversely affect our analysis, since it is more important that all relevant variables are included in the sets than that equal numbers of variables occur across the sets (Økland and Eilertsen 1994). Variation partitioning is considered to validly indicate the relative importance of the variable sets, whilst the absolute value of the figures obtained has little significance (Økland 2007). Adjustment of the sets as recommended by Peres-Neto et al. (2006) is not at present possible

for our specification of four variable sets and use of CCA, because no algorithm exists. However, the adjustment is not expected to significantly affect the results of our study, because of the large sample size used.

Species density, species records and number of threatened species were calculated from the species matrix to assess the explanatory contribution of the chosen sets. Species density is defined as the number of species per unit area (sampling plot) (Gotelli and Colwell 2001). Species records represent the number of records for a single fungus species per plot (one record is defined as one species record per piece of wood). Preliminary tests revealed no correlation between species records and the woody debris predictor variables such as volume or number of fractions. Threatened species were analysed using the number of red listed species (DGfM and NABU 1992) per plot. First, the influence of the selected environmental parameters (Table 1) on these three response values were analysed by fitting a generalized linear model. The distribution of species density and species records led us to apply Gaussian regression to these, and a log link function and Poisson regression to the number of rare species. However, one of the key assumptions made for statistical models of the type used here, is the independence of residuals (Dormann et al. 2007). This requirement was not necessarily fulfilled by our data, because the study plots were situated along transects. To overcome this difficulty, we used a general approach based on semiparametric spatial generalised linear models, which allow the use of spatially correlated data for the routine analysis. In this method spatial autocorrelation is alleviated by including a spatial surface into the regression model (Kneib et al. 2008). Assuming asymptotic normality of the estimated regression coefficients, confidence bands and p-values can be computed using the standard deviations obtained from the expected Fisher information matrix. The approach is implemented in the package “BayesX” (Fahrmeir et al. 2004, Kneib et al. 2008). Subsequent hierarchical partitioning (Chevan and Sutherland 1991) was performed for all significant variables ($p < 0.05$, Table. 4) resulting from the preliminary generalized linear models for species density, species records and threatened species. Hierarchical partitioning calculates the goodness-of-fit values for the entire hierarchy of models using all combinations of N independent variables. The hierarchical partitioning algorithm of Chevan and Sutherland (1991) is applied to the list of goodness-of-fit values, using the partition function, to return a simple table listing each variable and its independent contribution. The independent effects of the significant environmental variables were assigned to the sets: climate [C], forest structure [S] and habitat continuity [T]). We calculated the independent effects without the geographical variable set, because we used spatial GLMs, which already account for spatial autocorrelation.

Hierarchical partitioning was conducted using the ‘hier.part’-package (version 1.0-3) (MacNally and Walsh 2004) and the statistical software R 2.6.0 (RDevelopmentCoreTeam 2006).

3. Results

A total of 148 wood-inhabiting fungi species was found, represented by 9347 records on 290 plots. 28 threatened species were among the samples.

DCA (Fig. 1) reveals a general pattern indicating strong correlation of climate, forest structure and habitat continuity variables with the first axis, implying the existence of several biotic and abiotic gradients (Table 2). Most important factor along axis one is tree species density within woody debris, followed by the proportion of woody debris exposed to sunlight and precipitation (Table 2). Variation on the second axis depends primarily on the amount of woody debris, differentiated mainly in the upper altitudinal zones.

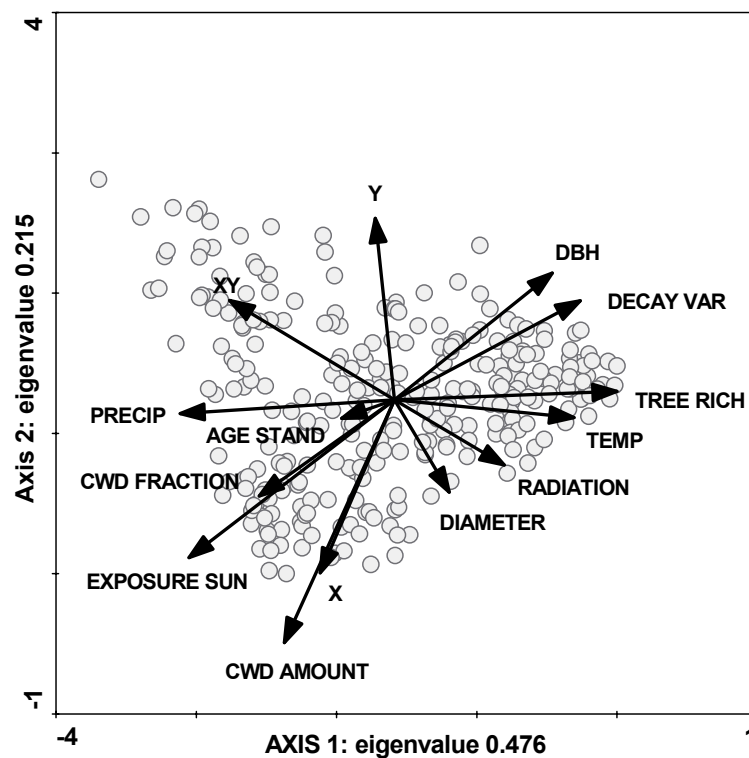


Fig.1: DCA ordination diagram of wood-inhabiting fungi communities in the Bavarian Forest. The biplot shows study plots and significantly correlated environmental variables (arrows) along the first two axes (eigenvalues are presented).

Tab. 2: Variables correlated with two DCA axes. Variables refer to the 0.1 ha plot. All variables are significant at a Bonferroni-corrected overall significance level $p=0.01$.

Variable	Coefficient	Axis
TREE RICH	0.600	DCA 1
PRECIP	-0.579	DCA 1
EXPOSURE SUN	-0.545	DCA 1
DECAY VAR	0.496	DCA 1
TEMP	0.485	DCA 1
DBH	0.418	DCA 1
CWD FRACTION	-0.360	DCA 1
X*Y	-0.451	DCA 1
RADIATION	0.300	DCA 1
AGE STAND	-0.142	DCA 1
CWD AMOUNT	-0.697	DCA 2
Y	0.530	DCA 2
X	-0.497	DCA 2
DIAMETER	-0.274	DCA 2

All environmental variables were used for variation partitioning by partial constrained ordination of the community composition and assigned to the classes presented in Table 1. The largest amount of variance was explained by the set of forest structure variables (35.2%), followed by the set of climate variables (12.5%) and habitat continuity variables (5.9%). Spatial variables (longitude and latitude) explained 11.5% (Table 3). The variance attributable to second, third and fourth order partial intersections of variable sets was always $< 8\%$. Spatial GLMs were run for the response variables (species density, species records and number of threatened species) and for predictors (all environmental variables) as (Table 1).

Tab.3: Partitioning of variation by partial constrained ordination (partial CCA) for wood-inhabiting fungi communities in the four sets of explanatory variables: climate [C], forest structure [S], habitat continuity [T] and spatial variables [G]. The denotation of the respective term calculated, the sum of all canonical eigenvalues (EV), the fraction of the total variance explained (FTVE), and the p-value of the respective term (p) are shown. Variation explained is given in inertia units as well as the fraction of the total variance explained (FTVE). The symbols ' $\cup$ ' and ' $\cap$ ' indicate unions and intersections of variable sets, while ' $|$ ' stands for the Boolean operator NOT and n.p. indicates that no test was performed. Explained variance is statistically significant at a Bonferroni-corrected p of 0.01 (Asterisks).

Denotation	EV	FTVE	p
C	0.271	*31.4	0.001
S	0.566	*65.6	0.001
T	0.203	*23.5	0.001
G	0.271	*31.4	0.001
$C (G \cup T \cup S)$	0.108	12.5	0.001
$S (G \cup T \cup C)$	0.304	35.2	0.001
$T (G \cup S \cup C)$	0.051	5.9	0.001
$G (T \cup S \cup C)$	0.099	11.5	0.001
$C \cap T (S \cup G)$	0.003	0.3	n.p.
$C \cap G (T \cup S)$	0.023	2.7	n.p.
$S \cap C (T \cup G)$	0.067	7.8	n.p.
$S \cap T (C \cup G)$	0.032	3.7	n.p.
$S \cap G (T \cup C)$	0.059	6.8	n.p.
$G \cap T (S \cup C)$	0.005	0.6	n.p.
$S \cap G \cap T C$	0.042	4.9	n.p.
$G \cap T \cap C S$	0.008	0.9	n.p.
$S \cap G \cap C T$	0	0	n.p.
$S \cap T \cap C G$	0.028	3.2	n.p.
$S \cap T \cap C \cap G$	0.034	3.9	n.p.

All climate variables have a positive influence on species density (Table 4). Furthermore, density is favoured by higher tree species density within woody debris and large mean diameter of woody debris. A negative influence could be detected for the factor woody debris exposed to sunlight. Species records increase with increasing values of potential sum of radiation and tree species density within woody debris (Table 4).

Tab. 4: Results of spatial GLM, based on 290 sampling plots. Black triangles indicate significant influence (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$): ▲ positive estimator / ▼ negative estimator; n.s. = non significant. Threatened species are according to the German red data book (DGfM and NABU 1992).

Dependent variable	TEMPERATURE	PRECIPITATION	POTENTIAL SUM OF RADIATION	AMOUNT OF WOODY DEBRIS	TREE SPECIES DENSITY	CWD FRACTION	EXPOSURE TO SUNLIGHT	DECAY VARIANCE	MEAN DIAMETER	DIAMETER BREAST HEIGHT	AGE OF STAND
	CLIMATE			STRUCTURE						HABITAT CONTINUITY	
Species density	▲***	▲*	▲**	n.s.	▲***	n.s.	▼***	n.s.	▲**	n.s.	n.s.
Species Records	n.s.	n.s.	▲*	n.s.	▲***	n.s.	▼**	n.s.	n.s.	▼**	n.s.
Number of Threatened Species	n.s.	▲**	n.s.	▲**	n.s.	n.s.	n.s.	▲*	n.s.	▲*	n.s.

Negative influence was revealed for the factor woody debris exposed to sunlight and for the habitat continuity factor maximum diameter at breast height. Threatened species profit from greater precipitation, a higher level of variability of decomposition stages and large amounts of woody debris.

Only the significant ($p < 0.05$) variables were considered for subsequent hierarchical partitioning and assigned to the sets of climate, forest structure and habitat continuity. The largest amount of variance for species density and records was explained by the set of forest structure variables (species density 64.7%; species records 78.1%). Second greatest explanatory power in the case of species density was revealed for the set of climate variables (35.3%), whereas no variance attributable to habitat continuity was discernible. Second highest degree of explanation for species records was attributable to habitat continuity variables (14.9%), whilst the set of climate variables explains 7.0%. All categories play a nearly equal role in explaining the occurrence of threatened species: habitat continuity variables, 34.6%; forest structure variables 33.8%; climate variables, 31.6%.

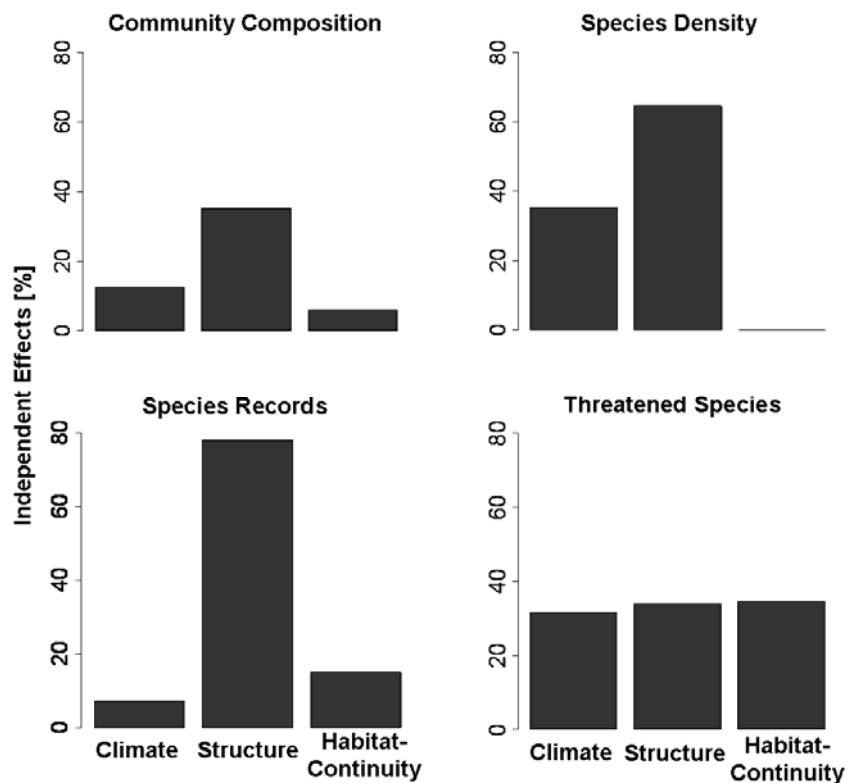


Fig.2: Explained variance (%) for wood-inhabiting fungi community composition according to variance partitioning by partial CCA in relation to the environmental set of variables divided into climate, forest structure and habitat continuity. Note that the graph for community composition lacks bars for geographical and unexplained variance. Species density, species records and threatened species examined with hierarchical partitioning in relation to the environmental set of variables divided into sets for climate, forest structure and habitat continuity. Note: methodology of calculation of independent effects for community composition differs from the others (see text).

4. Discussion

4.1 Fungi community compositions between climate change and human activity

The set of structure variables explains considerably more variation in the composition of wood-inhabiting fungi communities than the set of climate variables. DCA revealed the factors tree species density within woody debris and proportion of woody debris exposed to sunlight as probably the most important factors within forest structure. Thus it can be concluded that the most important factor on this level is the change of forest structure

represented by changes in tree species composition, most clearly seen in the clear threshold separating the lower mixed-montane forest from the high montane forest (Bässler et al. 2008). Tree species in the mixed-montane zone comprise mainly Norway Spruce (*Picea abies* (L.) H.Karst)), European Beech (*Fagus sylvatica* L.), with a few Silver Fir (*Abies alba* Mill.) and Sycamore (*Acer pseudoplatanus* L.), whereas forest of the high montane zone predominantly consists of Norway Spruce with sparse Mountain Ash (*Sorbus aucuparia* L.). Thus, the absence of beech dead wood in the high montane zone is the most important factor affecting wood-inhabiting fungi assemblages there, because the beech-specific taxa are lacking. Changes in environmental conditions acting on a global scale will probably in future affect wood-inhabiting fungi mainly by causing changes in forest structures. The most important phenomenon could be the upward shift of European Beech due to further warming (Grace et al. 2002). The effects on montane species should be assessed separately for each species. It can however be concluded that compositions of wood-inhabiting fungi communities are at present most affected by management activities which alter forest structures.

4.2 Driving factors and their effect on species density, species records and threatened species

Similarly to community composition, spatial GLM revealed the driving factors for species density and underlined that increasing representation of different tree species within woody debris leads to the presence of additional fungi species (Lindhe et al. 2004). Species density is clearly negatively affected by increasing exposure of woody debris to sunlight. This accord fully with a study from a hemi-boreal zone (Lindhe et al. 2004). Open edges with high insolation result in extreme and stressful conditions, because of large temperature fluctuations. Furthermore, solar radiation leads to desiccation of woody debris, and fungal decay processes depend heavily on wood moisture (Rayner and Boddy 1988). Open stands providing huge amounts of woody debris exist in a large part of the study area, as a result of bark beetle infestation during the last two decades. This woody debris seems to be very homogeneous, because the trees died within a similarly recent period and the material is still in the initial stages of decomposition (Bässler et al. 2008). The importance of decay level on fungi assemblages and diversity has been confirmed by several studies which emphasize that woody debris in more advanced stages of decomposition plays a key role in providing the structures that are necessary for a natural assemblage of fungi (Lindhe et al. 2004, Müller et al. 2007, Sippola and Renvall 1999). Studies on dead wood of beech, spruce or pine reveal that the decisive factor determining diversity seems to be presence of material at a medium

stage of decay (Bader et al. 1995, Müller et al. 2007). Species density was found to be higher on plots with large diameters of woody debris, which is interpreted as an indication of greater woody debris availability on these sites. This agrees with studies from spruce and pine dominated forests as well as from beech forests, if single samples are compared (Heilmann-Clausen and Christensen 2004, Lindhe et al. 2004), confirming that species richness is highly correlated with the amount of woody debris (Penttilä et al. 2004, Sippola and Renvall 1999, Sippola et al. 2004). All climate variables fitted in the spatial GLM were significant for species density and accounted for 35.3% of the explained variance. Species density may therefore profit from increasing temperatures and sum of radiation. It is surprising that no habitat continuity variable plays a determining role for species density and old growth forests therefore do not necessarily support more species.

Driving factors of species records within the set of forest structure variables are quite similar to those of species density, with the exception of species records reacting negatively to DBH. The most important categories of woody debris in the younger or medium aged stands as well as stands with continuous logging are small diameter fractions (branches). Fine woody debris plays an important role for wood-inhabiting fungi and should not be undervalued (Norden et al. 2004). Small diameter woody debris is especially important for the occurrence of common species (Kruys and Jonsson 1999). Rarefaction curves based on wood volume showed small trees and branches to host more species per unit volume than larger trees and logs (Heilmann-Clausen and Christensen 2004). According to that study, the number of species decreased on large trees per unit of surface area. This “surface area effect” explains the relatively high number of species in plots with small dimensioned dead wood. This finding could also apply to species records. Thus it can be assumed, that species records increase in younger and middle-aged stands because of increasing availability of fine woody debris.

In assessing potential effects of climate change, we considered the possibility that the number of threatened species might indicate the sensitivity of an area, after other (structural) variables were accounted for (Hannah et al. 2002). According to our findings, temperature has no effect on the number of threatened species. Only precipitation could be revealed as a positive estimator, but was expected to have no deciding influence, because the expected change for our region is only 6% (Spekat et al. 2007). One important factor positively influencing occurrence of threatened species is the total volume of woody debris, as also previously found for polypores in subxeric, mesic and herb-rich forests (Sippola et al. 2004). A key role for threatened species is also played by the decomposition stage, affecting these by presence / absence of advanced decay stages. This result agrees with those of earlier studies, where the

maximal incidence of threatened species on distinctly decayed trees, and their low frequency on newly dead trees, points to a general preference among threatened species for distinctly decayed wood (Bader et al. 1995, Heilmann-Clausen and Christensen 2005, Lindblad 1998, Sippola and Renvall 1999). It has often been stated that a preference of threatened species for coarse woody debris exists (Bader et al. 1995, Kruys and Jonsson 1999, Sippola and Renvall 1999), but this is not indicated by our GLM results. Our findings are however supported by a study of beech forests (Heilmann-Clausen and Christensen 2004). However, another important effect can be assumed to play its role here, in that occurrence of the red listed species *Phellinus viticola*, second most frequent species in our study, reduces the perceived importance of large woody debris. *P. viticola* is a typical high-montane and boreal fungus and is more common in the Bavarian Forest than in Scandinavia (Jahn 1969). *P. viticola* characteristically occurs on substrates of large dimensions (Krieglsteiner 2000), but in our study 87% of all *P. viticola* records were on branches with a median of substrate diameter of only 2cm. As GLM has shown, habitat continuity plays an important role for threatened species. The loss of habitat continuity due to intensive logging activity has the consequence of loss of threatened, wood-inhabiting fungi (Sippola et al. 2004).

Conclusion

In this study we tested on a regional scale the influence of climate on wood-inhabiting fungi as structure-dependent organisms useful for further interpretation of the impacts of climate change. Climate explains most spatial variability on a broad scale. However, at least on a small scale, structure-dependent organisms are more strongly influenced by their specific structural requirements than by general climate. The set of forest structure variables best explain the variance of species density and species records, as also of community composition. It can be concluded that direct, human activity such as logging, for example, which strongly influences supply of woody debris and degree of canopy cover, has the greatest impact on wood-inhabiting fungi. Most important for threatened species are habitat continuity variables. These results make it clear that it is not sufficient just to leave wood in the forest in order to protect threatened species - it is of great importance to maintain habitat continuity as well. These factors are more important than climate. To summarize: we conclude that the effects of global climate change on wood-inhabiting fungi communities are masked by the influence of forest structure and that climate change will have only an indirect, long-term effect by causing change in these structures.

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Estimation of the extinction risk of high montane species after global warming and comparison of their suitability as cross-taxon indicators

Claus Bässler^{1*}, Jörg Müller¹, Thomas Kneib², Torsten Hothorn² and Frank Dziöck³

* Corresponding author: claus.baessler@npv-bw.bayern.de

¹ Bavarian Forest National Park, Freyunger Str. 2, D-94481 Grafenau, Germany, Telephone: ++49-8552-9600-179, Fax: ++49-8552-9600100

² Institut für Statistik, Ludwigs-Maximilians-Universität München, Ludwigstr. 3, D-80539 München, Germany

³ Department of Biodiversity Dynamics, Technische Universität Berlin, Sekr. AB1, Rothenburgstr. 12, D-12165 Berlin, Germany

Abstract

Aim of this study is to model the occurrence of six high montane species representing ferns, vascular plants, wood inhabiting fungi, molluscs, saproxylic beetles and breeding birds under two global warming scenarios to estimate the extinction risk; second objective is the assessment of cross-taxon indicator suitability of the selected species for climate change monitoring in low mountain range forests in South-eastern Germany (Bavarian Forest National Park).

Using Bayesian methods that consider spatial structure, we tested the influence of temperature and other habitat variables using local geostatistical models. Applying generalized linear models with binomial error, the probability of occurrence for the high montane species was calculated under present conditions and for two scenarios of global warming. Cross taxon indicator suitability was tested using the discrimination results of the models.

Temperature was revealed as the main driver for all selected high montane species. For these species our statistical models predict a considerable risk of extinction within the Bavarian Forest National Park as a result of global warming. As a result of the essentially similar relationships with the environment exhibited by species characteristic of the high montane zone, their relative suitability as indicators of early signs of global warming can be considered to be indicated by the results obtained from the discrimination model. The choice of which indicators to use should involve a consideration of what sorts of monitoring systems are

already in local existence. As a rough assessment and prognosis, from 1.5 - 23.4 % of the species in the target groups may become extinct in the study area due to climate change. Red listed species are disproportionately sensitive, with an extinction risk ranging from 3.3 % to 75.0%.

Keywords: climate change, species distribution modelling, extinction risk, high montane species, indicators

Introduction

The evidence for climate change now appears to be overwhelming (Ipcc 2007b). There is broad evidence that anthropogenic climate change will lead to massive species extinction (Ipcc 2007a). Changes in the phenology and distribution of plants and animals are occurring in all well studied marine, freshwater, and terrestrial taxa. These observed changes are tending strongly in the directions predicted for global warming, and have been linked to local or regional climate change by correlation of climate change with biological variation, field and laboratory experiments, as well as physiological research: for review see (Walther et al. 2002, Parmesan 2006).

The latest scenarios predict further warming throughout the 21st century (Ipcc 2007b); the most likely mean value for the smallest increase on a global scale is 1.8 K, for the highest 4.0 K. It is thus likely that many species will undergo dramatic range shifts in future (Ipcc 2007a). Projections, mostly for larger spatial scales, have been used to produce estimates of impacts of climate change for a variety of taxonomic groups and for various parts of the world (Bakkenes et al. 2002, Peterson et al. 2002, Parmesan and Yohe 2003, Thomas et al. 2004, Jensen et al. 2008). Topographically isolated mountain ranges around the world, often with a high rate of endemism, are severely threatened by climate change (Williams et al. 2003, Thuiller et al. 2005, Rull and Vegas-Vilarrúbia 2006).

Various statistical techniques have been used to model probabilities of species occurrence in response to global warming (Lawler et al. 2006). Attempts to predict climate change impacts on biodiversity have often relied on approaches using species-climate envelope models, also known as ecological niche models (Pearson and Dawson 2003). Recent studies have questioned the validity of this approach, by pointing to the many factors other than climate that play an important part in determining species distributions, e.g. interactions between species, evolutionary change or differences in dispersal ability of individual species (Davis et al. 1998, Araújo et al. 2005, Hijmans and Graham 2006). The response of many species to

large scale climate is modified by smaller scale factors (Ellis et al. 2007). However, although the complexity of the natural system sets fundamental limits to predictive modelling, the approach is useful in obtaining a first approximate estimate for the potentially dramatic impact of climate change on biodiversity (Pearson and Dawson 2003).

There are several reasons why alpine and montane ecosystems should be preferred to lower altitudinal zones for monitoring climate change. Being characterised particularly by low temperatures, montane systems are generally considered especially sensitive to climate warming. Their ecological complexity is also comparatively low, with effects of abiotic factors found to be more important than biotic factors (Grabherr et al. 2000). Furthermore altitudinal sequences of thermal life zones on high mountains are, compared with latitudinal ones, more compressed and have smaller ecotones. Environmental gradients therefore occur along short distances, greatly reducing sampling effort and costs. Distribution of many species is limited by altitude, not only as an expression of climate parameters but also by limitation of resources (Grabherr et al. 1994); thus, species from mountains are unusually sensitive to climate change (Thuiller et al. 2005). According to this hypothesis some species should obviously lose parts of their range as a result of climate change. Mountain top species would seem to be particularly threatened by warming (Theurillat and Guisan 2001, Williams et al. 2003, Parmesan 2006, Pauli et al. 2007). The effects of warming are made worse by the disproportionately rapid decrease in available land surface area with increasing altitude. Species in lower mountain ranges are limited in how they can adjust their ranges in response to increasing temperature.

Broad consensus has been reached that models should be developed which can elucidate the correlations between climate and biophysical processes and thus increase our ability to predict the consequences of the effects of climate change on distribution of species and their habitats (Sutherland et al. 2006, Ipcc 2007a). These models must also be capable of linking the distribution of species to alternative scenarios of climate change (Lawler et al. 2006). Better information on climate sensitivity of species is essential in order to be able to detect responses of individual species to climate change, to assess “critical levels” and to develop anticipatory strategies. Thus there is a need to find appropriate indicators for the identification of the effects of climate change, to verify results from modelling and to prove the response of species (Kappelle et al. 1999, Sutherland et al. 2006), particularly those that possess some degree of specialisation (DeGroot et al. 1995). Until now, little attention has been paid to the cost-efficiency of indicators or the ease of inventory in relation to the identification of species. Numerous studies project and predict changes for species or selected taxonomic groups and

compare effects on taxa due to global warming in a general way, e.g. Bakkenes et al. (2002), Peterson et al. (2002), Jensen et al. (2008). On a regional scale, many studies also exist, but also deal only with single species or a single group of species e.g. (Peterson 2003, Ellis et al. 2007). Currently, the most relevant physical and temporal scales of ecological investigation are however local (Walther et al. 2002). Furthermore, at this local scale there is also a need to consider a variety of taxonomic groups (Ellis et al. 2007).

We expect a strong impact at a regional scale on various taxonomic groups, with some species becoming extinct due to global warming. Simple species-environment relationships for high montane species can be expected. In several taxonomic groups these seem to be dominated mainly by the effect of low temperatures. Thus we assume sensitive behaviour due to climate warming, with modifications to distribution in the form of decreasing area of occurrence. The selected species are hence good indicators at a regional scale, suitable for long term monitoring designed to validate results from modelling and to prove response of species to climate change. The same response driven by the same environmental factors occurs in all high montane species studied, so we expect most of these to be suitable as climate-sensitive indicators. They may assist in reducing the potentially high costs of climate change monitoring associated with species inhabiting more complex systems at lower altitudes.

Aim of this paper is to test the following hypotheses:

1. For high montane species (defined *a priori*) of low range mountains, temperature remains the dominating predictor even when a wide range of environmental factors is considered.
2. The extinction risks for species studied are similar under two climate change scenarios.
3. Species of the high montane zones, across a broad range of taxonomic groups, are generally suitable for use in climate change monitoring.

Material and Methods

Study area

The National Park “Bavarian Forest”, the oldest national park in Germany, is located in the south-eastern corner of Bavaria, at the border to the Czech Republic. The park covers approximately 24,000 ha at elevations from 650 m to 1450 m a.s.l. Total annual precipitation is between 1200 mm and 1800 mm depending on altitude. Mean annual temperature (1972-2001) varies between 3.8°C and 5.8°C (Bässler 2004). Geologically, the Bavarian Forest is the south-western part of the Bohemian Massif, consisting of granite and gneiss and therefore containing acidic soils. Above about 1100 m to 1200 m a.s.l. the stands are dominated by spruce *Picea abies*, with a low proportion of beech *Fagus sylvatica* and mountain ash *Sorbus*

aucuparia (high montane forest). Below this, the stands are dominated by spruce, beech and fir *Abies alba* (mixed montane forest) (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.

Species under study

All species considered in this study were sampled in the context of a broader program to characterise spatial variation of biodiversity across the National Park. For this program we established four transects across the altitudinal range of the park. Along these transects we located 293 plots at 100 m intervals (Bässler et al. 2008a). The number of plots sampled depended on the taxonomic group. For this reason we stratified the sample plots, selecting pre-stratified sub-samples with respect to the two main gradients (altitude and forest structure) for some groups. Vascular plants and ferns were mapped on 0.02 ha of all 293 plots following the methodology of Londo (1976) in a single survey, justified by the short growing season, in August 2006. Wood inhabiting fungi were also mapped and sampled for further laboratory determination on all plots on 0.1 ha in a single survey from August till October 2006. Birds were grid mapped quantitatively using the standardized area count method (Bibby et al. 1995) on a 1 ha grid on five visits to all plots. 173 of 293 plots were chosen for installation of flight interception traps (for Coleoptera etc.), one per plot from April to September 2007. Out of these 173 plots we selected 113 plots for hand sampling molluscs on 0.1 ha in September 2006 in addition to one pitfall trap per plot in July 2006.

We consulted the literature to identify which species can be considered to be high montane. One species was selected per taxonomic group for modelling. These are species which occur regularly within our study design (Table 3). *Athyrium distentifolium* is an arctic-alpine species (Oberdorfer 2001), restricted to higher elevation levels in the alps and low mountain ranges in Central Europe (Petermann and Seibert 1979, Haeupler and Schönfelder 1989, Wisskirchen and Haeupler 2000). According to Oberdorfer (2001) *Trientalis europaea* is an arctic-nordic species occurring in low mountain ranges in the southern part of Central Europe (Haeupler and Schönfelder 1989, Schönfelder and Bresinsky 1990) and distributed typically in the high montane zone in the study area (Petermann and Seibert 1979). The fungus *Hymenochaete fuliginosa* is indicated to be a typical high montane and alpine species (Breitenbach and Kränzlin 1986), mainly occurring above 1200 m a.s.l. in the study area (Luschka 1993). *Hymenochaete fuliginosa* is a threatened species considered in the red data book (DGfM and

NABU 1992). Available literature was examined by Müller et al. (2008) to characterize the general distribution of montane mollusc species. Of those found more regularly, only *Semilimax kotulae* is distributed in the high montane zone, and regarded as endemic to the Alpine-Carpathian area (Hässlein 1966, Sulikowska-Drozdz and Horsák 2007). *Semilimax kotulae* is considered as an endangered species in the red data book (Falkner et al. 2003). *Ampedus auripes* is described as a typical high montane species (Wurst and Kaupp 1995) and also listed as endangered (Schmidl et al. 2003). The song-bird *Turdus torquatus* occurs mainly in the Alps and in low mountain ranges on a European scale, at lower elevations in the North, its range restricted by temperature (Hagemeijer and Blair 1997). A recent study for Switzerland has indicated *Turdus torquatus* to be restricted to high montane levels, with a high dependency on temperature (von dem Bussche et al. 2008).

We summarized data for all species of the selected taxonomic groups for which documentation exists for the study area and identified those restricted to the high montane zone, as in the method of selection of species for further analysis (Supplementary Appendix 2). The following red data books were used as references in quantifying the proportion of red listed species: ferns and vascular plants (Schönfelder 1987), fungi (Schmid 1990), molluscs (Falkner et al. 2003), beetles (Schmidl et al. 2003) and birds (Bayerisches Staatsministerium für Umwelt 2005).

Environmental variables

All environmental variables derived from field measurement, aerial photographs (LIDAR data) and climate stations are listed in Table 1. Geographical coordinates and altitude were both generated using Geographical Information Systems (GIS). Basis of calculation was the Digital Terrain Model (DTM) with a cell size of 50 m.

To obtain reliable data for temperature we set up 30 data loggers in 2006 on representative sites across our altitudinal gradients. Additionally we used data from five meteorological stations in the region running since 2000 to extrapolate the data collected in 2006 and 2007 to averages for 2000-2007. From these data we calculated the mean annual temperature and developed a statistical model to predict the temperature for each sampled plot, using independent variables extracted from results of geostatistical modelling with the digital terrain model ArcEGMO (Becker et al. 2002, Pfützner 2002) (Supplementary Appendix 1). Basis for the precipitation model are 20 rain gauges in the study area. From this we calculated the mean sum of precipitation for the most complete time series 1980 - 2004 and developed a statistical model like that described for temperature to predict the mean annual sum of precipitation for

each sampled plot. Data for precipitation is available only for the time series until 2004, so for each plot we used mean annual temperature and mean annual sum of precipitation from the common time series 2000 - 2004 for further analyses.

Table 1: All environmental variables included in the spatial GLM for the selected species, their description and source.

Environmental variable	Description	Source	<i>Athyrium distentifolium</i>	<i>Trientalis europaea</i>	<i>Hymenochaete fuliginosa</i>	<i>Semilimax kotulae</i>	<i>Ampedus auripes</i>	<i>Turdus torquatus</i>
Temperature	Mean annual temperature 2000-2004 (°C)	ArcEcmo modelling	x	x	x	x	x	x
Precipitation	Mean sum of precipitation (2000-2004)(mm)	ArcEcmo modelling			x			
Radiation	Potential sum of radiation for the growing season (kwh m ⁻²)	GIS Model (DTM 25)	x	x	x	x	x	x
Soil water balance index	Soil water balance calculated after Ewald (2000) on a scale between 0 (dry) and 10 (wet)	Inspection of characteristics of the top soil as well as humus layer measurements in 2006	x	x		x		
pH value	pH value of the humus layer	4 soil samples per plot (Bundesministerium für Ernährung 1990), Laboratory analysis in 2006 1 M KCl, Hamilton glass electrode	x	x		x		
CEC	Cation exchange capacity (µeq/g), separated into litter and topsoil	Laboratory analysis, ICP-IES (Perkin Elmer Optima 3000), CHN-analyser LECO CHN-1000	x	x				
Base saturation	Base saturation (%), separated for litter and topsoil	4 soil samples per plot, Laboratory analysis, ICP-IES (Perkin Elmer Optima 3000), CHN-analyser LECO CHN-1000	x	x				
C/N ratio	Carbon (%) / Nitrogen (%) ratio of the humus layer	4 soil samples per plot, Laboratory analysis, ICP-IES (Perkin Elmer Optima 3000), CHN-analyser LECO CHN-1000	x	x				

Canopy Cover	Sample area shaded by horizontal projection of tree layer (upper L., middle L., under L.) separated for occurred tree species (leaves, branches, trunks) (%)	Visual estimation in 2006	x	x				
Age	Oldest tree in each sample plot	Forest inventory in 2002				x		
Diameter	Mean Diameter of woody debris, on sampling plots (0.1 ha)	Inventory of plots/measurement 2006			x			
Opening of canopy layer	Opening of canopy layer from areal photograph analyses ($\text{m}^2 \text{ha}^{-1}$)	Areal photography analysis by stereo analyst						x
Spruce woody debris (initial decay stage)	Amount of spruce dead wood >12cm within 0.1ha plot with a initial decomposition stage	Inventories of plots along transects in 2006					x	
Deciduous tree woody debris (initial decay stage)	Amount of deciduous tree dead wood >12cm within 0.1ha plot with a initial decomposition stage	Inventories of plots along transects in 2006					x	
Spruce woody debris (middle decay stage)	Amount of spruce dead wood >12cm within 0.1ha plot with a middle decomposition stage	Inventories of plots along transects in 2006					x	
Deciduous tree woody debris (middle decay stage)	Amount of deciduous tree dead wood >12cm within 0.1ha plot with a middle decomposition stage	Inventories of plots along transects in 2006					x	
Spruce woody debris (advanced decay stage)	Amount of spruce dead wood >12cm within 0.1ha plot with a middle decomposition stage	Inventories of plots along transects in 2006					x	
Deciduous tree woody debris (advanced decay stage)	Amount of deciduous tree dead wood >12cm within 0.1ha plot with a middle decomposition stage	Inventories of plots along transects in 2006					x	
Woody debris	Amount of dead wood >12cm within 0.1ha plot ($\text{m}^3 \text{ha}^{-1}$)	Inventory of plots along transects in 2006				x		
Decay level	Mean decay level within the sample plot (0.1 ha)	Inventory of plots along transects in 2006			x			
Sun exposure	Proportion exposure to sunlight of woody debris (%), on the sample plot	Inventory of plots along transects in 2006			x			
Snag	Amount of snags within the sample plot on 0.1ha ($\text{m}^3 \text{ha}^{-1}$)	Inventory of plots along transects in 2006			x			
Log	Amount of logs within the sample plot on 0.1ha ($\text{m}^3 \text{ha}^{-1}$)	Inventory of plots along transects in 2006			x			
Branch	Amount of branches within the sample plot on 0.1ha ($\text{m}^3 \text{ha}^{-1}$)	Inventory of plots along transects in 2006			x			
Stump	Amount of stumps within the sample plot on 0.1ha ($\text{m}^3 \text{ha}^{-1}$)	Inventory of plots along transects in 2006			x			
Tree richness woody debris	Tree richness within woody debris on 0.1 ha plot	Inventory of plots along transects in 2006			x			
Dead wood area	Area of dead wood killed by bark beetle (ha) on 1ha plot	Areal photography						x

NBAWW	Area of mature Spruce (ha) on 1ha plot	Areal photography					x	x
DDP	Penetration rate on 0.1 ha plot	Airborne laserscanner in 2006				x		
QHM	Mean vegetation height (m) on 1 ha plot	Airborne laserscanner in 2006						x
QHS	Standard deviation vegetation height on 1 ha plot	Airborne laserscanner in 2006						x
Plant species diversity	Shannon index of plant species diversity	Vegetation mapping in July 2006 using the Londo scale (Londo 1976)				x		

Variables of stand structure were recorded by measuring and visual inspection on each plot (0.1 ha size), supplemented by interpretation of aerial photographs using the stereo analyst tool (Mc Grath et al. 2004) within a 1 ha grid. 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 30cm depth. Before chemical analysis the samples were dried at 65°C for 5 days and sieved through a 2 mm mesh. 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 HNO₃ digestion (Bundesministerium für Ernährung 1990) with an ICP-IES (Perkin Elmer Optima 3000). The cations of all substrates were extracted with 1 M NH₄Cl for 2 hours on a rotation shaker (Bundesministerium für Ernährung 1990, Luehr and Böhmer 2000). Finally, cation exchange capacity, base saturation and C/N ratio were calculated. 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).

Species Modelling

To estimate the influence of climate change on the altitudinal distribution of the selected high montane species (see above) we first built logistic regression models (generalized linear models with an assumed binomial error distribution) using “BayesX” to predict the occurrence of these species in our sampling plots under consideration of all predictors in

Table 1. Logistic regression models are most suitable for binary response variables; they are robust against overfitting and yield parsimonious models (Hosmer and Lemeshow 2000). To avoid multicollinearity, we applied a two-sided rank correlation test after Spearman on the selected set of predictor variables, setting a limit for considering both correlated variables of $r_s=|0.7|$ (Fielding and Haworth 1995). However, one of the key assumptions in statistical models in the present context is the independence of residuals (Dormann et al. 2007), which was not necessarily true of our data. Therefore we used a semiparametric spatial generalised linear model. 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 based on the standard deviations obtained from the expected Fisher information matrix as implemented in the package “BayesX” (Fahrmeir et al. 2004, Kneib and Fahrmeir 2006, Kneib et al. 2008). Spatial generalized linear models (GLM) showed that temperature had an overall significant influence on the probability of occurrence, but in some cases a few other variables were also significant at a p-value of 0.05 (Table. 2). Therefore, in further analysis we included all other significant variables. In cases where variables other than temperature were significant, we calculated and ranked the explanatory power of these using hierarchical partitioning analyses (Chevan and Sutherland 1991, MacNally and Walsh 2004). Hierarchical partitioning was conducted with the ‘hier.part’-package (version 1.03) (MacNally and Walsh 2004) and the statistical software R 2.6.0 (RDevelopmentCoreTeam 2006). Since the results of the spatial GLM were specific to the locations where the data were collected, they are not suitable for a general predictive approach. To obtain the desired generalized model, we fitted a GLM using the estimated current mean annual temperature and other significant variables resulting from the first spatial GLM (Table 2), whilst excluding the spatial effects. This was then used to predict the probability of occurrence of the selected species for each plot. This method is a suitable modelling technique for the prediction of climate-induced range shifts, because relatively simple relationships to environmental gradients exist in the present study, as recommended by Lawler et al. (2006).

Two main criteria used to assess performance and quality of results of predictive models is calibration and discrimination (Pearce and Ferrier 2000, Reineking and Schröder 2003). We used Nagelkerke (R^2_N) to evaluate the calibration of our model and to measure the amount of explained variation (Nagelkerke 1991). Values exceeding 0.4 indicate a good calibration. The discrimination of our model was tested by calculating the AUC value (area under the receiver operation characteristics) which is based on the ROC (receiver operation characteristics) as a

threshold-independent criterion for model discrimination (Fielding and Bell 1997, Harrell 2001). An AUC value of 0.5 indicates a random prediction; $AUC > 0.8$ indicates an excellent and $AUC > 0.9$ an outstanding power of discrimination for the model (Hosmer and Lemeshow 2000). We applied Cohen's kappa, correct classification rate, sensitivity (true positive rate) and specificity (true negative rate) using a cut-off value $P_{crit}=0.5$ (Cohen 1960, Pontius 2000). It is standardised to become 1 at its maximum. Interpretation of the Kappa index follows Monserud and Leemans (1992). The calculation of performance criteria yields over-optimistic estimates if they are calculated on the training data only, so they must be validated. Because no external data were available in this study, an internal validation using a bootstrap resampling technique (Verbyla and Litvaitis 1989, Efron and R.J. 1993) with 1000 iterations has been undertaken (Schröder and Reineking 2004, Araújo et al. 2005).

In a final step we used two official scenarios (Ipcc 2007c) to predict the occurrence of the selected species on the sample plots after global warming. These two scenarios predict the increase of the mean annual temperature until 2100 using optimistic (increase by 1.8 K) as well as pessimistic assumptions (4.0 K). 1.8 K and 4 K were accordingly added to the estimated mean annual temperature and the occurrence of the selected species modelled using the model generated with the current annual temperature. Predictions of the three temperature scenarios were plotted against altitude. The general trend was described using a spline fit as a local smoother. To visualize the uncertainty of the general trend we constructed heuristic confidence bands using pointwise 95% prediction intervals calculated from the standard error of the predictions. The upper and lower bounds were again estimated using smoothing splines. Output from a regional climate model may be well suited to predicting changes in distribution of restricted species in regions with complex topography (Kueppers et al. 2005). The optimistic level of global warming considered in our study as one of two future scenarios is even in accordance with previously published local scenarios (Spekat et al. 2007), which are not however available for more pessimistic predictions. We did not consider changes in precipitation, because the expected changes for our region are only about 6% (Spekat et al. 2007). The analysis of temperature data by Bässler (2008) showed that the increase of mean annual temperature between 1948-2002 was the same in the three main altitudinal zones of the National Park (0.01 K year^{-1}). Thus, we assume that the same pattern of temperature increase will persist consistently for the entire study area in the future.

Finally, we used the models generated for each species to predict which species from other taxonomic groups might behave similarly. This permits an assessment of which species are suitable as indicators representing a wide variety of taxa. To validate the suitability we used

the AUC value, explained above. To test the differences between the species models against the occurrence of the remaining species (predictors) we performed analyses of variance (ANOVA) (Zar 1999) using the AUC values.

Results

The result of the spatial GLM showed strong dependency on temperature for all species (Table 2). For all species temperature had the highest p-value and an overall independent effect where other variables as well as temperature were significant. For *Trientalis europaea*, *Hymenochaete fuliginosa* and *Semilimax kotulae*, only temperature could be revealed as significant when other environmental variables were accounted for. Thus the first hypothesis could be accepted; temperature is the dominating predictor for the selected high montane species.

Table 2: Significant environmental variables as indicated by spatial GLM. Black triangles denote significant influence (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), upward pointing is positive estimator, downward pointing is negative estimator. Independent effect values (%) determined by hierarchical partitioning appear below the triangles.

Environmental variable	<i>Athyrium distentifolium</i>	<i>Trientalis europaea</i>	<i>Hymenochaete fuliginosa</i>	<i>Semilimax kotulae</i>	<i>Ampedus auripes</i>	<i>Turdus torquatus</i>
Temperature	▼** 57.6	▼*** 100	▼** 100	▼** 100	▼*** 97.1	▼*** 82.7
Radiation	▼* 25.0					
Canopy Cover	▼* 17.4					
Opening of canopy layer						▲** 17.3
Spruce woody debris (middle decay stage)					▲* 2.8	
Spruce woody debris (advanced decay stage)					▲* 0.1	

For all species, except *Semilimax kotulae* (0.855 = “excellent”) and *Hymenochaete fuliginosa* (0.697 = “not acceptable”), the AUC values are > 0.9 , thus indicating “outstanding” quality (Table 3). Good calibration and refinement of the models could be revealed with $R^2_N > 0.4$ for all species with exception of *Hymenochaete fuliginosa* (R^2_N 0.1). Following Cohen’s Kappa, a good degree of agreement could be revealed for all species with the exception of *Turdus torquatus* (poor degree of agreement) and *Hymenochaete fuliginosa* (no degree of agreement).

Table 3: Specifications of the selected models and number of presences/absences for species. AUC is the Area under the receiver operating curve, R^2_N is the calibration of the model according to (Nagelkerke 1991) and K is Cohen’s Kappa (Cohen 1960).

Species	Number of plots (presence/absence)	AUC	R^2_N	K
<i>Athyrium distentifolium</i>	273 (49/224)	0.933	0.610	0.628
<i>Trientalis europaea</i>	273 (33/240)	0.919	0.521	0.564
<i>Hymenochaete fuliginosa</i>	290 (28/262)	0.697	0.100	0
<i>Semilimax kotulae</i>	112 (70/42)	0.855	0.453	0.567
<i>Ampedus auripes</i>	177 (43/134)	0.915	0.604	0.613
<i>Turdus torquatus</i>	291 (22/269)	0.902	0.458	0.374

The probability of occurrence of the selected species decreased with temperature according to spatial GLM (Table 2). An increase in the mean annual temperature of 1.8 K will already lead to a decrease in the occupancy by about 25 % at altitudes of 1400 m, with the exception of *Semilimax kotulae* (Fig. 1). Nevertheless, within this optimistic scenario some sinks for cold air may act as refuges for *Semilimax kotulae* at lower altitudes, if one assumes 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 all selected species in the area covered by the National Park. Since there is a decrease of area with altitude (e.g. 9.5 % of area lies above 1200m a.s.l.), real current area of occurrence of the selected species is under 15 %, except for *Semilimax kotulae* (57 %) (Fig. 2). An increase in mean annual temperature of 1.8 K will push the selected species onto less than 3 % of the area, or in the case of *Semilimax kotulae* 12 %. Further warming under a 4.0 K scenario will lead to a decrease of occurrence of all species to below 1% of the area. Due to dissimilarity of the extinction risk for the species considered under the two warming scenarios, the second hypothesis must be discarded. Quality of predictions for all species except *Hymenochaete fuliginosa*, are at least “excellent” (AUC > 0.8) using the models of *Athyrium distentifolium*, *Trientalis europaeus* and *Ampedus auripes* (Fig. 3).

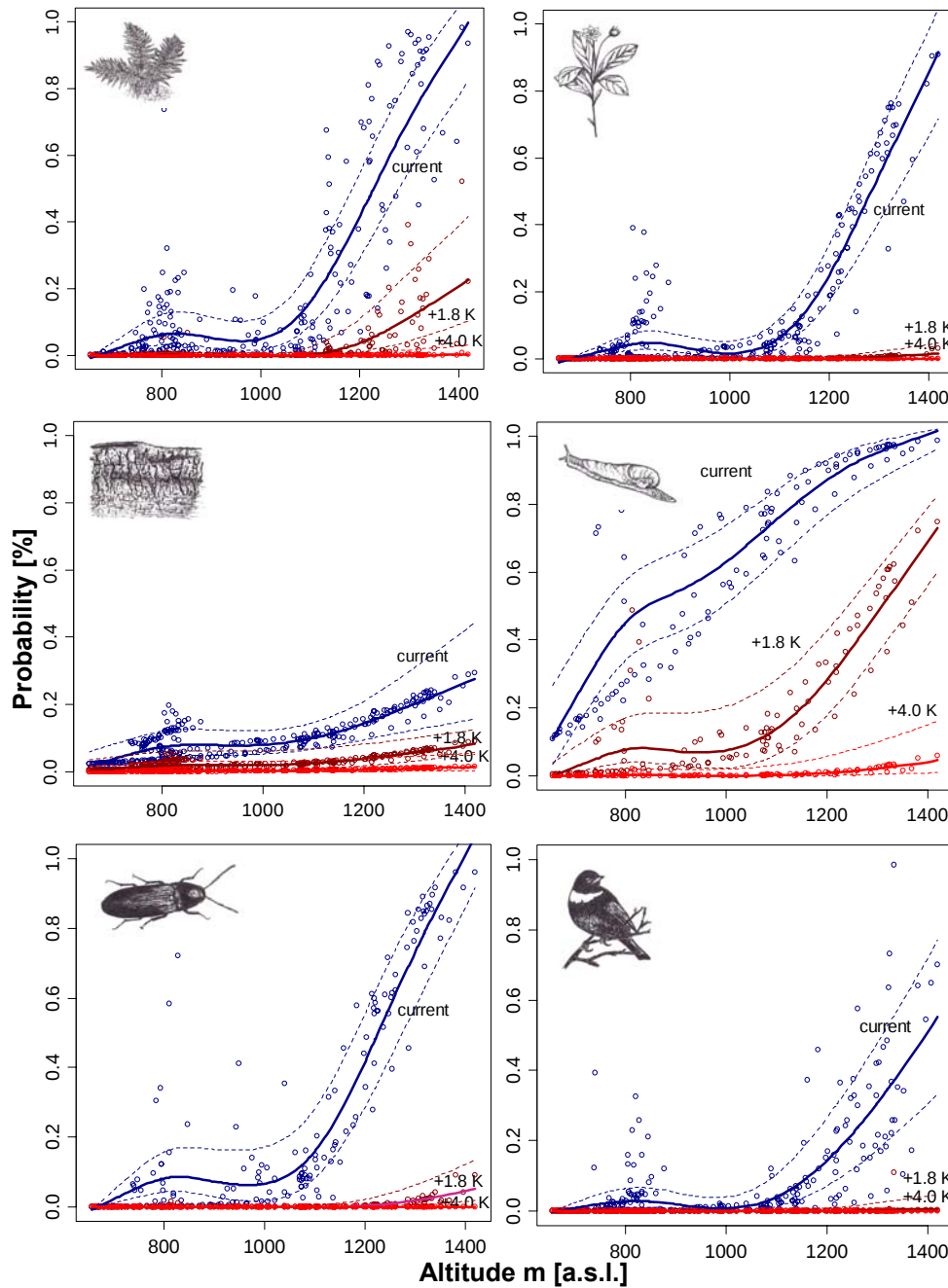


Fig. 1: The blue points represent the predicted probability of occurrences of *Athyrium distentifolium*, *Trientalis europaea*, *Hymenochaete fuliginosa*, *Semilimax kotulae* (Müller et al. 2008), *Ampedus auripes* and *Turdus torquatus* within the National Park “Bavarian Forest”, using annual mean temperatures for 2000 and 2004 for the sampling plots versus altitude of the plots. The curves are locally smoothed (spline fit) with heuristic confidence bands (for details of calculating these intervals see text). The other two groups of points and curves are predicted probability of occurrences under scenarios of global warming with an increase of the mean annual temperature of 1.8 K and 4.0 K.

The model of *Hymenochaete fuliginosa* predicts all species well, with AUC >0.85. *Semilimax kotulae* predicts on an “outstanding” level (>0.9) for all species, with exception of *Hymenochaete fuliginosa* (“acceptable”, AUC = 0.749). The model of *Turdus torquatus* predicts *Hymenochaete fuliginosa* acceptably (AUC = 0.7); in the other cases the AUC value ranges between 0.851 (“excellent”) and 0.911 (“outstanding”). No significant difference could be revealed for the models by analysis of variance (ANOVA) (Supplementary Appendix 3). Thus, the third hypothesis could be accepted.

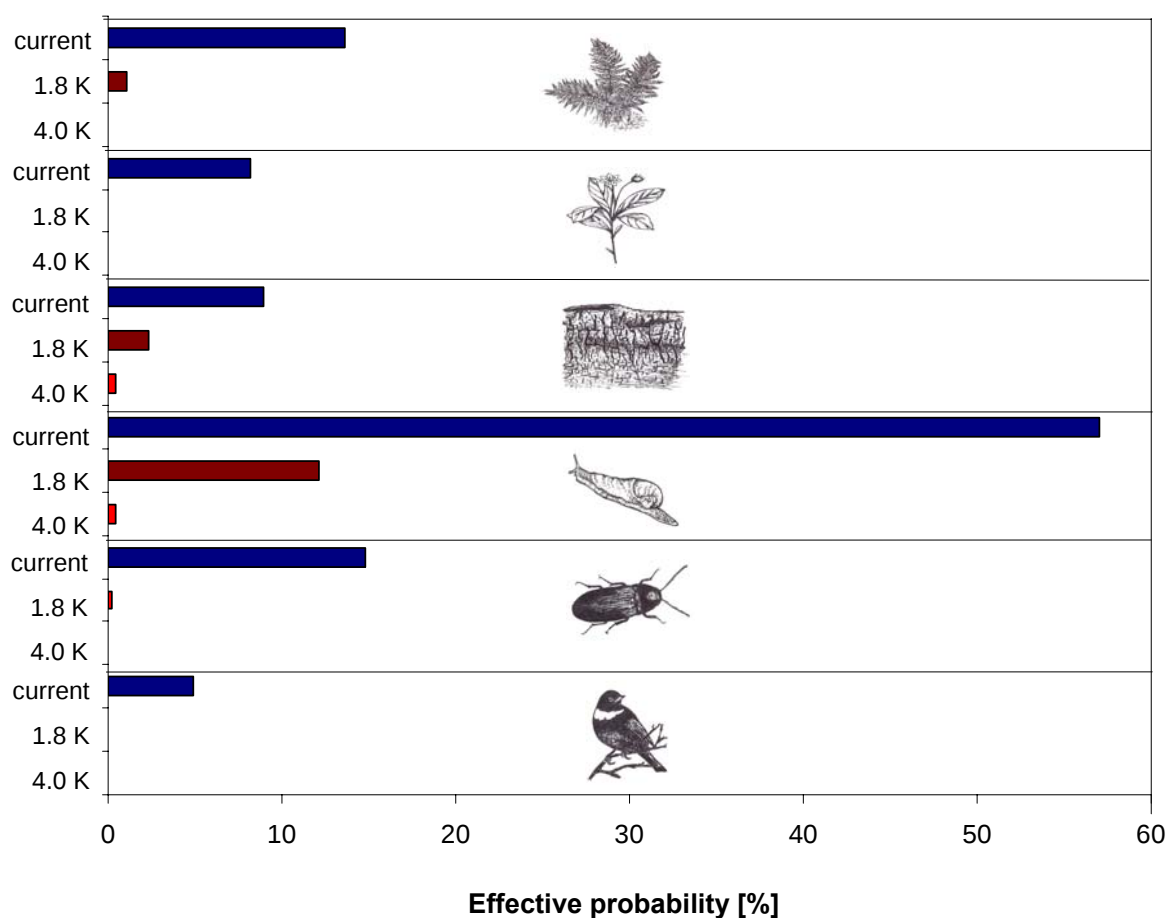


Fig. 2: Effective probability (%) (study area) for *Athyrium distentifolium*, *Trientalis europaea*, *Hymenochaete fuliginosa*, *Semilimax kotulae*, *Ampedus auripes* and *Turdus torquatus*, currently and as predicted under a 1.8K and 4.0K climate warming scenario, derived from the multiplication of the available area above a certain altitude by the proportion of probability calculated with the spatial GLM.

Discussion

High montane species: factors driving occurrence and suitability as climate change indicators

The species selected for more intensive study were those which occur regularly in our data set and according to existing information are high montane in distribution. As expected, decreasing temperature was the main determinant of occurrence for all six species. Predicted probabilities for the selected species show almost steadily increasing frequency of occurrence along the altitudinal gradient, with a clear lag in the mixed montane zone (Fig.1). But at approximately 800 m a.s.l. higher probabilities are revealed, caused by cold air sinks on valley sites, which are characteristic of the study area. A weaker correlation could only be detected for *Hymenochaete fuliginosa*, which failed to reach the 30% probability line on mountain tops, indicating its lesser suitability as an indicator, as supported by the poor discrimination (Fig.1, Table 3). A few less important explanatory variables could be found for *Athyrium distentifolium*, *Ampedus auripes* and *Turdus torquatus*. In contrast to the mixed montane zone, the high montane zone is characterized by more open stands, with openings in the canopy and reduced canopy cover. These habitat factors play a role for *Athyrium distentifolium*, known to prefer half shaded sites (Oberdorfer 2001) and *Turdus torquatus* with its core distribution in open forests, in the Alps often in close proximity to open landscape elements (von dem Bussche et al. 2008). The larval development of *Ampedus auripes* takes place in conifer wood (spruce, fir) at a medium to advanced stage of decay (Wurst and Kaupp 1995), as also supported by our findings. Availability of dead wood is thus important to this species.

One essential criterion of suitability as an indicator for global warming is sensitivity to temperature (DeGroot et al. 1995). This is fulfilled for all selected species. Recent studies have succeeded during the last decade in documenting range shifts in organisms and associated these with simultaneous climate change, but have also shown that a statistically significant change in abundance and distribution can not in every case be detected, in spite of regional climate change (e.g. 37% of the species studied by Parmesan and Yohe (2003)). In general, specialists are more sensitive than generalists (Juilliard et al. 2003). The adaptation to low temperatures permits species confined to the high montane zone to be regarded as specialists. Much knowledge of species distributions relies on observational data and on surveys. These data are often of little value in themselves because they yield only a description of the present situation (Juilliard et al. 2003).

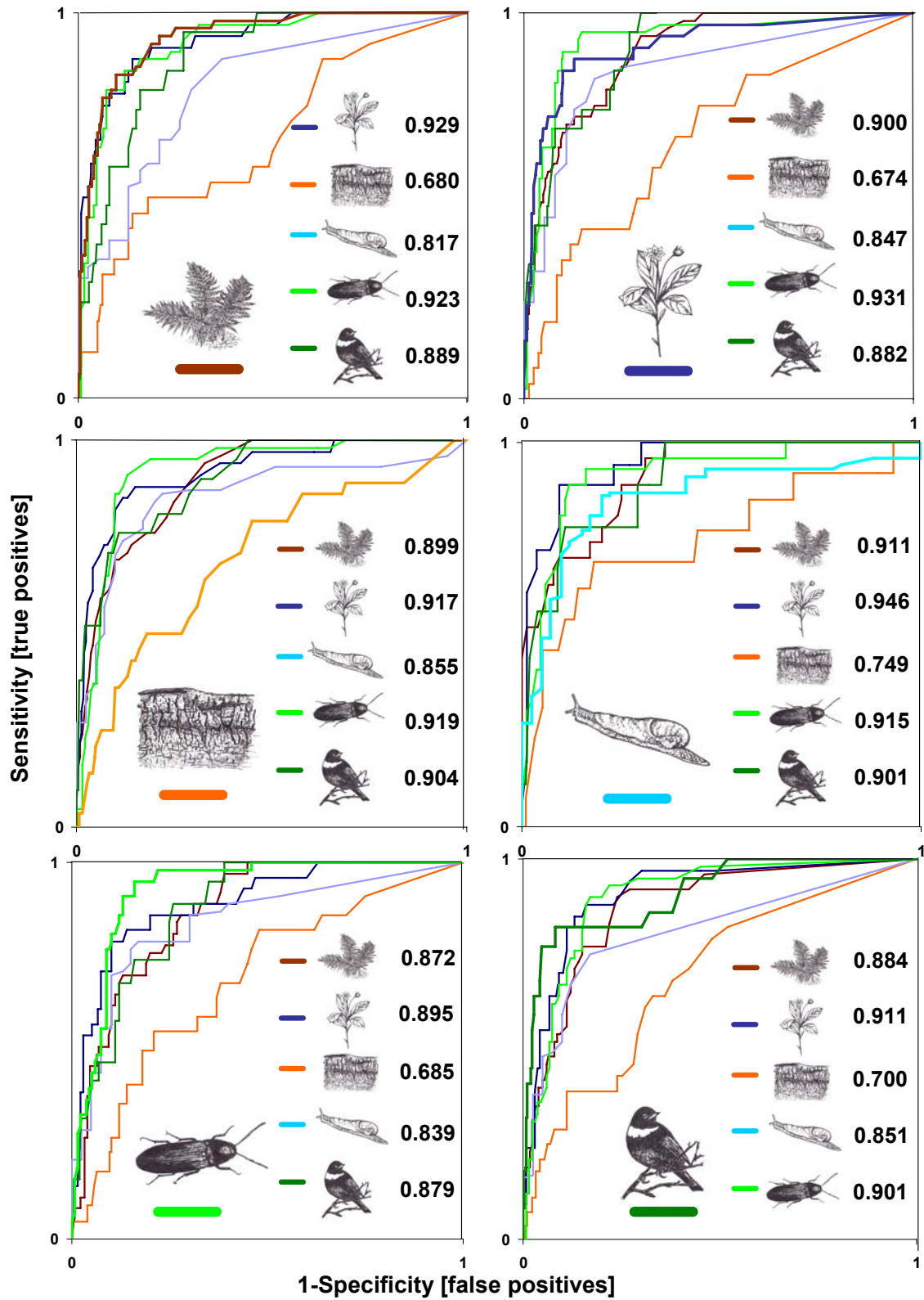


Fig. 3: ROC curves (receiver operation characteristics). The bold ROC curves are the models used; the others represent the model where the remaining species are used as predictors. Area under the receiver operating curve values (AUC) are given in bold.

Assessment of species vulnerability must be linked to quantitative predictors, to reveal the response along the predictor's gradient (Stenseth et al. 2002). This makes it necessary to focus more on species-environmental relationship analysis to answer the question of what makes some species more vulnerable and thus more suitable as indicators than others. We tested the suitability of the selected species as indicators for global warming, revealing strong temperature dependency even under consideration of other environmental variables. A further requirement for suitability as an indicator is that the resources necessary for development are widely present. This is especially important for woody debris dwelling species like fungi (e.g. *Hymenochaete fuliginosa*) and beetles (e.g. *Ampedus auripes*). Both species live in woody debris of spruce. This substrate occurs regularly in the study area, even in parts under continuous management, and thus does not limit their potential as suitable indicators.

Extinction risk for the revealed indicators

Almost all species considered in the present study are at present very common in the study area. As indicated by our exercise presented in Fig. 1,2, an increase in the mean annual temperature of 1.8 K will increase the risk of extinction for all species, with exception of the more moderate effect for *Semilimax kotulae* on a regional scale. Under pessimistic scenarios of climate warming, these species probably will not survive in the study region because an insufficient area of ground is in the highest altitudinal zones. Although the complete loss of its core environment may still not cause a species to immediately become extinct, it will certainly make that species extremely vulnerable. *Athyrium distentifolium* has a circumpolar distribution and is not rare, but restricted to montane-alpine zones and can accordingly be considered vulnerable to global warming throughout its range. Although *Trientalis europaeus* is a northern-temperate Eurasian species, it is not restricted to higher altitudes and occurs regularly in lowland areas, particularly on moors and heaths. Due to this distribution pattern, this species is not expected to become globally extinct. Occurrence of *Turdus torquatus* is temperature-restricted throughout its range (Hagemeyer and Blair 1997). In alpine areas of South and Central Europe *Turdus torquatus* usually breeds above the 800m altitudinal level. For this species, worldwide extinction is to be expected as a result of global warming, as recently assessed by Huntley et al. (2007). Globally, the main areas of *Hymenochaete fuliginosa* distribution are in Northern Europe, and it is almost confined to the montane-alpine zones. Only a few occurrences are reported in lowland areas. This species is also expected to be very vulnerable to further warming. *Semilimax kotulae* (Alpine-Carpathian endemic) and *Ampedus auripes* are globally very rare and restricted to montane and alpine ecosystems. Such species

are expected to be very vulnerable to climate change, with a high risk of worldwide extinction.

Extinction risk for high montane species

Arctic and low mountain range ecosystems underwent dramatic changes and are thus in general poor in species, an effect of the alternation of glacial and interglacial periods (Pleistocene) and, it is also assumed, by the warm conditions in postglacial periods (Quaternary) (Chapin and Körner 1994). This led to high extinction rates and survival of a few endemic, relict species. The magnitude of the current warming within such a short time frame on a global scale is unique in climate history and will certainly drive some species to extinction (Ipcc 2007b).

From the reference species lists for the study area we calculated for each taxonomic group the proportion of the species restricted to high montane levels as well as the proportion of the red listed high montane species, to roughly assess the potential for extinction due to climate change (Supplementary Appendix 2). Of all ferns- and vascular plants (200 species), 5.5 % are restricted to the high montane zone. The proportion of red data book species is about 11.4 %. Of all recorded fungi (1316 species), 1.5 % are restricted to the high montane zone and 3.3 % are in the red data book. For all documented molluscs (77 species), 23.4 % are restricted to the high montane zone, the proportion considering only the molluscs listed in the red data book is about 75 %. Of all documented beetles (814 species), 3.3% occur only in the high montane zone. About 8.0 % of species are listed in the red data book. Altogether, 76 breeding birds occur in the study area, with 3.9 % restricted to the high montane zone and around 3.8 % listed in the red data book. In summary: from 1.5 - 23.4 % of the target taxa considered may become extinct in the study area due to climate change. Red listed species are disproportionately sensitive, with an extinction risk of up to 75.0%. These extinction values indicate the potential for extinction as derived mainly from assumption of pessimistic SRES-scenarios (Ipcc 2007b, Spekat et al. 2007). On a European scale, the loss of species from mountains described as disproportionately sensitive to climate change may reach 60% (Thuiller et al. 2005). Projected percentage of extinction for different taxa and regions of the world range from 9 - 52 % depending on the chosen climate change scenario as well as uncertainties about dispersal capacity of many species (Thomas et al. 2004). According to this study, red data book species are also affected disproportionately. The reason why red listed species are so extremely affected can almost be explained alone by their restriction to montane-alpine zones and consequent rarity, sometimes they may be endemic taxa. In the

case of molluscs 15 of 18 high montane species are included in the red data book. Other studies support our assessment of extinction risks due to ongoing global warming. A study from the Australian tropical rainforest predicts, that even a 1 K increase will cause significant declines in range size in almost every species of regionally endemic vertebrate (Williams et al. 2003). Preliminary estimates for the Neotropical Guyana Highlands, based on representative endemic vascular plants, show that roughly 10-30% would loss their habitat with a 2-4 K temperature increase (Rull and Vegas-Vilarrúbia 2006).

Model criticism and validity

A variety of statistical techniques has been used to model the response of species to climate, e.g. Lawler et al. (2006, Pearson et al. (2006). We used GLM as the modelling technique because this is generally recommended as suitable for the prediction of climate-induced range shifts where relationships to environmental gradients are relatively simple (Thuiller 2003, Lawler et al. 2006). Predicting the impacts of climate change on the distribution of species at wider spatial scales is mostly based on the assumption that climate is the principle factor controlling species distribution and that distribution is therefore in dynamic equilibrium with the climate regime. Paleontological records of range changes associated with major climate shifts have been widely used both to highlight the strong correlation of climate variables with species ranges and to make predictions about responses of species ranges to present day climate warming e.g. Davis and Zabinski (1992). Such striking, repeatable patterns clearly indicate that climate is a strong range limiting factor. The general question is how sensitive are the model results to the assumption that the sampled distribution represents the real distribution? In the study of world-wide distribution of biomes, this assumption is probably not critical. But at a smaller scale the complexities of boundary determinants for species become more important for accurate prediction (Parmesan et al. 2005). Thus the response of many species to large scale climate will be modified by smaller scale factors (Ellis et al. 2007). Due to this effect and the local scale of our models we first assessed the importance of temperature when other habitat factors were accounted for. The scenario assumptions are based on the current species distribution patterns and consider only a change in temperatures. The scenario is not capable of predicting possible adaptation processes in the selected species. Although almost all models show good fit and discriminatory ability, additional uncertainties arise when making predictions into the future (Araújo et al. 2005). In predictive habitat distribution models, species distributions are assumed to be in equilibrium with the conditions present during the sampling period (Guisan and Thuiller 2005). While study of distributions

may have a high predictive value in describing potential habitat suitability under given conditions, it can not directly reveal the underlying process. Arctic and alpine species are relatively persistent or react slowly to alterations in environmental conditions (Guisan and Zimmermann 2000). Assuming a state of equilibrium is therefore less problematic. Mechanisms such as biotic and abiotic interactions, genetic variability and potential for evolutionary modification, dispersal and fragmentation are not taken into consideration directly, even though in general they are of high importance (Guisan and Thuiller 2005). Our study area is characterized in the high montane zone by unfragmented conditions, extending throughout the region, which increase possibilities for dispersal. Although evolutionary responses have been documented for some species (mainly insects), there is little evidence that observed genetic shifts are of the type or magnitude which can prevent the predicted species extinctions (Parmesan 2006). Dynamic simulation models represent an alternative approach to static distribution models. A way of integrating interactions to overcome the described problems could be the use of integrated systems of simultaneous regression equations (Guisan and Zimmermann 2000). Unfortunately, dynamic models require detailed data about the species, such as physiological parameters or interactions including competition, and are thus only applicable to a limited set of species. There is little doubt, that the impact of climate change on the region could conceivably be much more severe, as a result of several factors whose effects may compound each other. A further limitation is that predicting species distributions should be restricted to within the observed ranges of the predictor variables, because of the lack of information about responses outside those ranges (Thuiller et al. 2004). Aim of this study is to assess the impacts of climate change for the study area, as well as to identify suitable indicators for the same spatial scales with which to validate modelling results over time. All data for the model input and predictions have the same spatial scale. We have not considered potential climate change effects on vegetation types and primary production. It is to be expected that increased temperatures will lead to changes in plant community composition (Bässler et al. 2008b), possibly altering in this way the occurrence of high montane species.

Cross taxon suitability

The suitability of each of the selected species has already been discussed, but in a search for more flexibility and cost efficiency we also tested their cross taxon indicator suitability. A single species group rarely functions as a general indicator because of its usually low co-variation (Similä et al. 2006). Thus the most promising way of using an indicator species

group predictively appears to be with a subgroup of its own members, or with another taxonomic group sharing similar niche requirements. Our results show good co-variation between the species of different taxa as a result of similar response behaviour shared by cold-adapted high montane species. It can be concluded that it does not matter which of the species we studied is used as an indicator, as long as the discrimination of the models shows a similarly high quality ($AUC > 0.8$) (Hosmer and Lemeshow 2000). This condition is however not fulfilled by *Hymenochaete fuliginosa*.

Implications for monitoring

An accepted way of detecting changes in ecosystems caused by climate change under natural conditions is the use of long-term bio-monitoring (Grabherr et al. 1994, Harrison et al. 2001, Doran et al. 2003). But monitoring the entire system with regular replications is expensive and hard to accomplish even in very small areas (Lawton et al. 1998). In our case, for example, we surveyed 9300 fungi to identify *Hymenochaete fuliginosa* as a potential indicator, determined 27000 beetles from 180 flight interception traps to assess the value of *Ampedus auripes*, and collected 3400 mollusc individuals of 46 species to reveal *Semilimax kotulae* as an indicator. Our indicator species represent the key attributes of the ecological properties that are regarded as important. But other criteria are also important in deciding the suitability of an indicator for monitoring, such as easy and reliable identification. Until now, little effort has been expended on the cost-efficiency of indicators and ensuring the practicability of inventory by selecting easily identified species. Rapid and reliable assessment methods are however urgently needed to ascertain the impacts of climate change. When a range of different taxa is used for monitoring, it is not difficult to integrate their inventory with other biodiversity surveys or fieldwork undertaken throughout the year to reduce the necessary sampling effort. Most of our indicators are detectable throughout the year with the same reliability, and are easy to identify. To summarise: it can be stated that the easiest and most efficient method of monitoring is to map in a standardized way taxa which occur regularly in the study area, are very easy to identify and are found during the entire growing season. In the study area, *Athyrium distentifolium* or *Trientalis europaeus* are recommended as highly suitable, because they fulfil these conditions. Also recommended is the mapping of *Turdus torquatus*, which however would probably be most successful in spring. Our recommendations agree with the conclusions of (Juutinen and Mönkkönen 2004), who found that vascular plants and birds are the most cost-efficient indicators of species diversity. For *Semilimax kotulae* a standardized hand sampling strategy in early autumn (peak

of activity) (Uminski 1975, Müller et al. 2008) could also reduce the sampling effort and make it suitable as a target species. Highest sampling effort is to be expected for *Ampedus auripes*, where the huge numbers of insects collected in flight interception traps must first be sorted. In general, we should be giving more thought to the development of cheaper sampling methods, particularly for taxa having a large number of species, such as beetles (Juutinen and Mönkkönen 2004). As mentioned above, *Hymenochaete fuliginosa* is the only species which should not be considered for use as an indicator, because of its poor discrimination. This species is poorly predicted for by the other models. Furthermore, the model of *Hymenochaete fuliginosa* underestimates the occurrence of the other selected species.

We conclude that almost all of the selected species are good candidates for use as indicators in the rapid assessment of changes caused by climate change. It must however be borne in mind that studies on the performance of biodiversity indicators have shown that the use of only a very small number of indicator organisms is likely to result in an undetected loss of species and that a complete inventory of biodiversity is therefore still necessary if the objective is to retain all species in the landscape (Juutinen and Mönkkönen 2004). The species selected by us do not necessarily represent the overall biodiversity in the high montane zone. However, our results show similar response patterns for these species. The relatively simple and similar species-environmental relationships in the high montane zone, characterized by cold adaptation, lead us to expect similar responses for almost all species in this zone.

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SUPPLEMENTARY MATERIAL

Appendix 1: Modelling of the meteorological conditions

- The Model

The calculation of the meteorological conditions at each plot on the BIOKLIM transects was made with the geostatistical interpolation techniques included in the model ArcEGMO. This is a GIS-based, multi-scale modelling system for spatially simulating hydrological processes in river catchments (see Becker *et al*, 2002 and Pfützner, 2003), which has been adopted as the standard method for hydrological impact studies in the area of the Bavarian Forest National Park (Klöcking *et al.*, 2005).

The internal geostatistical interpolation techniques for regionalization of meteorological input, the “Quadrant Method” and the “Inverse Distance Weighting Method” (next neighbour method), were primarily developed for application in mesoscale hydrological models. Consequently, they operate rapidly and use commonly available meteorological data (e.g. from the German Meteorological Services DWD). Although a relatively dense sampling network exists for precipitation in Germany, the other main measured values are recorded only at major meteorological stations. To allow for the effects of different scales of spatial resolution for the individual weather values, a distinction is made between the regionalization of data for point measurements of precipitation (total volume measured by precipitation stations and meteorological stations) and climate sampling (only meteorological stations). Series of measurements of precipitation, air temperature, wind speed, air humidity or barometric pressure as well as total radiation or duration of sunshine can be expected to exist for the climate sampling points.

In the “Inverse Distance Weighting Method”, n is the number of climate measurement points closest to the plot under consideration and can be varied at will. The „Quadrant Method“ is based on values for a single station nearest to the central area, in each quadrant. Thus four stations are involved, when stations are located in all quadrants (Fig. 1).

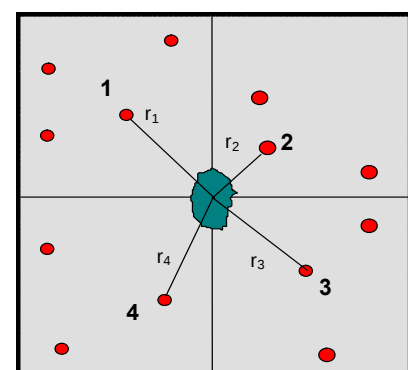


Fig. 1: Spatial distribution of measurement points around a sampling plot

Both methods employ vertical and horizontal distances between station and plot. The meteorological values P measured at the i stations are weighted according to Gl. (1) and allocated to the area of the plot. The sum of all weighting factors g is one.

$$P = \sum_{i=1}^4 g_i P_i \quad \text{with} \quad \sum_i g_i = 1 \quad (1)$$

Allocation of values to the plots takes place under consideration of local topography. It is known that a close correlation exists between altitude and precipitation, air temperature, relative humidity and partly also wind speed. For these values an average modification for each additional meter of altitude may be specified, where this is known for the study area. Alternatively, this modification may be made using the program, in the course of regression analysis. The consideration of dependence on altitude is based on annual averages derived from data for all stations which record that particular meteorological value. The correction of daily values is undertaken using the coefficients resulting from the linear regression between annual values and altitude.

It should be emphasized that considerable problems can be caused by a low density of meteorological stations and longer gaps in the data sets. This is particularly critical in the case of extreme precipitation events. Specific analyses of this problem have been performed in the Stepenitz Basin by Lahmer *et al.* (2000), using different interpolation methods: the quadrant method, two Kriging methods and several versions of the ‘next neighbour’ method. The quadrant method generally provides results which are almost as good as the more time-consuming Kriging methods.

- The data base

Tab. 1 presents an overview of the meteorological stations around the National Park and periods for which data are available. Fig. 2 shows their location and allocation to individual BIOKLIM transects.

Tab. 1: Meteorological Stations with air temperature measurements

ID	name	elevation	source	start	end	remark	parametrization
c_4489	Großer Arber	1446	DWD	198212	-		T 3, T 4
c_4490	Bodenmais AkkSt	648	DWD	195101	198112		
c_4491	Großer Falkenstein	1307	DWD	194701	198210		
c_4493	Zwieselberg	615	DWD	194801	200309		
c_4497	Zwiesel	612	DWD	199805	-	gaps 2003/2004	T 3, T 4
TWT	water reservoir Frauenau	695	WWA	1991	-		
NPV_1	Waldhäuser	940	DWD NPV	198001	-	device replacement 12/2003	T 1 + 2
							T 1 + 2
NPV_4	Klingenbrunn, Bhf.	759	NPV	198012	-	gap 5/2003-5/2004	T 1, T2, T3
NPV_5	Felsenkancel	1146	DWD	199712	200406		T 1 + 2
NPV_6	Waldschmidthaus	1350	NPV	199712	-	gaps, gap 9/2002- 6/2004	T 1, T2, T3
NPV_7	Gfeichtethöh	1165	NPV	1995	-	only summer	T 1 + 2
NPV_8	Feistenhang	869	NPV	1995	-	only summer	T 1 + 2
NPV_9	Hahnenfalz	752	NPV	1995	-	only summer	T 1 + 2
NPV_10	Hochfallen	761	NPV	1995	-	only summer	T 1 + 2
NPV_11	Schönort	901	NPV	1995	-	only summer	T 1 + 2
NPV_12	Messturm Schachtenau	857	NPV	199204	-	gaps	T 1 + 2
NPV_13	Lusen	1340	DWD	199712	200412		T 1 + 2
NPV_14	Taferlruck	771	LWF	198102	-	gap 2001/2002	T 1 + 2
LWF42	Racheldiensthütte	874	NPV	200410	-		T 1 + 2
K1	Transekte1	740	NPV	200610	-		T 1 + 2
K4	Transekte1	820	NPV	200610	-		T 1 + 2
K5	Transekte1	795	NPV	200610	-		T 1 + 2
K7	Transekte2	770	NPV	200610	-		T 1 + 2
K8	Transekte2	835	NPV	200610	-		T 1 + 2
K9	Transekte2	815	NPV	200610	-		T 1 + 2
K10	Transekte2	837	NPV	200610	-		T 1 + 2
K11	Transekte2	837	NPV	200610	-		T 1 + 2
K12	Transekte2	1290	NPV	200610	-		T 1 + 2
K14	Transekte2	1350	NPV	200610	-		T 1 + 2
K15	Transekte2	1420	NPV	200610	-		T 1 + 2
Ksee	Rachelsee	1090	NPV	200610	-		T 1 + 2
K16	Transekte3	680	NPV	200610	-		T 3
K17	Transekte3	730	NPV	200610	-		T 3
K18	Transekte3	765	NPV	200610	-		T 3
K19	Transekte3	1095	NPV	200610	-		T 3
K20	Transekte3	1100	NPV	200610	-		T 3
K21	Transekte3	1192	NPV	200610	-		T 3
K22	Transekte4	675	NPV	200610	-		T 4
K23	Transekte4	700	NPV	200610	-		T 4
K24	Transekte4	990	NPV	200610	-		T 4
K25	Transekte4	1145	NPV	200610	-		T 4
K26	Transekte4	1140	NPV	200610	-		T 4
K27	Transekte4	1112	NPV	200610	-		T 4
K28	Transekte4	1325	NPV	200610	-		T 3, T 4
K29	Transekte4	1325	NPV	200610	-		T 3, T 4

It is apparent that hardly any stations have measured air temperatures continually over a longer period. Derivation of long-term average temperature relationships for individual transect plots first became possible during the late 1990's, with more reliable series of data from a denser network.

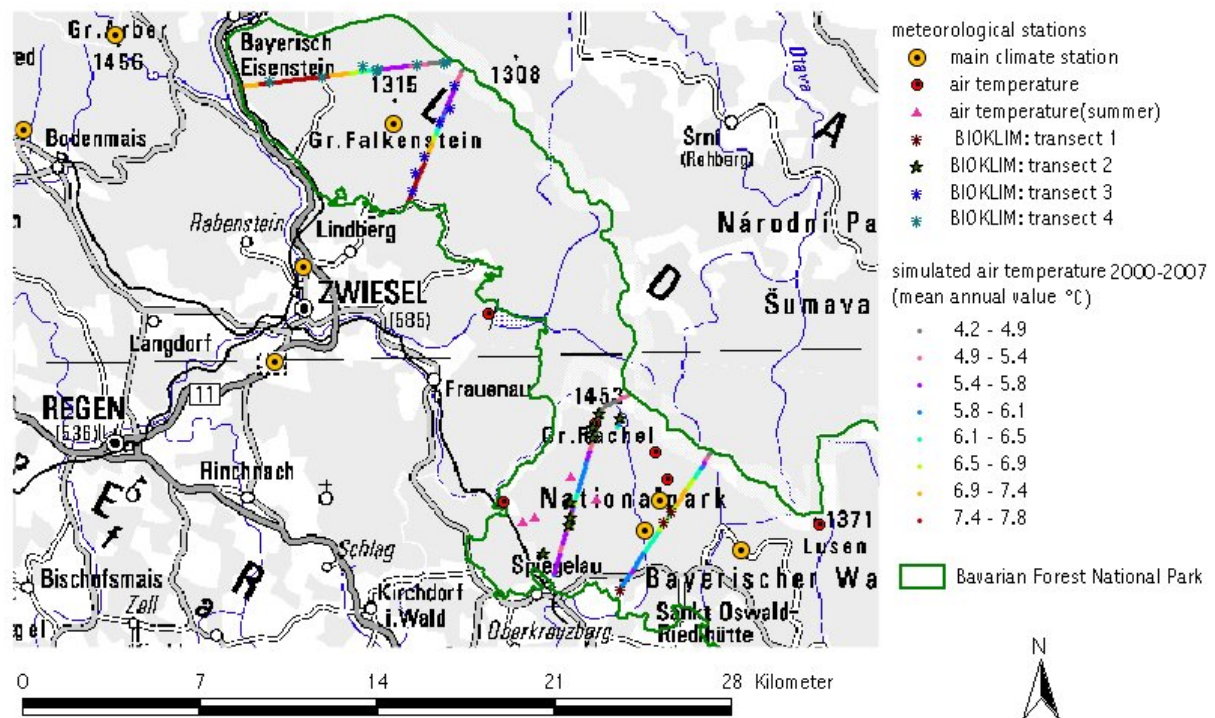


Fig. 2: BIODOL transects with the simulated mean annual temperatures (2000-2007) and the location of all meteorological stations in the area of the transects

Data processing, regionalisation of the point measurements

Measurements of air temperature and humidity at 30 minute intervals are available for all four transects from 10/2006 onwards. Daily values were aggregated from these (mean, minimum, maximum). On the basis of these measurement series for the period 1.10.2006 to 31.10.2007 and all further data available from the DWD, the National Park and the Bavarian Forest Agency (LWF), the spatial regression factor (dependence on altitude) was obtained, enabling further geostatistical regionalization. The nature of the topography called for separate simulations for each transect, using data for different weather stations. The weather stations used for individual transects are indicated in the last column of Tab. 1. The number of stations and the coefficients resulting from the linear regression between yearly values and altitude are presented for transects in Tab. 2.

Tab. 2: Overview of the transects.

Transect	region	Number of meteorological stations	Elevation gradient [°C/meter of altitude]
1 und 2	Große Ohe: T1: Plattenhausen T2: Rachel TS: Rachelsee	26	-0.00457
3	Scheuereck	10	-0.00416
4	Lattenberg, Nord-West-Flanke	10	-0.00401

The calculation of the long-term temperature conditions along the transects during the period 1980 – 2007 was undertaken using the above described „Quadrant Method“ in combination with the calculated elevation gradient. All series of temperature measurements were used, despite longer gaps, because of the low density of temperature observation stations in this period. A comprehensive analysis of the simulation results (Klöcking, 2008) indicated the reliability of the temperature conditions calculated at all 293 transect plots for the last 8 years (2000-2007). The regionalized results for the preceding years are less plausible, because of the insufficient data base. The mean annual temperature (2000-2007) for individual points on a transect lies between 4.2 and 7.8 °C, depending on altitude and exposition, as illustrated in Fig. 2.

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Appendix 2: Species of the investigated taxonomic groups restricted to the high montane zone in the study area. Bold type indicates red listed species (reference in text). We used the following sources for documentation of species occurrence in the National Park: Petermann and Seibert (1979) for ferns and vascular plants, Luschka (1993) for fungi, Strätz (2008, unpublished database) for molluscs, and Müller (2008, unpublished database) for beetles and birds.

Vascular plants and ferns	Fungi	Molluscs	Beetles	Birds
Athyrium distentifolium	Botryobasidium ellipsosporum	Arion alpinus	Trechus alpicola	Tetrao urogallus
Cardamine resedifolia	Bryochiton microscopicus	Causa holosericea	Pterostichus unctulatus	Turdus torquatus
Cryptogramma crispa	Calycina subtilis	Clausilia cruciata cruciata	Amara nigricornis	Anthus spinoletta
Homogyne alpina	Clitocybe phyllophila	Deroceras rodnæ	Sphaerites glabratus	
Huperzia selago	Epichloe typhina	Discus ruderatus ruderatus	Neuraphes coecus	
Ligusticum mutellina	Galerina mniophila	Isognomostoma isognomostomos	Anthophagus alpestris	
Pinus mugo Turra	Galerina subcerina	Macrogaster badia crispulata	Quedius punctatellus	
Soldanella montana	Hymenochaete fuliginosa	Macrogaster plicatula nana	Quedius obscuripennis	
Streptopus amplexifolius	Hyphodontia arguta	Macrogaster plicatula inuncta	Quedius alpestris	
Trientalis europaea	Inocybe subcarpata	Nesovitrea petronella	Quedius paradisiensis	
	Laccaria proximella	Patasina edentula liminifera	Bryophacis rufus	
	Mollisia palustris	Petasina unidentata subalpestris	Atheta allocera	
	Mycena excisa	Semilimax kotulae	Rhagonycha nigripes	
	Mycena laevigata	Urticicola umbrosus	Dasytes obscurus	
	Omphaliaster asterosporus	Vertico alpestris	Ampedus aethiops	
	Phellinus nigrolimitatus	Vertico modesta arctica	Ampedus auripes	
	Phlebiella pseudotsugae	Vertico substriata	Cis quadridens	
	Saccobolus neglectus	Vitrea subrimata	Xestobium austriacum	
	Tubulicrinis accedens		Hoplia argentea	
	Tubulicrinis hirtellus		Evodinus clathratus	

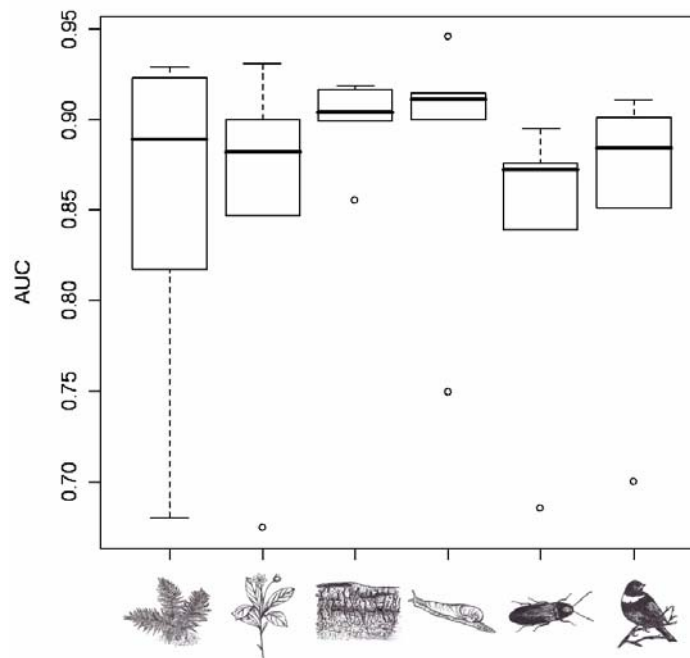
Luschka, N. 1993. Die Pilze des Nationalparks Bayerischer Wald im bayerisch-böhmischen Grenzgebirge. Hoppea, Denkschriften der Regensburger Botanischen Gesellschaft **53**:5-363.

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Strätz, C. 2008. Unpublished database

Müller, J.. 2008. Unpublished database

Appendix 3: ANOVA on the basis of the Area under the Receiver Operating curve values (AUC-values) of the species generalized linear models (from left *Athyrium distentifolium*, *Trientalis europaea*, *Hymenochaete fuliginosa*, *Semilimax kotula*, *Ampedus auripes* and *Turdus torquatus*) with the occurrence of the remaining species used as predictors.



Molluscs and climate warming in forest of a low mountain range

Müller Jörg^{1*}, Bässler Claus¹, Strätz Christian², Beate Klöcking³, Brandl Roland⁴

*Corresponding author

¹ National Park “Bavarian Forest”

Freyunger Str. 2

D-94481 Grafenau, Germany

Telephone: ++49-8552-9600-179

Fax: ++49-8552-9600100

Email: joerg.mueller@npv-bw.bayern.de

² Bureau for Ecological Studies

Oberkonnersreuther Str. 6a

D-95448 Bayreuth

bayreuth@bfoes.de

³ Bureau of Applied Hydrology

Murnauer Str. 102a

D-81379 Munich Germany

phone: ++49-89-71048872

fax: ++49-89-71048873

www.bah-muenchen.de

kloecking@bah-muenchen.de

⁴ Department of Animal Ecology, Faculty of

Biology, Philipps-University of Marburg,

Marburg, Germany

brandlr@staff.uni-marburg.de

ABSTRACT

Aim To assess the influence of the regional temperature gradient with altitude on species density and density of single species of molluscs in a mountain forest with acidic soil in Central Europe. Additional objectives: testing the influence of site-specific habitat factors by considering several habitat variables ranging from stand age to plant species richness; modelling of the occurrence of a high montane species under two climate warming scenarios to demonstrate differences in the extinction risk.

Location The forested low mountain range of the National Park “Bavarian Forest” in South-eastern Germany.

Methods Combined data from pitfall traps and time standardised hand sampling within 111 circular plots of 0.1 ha were analysed. Quantile regression was used to describe the influence of altitude and temperature. For testing influence of habitat variables we used a special Poisson and Gaussian regression approach that considers the spatial structure of the data. Using presence/absence data, we calculated the probability of occurrence of *Semilimax kotulae* (Westerlund 1883) under present conditions as well as two scenarios of climate warming.

Results Based on 3437 individuals and 46 species, density of individuals and species decreased with the altitude non-linearly. The slope of this decrease changed between 1100 and 1200 m a.s.l. Contrastingly, the density of *Semilimax kotulae* increased with altitude, but again with a change in the slope between 1100 and 1200 m a.s.l. Statistical modelling showed that especially habitat age is an important predictor for the density of many species. For the high montane species *Semilimax kotulae*, our statistical model predicts a considerable risk of extinction within the National Park “Bavarian Forest” as a result of global warming.

Main conclusions Global warming will lead to an overall increase in species density. However, species occurring only at higher elevations, such as the Central European endemic *S. kotulae*, will probably become extinct within the study area if global warming increases by +4.0 K.

Keywords

Altitudinal gradient, National Park “Bavarian Forest”, extinction risk, habitat tradition, *Semilimax kotulae*, spatial GLM

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). At their most extreme, these reorganizations may lead to a regional or even global extinction of some species (Bakkenes *et al.*, 2002; Berry *et al.*, 2002; Thomas *et al.*, 2004; Ipcc, 2007a). The understanding of these effects and the identification of indicators for global warming are considered to be among the most important tasks for ecologists, especially for those concerned with conservation (Sutherland *et al.*, 2006). Despite considerable advances in our general understanding of the relations between climate and species distribution at a worldwide scale (Gaston & Blackburn, 2000; Gillooly & Allen, 2007), our understanding of the local and regional effects of global warming is very sketchy (Grabherr *et al.*, 1994; Schrag *et al.*, 2007). In particular, the reorganizations of habitats by humans may override or reinforce the effects of global warming (Kappelle *et al.*, 1999; Travis, 2002).

High mountains show long altitudinal gradients and the majority of studies on relationships between climate and species have therefore concentrated on such areas (Kazakis *et al.*, 2007; Pauli *et al.*, 2007). However, the low mountain ranges of Central Europe comprise in total the largest area of all mountains in Europe (Cipra, 2007). As a result of their limited altitude, species restricted to the higher zones of these mountains seem to be vulnerable to local extinction by climate warming, because they have little possibility to shift their ranges upwards (Thomas *et al.*, 2004; Thuiller, 2007).

Molluscs are a suitable taxon for testing the influence of climate and habitat and for predicting changes in the extinction risks of high montane species with climate warming. It is well known that community composition, species richness or location and size of distributional ranges depend on climate (Tattersfield *et al.*, 2001; Aubry *et al.*, 2005). Previous studies in Europe identified molluscs as indicators for soil characteristics as well as for old forest stands (Kappes, 2005; Müller *et al.*, 2005b). This close correlation of mollusc distribution and habitats is in part due to their low dispersal propensity (Waldén, 1981). Furthermore, molluscs are comparatively easy to sample and to identify, thus making extensive sampling programmes feasible. Their low dispersal propensity leads to considerable genetic variation between neighbouring populations (Marten *et al.*, 2006). Similarly to plants (Matthies *et al.*, 2004), some of this variation will be adaptive for the local conditions (Calosi *et al.*, 2008). Therefore, especially in molluscs, global warming may lead to the extinction of locally adapted populations. Our study has three main aims:

1. To assess the regional influence of the temperature gradient with altitude on species density and density of single species in the “Bavarian Forest”, a low mountain range with acidic soils. Most Central European low mountain ranges possess acidic soils, which are sub-optimal for several plant and animal taxa, particularly molluscs. Previous studies of molluscs were mostly made in calcareous areas, because species richness under such conditions is attractively high. Our study therefore fills an important gap in the knowledge of this taxon.
2. To test the influence of site-specific habitat factors. We considered several habitat variables ranging from stand age to plant species richness.
3. To describe the changes in the extinction risk of a high montane species with global warming. Statistical modelling was used to assess the effects of the two official climate warming scenarios (Ipcc, 2007).

METHODS

Study area and study sites

The National Park “Bavarian Forest”, the oldest national park in Germany, is located in the south-eastern 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 1430 m a.s.l. Total annual precipitation is between 1200 mm and 1800 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 south-western part of the Bohemian Massif, consisting of granite and gneiss and therefore containing acidic soils (Table 1). Above about 1100 m to 1200 m a.s.l. the stands are dominated by spruce *Picea abies*, with a low proportion of beech *Fagus sylvatica* and mountain ash *Sorbus aucuparia* (high montane forest). Below this, the stands are dominated by spruce, beech and fir *Abies alba* (mixed montane forest) (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.

We sampled molluscs as part of a more comprehensive program to characterise spatial variation of biodiversity across the National Park. For this program 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 selected 111 plots that represented the major forest management types across the altitudinal

gradient (Fig. 1). Management types range 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.

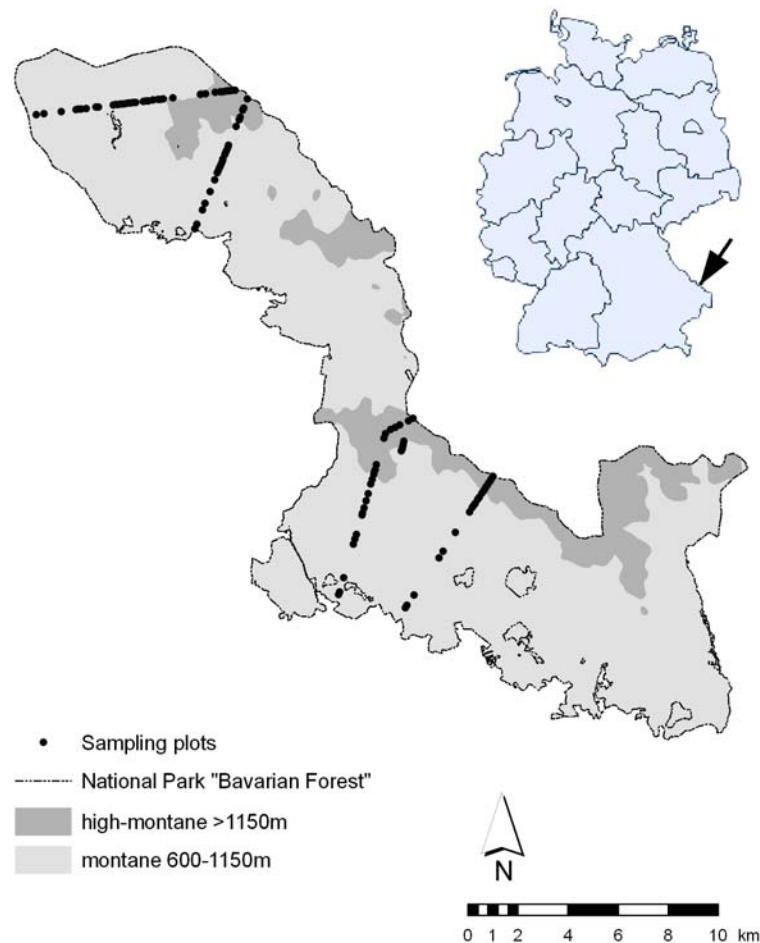


Fig. 1: Study area and plots (111 plots) used to sample molluscs along 4 altitudinal transects within the National Park "Bavarian Forest".

Sampling methods

Two sampling methods were used: Firstly, installation of one pitfall trap 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 in summer is not appropriate for all species and early autumn appears to be the best time to sample high montane molluscs (Uminski, 1975), hence use of

this combination of methods. 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; Hannemann *et al.*, 1992; Wiktor, 2000). For all subsequent analyses we totalled numbers of all individuals (density) and species (species density) across the two approaches. Species richness was estimated in terms of the residuals from the regression of species density versus density (Gotelli & Colwell, 2001). Effectively, we used density as a covariable.

Tab. 1: Definition, source and measurement of the environmental variables used for the analysis of density, species density and richness within the National Park “Bavarian Forest”

Environmental variable	Description	Source	Range total
Altitude	Height above sea level	Surface terrain model	655 – 1419 m
Temperature	Mean annual temperature 2000-2007	ArcEcmo modelling	4.1 -7.8°C
pH value of humus layer	pH value of Humus layer	laboratory analysis in 2006	2.3 - 4.42
Soil water balance index	Soil water balance calculated after Ewald inspection of characteristics of the (2000) on a scale between 0 (dry) and 10 top soil as well as pH 0.0 – 9.6 (wet)	measurements in 2006	
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	Inventory of plots along transects in 2006	0 - 708 m ³ ha ⁻¹
Opening of canopy layer	Percentage of signals arriving at 1 m above ground averaged across the 0.1 ha sampling plots	Airborne laser scanning in 2006	0.0 – 96.8 %
Plant species diversity	Shannon index of plant species diversity	Vegetation mapping in July 2006 using the Londo-scale.	0.0 - 3.13

For each plot we recorded coordinates and altitude using a GIS. To obtain reliable data for temperature and humidity, 30 data loggers were installed on representative sites across our altitudinal gradients during 2006. Additionally, we used data from five meteorological stations in the region operated since 2000 to adjust the data collected in 2006 to the average between 2000 and 2007. Note that values for temperature are higher than those reported in our general description above, which refer to the period 1970-2003. With these data we developed a statistical model to predict for each plot the mean annual temperature, using independent variables extracted from a terrain surface model (geostatistical modelling with ArcEGMO:

Becker *et al.*, 2002; Pfützner, 2002). These predicted values were used in all subsequent analyses (for details see Appendix S1 in Supplementary Material).

We collected random samples of litter of standard size within each plot in July 2006 which was then pooled for measurement of pH in the laboratory (Bässler *et al.*, 2008). Based on these results and visual inspection of soil characteristics using 4 cuts with a spade for each plot, we calculated an index of soil water balance on a rank scale from 0 (dry) to 10 (wet) following Ewald *et al.* (2000).

The age of stands was taken from the forest inventory data of the National Park. Data on coarse woody debris were collected in spring 2006 on all 293 plots of the transects (Bässler *et al.*, 2008). The openness of the canopy layer was measured using airborne laser scanning in summer 2006. Briefly, this method uses laser pulse (25 m^2) from which a lidar digital canopy model can be obtained. We calculated the percentage of laser pulse arriving at 1m above ground averaged across the 0.1 ha sampling plots (Hyde *et al.*, 2006). This is an inverse measure of canopy closure. Mature and dense stands therefore show low values, while stands with windthrow gaps or bark beetle infestation show high values. Composition of vegetation of each plot was sampled with standard methods in July 2006 and recorded on the Londo scale (Londo, 1976). Based on this we used the estimated Shannon-Index to describe plant diversity (Tab. 1)

To characterize the general distribution of montane species of molluscs, we examined the available literature (Murr & Royer, 1931; Rensch, 1937; Forcart, 1956; Hässlein, 1966; Kerney *et al.*, 1983; Uminski, 1983; Falkner, 1991) and unpublished data. From this analysis we found that *Semilimax kotulae* is the only montane species which occurs regularly throughout the sampling plots (see also Fig. 2). The altitudinal distribution of *S. kotulae* in Bavaria was analysed based on 47,279 mollusc records made between 1980-2007 throughout Bavaria across an altitudinal range of 110 m to 1740 m a.s.l. (Strätz, unpublished; see Appendix S2 in Supplementary Material).

Statistical analyses

The plots of density and species density *versus* the temperature gradient with altitude showed considerable scatter even at one altitudinal level. However, a visual inspection suggested a clear pattern of the maximum values with altitude. Therefore we used additive quantile regression smoothing (Koenker *et al.*, 1994) as implemented in the package “quantreg” in R 2.6.0 (Koenker, 2007); $\tau = 0.8$).

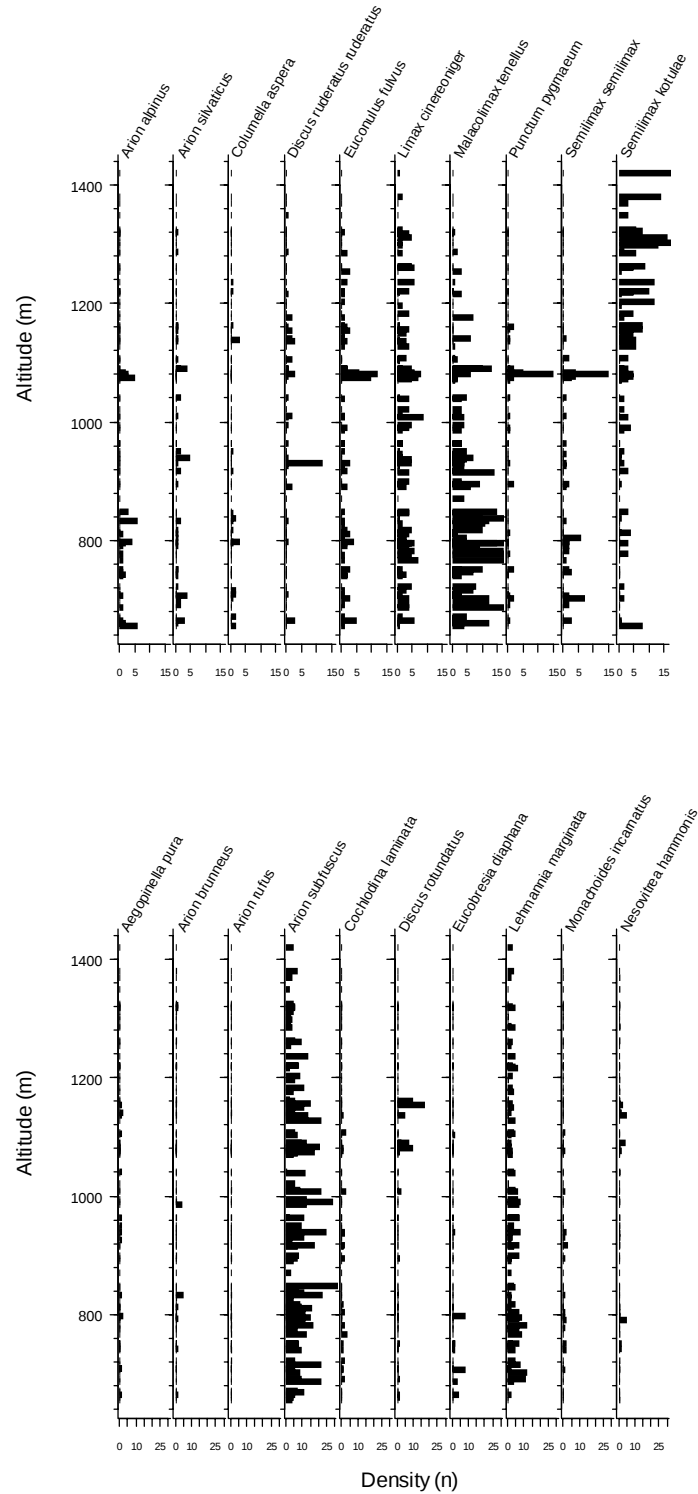


Fig. 2: Density of the more abundant species, which occurred in at least 10 sampling plots along altitudinal gradients within the National Park “Bavarian Forest” (each bar represents one of 111 plots; see Fig. 1). The upper part shows species where we found a significant relationship between density and temperature ($p < 0.1$). Otherwise, species are presented in alphabetical order (see also Tab. 2).

To analyse the relationships of total density, species density, species richness and densities of single species we used generalized linear models (GLM). We used a Poisson regression with a log link function for species density, species richness and single species density and gaussian regression for the total density of all molluscs (Quinn & Keough, 2002; Everitt & Hothorn, 2006). To allow a comparison of the estimators, all predictors were standardised to zero mean – unit variance. However, one of the key assumptions in statistical models in the present context is the independence of residuals (Dormann et al., 2007), which was not always the case with our data. Therefore we used a semiparametric spatial generalised linear model. 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 based on the standard deviations obtained from the expected Fisher information matrix as implemented in the package “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* (see above), we first used logistic regression implemented in “BayesX” to predict the occurrence of this species in our sampling plots under consideration of all available predictors (Table 1). This analysis showed that only temperature had a significant influence on probability of occurrence. Therefore we concentrated on temperature. Since the results of the spatial GLM were specific to the locations where the data were collected, they are not suitable for a general predictive approach. To obtain the desired generalized model, we fitted a GLM using the estimated current mean annual temperature whilst excluding the spatial effects (see above) and used this to predict the probability of occurrence of *S. kotulae* for each plot. In a final step we implemented in this model the values for temperature increase presented in two official scenarios (Ipcc, 2007b) to predict the occurrence of *S. kotulae* on the sample plots after global warming. These predict an increase in the mean annual temperature until 2100 of 1.8 K (optimistic assumptions) and 4.0 K (pessimistic assumptions). Predictions for the three temperature scenarios were plotted against altitude and the general trend described using a spline fit as a local smoother. To visualize the uncertainty of the general trend we 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 (for R-script see Appendix S3 in Supplementary Material). The optimistic global estimate of warming corresponds with existing local scenarios (Spekat *et al.*, 2007), which are not available for the pessimistic

scenario. We did not consider changes in precipitation, because the expected changes for our region are only 6% (Spekat *et al.*, 2007).

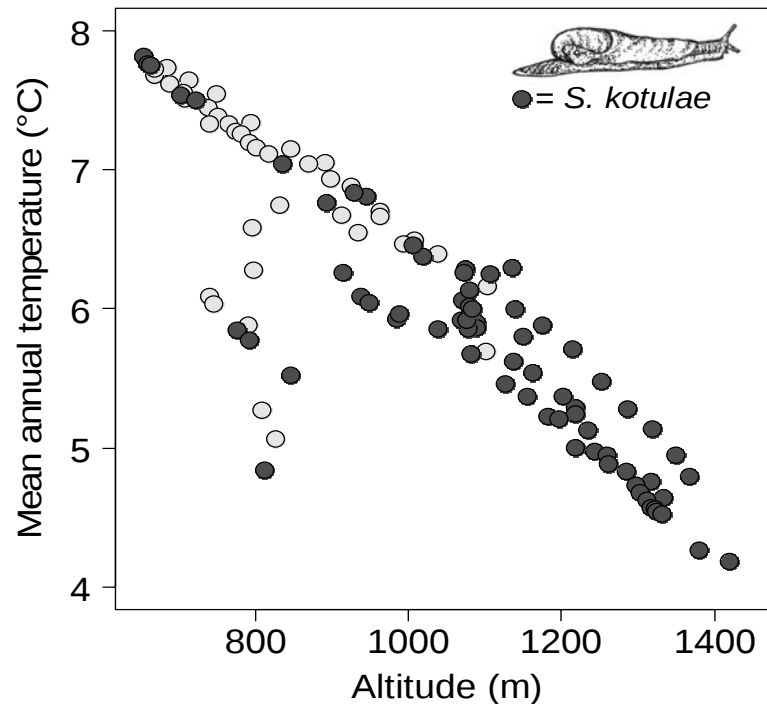


Fig. 3: Relation of mean annual temperature and altitude across the 111 sampling plots in the National Park “Bavarian Forest”. The outliers are typical sinks for cold air. Dark symbols indicate plots where we recorded *Semilimax kotulae*.

RESULTS

In total we sampled 3437 individuals of forty-six species (see Appendix S5 in Supplementary Material). On the individual plots we sampled between 7 and 96 individuals representing 3 to 27 species. Nine of the twenty more abundant species (at least ten occupied plots) showed a positive response ($p < 0.1$) to temperature (Fig. 2 above, Table 2) and only *Semilimax kotulae* showed a negative response (Fig. 2 above, Fig. 4a,b, Table 2). For the other ten species we failed to find a relationship between density and temperature (Fig. 2 below, Table 2).

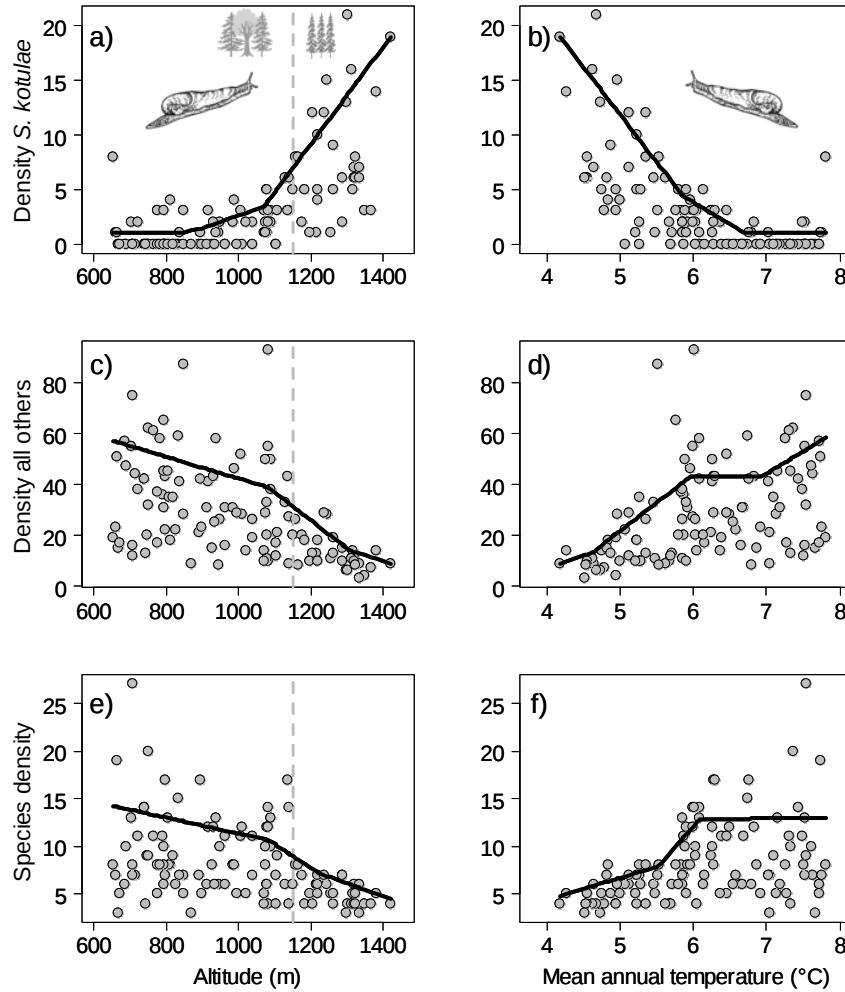


Fig. 4: Species density, density of *Semilimax kotulae* as well as density for all species (with exception *S. kotulae*) versus altitude and temperature across 111 plots sampled within the National Park “Bavarian Forest” (see Fig. 1). Lines are additive quantile regressions. The dashed line indicates the altitude of the change between mixed montane and high montane spruce forests (1150 m).

Obviously, temperature decreased with altitude of the sampled plots (Fig. 3). The outliers in Fig. 3 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 from moorland sites, which at ground level are also cold microhabitats (Fig. 3). For *S. kotulae* the relationships between density and altitude or temperature were non-linear (Fig. 4 a, b). The quantile regression showed a steeper increase of density with altitude above 1100 m or a decrease with temperature above 5.5 - 6.0°C. Species richness and density of all other molluscs (excluding *S. kotulae*) decreased with altitude and increased with temperature (Fig. 4 c-f). Again, these relationships were non-linear. For the common species, species density,

species richness, and total density the relationships with environmental variables listed in Table 1 were tested. In 13 models we found an increase with tree age. Temperature ranked second, based on the number of models with a significant temperature effect.

As noted in the introduction, the probability of occurrence of *S. kotulae* decreased with increasing temperature ($p = 0.03$; for all other variables $p > 0.25$) using spatial GLM. An increase in the mean annual temperature of 1.8 K will already lead to a decrease in frequency of about 50 % at altitudes of 1300 m (Fig. 5).

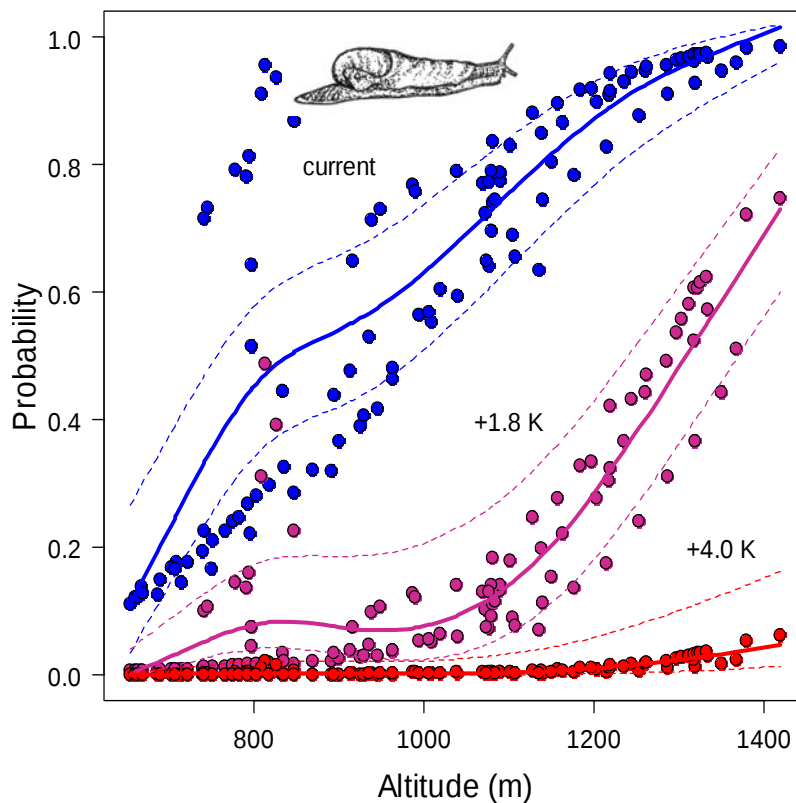


Fig. 5: The blue symbols indicate the predicted probability of occurrences of *Semilimax kotulae* across the 111 sampling plots versus altitude within the National Park “Bavarian Forest” using annual mean temperature. The blue curves are a local smoother (spline) with heuristic confidence bands (for details see Material and Methods as well as Appendix S3 in Supplementary Material). The other two groups of points and curves are predicted probability of occurrences for *S. kotulae* using scenarios of global warming with an increase of the mean annual temperature by 1.8 K and 4.0 K.

Note that most mountains in the region are below this altitude (Fig. 6). Nevertheless, within this optimistic scenario some sinks for cold air may act as refuges for *S. kotulae* at lower altitudes, if one assumes 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 area covered by the National Park (see also Appendix S4 in Supplementary material).

Tab. 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 effects with $p < 0.1$. Species density is the number of species per sampling area whereas for the estimation of species richness we included density as a covariable. For altitudinal distribution of species see Fig. 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
Density without <i>S. kotulae</i>		▲	10.0**	△		▲			
Species density		▲	0.29*		▲	▲			▲
Species richness		▲	0.17*		▲				▲
<i>Species shown in Fig. 2 above:</i>									
<i>Arion alpinus</i> , Pollonera 1887	X 23	▲	1.66**		▲	▲			
<i>Arion silvaticus</i> , Lohmander 1937	32	△	0.99					▲	▲
<i>Columella aspera</i> , Waldén 1966	X 18	▲	1.96*						
<i>Discus ruderatus ruderatus</i> , (W. Hartmann 1821)	X 27	▲	1.79**						▼
									-0.43*

		▲		▲		△	
	61	0.87**		0.20*	0.35**		0.24
<i>Euconulus fulvus</i> , (O. F. Müller 1774)		*			*		
	94	△	▲	▽	▲		
<i>Limax cinereoniger</i> , Wolf 1803		0.34	0.16*	-0.13	0.13*		
	79	▲	▲	▼	▲		
<i>Malacolimax tenellus</i> , (O. F. Müller 1774)		1.04**	0.18***	-	0.29**		
				0.35***	*		
	24	△	△	▲	▲	▼	
<i>Punctum pygmaeum</i> , (Draparnaud 1801)		0.69	0.33	0.36*	0.53**	-0.51*	
	28	▲			▲		▽
<i>Semilimax semilimax</i> , (J. Férussac 1802)		1.06*			0.31*		-0.38
	X 72	▼					
<i>Semilimax kotulae</i> , (Westerlund 1883)		-0.70*					
Species shown in Fig. 2 below:							
<i>Aegopinella pura</i> , (Alder 1830)	14						
	X 31			▲		△	
<i>Arion brunneus</i> , Lehmann 1862				0.33*		0.34	
<i>Arion rufus</i> , (Linnaeus 1758)	X 10						
	112		△	△	▲		
<i>Arion subfuscus</i> , (Draparnaud 1805)		0.08	-0.08	0.15**			
	20			▲	▽	▼	
<i>Cochlodina laminata</i> , (Montagu 1803)				0.52*	-0.72	-1.15*	
	30	▲		▲	▼	△	
<i>Discus rotundatus</i> , (O. F. Müller 1774)		0.59**		0.64**	-0.55*	0.37	
				*			
	13		▲				
<i>Eucobresia diaphana</i> , (Draparnaud 1805)			0.81**				
	90			▲		▼	
<i>Lehmannia marginata</i> , (O. F. Müller 1774)				0.23**		-0.39**	
				*			
<i>Monachoides incarnatus</i> , (O. F. Müller 1774)	16						△
							0.67
	40	▽		▲		▲	
<i>Nesovitrea hammonis</i> , (Ström 1765)		-0.32		0.51**		0.43*	
Sum of significance		10 (3)	3(4)	8(2)	13	2 (2)	3(3)
(almost significance)							5(1)

DISCUSSION

Even though the decrease of diversity along altitudinal gradients has fascinated biologists since Darwin, the reasons for these patterns are still disputed (Gaston, 2000). We found a non-linear decrease of species richness. Aubry *et al.* (2005) studied richness of molluscs in calcareous mountains in South-eastern France, where they found a plateau of species richness at elevations between 200 m and 1000 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 different to our study area, the distributional patterns with altitude in the two studies are very similar. We found a change in the slope of the general decrease of species richness with altitude at around 1150 m, the altitude where the switch from mixed montane to high montane forests also occurs. Some studies have already stressed the close correlation between altitudinal zonation of molluscs and plant communities (Coppo, 1984). Our study supports this finding.

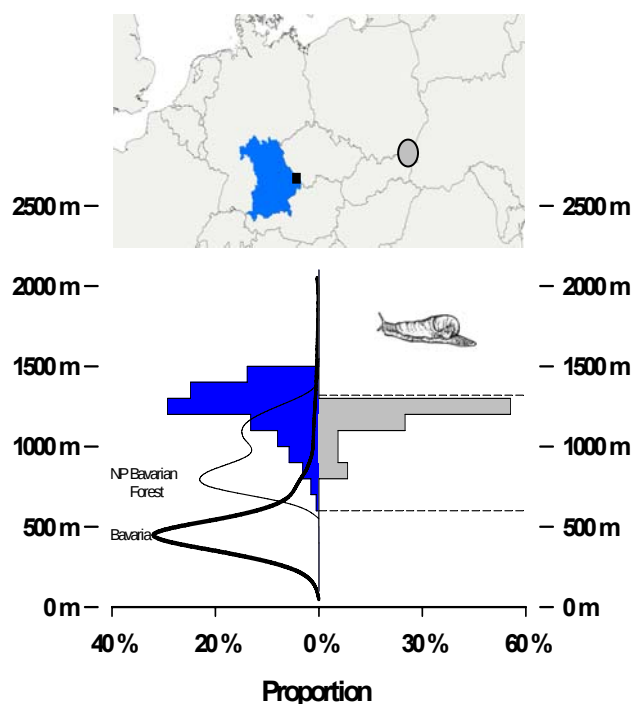


Fig. 6 (left) Altitudinal distribution of *S. kotulae* in Bavaria (see also Appendix S2 in Supplementary Material). The bold curve indicates the percentage of the land area versus altitude for Bavaria (data from Schlumprecht & Waeber, 2003). The black curve indicates percentage of area versus altitude for the National Park “Bavarian Forest”. The square in the map indicates the location of the National Park “Bavarian Forest”.

(right) Altitudinal distribution of *S. kotulae* in the East Carpathians Bieszczady National Park (Sulikowska-Drozd & Horsák, 2007). Percentage distribution is based on 167 individuals. The two lines indicate the altitudinal ranges of sampling.

Körner (2007) noted the difficulty of interpreting effects of non-climatic variables which are strongly correlated with elevation only within certain regions. This can modify altitudinal patterns of species diversity in such a way that climate seems to be unimportant, (Lee *et al.*, 2004). Nevertheless, Aubrey *et al.* (2005) suggest that climate and the availability of micro-habitats determines the number of species. Obviously our results support this idea. Temperature, soil water balance, age of trees and plant species diversity are significantly and positively correlated with the densities of several species. Habitat suitability should be even of more importance in our study than in the study of Aubrey *et al.* (2005). Our sample plots are all characterized by acidic conditions whereas molluscs often prefer habitats with high pH values (Wäreborn, 1969; Waldén, 1981; Coney *et al.*, 1982; Tappert, 2002; Martin & Sommer, 2004; Horsák, 2006). We found a positive relationship between mollusc occurrence and soil water content as well as diversity of plants, which agrees with other studies (Barker & Mayhill, 1999; Müller *et al.*, 2005b; Horsák, 2006).

In our tests of the correlation between plot characteristics and the densities of individual species, tree age was of overwhelming importance. Furthermore, density and species density also increased with tree age. The age of the oldest tree in a stand is a surrogate of habitat continuity in forests (Speight, 1989; Sverdrup-Thygeson & Lindenmeyer, 2003; Müller *et al.*, 2005a). This high level of 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 (Müller *et al.*, 2005b; Bußler *et al.*, 2007). The importance of habitat tradition to molluscs has at least three components: Firstly, some species feed on the bark of old broadleaved trees (e.g. *Lehmannia marginata*, *Clausilia cruciata cruciata*) and therefore require veterans. 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 *et al.*, 2006). But 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; Pettersson *et al.*, 1995; Ulikzka & Angelstam, 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 of species density and 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, some species will be able to increase their altitudinal range of occurrence. Secondly, new species will be able to invade the area (including alien species such as *Arion lusitanicus*). Therefore, viewed naively, climate warming will be a positive phenomenon if one considers only species richness. However, species adapted to montane habitats are often adapted to cooler climates and climate warming may lead to their local extinction, especially because the available area suitable to them also decreases with altitude (Fig. 6). We have one such species in our data set: *Semilimax kotulae*.

S. kotulae is endemic to the Alpine-Carpathian area and occurs at altitudes above 600 m (Fig. 6). Populations between 500 and 600 m exist in sites where cold air emanates from block fields (Hässlein, 1966), which is fully in line with our results. When we compared our data with data from the East Carpathians (Sulikowska-Drozd & Horsák, 2007), we found a very similar pattern of altitudinal distribution of *S. kotulae* (Fig. 6), which suggests that this species may be a suitable indicator for the fate of montane species affected by global warming (see also De Groot *et al.*, 1995; Kappelle *et al.*, 1999). As indicated by our exercise presented in Fig. 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, other montane species too. Under pessimistic scenarios of climate warming, *S. kotulae* will only survive in regions that provide sufficient areas at higher altitudes (Alps). Sites with special, cool climates in low mountain ranges will lose their suitability (Fig. 5).

The upper altitudinal zones of the low mountain ranges in Central Europe are not species rich when compared to lowland forests. Nevertheless, some species are restricted to this zone. Their present range of occurrence is between 1100 m and 1400 m a.s.l., so that these species have no possibility of an upward escape with rising temperatures; these mountain ranges are simply too low. Hence global warming will make impossible one of the major aims of the National Park “Bavarian Forest”: the conservation of species assemblages of the high montane zone.

Acknowledgements

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SUPPLEMENTARY MATERIAL

Appendix S1: Modelling of the meteorological conditions

The Model

The calculation of the meteorological conditions at each plot on the BIOKLIM transects was made with the geostatistical interpolation techniques included in the catchment model ArcEGMO. This is a GIS-based, multi-scale modelling system for spatially simulating hydrological processes in river catchments (see Becker *et al*, 2002 and Pfützner, 2003), which has been adopted as the standard method for hydrological impact studies in the area of the Bavarian Forest National Park (Klöcking *et al.*, 2005).

The internal geostatistical interpolation techniques for regionalization of meteorological input, the “Quadrant Method” and the “Inverse Distance Weighting Method” (next neighbour’ method), were primarily developed for application in mesoscale hydrological models. Consequently, they operate rapidly and use commonly available meteorological data (e.g. from the German Meteorological Services DWD). Although a relatively dense sampling network exists for precipitation in Germany, the other main measured values are recorded only at major meteorological stations. To allow for the effects of different scales of spatial resolution for the individual weather values, a distinction is made between the regionalization of data for point measurements of precipitation (total volume measured by precipitation stations and meteorological stations) and climate sampling (only meteorological stations). Series of measurements of precipitation, air temperature, wind speed, air humidity or barometric pressure as well as total radiation or duration of sunshine can be expected to exist for the climate sampling points.

In the “Inverse Distance Weighting Method”, n is the number of climate measurement points closest to the plot under consideration and can be varied at will. The „Quadrant Method“ is based on values for a single station nearest to the central area, in each quadrant. Thus four stations are involved, when stations are located in all quadrants (Fig. 1).

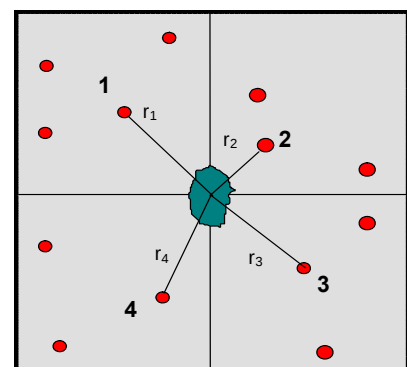


Fig. 1: Spatial distribution of measurement points around a sampling plot

Both methods employ vertical and horizontal distances between station and plot. The meteorological values P measured at the i stations are weighted according to Gl. (1) and allocated to the area of the plot. The sum of all weighting factors g is one.

$$P = \sum_{i=1}^4 g_i P_i \quad \text{with} \quad \sum_i g_i = 1 \quad (1)$$

Allocation of values to the plots takes place under consideration of local topography. It is known that a close correlation exists between altitude and precipitation, air temperature, relative humidity and partly also wind speed. For these values an average modification for each additional meter of altitude may be specified, where this is known for the study area. Alternatively, this modification may be made using the program, in the course of regression analysis. The consideration of dependence on altitude is based on annual averages derived from data for all stations which record that particular meteorological value. The correction of daily values is undertaken using the coefficients resulting from the linear regression between annual values and altitude.

It should be emphasized that considerable problems can be caused by a low density of meteorological stations and longer gaps in the data sets. This is particularly critical in the case of extreme precipitation events. Specific analyses of this problem have been performed in the Stepenitz Basin by Lahmer *et al.* (2000), using different interpolation methods: the quadrant method, two Kriging methods and several versions of the 'next neighbour' method. The quadrant method generally provides results which are almost as good as the more time-consuming Kriging methods.

- The data base

Tab. 1 presents an overview of the meteorological stations around the National Park and periods for which data are available. Fig. 2 shows their location and allocation to individual BIODIVERSITY transects.

Tab. 1: Meteorological Stations with air temperature measurements

ID	name	elevation	source	start	end	remark	parametrization
c_4489	Großer Arber	1446	DWD	198212	-		T 3, T 4
c_4490	Bodenmais AkkSt	648	DWD	195101	198112		
c_4491	Großer Falkenstein	1307	DWD	194701	198210		
c_4493	Zwieselberg	615	DWD	194801	200309		
c_4497	Zwiesel	612	DWD	199805	-	gaps 2003/2004	T 3, T 4
TWT	water reservoir Frauenau	695	WWA	1991	-		
NPV_1	Waldhäuser	940	DWD NPV	198001	-	device replacement 12/2003	T 1 + 2
							T 1 + 2
NPV_4	Klingenbrunn, Bhf.	759	NPV	198012	-	gap 5/2003-5/2004	T 1, T2, T3
NPV_5	Felsenkancel	1146	DWD	199712	200406		T 1 + 2
NPV_6	Waldschmidthaus	1350	NPV	199712	-	gaps, gap 9/2002- 6/2004	T 1, T2, T3
NPV_7	Gfeichtethöh	1165	NPV	1995	-	only summer	T 1 + 2
NPV_8	Feistenhang	869	NPV	1995	-	only summer	T 1 + 2
NPV_9	Hahnenfalz	752	NPV	1995	-	only summer	T 1 + 2
NPV_10	Hochfallen	761	NPV	1995	-	only summer	T 1 + 2
NPV_11	Schönort	901	NPV	1995	-	only summer	T 1 + 2
NPV_12	Messturm Schachtenau	857	NPV	199204	-	gaps	T 1 + 2
NPV_13	Lusen	1340	DWD	199712	200412		T 1 + 2
NPV_14	Taferlruck	771	LWF	198102	-	gap 2001/2002	T 1 + 2
LWF42	Racheldiensthütte	874	NPV	200410	-		T 1 + 2
K1	Transekte1	740	NPV	200610	-		T 1 + 2
K4	Transekte1	820	NPV	200610	-		T 1 + 2
K5	Transekte1	795	NPV	200610	-		T 1 + 2
K7	Transekte2	770	NPV	200610	-		T 1 + 2
K8	Transekte2	835	NPV	200610	-		T 1 + 2
K9	Transekte2	815	NPV	200610	-		T 1 + 2
K10	Transekte2	837	NPV	200610	-		T 1 + 2
K11	Transekte2	837	NPV	200610	-		T 1 + 2
K12	Transekte2	1290	NPV	200610	-		T 1 + 2
K14	Transekte2	1350	NPV	200610	-		T 1 + 2
K15	Transekte2	1420	NPV	200610	-		T 1 + 2
Ksee	Rachelsee	1090	NPV	200610	-		T 1 + 2
K16	Transekte3	680	NPV	200610	-		T 3
K17	Transekte3	730	NPV	200610	-		T 3
K18	Transekte3	765	NPV	200610	-		T 3
K19	Transekte3	1095	NPV	200610	-		T 3
K20	Transekte3	1100	NPV	200610	-		T 3
K21	Transekte3	1192	NPV	200610	-		T 3
K22	Transekte4	675	NPV	200610	-		T 4
K23	Transekte4	700	NPV	200610	-		T 4
K24	Transekte4	990	NPV	200610	-		T 4
K25	Transekte4	1145	NPV	200610	-		T 4
K26	Transekte4	1140	NPV	200610	-		T 4
K27	Transekte4	1112	NPV	200610	-		T 4
K28	Transekte4	1325	NPV	200610	-		T 3, T 4
K29	Transekte4	1325	NPV	200610	-		T 3, T 4

It is apparent that hardly any stations have measured air temperatures continually over a longer period. Derivation of long-term average temperature relationships for individual transect plots first became possible during the late 1990's, with more reliable series of data from a denser network.

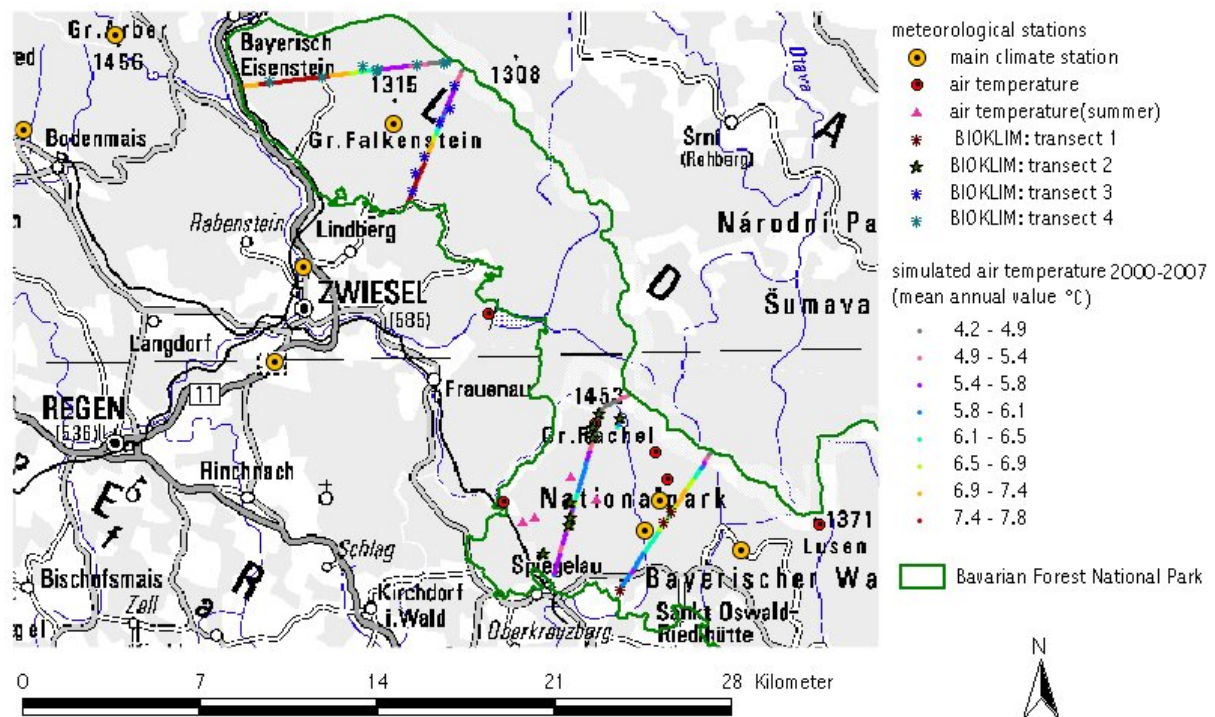


Fig. 2: BIODOL transects with the simulated mean annual temperatures (2000-2007) and the location of all meteorological stations in the area of the transects

Data processing, regionalisation of the point measurements

Measurements of air temperature and humidity at 30 minute intervals are available for all four transects from 10/2006 onwards. Daily values were aggregated from these (mean, minimum, maximum). On the basis of these measurement series for the period 1.10.2006 to 31.10.2007 and all further data available from the DWD, the National Park and the Bavarian Forest Agency (LWF), the spatial regression factor (dependence on altitude) was obtained, enabling further geostatistical regionalization. The nature of the topography called for separate simulations for each transect, using data for different weather stations. The weather stations used for individual transects are indicated in the last column of Tab. 1. The number of stations and the coefficients resulting from the linear regression between yearly values and altitude are presented for transects in Tab. 2.

Tab. 2: Overview of the transects.

Transect	region	Number of meteorological stations	Elevation gradient [°C/meter of altitude]
1 und 2	Große Ohe: T1: Plattenhausen T2: Rachel TS: Rachelsee	26	-0.00457
3	Scheuereck	10	-0.00416
4	Lattenberg, Nord-West-Flanke	10	-0.00401

The calculation of the long-term temperature conditions along the transects during the period 1980 – 2007 was undertaken using the above described „Quadrant Method“ in combination with the calculated elevation gradient. All series of temperature measurements were used, despite longer gaps, because of the low density of temperature observation stations in this period. A comprehensive analysis of the simulation results (Klöcking, 2008) indicated the reliability of the temperature conditions calculated at all 293 transect plots for the last 8 years (2000-2007). The regionalization results for the preceding years are less plausible, because of the insufficient data base. The mean annual temperature (2000-2007) for individual points on a transect lies between 4.2 and 7.8 °C, depending on altitude and exposition, as illustrated in Fig. 2

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Appendix S2 Altitudinal distribution of *S. kotulae*

The altitudinal distribution is based on 47,279 records of molluscs made in South-east Germany. (Strätz, unpublished). Data were collected between 1980-2007. First, we divided the altitudinal range into bands of 100 m. For each band *i* we summed all records of molluscs as well as all records of *S. kotulae*. Sampling frequency differed considerably between bands. We used the approach of Samietz (2005) to correct for such differences:

$$PS_i = \frac{RS_i}{Pm_i * \sum_{i=1}^n \frac{RS_i}{Pm_i}}$$

PS_i = Corrected percentage of *S. kotulae* in altitudinal band *i*.

RS_i = Records of *S. kotulae* in band *i*.

Pm_i = Percentage of all mollusc records in belt *i*.

n = number of altitudinal belts

Fig. 6 plots the PS_i values.

No data were available for the altitudinal belts between 1500-1700m in Bavaria.

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Appendix S3 R-script for local smoother with confidence bands.

The data are stored in the file Semkot.Rdata with the three variables Semkot, Temp and NN. Semkot codes the presence and absence of *Semilimax kotulae* across plots. Temp contains the temperature data and NN the altitude in m. Data can be extracted from **Appendix S5** Species versus plot matrix.

```
#prediction of Semilimax kotulae under current and two global warming szenarios
#based on Mean annual temperature calculated with ArcEcmom based on data from 2000-2007

load("Semkot.Rdata")

par(mfrow=c(1,2))

prog <- glm(Semkot ~ Temp, data = Semkot, family = binomial())

# Prediction of the response
fi <- predict(prog, type = "response")

plot(Semkot$Temp, fi, ylim = c(0, 1), xlab= "Altitude (m.a.s.l.)", ylab= "Probability",cex.lab=1.2,
cex.axis=1.3)
fi.se <- predict(prog, type = "link", se.fit=TRUE)
fi.lower <- fi.se$fit - 1.96*fi.se$se.fit
fi.lower <- exp(fi.lower)/(1+exp(fi.lower))
fi.upper <- fi.se$fit + 1.96*fi.se$se.fit
fi.upper <- exp(fi.upper)/(1+exp(fi.upper))
points(Semkot$Temp,fi.lower, cex=0.6)
points(Semkot$Temp,fi.upper, cex=0.6)

###Addition of the expected global warming after Ipcc 2007

# value of temperature increase +1.8 and +4.0K
incr1 <- 1.8
incr2 <- 4

# new dataframe with new temperature +1.8K
tmp1 <- Semkot
tmp1$Temp <- tmp1$Temp + incr1
# prediction for +1.8K
pred <- predict(prog, newdata = tmp1, type = "response")
pred.se <- predict(prog, newdata = tmp1, type = "link", se.fit=TRUE)
pred.lower <- pred.se$fit - 1.96*pred.se$se.fit
pred.lower <- exp(pred.lower)/(1+exp(pred.lower))
pred.upper <- pred.se$fit + 1.96*pred.se$se.fit
pred.upper <- exp(pred.upper)/(1+exp(pred.upper))

# new dataframe with new temperature +4.0K
tmp2 <- Semkot
tmp2$Temp <- tmp2$Temp + incr2
# prediction for +4.0K
pred2 <- predict(prog, newdata = tmp2, type = "response")
pred2.se <- predict(prog, newdata = tmp2, type = "link", se.fit=TRUE)
pred2.lower <- pred2.se$fit - 1.96*pred2.se$se.fit
pred2.lower <- exp(pred2.lower)/(1+exp(pred2.lower))
pred2.upper <- pred2.se$fit + 1.96*pred2.se$se.fit
pred2.upper <- exp(pred2.upper)/(1+exp(pred2.upper))

###plot of the current and expected probability of S. kotulae among the altitude

win.metafile("ProbabilitySemkot.wmf")
par(las=1,cex.lab=1.5, cex.axis=1.2)

plot(Semkot$NN, fi, ylim = c(0, 1), xlab= "Altitude a.s.l (m)", ylab= "Probability",cex=1.5,pch=21,
bg="blue")
points(tmp$NN, pred, cex=1.5,pch=21, bg="maroon3")
points(tmp2$NN, pred2, cex=1.5,pch=21, bg="red")

text(1000,0.9,"current",cex=1.2)
text(1100,0.4,"+1.8 K",cex=1.2)
text(1350,0.2,"+4.0 K",cex=1.2)

lines(smooth.spline(Semkot$NN, fi,df=5),lwd=3, col="blue")
```

```
lines(smooth.spline(Semkot$NN, fi.upper, df=5), lty=2, col="blue")
lines(smooth.spline(Semkot$NN, fi.lower, df=5), lty=2, col="blue")

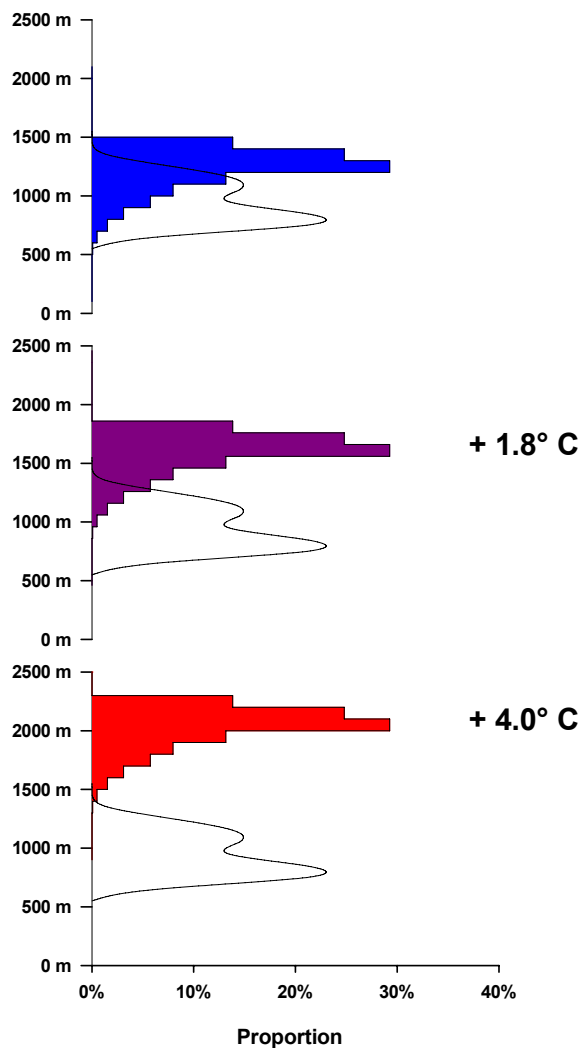
lines(smooth.spline(tmp$NN, pred, df=5), lwd=3, col="maroon3")
lines(smooth.spline(tmp$NN, pred.upper, df=5), lty=2, col="maroon3")
lines(smooth.spline(tmp$NN, pred.lower, df=5), lty=2, col="maroon3")

lines(smooth.spline(tmp2$NN, pred2, df=5), lwd=3, col="red")
lines(smooth.spline(tmp2$NN, pred2.upper, df=5), lty=2, col="red")
lines(smooth.spline(tmp2$NN, pred2.lower, df=5), lty=2, col="red")

dev.off()
```

Appendix S4 Shift of *Semilimax kotulae* distribution caused by global warming.

Blue area shows the current altitudinal distribution of *S. kotulae* in the Bavarian Forest National Park. The curve shows the area at different altitudes within the National Park. The lower two graphs show two scenarios of global warming of +1.8K and +4.0K. Note the highly reduced overlap under the last scenario.



Appendix S5 Species *versus* plot matrix

[illegible]

[illegible]

[illegible]

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				
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			