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DIPLOMARBEIT

Species richness and composition of bird assemblages along an elevational gradient in the Eastern Alps (National Park Gesäuse, Austria)

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Abstract

Most studies about changes of bird species richness along elevational gradients were carried out in tropical regions, whereas quantitative information is scarce for temperate mountain ranges such as the Alps. We conducted standardized bird surveys using point censuses along an elevation gradient in the Eastern Alps to study changes of species richness, species composition and relative abundance of feeding guilds. Additionally, we related altitudinal changes of the avifauna to changes of biotic (vegetation structure) and abiotic variables (area of elevation belts).

The investigated altitudinal gradient consisted of three different elevation transects in the National Park Gesäuse (Styria, Austria) on the southern slopes of the Buchstein massif covering an altitudinal range between >500 m (valley floor of Ennstal) to 2,035 m a.s.l. (summit of Tamischbachturm, 2 transects) and 1,928 m a.s.l. (rocky massif of Großer Buchstein, 1 transect), respectively. In total 87 census points were selected along the three transects. Birds were recorded visually and acoustically between 3rd April and 25th July at each census point during three 10 min-observation units. For each bird it was noted if it was recorded within or outside a radius of 50 m around the census point. The following habitat parameters were measured or estimated for each census point: altitude a.s.l., distribution of tree diameters, maximum height of woody vegetation, species richness of woody plants and tree density. Furthermore, for all 100 m-elevation belts their total area and the southern slope area [km²] were extracted from digitalized maps.

A total of 40 breeding bird species were recorded. Species richness did not decline linearly but showed a plateau between 500 and 1,200 m, where an average of 10 species per census point was recorded. From 1,200 m towards higher altitudes species numbers decreased continuously, reaching a minimum of 1-2 species per census point at the highest elevations. Beside the factors altitude and area per altitudinal zone, which accounted for most of the variation of species richness, the variables vegetation height [m], tree density, tree diameter [cm] and woody plant species diversity proved to influence richness of bird assemblages. A comparison of breeding bird species composition between census points based on Bray-Curtis similarity indices demonstrated significant differences between the forest belt and the zone above the timberline, and within the forest belt between mixed forest and coniferous woodlands. Species composition was significantly related to altitude, woody plant species richness and maximum height of woody vegetation. Differences of the relative abundance of feeding guilds between elevation belts mirrored changes of habitat structure, e.g. insectivorous stem climbers disappeared at the timberline. Regarding absolute numbers of individuals a significant decrease of omnivores, ground-dwelling insectivores and insectivores foraging within the vegetation could be observed. Insectivorous stem climbers reached their highest abundances at mid-elevations, perhaps indicating an intensive forest use until recently at lower elevations.

Zusammenfassung

Während aus tropischen Gebirgen detaillierte Studien über Veränderungen des Artenreichtums von Vögeln entlang von Höhengradienten vorliegen, sind quantitative Informationen aus Gebirgen der temperaten Zone, wie den Alpen, spärlich. Mittels Punkt-Stopp-Zählungen wurden Vogelgemeinschaften entlang eines

Höhengradienten in den Ostalpen erfasst, um Veränderungen des Artenreichtums, der Artenzusammensetzung und der Struktur von Nahrungsgilden zu untersuchen. Zusätzlich wurde die Bedeutung verschiedener biotischer (Vegetationsstruktur) und abiotischer (Fläche pro Höhenzone) Variablen für Veränderungen der Vogelgemeinschaften getestet.

Die Untersuchung wurde im Nationalpark Gesäuse (Steiermark) im Bereich des südlichen Buchsteinmassivs durchgeführt. Vogelzählungen erfolgten entlang von drei Höhengradienten, die vom Boden des Ennstals (>500 m) auf den Tamischbachturm (2.035 m, 2 Gradienten) beziehungsweise bis zum Felsmassiv des Großen Buchsteins (1.929 m, 1 Gradient) hinaufreichten. Insgesamt wurden entlang der drei Höhentransekte 87 Beobachtungspunkten eingerichtet. Die Erfassung von Vögeln an den Beobachtungspunkten erfolgte für jeweils 10 min optisch und akustisch an drei Terminen zwischen dem 3. April und dem 25. Juli 2006. Zusätzlich wurde die Entfernung des Vogels vom Beobachtungspunkt (innerhalb oder außerhalb 50 m-Radius) notiert. Folgende Habitatparameter wurden für jeden Zählpunkt gemessen oder geschätzt: Höhe ü. NN, Verteilung der Baumstammdurchmesser, maximale Höhe der Gehölzvegetation, Baum- und Gehölzartenreichtum und Baumdichte. Außerdem wurden die Gesamtfläche des Buchsteinmassives und die Fläche des Südhangs jeweils für jede einzelne 100 m-Höhenzone mit Hilfe von digitalen Karten ermittelt.

Insgesamt konnten 40 Brutvogelarten innerhalb der 50 m-Radien gezählt werden. Der Artenreichtum nahm mit zunehmender Höhe nicht kontinuierlich ab, sondern zeigte ein Plateau zwischen 500 und 1200 m mit durchschnittlich 10 nachgewiesenen Arten pro Beobachtungspunkt. Danach erfolgte eine signifikante Abnahme des Artenreichtums bis in die höchsten untersuchten Lagen. Außer den Habitatvariablen Höhe ü. NN und Fläche pro Höhenzone, die den größten Beitrag zur Erklärung der Veränderungen des Vogelartenreichtums leisteten, konnten signifikante Zusammenhänge mit Vegetationshöhe, Baumdichte, Baumdurchmesser, Gehölzartenreichtum und Habitatdiversität gefunden werden. Ein Vergleich der Vogelartenzusammensetzung zwischen Beobachtungspunkten mittels Bray-Curtis Ähnlichkeiten, zeigte einen deutlichen Effekt der Vegetationsstruktur auf die Artenzusammensetzung auf. Signifikante Unterschiede konnten zwischen den Habitattypen der Waldzone und den Beobachtungspunkten oberhalb der Waldgrenze und zudem zwischen Misch- und Nadelwald gefunden werden. Signifikante Effekte auf Veränderungen der Artenzusammensetzung konnten neben der Höhe ü. NN, für Gehölzartenvielfalt und Vegetationshöhe belegt werden. Unterschiede der relativen Abundanzen von Nahrungsgilden zwischen Höhenstufen spiegelten Veränderungen der Habitatstruktur wieder. Zum Beispiel verschwanden insektivore Stammkletterer oberhalb der Waldgrenze. Individuenzahlen von omnivoren und insektivoren Vögeln, die am Boden oder in der Vegetation nach Nahrung suchen, nahmen signifikant mit zunehmender Höhe ab. Insektivore Stammkletterer hingegen erreichten ihre höchsten Abundanzen in mittleren Höhenlagen, möglicherweise bedingt durch die intensive Nutzung der Wälder tieferer Lagen bis in neuere Zeit hinein.

Keywords: area; birds; elevational gradient; feeding guilds; species richness; species composition; The Alps

Introduction

Some of the most general features of life on earth are changes of abundance and diversity of organisms along the earth's major environmental gradients, including those of elevation (Brown 2001). The significant change of abiotic and biotic environmental variables along elevational gradients strongly affects patterns of abundance, distribution and diversity of most organisms. As emphasized by Brown & Lomolino (1998), lower elevational zones usually differ from higher altitudes by: (1) a greater total amount of resources and population numbers; (2) more refugia and space for species with larger home ranges; (3) greater habitat diversity; and (4) a greater potential for serving as target for potential immigrants. Compared to lower vegetation belts, montane ecosystems are small and isolated (Mac Arthur 1984), which, according to the theory of island biogeography (MacArthur & Wilson 1967), should negatively affect species richness. However, not all environmental variables change continuously with increasing altitude. For example, precipitation and related ecologically relevant variables (e.g. soil moisture and evapotranspiration) typically show a maximum at intermediate elevations. Consequently, some variables such as primary productivity and plant species richness reach highest values at mid-elevations (Able & Noon 1976; Rahbek 1995; Brown 2001; Ding et al. 2005; Lomolino et al. 2006), which may partly explain the commonly found mid-elevation peak of species richness (e.g., Rahbek 2005).

Most studies on changes of bird communities along elevational gradients were conducted in tropical and subtropical regions, like Peru (Terborgh 1971, 1977), Ecuador (Paulsch & Müller-Hohenstein 2008), Costa Rica (Blake & Loiselle 2000; Chaves-Campos 2003, 2004), Bolivia (Kessler et al. 2001; Herzog et al. 2005), Mexico (Navarro, 1992), India (Raman et al. 2005) and Taiwan (Lee et al. 2004; Ding et al. 2005). In contradiction, studies on elevational changes of bird assemblages from the temperate zone are scarce and confined to few mountain ranges (e.g. Rahbek 1995), including mountain ranges in the United States (Able and Noon 1976), the Alps (Wartmann & Furrer 1977, 1978; Winding et al. 1993; Hochrathner 1997; Oberwalder et al. 2002; Reboud & Frochot 1998; Sergio & Pedrini 2007) and the Carpathians (Głowaciński & Profus 1992).

This study aimed to quantify avifaunal changes along an elevational gradient in the Eastern Alps. Particularly, the following questions were addressed:

(1) How does bird species richness change along the elevation gradient?

Two major patterns of changing bird species richness along elevational gradients can be found: a continuous decrease of species numbers with increasing altitude (e.g. Terborgh 1977, MacKinnon & Phillips 1993, Sackl & Samwald 1997; Sergio & Perdini 2007) and a mid-domain peak (Rahbek 1997; Heaney 2001; MacKinnon & Phillips 1993, Nor 2001; Rickart 2001; Sanchez-Cordero 2001; Sanders 2002; Herzog et al. 2005; Ding et al. 2005). A hump-shaped altitudinal species-richness pattern is the most common (c. 50%), with a monotonic decreasing pattern also frequently (c. 25%) reported (Rahbek 2005). However, the emerging pattern is strongly influenced by the spatial grain and extent (Rahbek 2005). Although (qualitative or semi-quantitative) information on the vertical distribution of species in the Alps can be extracted from published breeding atlases for the areas of Switzerland (Schmid et al. 1998), Austria (Dvorak et al. 1993) and individual Austrian provinces (Styria: Sackl & Samwald 1997; Upper Austria: Brader & Aubrecht 2003; Carinthia: Feldner et al. 2006) detailed quantitative studies on changes of bird communities on smaller spatial scales covering elevational gradients ranging from the valley floor to the summits of individual mountain massifs are missing. This case study from Eastern Austria contributes to fill part of this information gap.

(2) Which abiotic and biotic habitat variables reliably predict changes of bird species richness along the environmental gradient?

Because of the conical shape of mountains, area is decreasing with elevation (Lomolino et al. 2006). However, depending on the shape of a studied mountain massif, area may not decline continuously, thereby affecting elevational patterns of species richness due to the well-established species-area relationship (Lomolino 2001). However, area is not the only factor contributing to explain variability of species richness between different altitudes. Close relationships can exist between species richness and changing habitat complexity (Rahbek 1995). For example, decreasing height of woody vegetation from the valley floor towards higher altitudes can reduce the extent of vertical stratification of vegetation structure thereby most likely reducing the diversity of microhabitats available to birds. Furthermore, differences of tree density and plant species richness between elevation belts may influence the structural heterogeneity and the diversity of available food sources and nesting sites.

(3) How does species composition of bird communities change between altitudes?

Terborgh & Weske (1975) mentioned three principal factors influencing altitudinal structuring of communities: abrupt changes of habitats, gradual changes in environmental parameters and competition. Navarro (1992) emphasized the vertical distribution of vegetation zones as important factor for explaining altitudinal distribution of species and species turnover between elevation belts. In the Alps significant changes of bird species composition may be particularly related to the dramatic structural change of vegetation at the timberline. However, also less sharp ecotones such as the transition zone from mixed to coniferous forest may be characterized by a conspicuous change of bird species composition.

(4) Does the response to altitude differ between feeding guilds and functional groups?

The abundance of feeding guilds can strongly depend on habitat structure (Wartmann & Furrer 1978; Hochrathner 1997; Brunner 1998, 2001), which changes with increasing altitude, thereby differentially altering the available amount of food resources for feeding guilds and the vegetation structures required for foraging by different functional groups along the elevation gradient (Blake & Loiselle 2000). Particularly the change of vegetation structure from the upper montane forest towards the dwarf pine zone at the timberline may not only influence species richness and composition but also may significantly affect the abundance of feeding guilds and functional groups.

Methods

Study area

The study area was located in the National Park Gesäuse (NPG), Province Styria, (Austria). The park founded on 26th October 2002 is part of the Ennstal Alps and consists of two massifs, the Buchstein and the Hochtor massif, covering a total area of about 110.5 km^2 and an elevational range between 490 and 2,370 m a.s.l. The river Enns has cut a steep V-shaped valley between the two massifs. Geologically, NPG belongs to the Northern Limestone Alps (http://www.nationalpark.co.at/en/index.php).

The Gesäuse is influenced by a mild and damp central European and oceanic climate; westerly winds bring fronts of rain from the Atlantic Ocean. The Northern Limestone Alps are part of a “stacking area” (Wakonigg 1978), where clouds from the north pile up on the mountain range causing periods of precipitation. Precipitation varies from 1,200 to more than 2,500 mm per year, and its quantity increases with height above sea level (http://www.nationalpark.co.at/en/index.php). In spring weather conditions change frequently and snowfall until the valley floor is no exception (Kollmann 1975). The survey area does not belong to the central “stacking area”, because it is situated in the outskirts of the Northern Limestone Alps. For this reason the phenomenon described above occurs in an alleviated form (M. Seiss, pers. comm.).

The land cover of NPG is predominated by woodland (50 % of total area), alpine areas (31.0 %), scrub-land (13.5 %) and high pastures and meadows (5.0 %). Due to the difficult access to the forested areas on the steep slopes on both sides of the Enns Valley, a large proportion of these forests is relatively undisturbed (http://www.nationalpark.co.at/en/index.php). Based on vegetation structure, Fischer et al. (1994) distinguished three altitudinal zones. The montane zone (“Montanstufe”) ranges from an altitude of 600 m to the timberline situated between 1,500 (lower limit) and 2,000 m (upper limit). At lower elevations (up to 800-900 m) forests are dominated by *Fagus sylvatica*; higher elevations are characterized by *Picea abies-Abies alba* stands, *Picea abies-Larix decidua* stands or stands only dominated by

Picea abies. The most common societal grouping in NPG is *Picea abies-Abies alba-Fagus sylvativa* wood, but this mixed woodland was often replaced by artificial *Picea abies* stands. On steep slopes *Erica carnea-Pinus sylvestris* wood can be found on southern slopes (M. Seiss, pers. comm.). In the subalpine belt (lower limit in NPG: 1,500 m) the number of trees is declining and *Pinus mugo* stands are increasingly dominating. At even higher altitudes, in the alpine zone (lower limit in NPG: c. 1,800 m), dwarf-shrubs, alpine meadows, rocky elements and some isolated *Pinus mugo* stands are developed. The natural timberline in the central Alps is at an altitude of about 2,000 m, whereas in the Northern Limestone Alps the timberline is depressed to an altitude of 1,800 m (Maurer 1981). Because of the site-specific relief shape and due to former conversion of forest to pastures, the timberline in NPG is situated predominantly at an altitude of 1,600 m or even lower (at c. 1,500 m) as in the study area.

Study sites

All study sites were situated on the southern slope of the Buchstein massif, where standardized bird observations were conducted along three trails reaching from the valley floor (>500-600 m) either to the peak of Tamischbachturm (2,035 m a.s.l., 2 trails) or to the summit of Großer Buchstein (1,928 m a.s.l., 1 trail). The three elevational transects mainly followed common hiking routes to save time by better accessibility. All three trails had almost the same exposition: (1) Gstatterboden to Tamischbachturm (TW) − southwest, (2) Hieflau-Tamischbachturm (TE) − southeast, and (3) Gstatterboden to Großer Buchstein (B) − southeast to southwest.

A maximum of three census points were selected per 100 m elevational belt along each trail. Due to local circumstances (steep slopes, wide avalanche valleys) less census points could be established in individual elevation belts and the minimum recommended distance between census points of 300 m in woodlands (Südbeck et al. 2005) was not always achieved. Points were localized based on the Austrian Map ÖK 1:50000 and the hiking map “Alpenvereinskarte Ennstaler Alpen Gesäuse 1:25000”. A total of 27 census points were selected along trail B, 33 along TW and 27 along TE (Fig. 1). For all 87 census points coordinates were measured with a GPS (Garmin 12 CHANNEL) and rechecked with ArcGIS 9 (ArcMap).

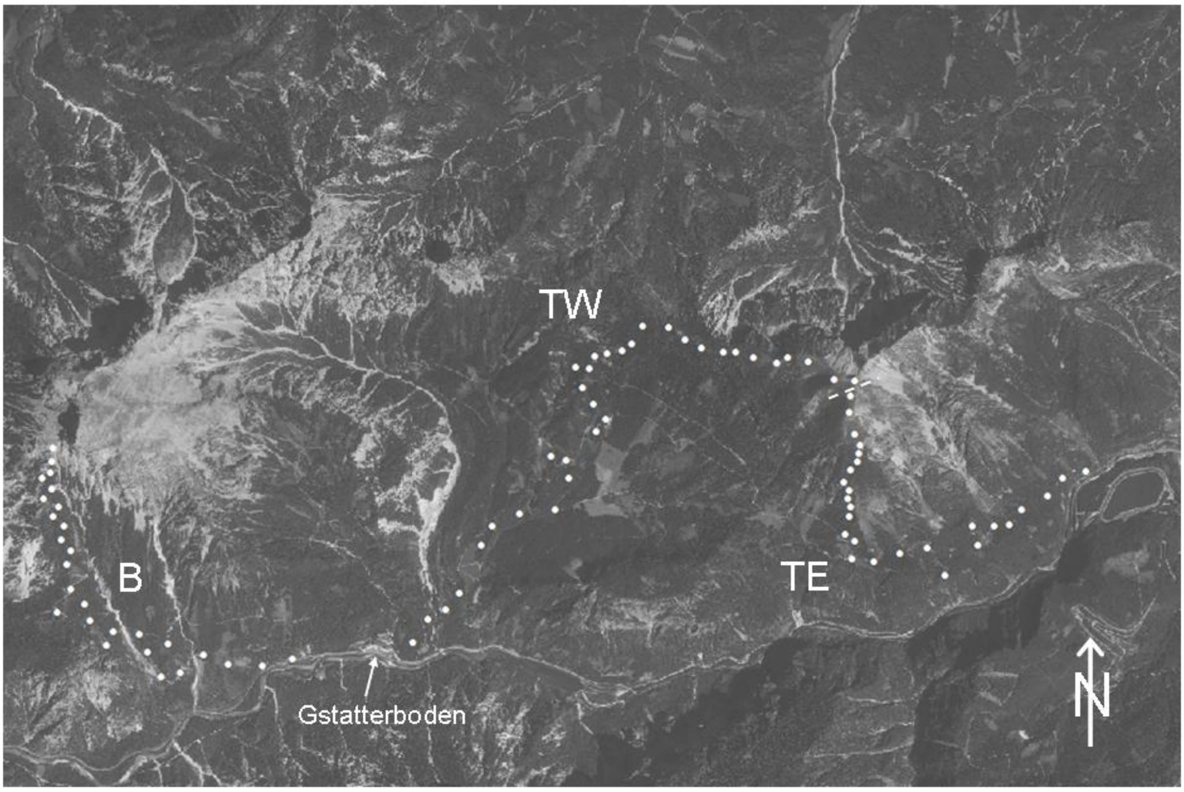

Figure 1. Survey area with selected bird census points along trails to the summits of Großer Buchstein (B) with 27 census points, Tamischbachturm-West (TW) with 33 census points and Tamischbachturm-East with 27 census points.

Bird survey method

Birds were surveyed three times at each census point between 3rd April and 25th July at a total of 37 days. The minimum period elapsing between two counts at the same census point was two weeks. Due to the delayed breeding activities of birds and the danger of avalanches until late spring at higher altitudes, point counts above the timberline started later in the season, at 19th of June.

During 10-min observation units all birds recorded visually and acoustically were noted. Unfamiliar voices were tape-recorded using an Olympus Digital Voice Recorder VN-480 PC and identification was checked afterwards using tape records by Roché (2000). Whenever possible, details such as sex and behavior indicating breeding activity were noted. Additionally, it was estimated if the recorded bird was within or outside a radius of 50 m around the census point. If not mentioned otherwise, analyses are based on counts of birds recorded within a radius of 50 m.

Breeding status of bird species was assumed for individual census points when courtship (such as singing) or breeding behavior (such as carrying nesting material or food) was noticed, or when a species was recorded during at least two different counts. For *Loxia curvirostra* breeding was only assumed when courtship or breeding behavior was observed, because even the observation of birds during several counts does not reliably indicate breeding activity due to the unusual breeding phenology of the species (e.g. Südbeck et al. 2005).

To quantify total bird species richness for individual 100 m-elevation belts (total of 15 belts), records from all census points within the respective elevation belt were taken into account. Bird species were counted for individual 100 m-elevation belts even when not recorded, but observed in the adjacent lower and upper 100 m-elevation belts (compare Appendix 1). Their occurrence in neighboring elevation belts indicates that they potentially can occur at intermediate altitudes but perhaps remained unrecorded due to an inadequate temporal or spatial sampling effort. Only adjacent elevation belts were considered to account for the possibility of true disjunct vertical distributions of species (as documented e.g. for *Phoenicurus ochruros*, Glutz von Blotzheim 2001).

Feeding guild and functional group affiliation

To analyze changes of abundance of feeding guilds and functional groups along the elevation gradient, all observed breeding bird species counted at census points within a radius of 50 m were assigned to five groups based on their feeding preferences in spring and early summer and the habitat structures used during foraging (according to Glutz von Blotzheim 2001): (1) omnivorous species; (2) ground-dwelling insectivorous species; (3) insectivorous stem climbers; (4) insectivorous species searching for food in the vegetation (e.g. leaf gleaners); (5) granivorous species.

Measured habitat variables

(1) Altitude was measured for each bird census point with an altimeter (HiTRAX) and GPS (Garmin 12 CHANNEL).

(2) Area of 100 m-elevation belts was calculated with a GIS application for the entire Buchstein Massif and its southern slope only.

(3) Stem perimeters (at breast height) of a maximum of 16 trees were measured per census point. Therefore, refering to the central census point a reference point each in the direction North, East, South and West was established at a distance of 20 m. For the sectors North-East, South-East, South-West and North-West the four closest trees with a stem diameter of ≥ 10 cm to each reference point and within a distance of ≤25 m were measured.) For further analyses all measured stem perimeters were transferred to diameters in breast height (DBH).

(4) Maximum height of woody vegetation was estimated for each census point.

The following habitat variables (5–9) were quantified for census points by measurements within a 6 m wide corridor along four 30 m transects orientated from the bird census point in the cardinal directions North, East, South and West resulting in a total area of 684 m² (= 720 m² without 36 m² overlap of transects). Afterwards the variables were converted to values per 100 m².

(5) Tree species richness was quantified as total number of tree species with a DBH ≥ 10 cm.

(6) Tree density was measured by counting all trees with DBH ≥ 10 cm.

(7) Proportion of coniferous trees of was calculated as percentage of total number of counted trees.

(8) Percentage of area covered with dwarf pine (*Pinus mugo)* stands was estimated.

(9) Woody plant species richness was quantified for census points above the timberline including *Pinus mugo*.

Additionally the importance of woody debris was quantified as the number of death trees with DBH ≥10 cm lying and standing per 100 m². However, due to the overall very small numbers of dead trees this variable was not included in further analyses.

Vegetation type affiliation of bird census points

Bird census points were assigned to the forest belt when no dwarf pines were found within a radius of 50 m. All points with dwarf pines were classified as located above the timberline. Based on the numbers of trees counted within the transect area of 684 m^2 (see above), census points within the forest belt were assigned to coniferous woodland (<10 % deciduous trees) and mixed forest (>10 % deciduous trees). Above the timberline the estimated area covered by dwarf pines was used to assign census points to habitat types: dwarf pine belt (dwarf pine cover: >40 %), alpine meadows with isolated dwarf pine stands (<40 %) and alpine meadows and rocks (no dwarf pines).

To measure habitat heterogeneity of single 100 m-elevation belts, the mean similarity of woody plant species composition (quantified as mean Sørensen similarities) of all census points within the respective 100 m-elevation belts was calculated.

Statistical analysis

When not mentioned otherwise analyses were carried out with the program Statistica 7.1 (StatSoft 2005). When data were not normally distributed, adequate data transformations were used to achieve normal distribution. When normal distribution could not be achieved, non-parametric statistical tests were used for data analyses.

To test for effects of biotic habitat variables on bird species richness of 100 m-elevation belts, mean variable values per census point were calculated for each elevation belt.

Generalized linear models (GLMs) were calculated to test simultaneously for relationships between habitat variables and bird species richness by including all predictor variables. Then a ‘step-down’ approach was used to determine the minimum adequate model and hence identify which habitat variables had the strongest influence on species richness of 100 m-elevation belts or census points. Each predictor variable was excluded from the model in turn. The removed variable causing the least influence on overall model deviance according to Akaike Information Criterion (Crawley 1993) was removed and the process repeated again. This was continued until only habitat variables remained in the model that significantly affected bird species richness.

Differences of breeding bird species composition between census points were quantified by Bray-Curtis similarities (based on square-root transformed abundance data). A non-parametric multi-dimensional scaling (NMDS) ordination calculated with Statistica 7.1 (Statsoft 2005) was used to visualize similarities of species composition between census points. A one-way ANOSIM was calculated with the program Primer v5 (Clarke & Gorley 2001) to test for differences of species composition between census points assigned to different vegetation zones. A Spearman matrix rank correlation (performed with 999 permutations) was used to test if similarity of species composition (quantified by Bray-Curtis similarities) between census points was affected by spatial autocorrelation. The matrix rank correlation was performed with the software Primer v5 (Clarke & Gorley 2001). Furthermore, partial Mantel tests were conducted to test if relationships between bird species composition and habitat variables remained significant after corrected for spatial autocorrelation of census points. Partial Mantel test were calculated with the software zt (Bonnet & Van de Peer 2002). Geographical distances between census points were extracted from digital maps with ArcGIS (ArcMap).

Results

Species richness of elevation belts: effects of altitude, area and habitat diversity

For measuring recorded and estimated species richness of 100 m-elevation belts observations outside the 50 m radius around census points were included when located within the respective 100 m-elevation belt. The smaller number of available census points in the lowest (<600 m) and the highest elevation belts (>1,900 m) can potentially cause an underestimation of species richness, when interpolating vertical ranges of species. The missing bird records from adjacent elevation belts below and above, respectively, potentially bias species richness estimated for lowest and uppest 100 m-elevation belts. Therefore, these elevation belts were not considered in all further analyses. For the remaining thirteen 100 m-elevation belts, both measures of species richness, recorded and estimated species numbers, were highly correlated (r = 0.95, N = 13, p < 0.001).

Species richness significantly declined with increasing elevation along the entire altitudinal gradient (recorded species: r_s = -0.86, N = 13, p < 0.001; estimated species: r_s = -0.79, N = 13, p = 0.001). However, between 600 and 1,200 m recorded species numbers were not significantly affected by altitude (r_s = 0.15, N = 6, p = 0.770) and estimated species richness even increased significantly with increasing altitude (r_s = 0.88, N = 6, p = 0.021). Highest species richness was reached at the transition zone between deciduous and coniferous forest at >1,100–1,200 m, where 31 and 33 species were observed and estimated, respectively (Fig. 2a). From 1,200 m towards the highest altitudes species richness decreased monotonously (recorded species: r_s = -0.99, N = 7, p < 0.001; estimated species: r_s = -0.99, N = 7, p < 0.001). The linear decline of species numbers recorded and estimated for 100 m-elevation belts was only interrupted by a less rapid decrease of species numbers as expected by a linear model just below the timberline at >1,400-1,500 m (Fig. 2a).

An even closer relationship was found between species richness and total area ($\log_{10}$-transformed) (recorded species: r = 0.95, N = 13, p < 0.001; estimated: r = 0.97, N = 13, p < 0,001) and southern slope area ($\log_{10}$-transformed) of 100 m-elevation belts (recorded species: Fig. 2c; estimated: Fig. 2d). Total and southern slope area of 100 m-elevation belts did not decrease continuously from the valley floor towards higher altitudes but reached their maximum at an altitude between 1,000 and 1,100 m (Fig. 2b).

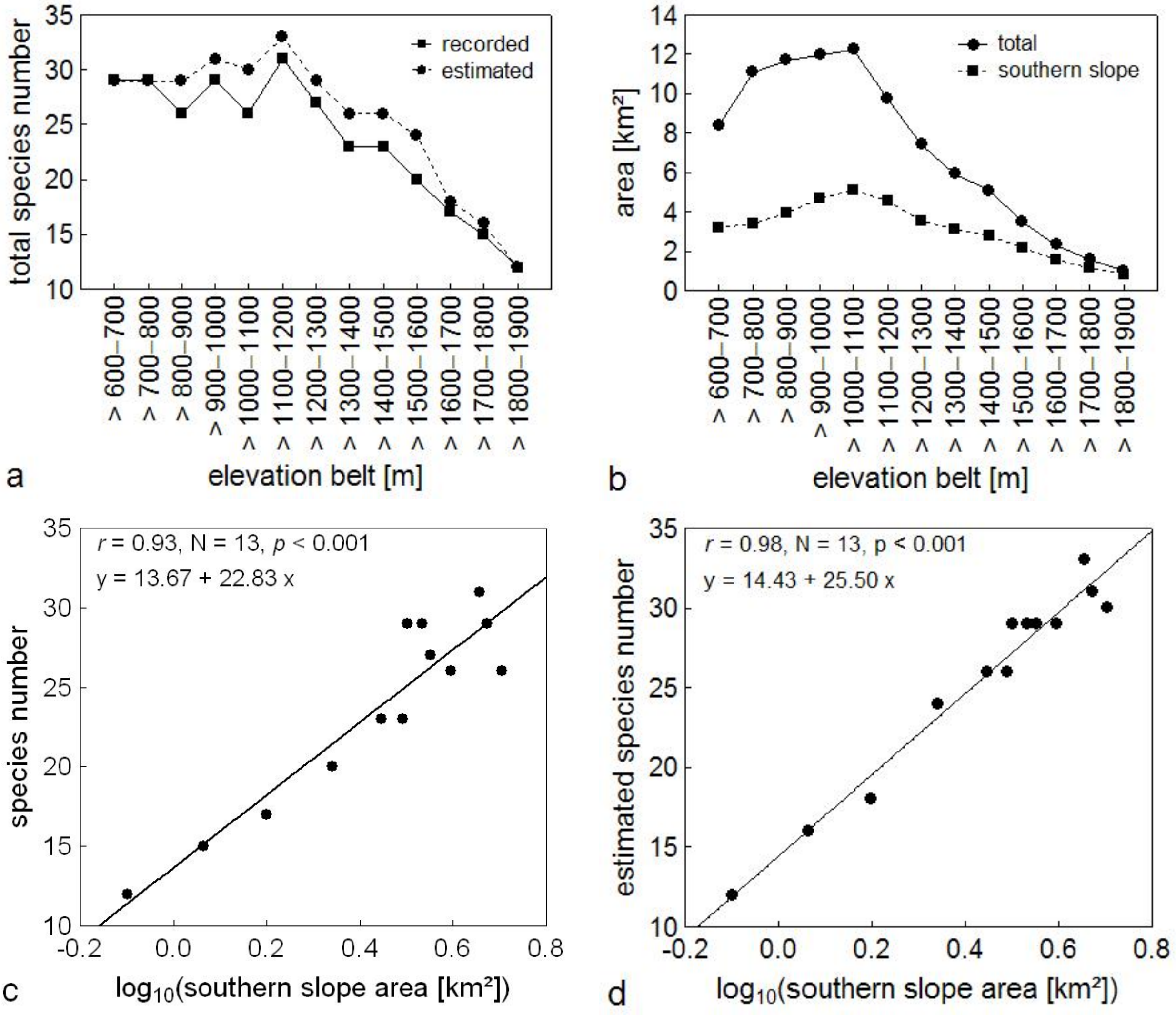

Figure 2. Effects of altitude and area on bird species richness. (a) Bird species richness recorded and estimated for 100 m-elevation belts. (b) Total area and southern slope area of 100 m-elevation belts. Relationship between birds species richness recorded (c) and estimated (d) for 100 m-elevation belts and area of southern slope ($\log_{10}$-transformed).

The mean Sørensen similarity for woody vegetation between census points showed a significant overall increase from lower to upper 100 m-elevation belts ($r_s = 0.91$, N = 13, $p < 0.001$) indicating decreasing habitat diversity and increasing similarity at higher altitudes (Fig. 3a). Bird species numbers recorded for 100 m-elevation belts decreased significantly with increasing mean Sørensen values of woody vegetation

(Fig. 3b). A similar negative response to decreasing habitat diversity was found for estimated bird species richness (*r* = -0.91, N = 13, $p < 0.001$).

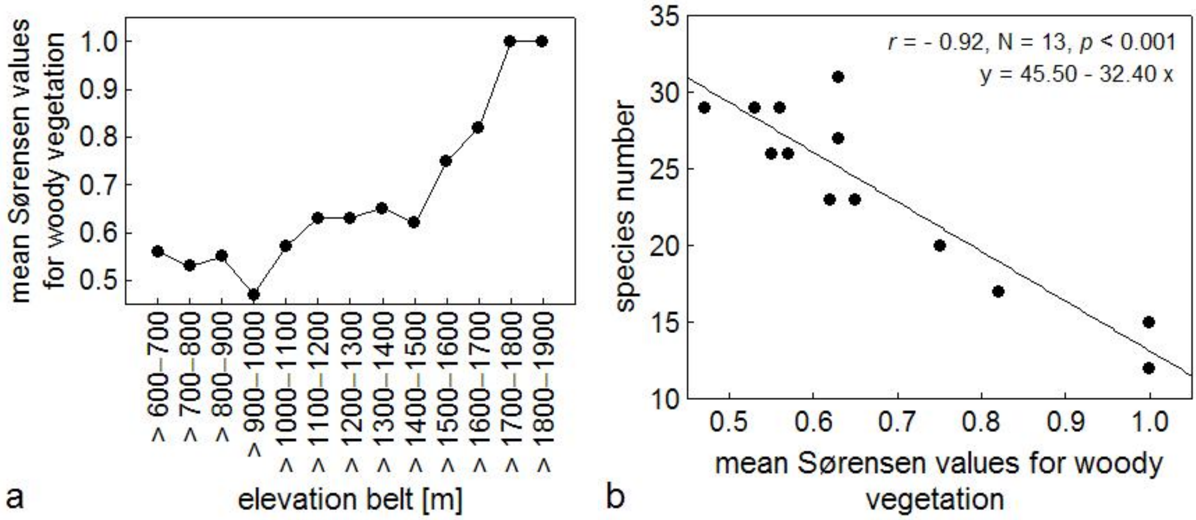

Figure 3. Change of habitat diversity (quantified as mean Sørensen similarity for woody vegetation) of 100 m-elevation belts along the elevational gradient (a) and its relationship with recorded birds species richness (b).

GLMs were calculated to test synchronously for effects of altitude, area and habitat diversity (quantified as mean Sørensen similarity for woody vegetation) of 100 m-elevation belts on species richness of breeding birds. The minimum adequate GLM model showed that area of 100 m-elevation belts and altitude significantly affected bird species richness, while habitat diversity did not prove to contribute significantly to improving the model (Tab. 1). The effect of area and altitude on bird richness proved to be very similar independently of the used richness measure, recorded or estimated species numbers (Tab. 1). The same variables remained significant in the final model, when GLMs were calculated with total areas instead of southern slope areas of 100 m-elevation belts (data not shown).

Table 1. Relationships between species richness of breeding birds in 100 m-elevation belts (N = 13) and the variables altitude, southern slope area [km^2] (log_{10}-transformed) and mean Sørensen similarities of woody vegetation tested with generalized linear models (GLM) separately for recorded and estimated species numbers. Resulting models selected by a "step-down" approach (see text) are ranked according to Akaike information criterion (AIC). The final model (all variables significant) is printed bold.

Richness measure	Included variables	AIC	*p*
Recorded species	altitude, area, similarity of woody vegetation	69.39	<0.001
	altitude, area	**68.14**	**<0.001**
	Area	73.47	<0.001
Estimated species	altitude, area, similarity of woody vegetation	65.97	<0.001
	altitude, area	**64.80**	**<0.001**
	area	69.27	<0.001

Species richness of census points: effects of altitude and vegetation

A total of 40 breeding bird species, excluding records of eight species for which breeding appeared to be unlikely, were recorded at the 87 census points within the 50 m radius. The number of breeding bird species recorded at census points decreased significantly from the valley floor towards the highest elevations (r_s = -0.70, N = 87, $p < 0.001$). However, species richness did not decline linearly from the lowest to the highest census points. Between 500 and c. 1,150 m with a mean bird species number per census point (± SD) of 10.1 (± 2.4) no clear pattern was found and species numbers recorded per census point varied strongly (Fig. 4). Within this elevation range species numbers recorded per census point even showed a weak positive trend with increasing elevation (r_s = 0.26, N = 45, p = 0.078). From 1,150 m towards the highest altitudes, species numbers per census point decreased continuously (r_s = -0.82, N = 42, $p < 0.001$) reaching a minimum of only two species per census point at elevations around 2,000 m (Fig. 4).

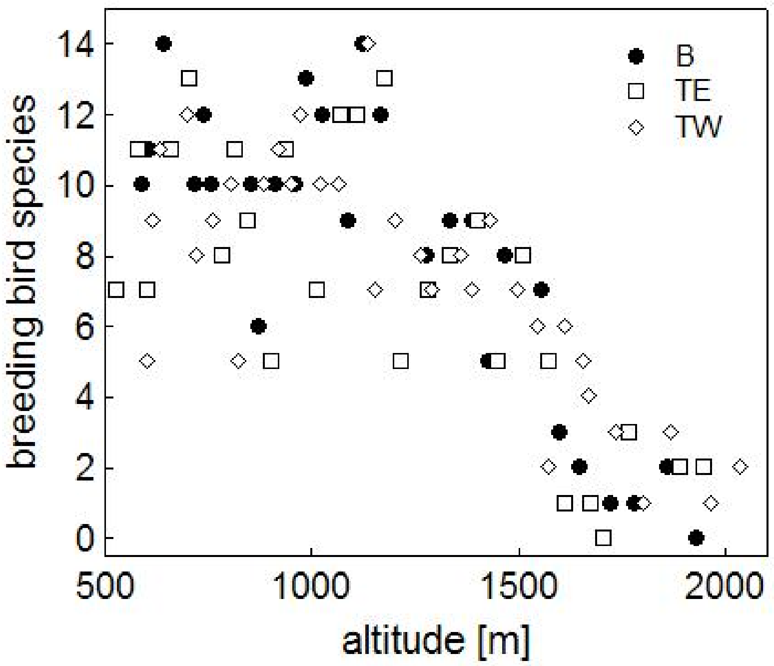

Figure 4. Numbers of breeding bird species recorded at census points in different altitudes along three elevation transects indicated by different symbols: B = Großer Buchstein, TE = south-eastern slope of Tamischbachturm, TW = south-western slope of Tamischbachturm.

To test for effects of the habitat variables altitude, tree species richness and maximum height of woody vegetation on species richness of breeding birds recorded at census points, GLMs were calculated including all habitat variables and all possible subsets. Only the variables altitude and maximum vegetation height remained in the minimum adequate GLM (all variables significant), which was selected by the "step-down" approach (Tab. 2). Although tree species richness appeared to be redundant in explaining variability of bird species richness, it proved to be positively correlated with bird richness in an univariate test ($r = 0.52$, N = 84, $p < 0.001$).

Table 2. Relationships between numbers of breeding bird species recorded at census points and the variables altitude, tree species richness and maximum height of vegetation tested with generalized linear models (GLM). Resulting models selected by a "step-down" approach (see text) are ranked according to Akaike information criterion (AIC). The final model (all variables significant) is printed bold.

Variables included	**AIC**	***p***
altitude, tree species richness, max. vegetation height	385.58	<0.001
altitude, max. vegetation height	**384.02**	**<0.001**
max. vegetation height	397.42	<0.001

Overall, maximum height of vegetation decreased with increasing altitude but remained relatively stable between the valley floor and ca. 1,500 m (Fig. 5a). The number of breeding bird species recorded at census points increased with increasing maximum height of woody vegetation (Fig. 5b).

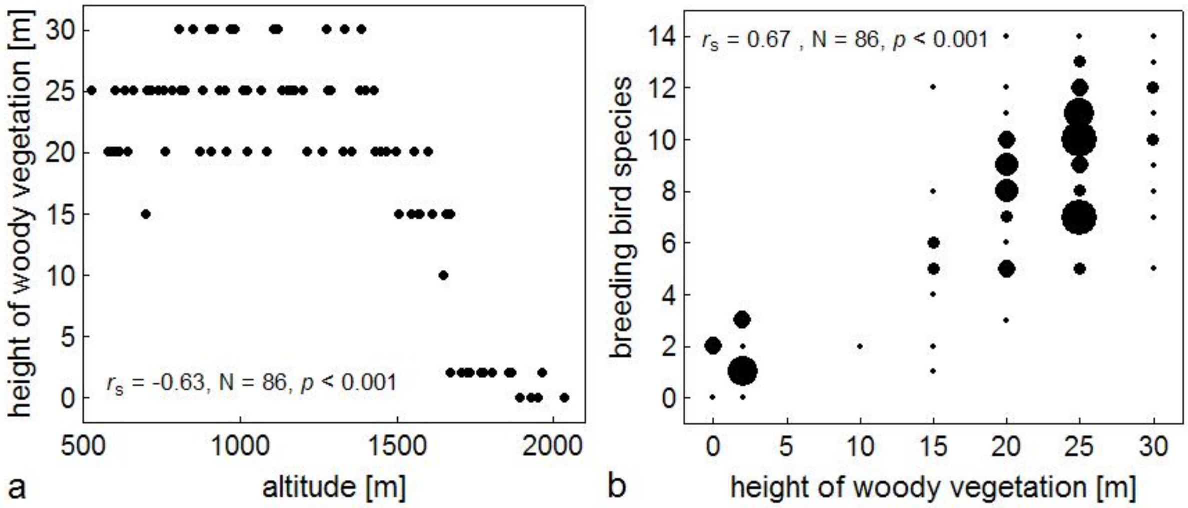

Figure 5. Change of maximum height of woody vegetation at census points along the altitudinal gradient (a) and the relationship between bird species richness and maximum height of wood vegetation (b). For both graphs results of Spearman rank correlations are provided. Larger bubbles in Fig. 5a indicate a larger number of census points.

Because of a sharp transition between forest belt and mountain pine belt between 1,400 and 1,600 m (compare rapid decline of maximum height of woody vegetation in Fig. 5a), different habitat variables may affect bird species richness above and below the timberline. Therefore, effects of habitat variables on bird species numbers were analyzed separately for census points below and above the timberline.

For evaluating the importance of six habitat variables (Tab. 3) on bird species richness of census points within the forest belt, we again calculated GLMs including all variables and all possible subsets. In the minimum adequate model (all varbiables significant) two variables remained, mean DBH and tree density (Tab. 3). Bird species richness proved to be negatively related to tree density (Fig. 6), while an univariate correlation between bird species richness and mean DBH (square root transformation) did not achieve a significant level (r = -0.17, N = 60, p = 0.188).

Table 3. Relationships between numbers of breeding bird species recorded at census points within the forest belt (N = 60) and the variables altitude, tree species richness, maximum height of woody vegetation, mean tree DBH (square-root transformed), tree density (square-root transformed), proportion of coniferous trees (arcsin transformed) tested with generalized linear models (GLM). Resulting models selected by a "step-down" approach (see text) are ranked according to Akaike information criterion (AIC). The final model (all variables significant) is printed bold.

Variables included	**AIC**	***p***
altitude, mean tree DBH, tree density, proportion of coniferous trees, max. height of woody vegetation, tree species richness	268.70	0.002
altitude, mean tree DBH, tree density, proportion of coniferous trees, max. height of woody vegetation	266.85	<0.001
altitude, mean tree DBH, tree density, max. height of woody vegetation	266.17	<0.001
altitude, mean tree DBH, tree density	266.45	<0.001
mean tree DBH, tree density	**267.05**	**<0.001**
tree density	274.84	0.013

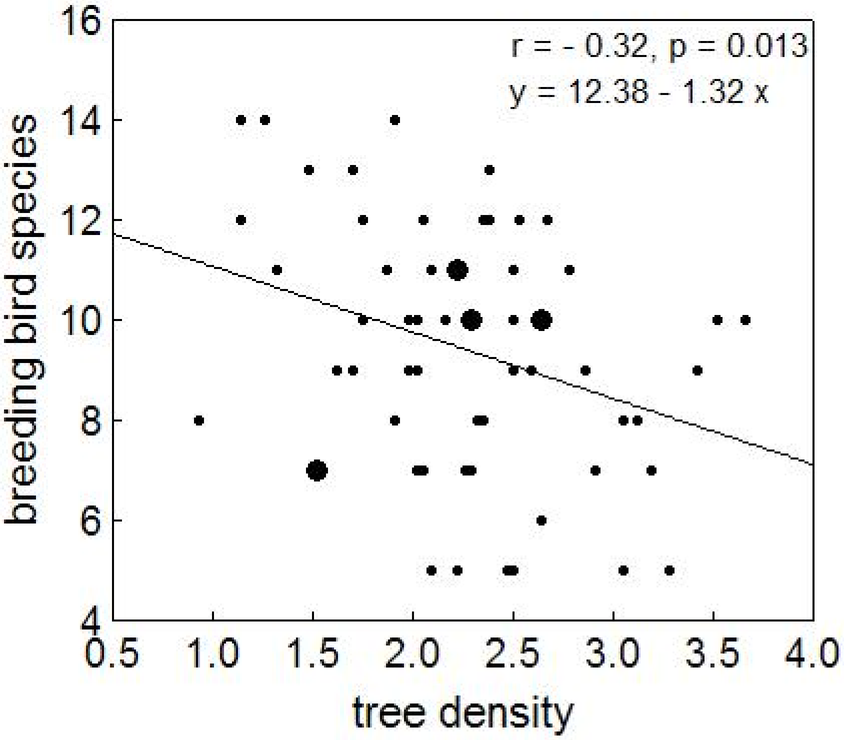

Figure 6. Relationship between number of breeding bird species recorded at individual census points (N = 60) and tree density. Larger bubbles indicate a larger number of census points.

Three habitat variables, altitude, tree species richness and maximum height of woody vegetation, were tested for their potential to explain variability of breeding bird richness at census points above the timberline calculating GLMs including all variables and all possible subsets, respectively. Two variables, altitude and tree species richness, remained in the minimum adequate model (all variables significant). Bird species richness at census points above the timberline was negatively correlated with altitude ($r = -0.65$, N = 26, $p < 0.001$) and positively related to increasing tree species richness (Fig. 7).

Table 4. Relationships between numbers of breeding bird species recorded at census points above the timberline (N = 26) and the variables altitude, tree species richness and maximum height of woody vegetation (square-root transformed) tested with generalized linear models (GLM). Resulting models selected by a "step-down" approach (see text) are ranked according to Akaike information criterion (AIC). The final model (all variables significant) is printed bold.

Variables included	**AIC**	***p***
Altitude, tree species richness, max. height of woody vegetation	98.58	<0.001
altitude, tree species richness	**97.16**	**<0.001**
altitude	98.60	<0.001

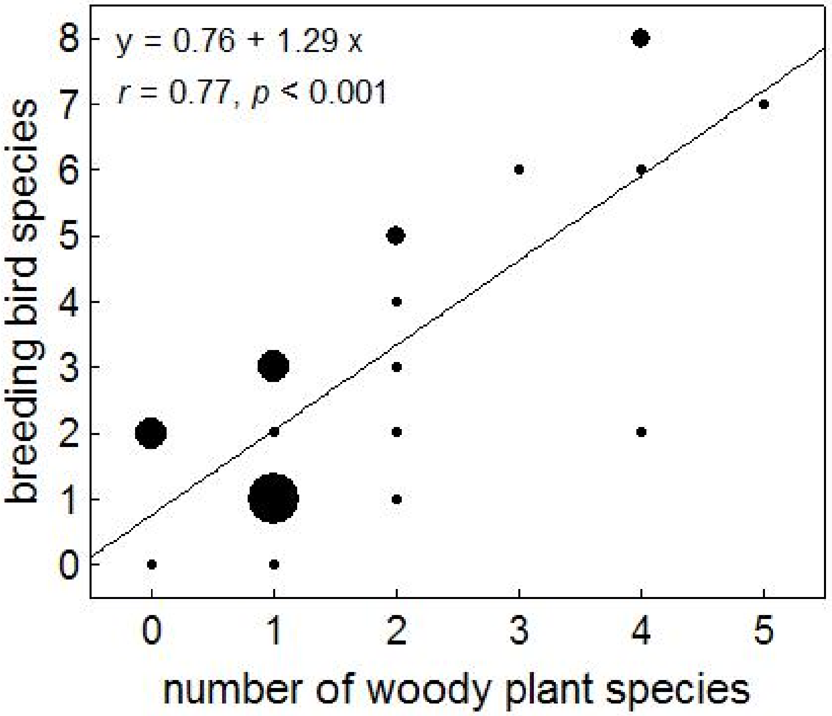

Figure 8. Relationships between breeding bird and number of woody plant species species recorded at individual census points (N = 26). Larger bubbles indicate a larger number of census points.

Effects of altitude and vegetation structure on bird species composition

A NMDS plot based on Bray-Curtis similarities was used to visualize differences of species composition between census points and habitat types (Fig. 9). Bird species composition of census points was significantly affected by the six habitat types (one-way ANOSIM: global $r = 0.47$, $p = 0.001$) pre-defined as (1) mixed forest woodland, (2) coniferous woodland, (3) succession sites within the forest belt, (4) dwarf pine belt, (5) alpine meadows with isolated dwarf pine stands and (6) alpine meadows with rocks. Species composition differed significantly between most of the classified habitat types (Tab. 5). Succession sites were one exception. They appeared to be characterized by a species composition intermediate between mixed forest (at lower altitudes) and coniferous forest (at higher altitudes; compare Fig. 9) and did not differ significantly from both old-grown forest types (Tab. 5). Another exception was the habitat type defined as alpine meadows with dwarf pine stands. Its species composition did not differ significantly from both other classified habitat types located above the timberline, the dwarf pine belt and alpine meadows with rocks (Tab. 5). The NMDS plot indicates that its species composition was intermediate between these two other habitat types (Fig. 9).

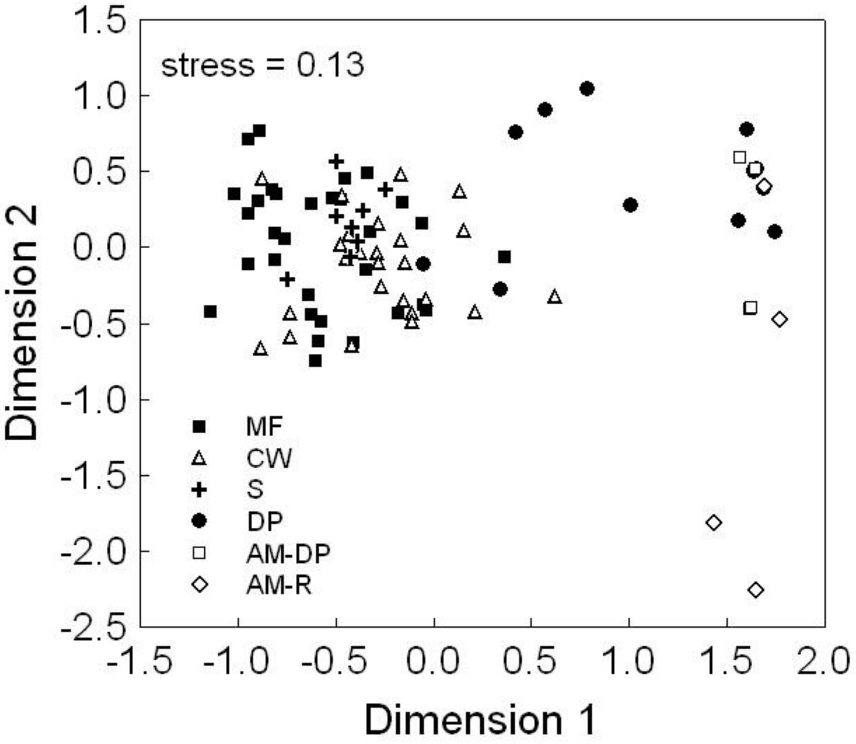

Figure 9. Two-dimensional NMDS plot based on Bray-Curtis similarities for species composition of breeding bird assemblages. Different symbols indicate different habitat types: MF – mixed forest, CF – coniferous forest, S – succession sites, DP – dwarf pine belt, AM-DP – alpine meadows & dwarf pine stands, AM-R – alpine meadows & rocks.

Table 5. Pairwise comparisons (one-way ANOSIMs) of species composition between census points belonging to the six pre-defined habitat types. Significant differences are printed in bold.

Pairwise comparisons of habitat types	***r***	***p***
MF vs. S	-0.09	0.829
MF vs. CF	**0.12**	**0.002**
MF vs. DP	**0.82**	**0.001**
MF vs. AM-DP	**0.97**	**0.001**
MF vs. AM-R	**0.99**	**0.001**
S vs. CF	0.02	0.420
S vs. DP	**0.71**	**0.001**
S vs. AM-DP	**1.00**	**0.002**
S vs. AM-R	**0.91**	**0.002**
CF vs. DP	**0.78**	**0.001**
CF vs. AM-DP	**0.95**	**0.001**
CF vs. AM-R	**0.99**	**0.001**
DP vs. AM-DP	0.11	0.241
DP vs. AM-R	**0.47**	**0.017**
AM-DP vs. AM-R	0.31	0.086

Bray-Curtis similarities for breeding bird species assemblages and geographic distances between census points were significantly correlated (Spearman matrix rank correlation: *Rho* = 0.065, *p* = 0.025) indicating a weak spatial autocorrelation of sites. Therefore, to test which habitat variables potentially affect species composition, we conducted partial Mantel tests between the Bray-Curtis similarity matrix and three distance matrices for the habitat parameters altitude, maximum height of woody vegetation and number of woody plants species, respectively, corrected for spatial autocorrelation. As indicated by the calculated partial Mantel tests, all habitat parameters significantly affected bird species composition. However, according to the partial correlation coefficients the relationships between bird species richness and the two variables maximum vegetation height and altitude, respectively, is much stronger than with tree species richness (Tab. 6).

Table 6. Results of partial Mantel tests between Bray-Curtis similarities for species assemblages of breeding bird and habitat variables corrected for geographic distances between census points.

Habitat variables	r_{part}	p
Tree species richness	-0.25	< 0.001
Max. height of woody vegetation	-0.60	< 0.001
Altitude	-0.57	< 0.001

Feeding guilds

A comparison of the mean relative abundance of feeding guilds per census point between altitudinal zones (including only breeding bird species within the 50 m radius) showed no prominent overall trend along the elevation gradient, except a distinct change of feeding guild composition close to the timberline. At higher elevations only few species remained, exclusively represented by insectivorous birds (Fig. 10) searching for arthropods on the ground (e.g., *Anthus spinoletta* and *Prunella collaris*).

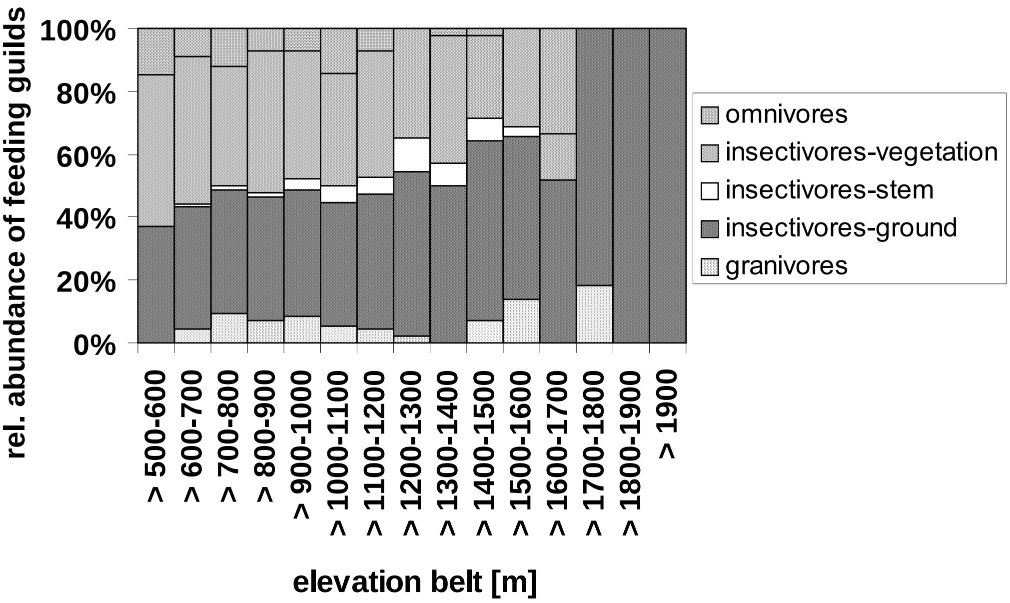

Figure 10. Mean relative abundance of feeding guilds/functional groups per census point in 100 m-elevation belts.

The absolute numbers of individuals per census point decreased significantly with increasing altitude in ground-dwelling insectivores (r_s = -0.64, N = 15, $p < 0.01$), insectivores foraging within the vegetation (r_s = -0.90, N = 15, $p < 0.001$) and omnivores (r_s = -0.64, N = 15, $p < 0.01$; Fig. 11). Two feeding guilds, granivorous birds (r_s = -0.48, N = 15, $p = 0.068$) and insectivorous stem climbers (r_s = -0.23, N = 15, $p = 0.414$), did not show a negative response to increasing altitude. While the mean abundance of granivores did not show a clear elevational pattern, insectivorous stem climbers showed a prominent mid-elevation abundance peak (Fig. 11).

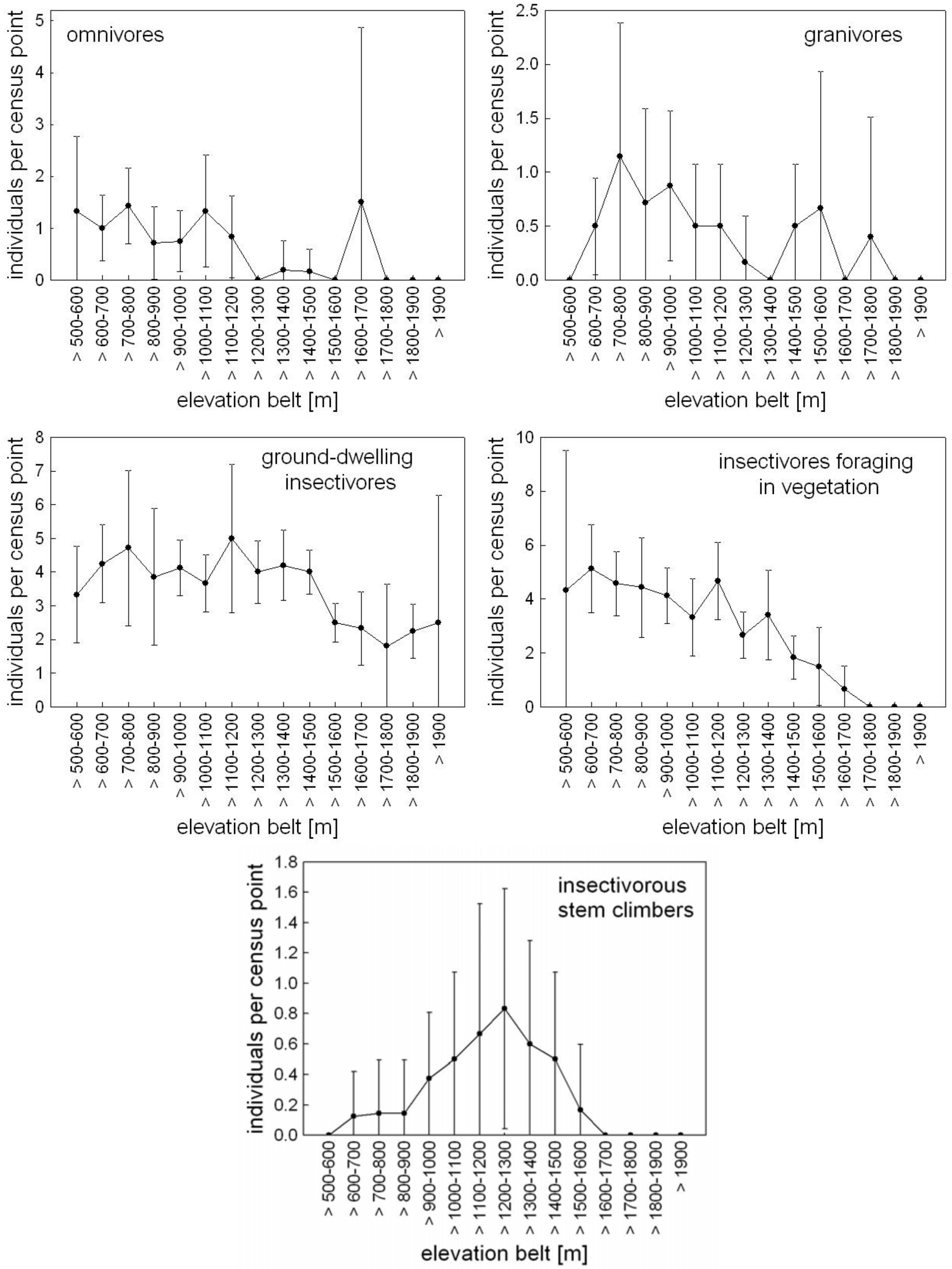

Figure 11. Changes of mean numbers of individuals per census point ± 95% CI along the elevation gradient for five different feeding guilds/functional groups. Mean numbers are calculated for 100 m-elevation belts.

Discussion

Elevational species richness pattern

Rahbek (1995) conducted an extensive literature review including studies on changes of species richness covering a wide range of taxonomic groups, biomes, and spatial scales. While a monotypic decline in species numbers with increasing elevation often was considered a general pattern (e.g., Able & Noon 1976; Brown & Gibson 1983; Rohde 1992; Stevens 1992), Rahbek (1995) demonstrated that hump-shaped relationships with maximum species numbers at mid-elevations are the most common elevational species richness pattern. Depending on the spatial grain and the size of the surveyed study area, different elevational richness patterns were reported for birds: (a) an overall decline of species richness with increasing altitude (Terborgh 1971, 1977; Diamond 1973; Able & Noon 1976; Rahbek 1997; Patterson et al. 1998; Reboud & Frochot 1998; Sergio & Pedrini 2007), (b) a plateau of species richness at lower altitudes then declining towards the highest elevations (Navarro S. 1992; Blake & Loiselle 2000; Herzog et al. 2005) and (c) a mid-elevation peak of species richness (Rahbek 1995, 1997; Kessler et al. 2001; Lee et al. 2004; Ding et al. 2005).

Independent of the spatial scale (census points vs. elevation belts) in this study on changes of bird communities across an elevation gradient at the southern Buchstein massif in Gesäuse National Park, species richness of breeding birds showed a plateau between 500 and 1,200 m before a nearly monotypic decline was observed. As emphasized by Grytnes & Vetaas (2002), interpolated species presence between maximum and minimum observed elevations – as used by this study for estimating species richness of 100m-elevation belts – can cause an artificial hump in the species-elevation curves. However, in our study the change of bird richness per evelation belt remained very similar independent of the used richness measure, interpolated or recorded species richness.

The most obvious (but weak) deviations of changes in bird species richness between neighboring altitudes detected across our elevational gradient – beside the generally monotypic decline of bird richness with increasing altitude above the timberline –

occurred at two ecotones: (1) the transition zone between mixed forest and coniferous woodland and (2) the timberline. Able & Noon (1976) emphasized the importance of ecotones for the vertical distribution of birds. They found the highest aggregation of vertical distribution borders at ecotones. Transition zones between two vegetation belts can be characterized by a spatially meshed distribution of different vegetation types. This may generate a vertical overlap of bird species belonging to lower and upper vegetation belts resulting in a species richness within such transition zones, which is deviating from the expected pattern when only taking into account elevations below and above these ecotones. However, an increase of species richness due to the overlap of species assemblages characteristic for adjacent elevation zones proved to be more prominent in other studies. For example, Nor (2001) found the maximum species richness for small mammals at Mount Kinabalu (East Malaysia) at the overlapping zone between highland and lowland assemblages. The area of much overlapping of species´ vertical distribution ranges occurred at elevations where climate and vegetation change rapidly from lowland to montane forest types (Nor 2001).

Effects of elevation belt area on species richness

Rahbek (2005) underlined the strong influence of spatial scale on emerging patterns of species richness. This also can cause methodological problems when comparisons of elevational patterns of species richness do not consider effect of different sampling effort and/or area on species richness (Rahbek 1995). Failure to standardize data to account for sampling effort (Gotelli & Colwell 2001) and area (Rahbek 1995, 1997) can cause artefactual results. To overcome such pitfalls, Rahbek (1997) analyzed a data set largely devoid of sampling biases on the elevational distribution of Neotropical land birds. After controlling for the surface area of each elevational belt, the emerging regional-scale relationship between species richness and elevation was hump-shaped with a maximum at ca 1000 m. In our study, sampling area and sampling effort were identical for census points and at least very similar for 100 m-elevation belts. For quantifying species richness of elevation belts, potential effects of varying sampling causing differences in species inventory completeness were additionally reduced by interpolating vertical ranges of species. Therefore, both factors potentially “biasing” richness patterns should be negligible.

However, our results still showed a strong effect of area on bird species richness of individual elevation belts indicating that also species density is strongly affected by elevation belt area.

On larger scales, a monotypic decline of species richness with increasing elevation was found for breeding birds in Styria (Sackl & Samwald 1997) and central-eastern Italian Alps (Sergio & Pedrini 2007). However, both studies did not take in account area varying between different elevation belts, although area can have a prominent effect on species richness patterns (Rahbek 1995, 2005). In our study, total area of individual elevation belts best predicted variation of bird richness between elevation belts, although the actually surveyed area remained approximately the same. Rahbek (1995) explained the strong effect of area on species richness along elevation gradients by arguing that area often shows a decrease with elevation because of a generally steeper terrain toward the highest peaks. However, as demonstrated by our study region, area does not necessarily decrease continuously with increasing elevation, but can be highest at mid-elevations. This can cause elevational species richness patterns which are characteristic for a certain locality such as the Buchstein maasif but do not necessarily reflect a more common pattern typical for an entire mountain range or an entire biogeographical region.

Effects of elevational differences of vegetation

On larger geographic scales topographic heterogeneity and habitat diversity are well established as predictors of spatial changes in bird species richness (Rahbek & Graves 2001). However, habitat diversity is generally closely related to topographic heterogeneity (Rahbek & Graves 2001). Along elevational gradients decreasing habitat heterogeneity, diversity and complexity towards higher altitudes can be major reasons for a decline of bird richness (e.g. Able & Noon 1976; Stotz et al. 1996). Lomolino (2001) emphasized that gamma diversity should vary directly with the total available area of each elevational zone and should peak at those zones, that cover the largest area. We used differences in species composition of woody plants within elevation belts to quantified changes of habitat diversity across the elevation gradient. Bird richness of elevation belts proved to be highly related to habitat diversity when tested by a univariate model. However, in a multiple analysis with area, altitude and mean similarity of wood plant assemblages, the later proved to be redundant for predicting changes of bird richness across the elevation gradient.

At the spatial level of census points in this study bird richness was positively related to maximum tree height and tree species richness. Both vegetation parameters decreased with increasing altitude with a particularly steep decline at the timberline. Terborgh (1977) showed a strong relation between bird species richness and the number of vegetation layers, a measurement of structural diversity of the vertical forest cover dimension. The number of vertical strata of habitats should be related to the maximum vegetation height, which was used as habitat parameter in our study. Additionally, structural diversity should also be related to tree species richness. Tree species richness is often used as surrogate for habitat complexity and diversity of available resources (food, nesting sites etc.). A positive relationship between tree species richness and richness of bird assemblages was found for forest types in lowland areas (Poulsen 2002). Furthermore, for other vertebrates such as small mammals it was recorded that highest species richness occurred at elevations, where plants reached their maximum diversity (Heaney 2001; Nor 2001; Sánchez-Cordero 2001; Li et al. 2003). The importance of the habitat structure for bird species richness was emphasized by other studies (Scherzinger 1985), particularly for explaining changes of species richness across elevational gradients in the Alps (Wartmann & Furrer 1977; Winding et al. 1993; Brunner 1998).

Within the woodland belt tree density and tree diameter had striking significant influence on bird species richness. Tree density plays an important role as parameter describing the vegetation structure and is related to many other factors such as canopy closure, light regime (net primary production), understorey vegetation, and microclimate. When large trees are missing, tree density is often increased (Poulsen 2002). Furthermore, Poulsen (2002) showed that the number of tree size-classes is positively correlated with bird abundance and species richness. The positive effect of a higher number of tree size classes on bird richness most likely describe the same relationship reported between the number of vegetation layers and bird species by Terborgh (1977). A higher number of tree size classes most likely results in a higher vertical habitat complexity and vertical stratification.

Above the timberline, the number of woody plant species positively affected to bird species richness. This is not surprising when taking into account that individual trees may represent an important structural component within otherwise relatively homogeneous habitats dominated by *Pinus mugo*. Individual trees may provide important resources such as perching and nesting sites for bird species.

Changes of species composition of bird communities between altitudes

A study on changes of different plant and moth taxa across a habitat disturbance gradient in a montane forest in Ecuador demonstrated that different drivers may shape changes of species richness and species composition (Nöske et al. 2008). Also our data on elevational changes of bird assemblages indicate that both community parameters appear to respond largely independently from each other to changing elevation. While an obvious decrease of species richness was only recorded for higher elevations, species composition differed significantly between most pre-defined habitat types. This does not only emphasize that vegetation structure has a major effect on composition of bird assemblages but also that a prominent species turnover can occur within elevational zones where no significant elevational changes of species richness can be detected. The importance of vegetation parameters for the structure of bird assemblages was also demonstrated by the close relationship between species composition and maximum height of woody vegetation found in this study. Vegetation height explained nearly as much of the variation in species composition than elevation.

Our results showed that vegetation zones were characterized by distinct bird species assemblages. As emphasized by Terborg (1985) temperate forests contain relatively few tree species, and stands that are nearly “monocultures” are prevalent at high elevations. Therefore, not only structural changes at the timberline but also at ecotones such as in the transition zone between deciduous and coniferous forest may have significant effects on bird species composition. For example, several insectivorous birds have been shown to forage preferentially in certain tree species in a mixed deciduous forest in North America (Holmes et al. 1979, Holmes & Robinson 1981). Such preferences may limit the elevational distribution for bird species which depend on certain tree species at least in temperate mountain ranges. Due to the high species richness of trees and the high diversity of their foliage, such preferential foraging may be less developed in tropical birds. Consequently, structural changes characterizing tropical ecotones may have less significance for elevational distribution limits of birds than the transition from broad-leafed to needle-leafed forest at elevation gradients in temperate mountains.

That changes of vegetation type are major drivers for species composition was also emphasized by studies reporting a particular high species turnover across the elevation gradient at ecotones (Able & Noon 1976; Wartmann & Furrer 1977; Głowaciński & Profus 1992; Navarro S. 1994; Blake and Loiselle, 2000). In our study species composition differed significantly between all pre-defined habitats below and above the timberline underlining the importance of the change of vegetation structure at the timberline already emphasized by Wartmann & Furrer (1977).

Habitat discontinuities along the elevational gradient can have a significant influence for determining vertical distribution limits of species (Able & Noon 1976) resulting in particularly high species turnover rates at ecotones with sharp borders between vegetation belts such as at the timberline of temperate mountains ranges. However, also species turnover at the timberline can be less prominent than expected depending on the regional situation. For example, Głowaciński & Profus (1992) could not record a prominent avifaunal change at the timberline ecotone in the Carpathian mountains because of a more continuous transition from mountain forests to shrubs and meadows of the alpine zone. Patterson et al. (1998) reported a similar observation for the transition from elfin forest to *puna* grassland at about 3,200 m in the Andes of southeastern Peru. The transition between these two vegetation belts was the most obvious along the studied elevational gradient in terms of vegetation structure and the *puna* fauna is strongly distinguished from the fauna of the forested slope. However, the transition zone was only weakly marked in analysis of both bird and mammal assemblages perhaps reflecting the interdigitation of forest and grassland habitats across several hundred meters (Patterson et al. 1998). That the upper montane forest is rather meshed with dwarf pine areas than sharply separated from dwarf pine areas at the timberline is also indicated by our data on the change of woody vegetation height and dwarf pine cover across the elevation gradient at the southern slopes of Buchstein massif. Both variables indicate an interdigitation between 1,450 and 1,650 m. Therefore, differences in species composition may be less distinct when using elevation zones to group or census point inventories than, as done in this study, to affiliate them with pre-defined habitat types.

Feeding guilds

Other studies demonstrated that changes of species richness and abundance of different feeding guilds do not have to be congruent (Terborgh 1977). The study by Terborg (1977) along an Andean elevation gradient demonstrated a different response of the three investigated feeding guilds to elevation. Only species richness of insectivores showed a dramatic decline with increasing altitude, while frugivorous and nectarivorous bird richness showed a weak decline and no abundance change, respectively. However, Terborgh (1977) did not quantify abundance changes of different guilds across the elevational gradient, which is of higher ecological relevance than richness. In our study changes of the relative abundance of feeding guilds did not show a clear pattern across the entire elevational gradient, except of a dominance of insectivorous ground-dwelling birds in the highest elevation belts. However, a comparison of the mean abundance per census point demonstrated that feeding guilds respond differentially to changing elevation. While the abundance of omnivores, granivores and ground-dwelling insectivores did not show a distinct pattern of change with increasing elevation, insectivores foraging in the vegetation declined prominently. Due to the decreasing number of vegetation layers a related decrease of total insect biomass with increasing altitude could be one reason. Furthermore, a limited availability of nesting sites at higher altitudes can negatively affect the abundance of insectivores depending on their nesting mode. For example, all five tit species (*Parus* spp.) depend on tree holes which may become a decreasingly spare resource with increasing altitude and are missing completely at many sites above the timberline.

The most remarkable pattern was the mid-elevation abundance peak found for insectivorous stem climbers (woodpeckers and *Certhia familiaris*). While the availability of suitable nesting trees may explain the decrease of this feeding guild from c. 1300 m towards higher altitudes, because all species exclusively breed in tree cavities, the decrease from mid-elevations towards the valley floor remains unexplained. Perhaps the low abundance of insectivorous stem climbers at lower elevations is reflecting a more intensive forest until recently resulting in a low availability of dead wood, which represents an important source for food (wood-boring insects) for species such as woodpeckers. That the amount of dead wood can have significant effects on species richness, composition and abundances was already demonstrated by other studies (Scherzinger 1996; Sauberer et al. 2007).

Main conclusions

This study at Gesäuse National Park in the eastern Alps demonstrated the importance of spatial scale, regional topography, area and vegetation cover for changes of bird assemblages across elevational gradients. However, several other factors might additionally affect bird species richness and composition, which were not considered by this study. For example, beside ecotones interspecific competition may be an important factor for determining vertical distribution limits of birds, thereby affecting changes of species composition across elevation gradients. However, Terborgh (1985) emphasized that ecotones have a much greater importance for explaining lower and upper limits of the elevational distribution in birds of temperate mountain ranges than in the tropics. He argued that reasons probably involve the character of temperate ecotones as well as the greatly reduced species density. In contrast, in tropical regions direct and diffuse competition exclusion might be of overriding importance to explain changes of species composition across elevational gradients.

Also human impact on the natural vegetation cover during the last decades and centuries can have affected patterns of species richness, which can be observed today across elevational gradients (e.g. Kessler et al. 2001). The highest abundance of insectivorous stem climbers (depending on dead wood) at mid-elevations could indicate that human impact due to intensive forest use particularly affected the structure of bird communities at lower elevations. Comparisons of disturbed and at least near-natural habitats in different altitudes have to quantify how anthropogenic disturbance and conversion of natural forests to production forests affect patterns of bird richness, species composition and vertical distribution of individual species across elevation gradients. Also a prominent mid-elevation peak of Red-List bird species at the southern Buchstein massif (Klosius, unpublished data) could indicate that bird communities at lower elevations already miss most of the more specialized endangered species, perhaps as result of a long lasting anthropogenic disturbance at lower elevations.

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References

Able, K. P. and Noon, B. R. 1976. Avian community structure along elevational gradients in the Northeastern United States. Oecologia 26: 275–294

Blake, J. G. and Loiselle, B. A. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. The Auk 117: 663–686

Blotzheim von, U. N. G. 2001. Handbuch der Vögel Mitteleuropas. e-Book-Linzenzausgabe. Vogelzug Verlag

Bonnet, E. and Van de Peer, Y. 2002. zt: a software tool for simple and partial Mantel tests. Journal of Statistical Software 7: 1–12

Brader, M. and Aubrecht, G. 2003. Atlas der Brutvögel Oberösterreichs. Biologiezentrum der OÖ Landesmuseen, Linz

Brehm, G, Colwell, R. C. and Kluge, J. 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. Global Ecology and Biogeography 16: 205–219

Brose, U. and Martinez, N. D. 2004. Estimating the richness of species with variable mobility. Oikos 105: 292–300

Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. Global Ecology & Biogeography 10: 101-109

Brown, J. H. and Gibson, A. C. 1983. Biogeography. Mosby.

Brown, J. H. and Lomolino, M. V. 1998. Biogeography. 2nd edn. Sinauer, Sunderland, Massachusetts.

Brunner, H. 1998. Ökologisch-faunistische Untersuchungen der Vogelwelt (Aves) in Gebirgslebnsräumen der Seckauer Alpen (Niedere Tauern, Österreich). Mitteilungen naturwissenschaftlicher Verein Steiermark Band 128: 227–243

Brunner, H. 2001. Vogelgemeinschaften an der oberen Waldgrenze unter dem Einfluss traditioneller und moderner Landnutzung im Nockgebiet (Kärnten, Steiermark). Carinthia II 191./111. Jahrgang: 533–544

Chaves-Campos, J. 2003. Changes in abundance of crested guan (*Penelope purpurascens*) and black guan (*Chamaepetes unicolor*) along an altitudinal gradient in Costa Rica. Ornithologica Neotropical 14: 195–200

Chaves-Campos, J. 2004. Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient. Ornitologia Neotropical. 15: 433–445

Clarke, K.R. and Gorley, R.N. 2001. PRIMER v5: user manual/tutorial. Primer-E, Plymouth

Colwell, R. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15: 70–76

Crawley, M. J., 1993. GLIM for Ecologists. Blackwell Science, Oxford.

Cyr, A. and Oelke, H. 1976. Vorschläge zur Standardisierung von Biotopbeschreibungen bei Vogelbestandsaufnahmen im Waldland. Die Vogelwelt 5: 161–175

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179: 759–769

Ding, T., Yuan, H., Geng, S., Lin, Y. and Lee, P. 2005. Energy flux, body size and density in relation to bird species richness along an elevational gradient in Taiwan. Global Ecology and Biogeography 14: 299–306

Dvorak, M., Ranner, A. and Berg, H. M. 1992. Atlas der Brutvögel Österreichs. Ergebnisse der Brutvogelkartierung 1981-1985 der Österreichischen Gesellschaft für Vogelkunde. Umweltbundesamt, Wien

Feldner, J., Rass, P., Petutschnig, W., Wagner, S., Malle, G., Buschenreiter, R. K., Wiedner P. and Probst, R. 2006. Avifauna Kärntens: Die Brutvögel. Naturwissenschaftlicher Verein für Kärnten, Klagenfurt

Fischer, M. A. 2005. Exkursionsflora von Österreich, Liechtenstein und Südtirol. Oberösterreichische Landesmuseen, Linz

Fischer, S., Flade M, and Schwarz, J. 2005. Punkt-Stopp-Zählung. In: Südbeck, P., Andretzke, H. Fischer S., Gedeon K., Schikore T., Schröder K. and Sudfeldt, C. (eds.). Methodenstandards zur Erfassung der Brutvögel Deutschlands. Radolfzell

Głowaciński, Z. and Profus, P. 1992. Structure and vertical distribution of the breeding bird communities in the polish Tatra National Park. Ochrona Przyrody 50, CZ. I: 65–94

Grytnes, J. A. and Vetaas, O. R. 2002. Species richness and altitude: A comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. The American Naturalist 159: 294–304

Heaney, L. R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Global Ecology and Biogeography 10: 15–39

Herzog, S. K., Kessler, M. and Bach, K. 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevational plateau. Ecography 28: 209–222

Hochrathner, P. 1997. Qualitative und quantitative Erhebung der Avifauna auf drei ausgewählten Untersuchungsflächen im Sengsengebirge (Transektgebiet) – subalpin bis alpin (Oberösterreich). Vogelkundliche Nachrichten Oberösterreich. Naturschutz aktuell 5: 9–39

Kessler, M., Herzog, S. K., Fjeldså, J. & Bach, K. 2001. Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. Diversity and Distributions 7: 61–77

Kluge, J., Kessler, M. and Dunn, R. R. 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Global Ecology and Biogeography 15: 358–371

Kollmann, W. 1975. Hydrologie der nördlichen Gesäuseberge. Doctoral thesis. Universität Graz

Lee, P.-F., Ding, T.-S., Hsu, F.-H. and Geng, S. 2004. Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization. Journal of Biogeography 31: 307–314

Li, J. S., Song, Y. L. and Zeng, Z. G. 2003. Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. Global Ecology and Biogeography 12: 449–460

Lomolino, M. V., Riddle, B. and Brown, J. 2006. Biogeography. Sinauer Associates, Sunderland, MA, U.S.A.

Lomolino, M. V. 2001. Elevational gradients of species-density: historical and prospective views. Global Ecology & Biogeography 10: 3–13

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. John Wiley, London

MacArthur, R. H. 1984. Geographical Ecology: Patterns in the Distributions of Species. Princeton Univ. Press, Princeton

Maurer, W. 1981. Die Pflanzenwelt der Steiermark und angrenzender Gebiete am Alpenostrand. Verlag für Sammler, Graz

MacKinnon, J. and Phillips, K. 1993. A field guide to the birds of Sumatra, Java and Bali. Oxford University Press, New York

McCain, C. M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. Journal of Biogeography 31: 19–31

Navarro S., A. G. 1992. Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. The Condor 94: 29–39

Nor, S. M. 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. Global Ecology and Biogeography 10: 41–62

Nöske, N. M., Hilt, N., Werner, F. A., Brehm, G., Fiedler, K., Sipman, H. J. M. and Gradstein, S. R. 2008. Disturbance effects on diversity in montane forest of Ecuador: sessile epiphytes vs. mobile moths. Basic and Applied Ecology 9: 4–12

Oberwalder, J., Lair, C., Föger, M. and Pollheimer, M. 2002. Siedlungsökologie von Drosseln *Turdus* sp. entlang eines alpinen Höhengradienten. Der Ornithologische Beobachter 99: 205–220

Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. and Pacheco, V. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. Journal of Biogeography 25: 593–607.

Pauli, H., Gottfried, M., Reiter, K., Klettner, C. and Grabherr, G. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. Global Change Biology 13: 147–156

Paulsch, D. and Müller-Hohenstein, K. 2008. Bird species distribution along an altitudinal gradient in Southern Ecuador and its functional relationships with vegetation structure. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds.), Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies 198. Pp. 149–156. Springer-Verlag, Berlin

Poulsen, B. O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biodiversity and Conservation 11: 1551–1566

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18: 200–205

Rahbek, C. 1997. The relationship among area, elevation and regional species richness in neotropical birds. American Naturalist 149: 875–902.

Rahbek, C. & Graves, G. R. 2001. Multiscale assessment of patterns of avian species richness. Proceedings of the National Academy of Sciences of the United States of America 98: 4534–4539.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8: 224–239.

Raman, S. T. R., Joshi, N. V. and Sukumar, R. 2005. Tropical rainforest bird community structure in relation to altitude, tree species composition, and null models in the Western Ghats, India. Journal of the Bombay Natural History Society 102: 145–157

Reboud, C. and Frochot, B. 1998. Gradient d'altitude de la richesse spécifique des oiseaux: utilization de données partielles du nouvel atlas des oiseaux nicheurs de la région Rhône-Alpes. Bulletin de la Sociéte Zoologique de France 123: 361–372

Rickart, E. A. 2001. Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. Global Ecology and Biogeography 10: 77–100.

Roché, J. C. 2000. Die Vogelstimmen Europas auf 4 CDs. Franckh-Kosmos Verlags GmbH & Co., Stuttgart.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65: 514–527.

Sackl, P. and Samwald, O. 1997. Atlas der Brutvögel der Steiermark. BirdLife Österreich, Landesgruppe Steiermark und Landesmuseum Joanneum. Austria medien service, Graz.

Sánchez-Cordero, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. Global Ecology and Biogeography 10: 63–76

Sanders, N. J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography 25: 25–32

Sauberer, N., Hochbichler, E., Milasowszky, N., Panagoitis, B. and Sachslehner, L. 2007: Nachhaltiges Waldbiomassenmanagement im Biosphärenpark Wienerwald. Verlag der Österreichischen Akademie der Wissenschaften, Wien

Schmid, H., Luder, R., Naef-Daenzer, B., Graf, R. and Zbinden, N. 1998. Schweizer Brutvogelatlas: Verbreitung der Vögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996 = Atlas des oiseaux nicheurs de Suisse. Schweizerische Vogelwarte Sempach, Sempach

Scherzinger, W. 1985. Die Vogelwelt der Urwaldgebiete im Inneren Bayrischen Wald. Heft 12, Schriftenreihe des Bayrischen Staatsministeriums für Ernährung, Landwirtschaft und Forsten

Scherzinger, W. 1996. Naturschutz im Wald: Qualitätsziele einer dynamischen Waldentwicklung. Ulmer Verlag, Stuttgart

Sergio, F. and Pedrini, P. 2007. Biodiversity gradients in the Alps: the overriding importance of elevation. Biodiversity & Conservation 16: 3243–3254

StatSoft. 2005. STATISTICA for Windows, 7.1. StatSoft Inc., Tulsa, Oklahoma

Stotz, D. F., Fitzpatrick, J. W., Parker III, T. A. and Moskovits, D. K. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago

Svensson, L., Grant, P. J., Mullarney K. and Zetterström, D. 1999. Der neue Kosmos Vogelführer. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Terborgh, J. 1971. Distribution on environmental gradients; theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 53: 23–40

Terborgh, J. 1977. Bird species diversity of an Andean elevational gradient. Ecology 58: 1007–1019

Terborgh, J. 1985. The role of ecotones in the distribution of Andean birds. Ecology 66: 1237-1246

Terborgh, J. and Weske, J. S. 1975. The role of competition in the distribution of Andean birds. Ecology 56: 562–576

Wakonigg, H. 1978. Witterung und Klima in der Steiermark. Arbeiten aus dem Institut für Geographie der Universität Graz

Wartmann, B. und Furrer, R. K. 1977. Zur Struktur des Avifauna eines Alpentales entlang des Höhengradienten. Veränderungen zur Brutzeit. Der ornithologische Beobachter 74: 137–160

Wartmann, B. und Furrer, R. K. 1978. Zur Struktur der Avifauna eines Alpentales entlang des Höhengradienten. Ökologische Gilden. Der ornithologische Beobachter 75: 1–9

Winding, N., Werner, S., Stadler, S. and Slotta-Bachmayr, L.1993. Die Struktur von Vogelgemeinschaften am alpinen Höhengradienten: Quantitative Brutvogel-Bestandsaufnahmen in den Hohen Tauern (Österreichische Zentralalpen). Wissenschaftliche Mitteilungen aus dem Nationalpark Hohe Tauern Bd. I: 106–124

Appendix 1. Total number of bird species (= 53 species) recorded within individual elevation belts including all observations. Cells filled black represent elevation belts where the species was recorded, cells in grey indicate elevation belts for which the occurrence appears to be likely.

Species	100 m-elevation belt														
	> 500-600	> 600-700	> 700-800	> 800-900	> 900-1000	> 1000-1100	> 1100-1200	> 1200-1300	> 1300-1400	> 1400-1500	> 1500-1600	> 1600-1700	> 1700-1800	> 1800-1900	> 1900
Corvus corone corone	■	■	■	▒	■										
Erithacus rubecula	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
Fringilla coelebs	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
Motacilla cinerea	■														
Parus ater	■	■	■	■	■	■	■	■	■	■	■	■	■		
Parus major	■	■	■	■	■	■	■	■	▒	■	■				
Parus palustris	■	■	■	■	■										
Phylloscopos bonelli	■	■	■	■	■	▒	■	■	■	■					
Phylloscopos collybita	■	■	■	■	■	■	■	■	■	■	■	■	▒	■	
Phylloscopos trochilus	■	■	■	■	■	▒	■			■	■				
Prunella modularis	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Pyrrhula pyrrhula	■	■	■	■	■	■	■	■	▒	■	■	■			
Regulus ignicapillus	■	■	■	■	■	■	■	■							
Sylvia atricapilla	■	■	■	■	■	■	■	■	■	■	■				
Troglodytes troglodytes	■	■	■	■	■	■	■	■	■	■	▒	■	■		
Turdus merula	■	■	■	■	■	■	■	■	■	■	▒	■			
Turdus philomelos	■	■	■	■	■	■	■	■	■	▒	■	■			
Carduelis chloris		■			■										
Certhia familiaris		■	■	■	■	■	■	■	■	■	■				
Columba palumbus		■	■	■	▒	■	■								
Cuculus canorus		■			■	■	■	■	■	▒	■				
Dryocopus martius		■	■	■	▒	■	▒	■							
Nucifraga caryocatactes		■	■	■	■	■	■	■	■	■	▒	■			
Parus montanus		■	■	■	■	■	■	■	■	▒	■				
Phoenicurus ochruros		■										■	■	■	■
Picus viridis		■	■	▒	■	▒	■	■							
Regulus regulus		■	■	■	■	■	■	■	■	■	■				
Sylvia borin		■					■								
Sylvia curruca		■					■	■	▒	■	■	■	■	■	
Turdus viscivorus		■	■	■	■	■	■	■							
Anthus trivialis			■	■	■	■	■	■	■	■					
Dendrocopos leucotos			■												
Garrulus glandarius			■				■								
Parus cristatus			■	■	■	■	■	■	■	■	▒	■			
Picus canus			■	▒	■	▒	■	▒	■						
Buteo buteo				■	■	■	■	▒	■						
Falco tinnunculus				■					■						
Dendrocopos major					■										
Picoides tridactylus						■	▒	■	■						
Tetrao urogallus						■									

Turdus torquatus						■	■	■	■	■	■	■	■	■	
Emberiza citrinella							■								
Loxia curvirostra								■	■	■	■	■	■	■	■
Tetrao tetrix									■	■	■	▨	■		
Carduelis flammea										■	■	■	■	■	■
Certhia familiaris										■					
Montifringilla nivalis										■	■				
Corvus corax												■	■		
Anthus spinoletta													■	■	■
Prunella collaris													■	■	■
Pyrrhocorax graculus													■	■	■
Lagopus mutus															■
Tichodroma muraria															■
	12	6	7	5	4	9	2	6	8	4	4	11	5	6	5

Lebenslauf

Name:	Hella Klosius
Geburtsdatum:	14.12.1980
Geburtsort:	Reps (Rumänien)
Staatsbürgerschaft:	Deutsch
Familienstand:	ledig
Religion:	evangelisch A.B.
Schulausbildung:	
1987-1991	VS Neuburg/Do.(Deutschland) VS Neuhaus/Klb. (Österreich)
1991-1993	HS Neuhaus/Klb.
1993-1999	BG/BRG Oberschützen Matura: 10.06.1999
Berufliche Bildung:	
1999/2000	2 Semester Studium der Landschaftsplanung Landschaftspflege an der Uni für Bodenkultur
WS 00/01-SS 08	Diplomstudium der Biologie (Ökologie) an der Uni Wien
Berufserfahrung:	
Ferialpraktika:	
Juli/August 2002	auf einem Bergbauernhof in der Schweiz im Kanton Uri (Isenthal, Gitschenen)
Juli 2003	im NABU Wallnau Wasservogelreservat (Fehmarn, Ostseeinsel)
August 2003	auf der Agrarbezirksbehörde Gmunden
Sommer 2004/05	Mitarbeit auf der Beringungsstation des Vereines Auring in Hohenau an der March
Sonstige Erfahrungen:	Mitarbeit bei Bird Life, ornithologischen Erhebungen, bei den Ökopädagogen des Vereines Auring
Seit April 2007	Mitarbeiterin beim Landgut Cobenzl
Besondere Kenntnisse, Fähigkeiten:	Englisch, Französisch Microsoft Office, Open Office, Photoshop Basiskenntnisse in Statistik und GIS Führerschein B
Hobbys und Interessen:	Wandern, Musizieren, Fotografieren, Sport, Kunst und Kultur, Lesen, Reisen, Gartenarbeit, Kochen