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Diversity of diurnal Lepidoptera across an elevational gradient above the timberline: a case study from the Austrian Alps

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Diversity of diurnal Lepidoptera across an elevational gradient above the timberline: a case study from the Austrian Alps

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Abstract

Only few empirical studies described changes of species richness and composition, and the complex interplay of environmental predictors and Lepidoptera distribution patterns, across altitudinal gradients in the Alps. This study focuses on the altitudinal distribution of diurnal Lepidoptera above the timberline on Mount Schrankogel (3,497m) in the Stubaier Alps (Tyrol/Austria). Diurnal Lepidoptera assemblages were surveyed in June and July 2009 along 25 horizontal line transects of 100m length, covering an elevational gradient between 2,050 and 3,200 m asl. A total number of 75 diurnal Lepidoptera species (1,087 sightings) belonging to 15 families were recorded. Lepidoptera species richness and abundance decreased continuously with increasing altitude, decreasing plant richness, nectar availability and vegetation cover. Lepidoptera species composition changed continuously across the elevational gradient resulting in a proportionally higher dissimilarity of species assemblages at larger altitudinal distances between transects. Furthermore, species richness of Lepidoptera decreased in similar ways towards higher altitudes independently if only species with monophagous, oligophagous or polyphagous larvae were considered. These results are consistent with the expectation of a continuous ecotone connecting alpine to subnival habitats, and do not support the idea of sharply defined biotic zones.

A long-term monitoring scheme should be implemented to quantify potential upward shifts of altitudinal distribution of alpine Lepidoptera species reflecting a response to the already documented upward migration of plant species corresponding to climate change.

Keywords

Diurnal Lepidoptera, species richness, species composition, elevational gradient, alpine environment, timberline, plant richness, nectar availability

Zusammenfassung

Bisher existieren nur wenige quantitativ-empirische Arbeiten, die sich mit den Veränderungen von Artenreichtum und Artenzusammensetzung sowie dem komplexen Zusammenspiel von Umweltvariablen und Verbreitungsmustern von Lepidopteren in den Alpen beschäftigen. Die vorliegende Studie untersucht die Höhenverbreitung tagaktiver Schmetterlinge oberhalb der Waldgrenze am

Schrankogel (3.497m) in den Stubaier Alpen (Tirol/Österreich). Zönosen tagaktiver Schmetterlinge wurden im Juni und Juli 2009 entlang von 25 Linientransekten, mit einer Länge von je 100 m, die einen Höhengradient zwischen 2.050 und 3.200 m abdecken, erforscht. Insgesamt wurden 75 tagaktive Schmetterlingsarten (1.087 Einzelsichtungen) aus 15 Familien nachgewiesen.

Die Ergebnisse zeigen eine kontinuierliche Abnahme des Artenreichtums und der Abundanz der Schmetterlinge mit zunehmender Höhe. Weiters ist ein positiver Zusammenhang zwischen Artenreichtum und der Nektarverfügbarkeit, der Vegetationsbedeckung und dem Pflanzenartenreichtum zu erkennen. Die Artenzusammensetzung von Schmetterlingen ändert sich kontinuierlich entlang des Höhengradienten. Dies wird durch eine steigende Unähnlichkeit innerhalb der Schmetterlingsgesellschaften mit zunehmender Vertikaldistanz zwischen den Transekten sichtbar. Eine ähnlich kontinuierliche Abnahme des Artenreichtums von Lepidopteren mit zunehmender Höhe lässt sich erkennen, wenn man den Artenpool gemäß der larvalen Ressourcenansprüche in 3 Phagie-Klassen unterteilt (monophag, oligophag, polyphag). Diese Ergebnisse stützen die Annahme eines kontinuierlichen Ökotons von der alpinen in die subnivale Vegetation und geben keine Hinweise auf scharfe zonale Grenzen.

Ein langfristiges Monitoring wäre hilfreich, um die mögliche Höhenverschiebung von Verbreitungsmustern alpiner Schmetterlingsarten zu dokumentieren, welche einher gehen mit der bereits vielseitig bestätigten Wanderung von Pflanzenarten in höhere Lagen auf Grund des Klimawandels.

Introduction

The distribution of high mountain ecosystems reaches from tropical to polar zones (Pauli et al. 2009). These alpine landscapes are generally regarded as hot spots of biodiversity (Grabherr et al. 2000a) with a high level of endemism but are actually going through a series of severe changes. For instance, the treeline is shifting upwards because of the rapidly declining use of alpine pastures for livestock rearing, which formerly lowered the timberline by humans to increase the area available for grazing (Dirnböck et al. 2003). Further, ecosystems of alpine regions are exceptionally susceptible to climate change because of their isolated and fragmented location and the influence of multiple environmental stress factors (Watson et al. 1997; Huber et al. 2007).

Insects in alpine environments have to deal with harsh climate conditions, such as high solar radiation intensity and short vegetation periods. However, one of the most important ecological factors for such ectothermic organisms is temperature (Sinclair et al. 2003; Karl & Fischer 2008). In alpine environments the annual mean temperature decreases about 1°C per 100 meters with increasing altitude (Geiger 1965; Roland 2006). To survive, alpine insects have evolved different adaptations to compensate for lower temperatures at higher altitudes, for instance behaviourally by basking (Clench 1966; Kevan & Shorthouse 1970; Heinrich 1993), physiologically through shivering (Heinrich 1986, 1993) and morphologically by means of thermal melanism (Roland 1982, 2006). With increasing altitude, the proportion of univoltine butterflies increases and generally the adult phase starts later in the year and is of shorter duration (Shapiro 1975).

Several studies on relationships between animal diversity and habitat variables along elevational gradients can be found for the Neotropis (e.g. Rahbek 1997; Brehm & Fiedler 2003), but information is limited for the Alps. In this study, we document the elevational patterns of Lepidoptera species richness above the timberline, attempting to understand the elevational distributions of Lepidoptera assemblages, and examine effects of habitat parameters and climatic factors on Lepidoptera diversity along an elevational gradient in the Austrian Alps. Particularly, the following hypotheses were tested:

(1) Species richness of diurnal Lepidoptera is declining with increasing altitude. Besides change in various climate variables, plant species richness, vegetation cover and nectar availability are important drivers of Lepidoptera diversity. Decline of temperature with increasing altitude possibly shapes the upper distribution margin of many ectotherm insects such as butterflies and moths. As mentioned by Hurlbert (2004), the species–energy theory predicts a positive relationship between species richness and available energy. Hence, the typically declining plant species richness towards higher altitudes may additionally have a negative effect on herbivore communities (Lawton et al. 1987). For the fraction of nectarivorous species also a decreasing availability of nectar sources at higher altitudes may cause a decrease of species diversity. A declining vegetation cover may have negative effects on the abundance of herbivorous insects such as the majority of Lepidoptera. According to the more-individuals – hypothesis (Srivastava & Lawton 1998) a generally higher abundance of Lepidoptera, therefore, may cause a higher species richness at lower altitudes with a higher density of ground vegetation.

(2) There is a continuous change of Lepidoptera species composition along the altitudinal gradient above the timberline. The harsher environment at higher altitudes may not only cause a decline of Lepidoptera diversity but also may require specific adaptations on low temperatures and a shorter vegetation period. Consequently, climatic conditions at higher altitudes may favor a different species assemblage with a higher proportion of “high-altitude specialists”. However, because the climatic conditions do not change abruptly but continuously, also Lepidoptera species composition may not change rapidly but most likely is related to the gradual changes in vegetation composition.

(3) Polyphagous species (generalists) become more dominant than oligophagous- and monophagous species (specialists) towards higher altitudes. The higher vegetational heterogeneity at lower altitudes may favor a higher proportion of specialists occupying smaller niches than in habitats at higher altitudes. This can be reflected by a change in the extent of larval food plant specialization. Therefore, we expect a decreasing proportion of host plant specialization towards higher altitudes.

Material and Methods

Study area and study sites

The study area is located on Mount Schrankogel, Stubaier Alps, Tyrol, Austria (11°05'58''E, 47°02'41''N; 3,497 m asl.), one of the highest mountains of the Austrian Alps. Mount Schrankogel is a GLORIA site (Global Observation Research Initiative in Alpine Environments), established in 1994. The purpose of GLORIA is to establish an internationally coordinated network monitoring effects of climate change on a global scale. The research initiative takes advantage of the high sensitivity of alpine ecosystems to climate change (Grabherr et al. 2000b). Study sites selected for this study on Lepidoptera are located above the timberline between 2,050 and 3,200 m asl. on the south and west flanks of Mt. Schrankogel (Fig. 1) where a vegetation characteristic for the central siliceous high Alps can be found.

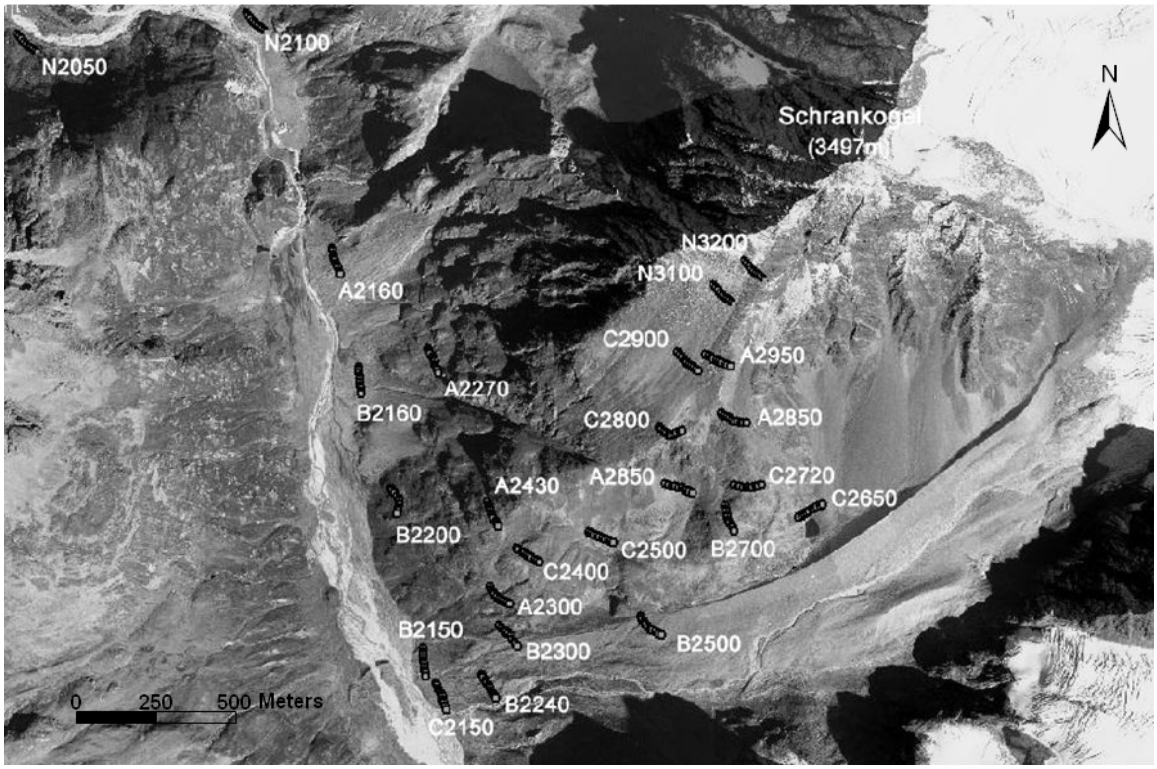

Fig. 1. Study area at Mt. Schrankogel, Tyrol, Austria showing the locations of all 25 sampling transects. Additionally, all transect codes are provided (numbers indicate the altitude in meters of the transects).

The study sites represent 25 horizontal line transects, 21 already established and marked in 2008 in the framework of a plant mapping project (Hofer & Scholz 2010). Therefore, detailed floristic data were available for these 21 study sites located between 2,150 and 2,950 m. Another 4 transects were established in 2009 at altitudes of 2,050, 2,100, 3,100 and 3,200 m to expand the altitudinal gradient for this study on Lepidoptera. All transects had a length of 100 meters. Habitat features of all study sites are documented in Appendix A.

Lepidoptera sampling

The sampling of Lepidoptera was conducted between 17 June and 1 August 2009. Each transect was visited three times (for sampling dates see Appendix A). It was planned to visit all transects before starting the next sampling round. However, due to unpredictable weather conditions sometimes this order could not be retained (compare sampling dates provided in Appendix A). Transect runs were only made between 09:30 and 17:00 during suitable weather conditions (in sunshine). The duration of one transect run was approximately 20 minutes. When weather conditions became worse (e.g. clouds covered the sun) Lepidoptera sampling was stopped and continued only after the conditions became again suitable for supporting flight activity of diurnal Lepidoptera. Lepidoptera were recorded up to 5 meters on both sides along the transect (area about 1,000 m² per transect). Lepidoptera were identified on the wing or caught with a sweep net for further identification. If a proper determination was impossible in the field voucher specimens were collected for later identification in the laboratory. Whenever necessary to validate preliminary identification of similar species, genitalia dissections were done (e.g. some *Pyrgus* species, Hesperiidae). Butterflies and moths were identified according to Stettmer et al. (2007), Fajcik (1998, 2003) and Slamka (1995).

Recorded biotic and abiotic variables

For each transect the following variables were measured or estimated: altitude, inclination, nectar availability, plant cover, open ground cover, rock cover and signs of pasturing. Altitude was measured by GPS; inclination was classified on a scale from 1 (flat) to 5 (very steep). During each of the three transect runs nectar

availability was ranked on a scale between 0 (absence of nectar sources) to 5 (very high density of flowering plants). The mean nectar availability was used for all further analyses. Plant cover, open ground cover and rock cover was estimated as percentage of the total "transect area" of 10 x 100 m, signs of pasturing were classified as 0 (no cattle excrements) to 3 (excrements covering larger part of the study site).
Furthermore, cloudiness and wind force were estimated during all transect runs. Cloudiness was estimated as the fraction of sky obscured by clouds in eighths (0 – cloudless; 8/8 – closed cloud cover); wind force was classified according to the Beaufort-scale ranging between 0-12. However, transect runs were only done during wind forces between 0 and 5.

Statistical analysis

The completeness of the total species inventory was estimated with the richness estimators Chao 2 and jacknife 2. These abundance-based estimators were identified as best richness estimators by Walther & Moore (2005). Both estimators and species-accumulation curves were computed using the software EstimateS version 8.00 (Colwell 2006). Samples were randomized 50 times without replacement.

To test for univariate relationships between species numbers or abundance (sum of all individuals counted during the three transect walks) and biotic or abiotic variables linear regression models were calculated. Also changes of abiotic variables across the altitudinal gradient were analyzed by linear regressions. If variables were not normally distributed, respective data transformations were applied to achieve normal distribution. Generalized linear models (GLMs) were calculated to test for multiple effects of environmental variables on species richness or abundance of Lepidoptera. Only predictor variables which proved to have significant effects in calculated univariate regressions were included in the calculated GLMs. When testing for effects of species richness, Lepidoptera abundance was included as predictor variable. For testing effects of nectar availability on species richness only nectarivorous Lepidoptera were considered. All regression analyses were performed using Statistica 7.1 (StatSoft Inc 2005).

Bray-Curtis similarities for Lepidoptera and plant communities were calculated for all possible site pairings using the software Primer 5.2 (Clarke & Gorley 2001). The resulting similarity matrix for Lepidoptera was used to compute a non-metric multidimensional scaling (NMDS) plot with Statistica 7.1 (StatSoft Inc 2005) to visualize similarity relationships between Lepidoptera communities sampled at individual transect sites. Because the produced two dimensional scaling plot has a stress value (a measure of poorness-of-fit) of <0.20 it was considered to adequately visualize species composition relationships (Clarke 1993). Dimension 1 and Dimension 2 values of the plot were related to habitat values to identify potential drivers shaping changes of species composition across the studied elevational gradient. Spearman matrix rank correlations were calculated to test for relationships between the Lepidoptera similarity matrix and distance matrices (Euclidian distances) of habitat parameters by the software Primer 5.2.

To achieve useful measures for plant species richness and composition very rare plant species (23 species) occurring only in one individual on one transect were not considered. Such rare species may strongly affect plant diversity measures although they most likely will not have any prominent effect on Lepidoptera communities. Lepidoptera species were assigned to three different groups according to their larval hostplant specificity: monophagous species (only feeding on one plant genus), oligophagous species (feeding on different plant genera belonging to the same family) and polyphagous species (feeding on >1 plant family; Schaefer 2003).

Results

A total of 1,117 individuals of 87 Lepidoptera species (including 12 exclusively nocturnal species flushed from the vegetation) were observed along the 25 transects between 2,050 and 3,200 m (Appendix B). Diurnal Lepidoptera were represented by 75 species (including 3 migratory species). A total of 15 Lepidoptera families were recorded: Hesperidae (6 species), Lycaenidae (5), Nymphalidae (22), Papilionidae (2), Pieridae (6), Arctiidae (4), Geometridae (14), Hepialidae (1), Noctuidae (3), Pterophoridae (1), Pyralidae (16), Zygaenidae (1), Gelechiidae (1), Psychidae (1) and Tortricidae (2). Only 3 specimens belonging to 2 different species (“spec. 1”, “spec. 2”) could not be designated to species due to their heavily damaged wings.

Species richness and abundance

The shape of the calculated species accumulation curves for all transects (excluding migratory species) indicate that the total species assemblage is still incompletely sampled, independently if all or only diurnal species were considered (Fig. 2). However, when excluding nocturnal species the species completeness slightly increased from 67.8 (Jack2)–78.5 % (Chao2) to 72.6 (Jack2)–84.3 % (Chao2) indicating that this group was inadequately sampled by our transect walks. Therefore, for all further analyses, additionally to migratory Lepidoptera, also nocturnal species were excluded.

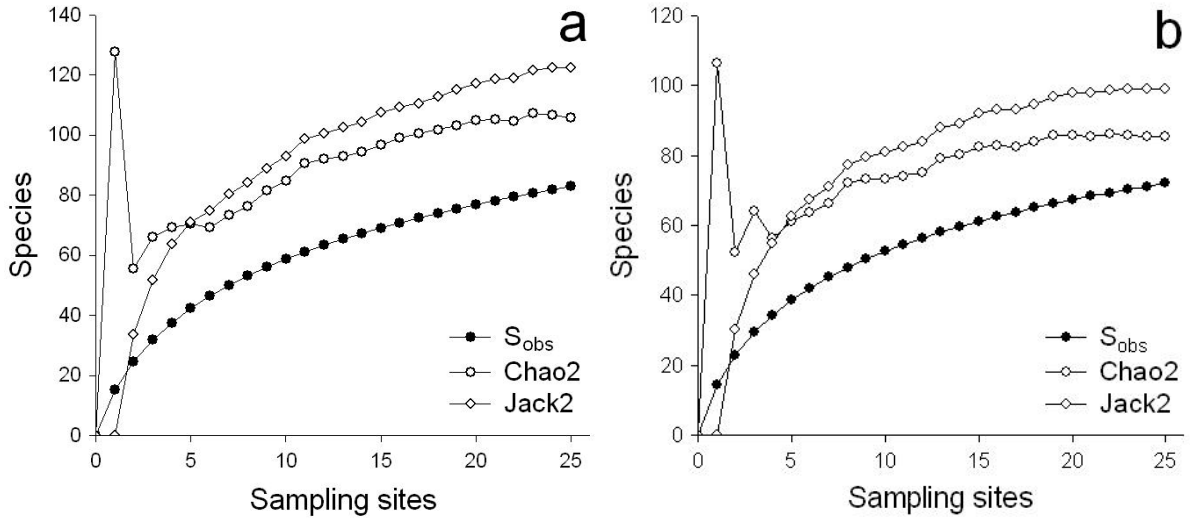

Fig. 2. Accumulation curves for richness (excluding all migratory species) of all Lepidoptera species (a) and only diurnal species (b) sampled by transect walks across the entire altitudinal gradient ranging from 2,050 to 3,200 m asl.

Species richness recorded for individual transects declined significantly with increasing altitude (Fig. 3a), while the number of counted individuals did not change significantly, although highest Lepidoptera abundance was observed at lower elevations (Fig. 3b).

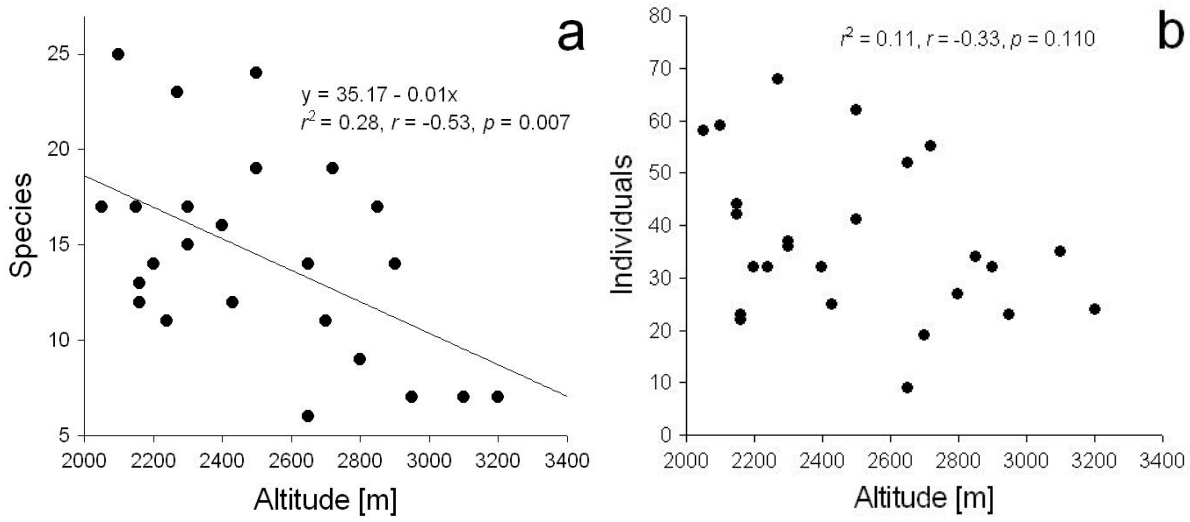

Fig. 3. Relationship between the total number of Lepidoptera species (a) and individuals (b) observed per transect and altitude. Additionally results of linear regressions and the respective regression functions and curves (only when a significant level was achieved) are shown.

Furthermore, species richness was positively related to the abundance of Lepidoptera (Fig. 4).

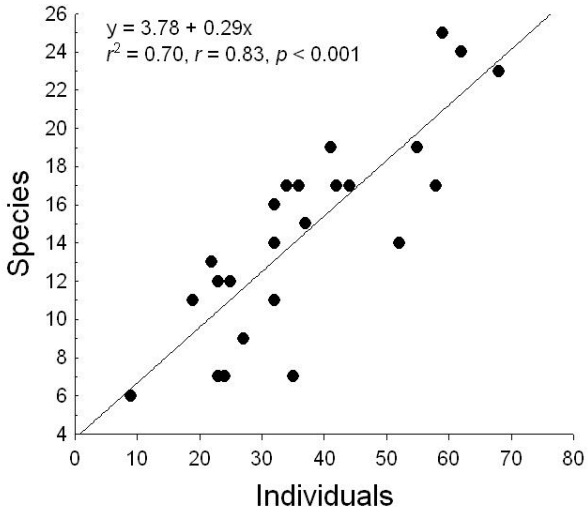

Fig. 4. Relationship between species richness of Lepidoptera and abundance described by a linear regression model.

To test for a potential effect of weather variables (cloud cover, wind speed) on the total number of individuals recorded during the three counts per transect a GLM was applied. Altitude, mean cloud cover (N = 3 transect counts) and mean wind speed (N = 3 transect counts) were included as predictor variables. The results do not indicate any effect of the two weather variables on Lepidoptera abundance (Tab. 1).

Table 1. Results of a GLM testing for effects of altitude and weather variables (cloud cover and wind speed) on the total number of observed individuals per 100 m transect.

Variables	df	MQ	*F*	*p*
Constant	1	2435.87	11.32	0.003
Altitude	1	302.65	1.41	0.249
Cloud cover	1	121.44	0.56	0.461
Wind speed	1	153.94	0.72	0.407
Error	21	215.14		

Altitudinal changes of habitat parameters

Plant species richness (excluding rare species with only one individual per transect) and nectar availability decreased continuously with increasing altitude (Fig. 5). Also vegetation cover and the variable pasture signals decreased significantly with increasing altitude. Inclination, open ground and the area of exposed rock increased significantly with increasing altitude (Table 2).

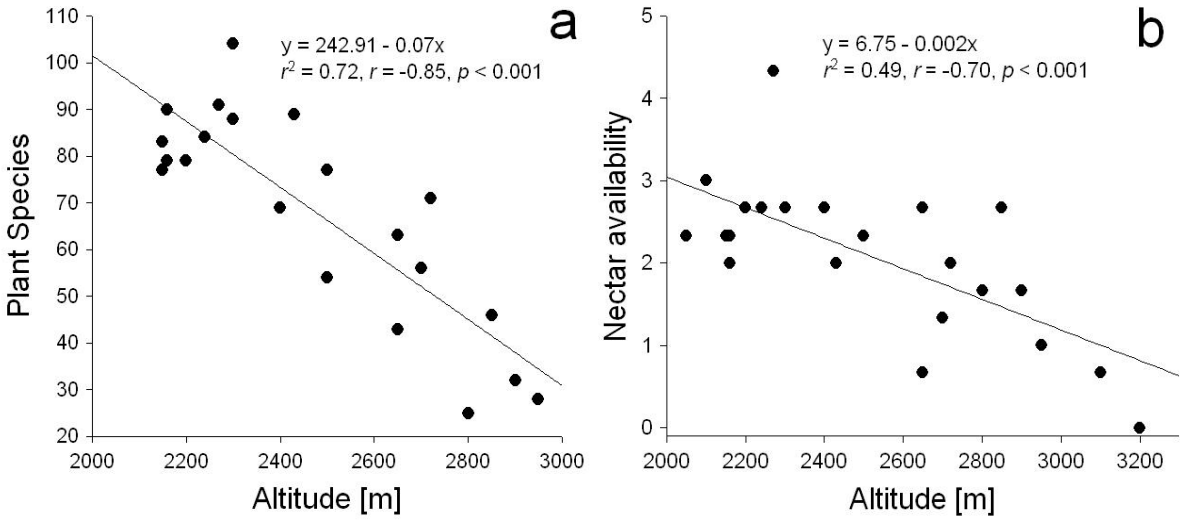

Fig. 5. Changes of plant species richness (a) and nectar availability ranging from 0 (no nectar sources) to 5 (very high density of flowering plants) (b) across the altitudinal gradient described by a linear regression function.

Table 2. Results of linear regressions of various habitat variables on altitude.

Parameter	***r*²**	***r***	***p***	**Regression function**
Vegetation cover (arcsin x transformed)	0.48	-0.69	< 0.001	y = 2.22 - 0.001x
Inclination	0.27	0.52	0.008	y = -0.69 + 0.01x
Open ground (arcsin x transformed)	0.25	0.50	0.011	y = -0.70 + 0.01x

Rock cover (arcsin x transformed)	0.46	0.67	< 0.001	y = -88.52 + 0.05x
Pasturing	0.28	-0.53	0.007	y = 2.22 - 0.001x

Relationships between habitat parameter and Lepidoptera diversity

Diversity of Lepidoptera increased with increasing plant species richness (Fig. 6a) and increasing nectar availability (only nectarivorous species considered; Fig. 6b). Furthermore, Lepidoptera species richness was positively related to vegetation cover (linear regression: r^2 = 0.41, r = 0.63, p<0.001; y = 7.91-0.12x) and negatively related to the proportion of exposed rock (r^2 = 0.42, r = -0.65, p<0.001; y = 19.20-9.21x). No relationship was found between Lepidoptera richness and the proportion of open ground (linear regression: r^2 = 0.03, r = -0.17, p=0.416) and inclination (r^2 = 0.05, r = -0.22, p=0.283). A weak positive relationship was found between grazing intensity and Lepidoptera richness (r^2 = 0.18, r = 0.43, p=0.034). However, this relationship did not remain significant after applying a Bonferroni correction.

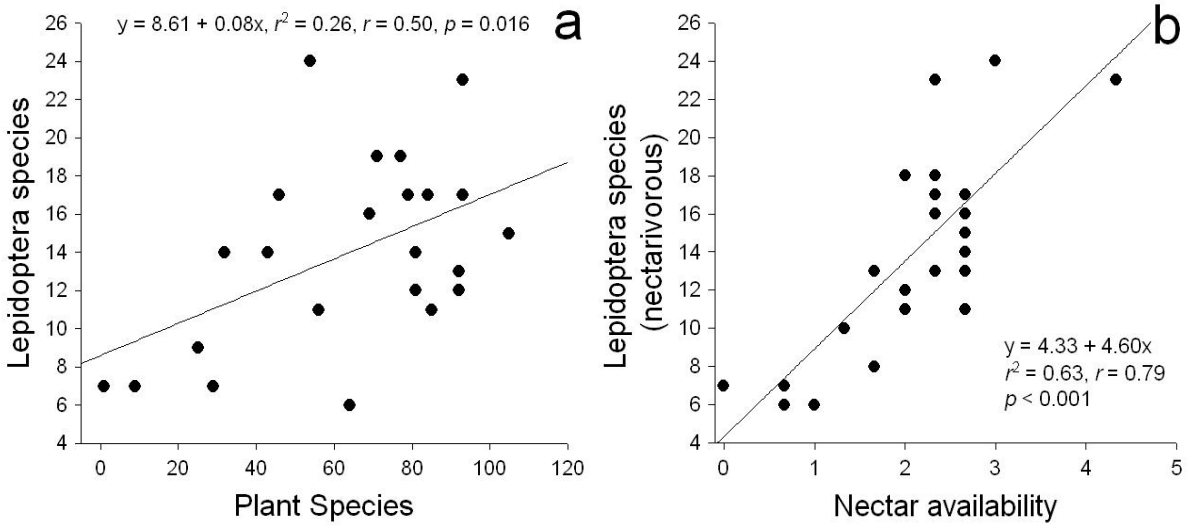

Fig. 6. Relationship between Lepidoptera species richness and plant species richness (a) and nectar availability (b). For the later regression analysis only Lepidoptera species with a functional proboscis were considered. Additionally, result of linear regressions and the respective regression curves are provided.

Because all habitat variables strongly affecting Lepidoptera richness – as indicated by univariate regression analyses – are correlated with altitude, we additionally tested their effect on the standardized residuals of Lepidoptera species richness on altitude. No relationships were found between the residuals of Lepidoptera richness

and plant richness (r^2 = 0.01, r = -0.11, p=0.641), vegetation cover (r^2 = 0.10, r = 0.31, p=0.126) and the area rock of exposed rock (r^2 = 0.11, r = -0.33, p=0.105). However, a strong positive relationship was found between residuals of Lepidoptera species numbers and Lepidoptera abundance (Fig. 7).

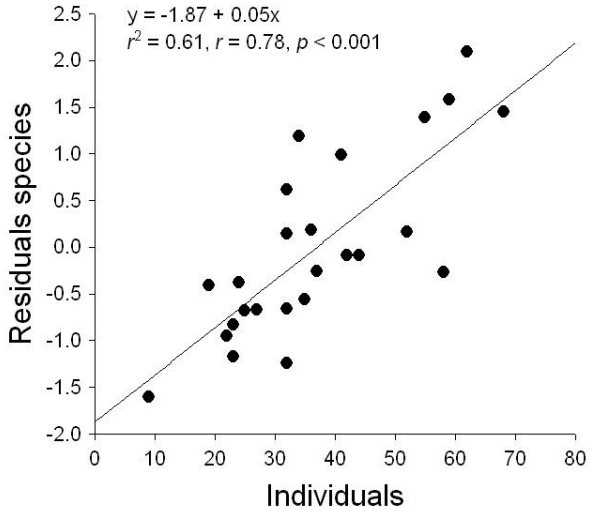

Fig. 7. Relationship between residuals of Lepidoptera species numbers on altitude and total Lepidoptera abundance described by a linear regression.

When considering only nectarivorous Lepidoptera (residuals of species numbers on altitude), again no effects were found for plant richness (r^2 < 0.01, r = -0.06, p=0.804), vegetation cover (r^2 = 0.10, r = 0.33, p=0.111) and the area rock of exposed rock (r^2 = 0.11, r = -0.33, p=0.107), but a positive relationship was found between richness of nectarivorous Lepidoptera and nectar availability (Fig. 8) and abundance (Fig. 9). When calculating a GLM testing for effects of nectar availability and the abundance of nectarivorous Lepidoptera on the residuals of nectarivorous Lepidoptera richness on altitude (multiple r = 0.77, F = 15.82, p < 0.001), only the abundance of diurnal Lepidoptera remained as significant explanatory variable (Table 3), most likely because abundance itself was highly correlated with nectar availability (Fig. 10).

Table. 3. Results of GLM testing for effects of nectar availability and the abundance of nectarivorous Lepidoptera on the residuals of nectarivorous Lepidoptera richness on altitude.

Variable	df	MQ	*F*	*p*
Constante	1	10.03844	23.41607	0.000078
Individuals of nectarivorous species	1	8.12123	18.94390	0.000255
Nectar availability	1	0.00212	0.00494	0.944578
Error	22	0.42870		

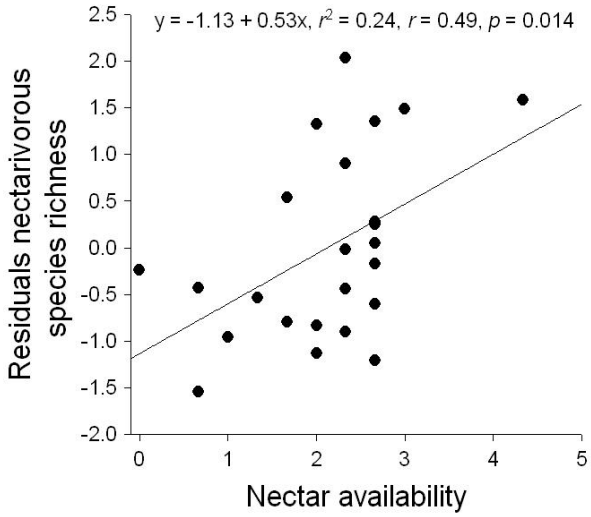

Fig. 8. Relationship between standardized residuals of nectarivorous Lepidoptera richness on altitude and nectar availability described by a linear regression.

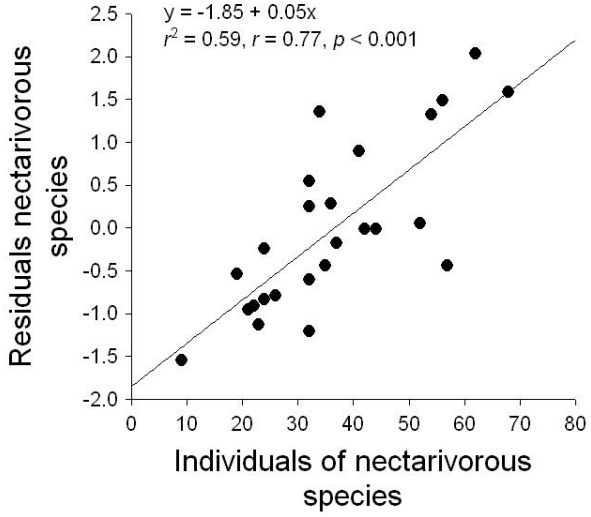

Fig. 9. Relationship between standardized residuals of nectarivorous Lepidoptera richness on altitude and abundance of nectarivorous Lepidoptera described by a linear regression.

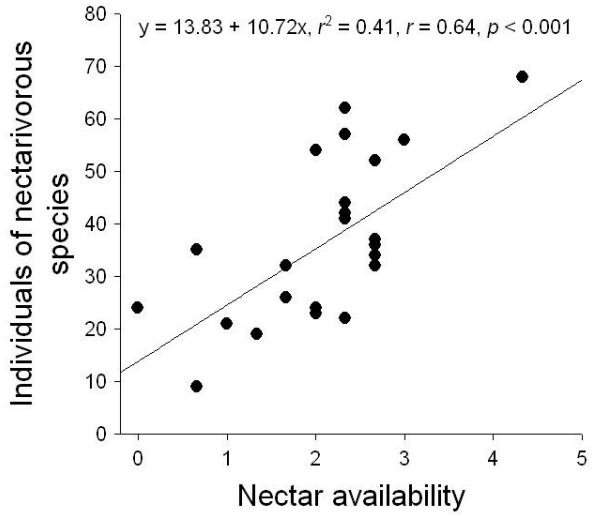

Fig. 10. Relationship between abundance of nectarivorous Lepidoptera and nectar availability described by a linear regression model.

Species composition: Effects of altitude and habitat variables

The NMDS ordination based on Bray-Curtis similarities indicate a continuous change from lower towards higher altitudes from the left towards the right side of the ordination plot (Fig. 11). This visual impression is confirmed by a significantly positive correlation between the Dimension 1 values and altitude (Fig. 12). However, also other habitat variables closely related to altitude, such as vegetation cover and the area of exposed rocks and (nectar availability) were highly correlated with Dimension 1 values (Appendix C). In contradiction, none of our habitat variables was related to Dimension 2 values after applying Bonferroni correction (Appendix C).

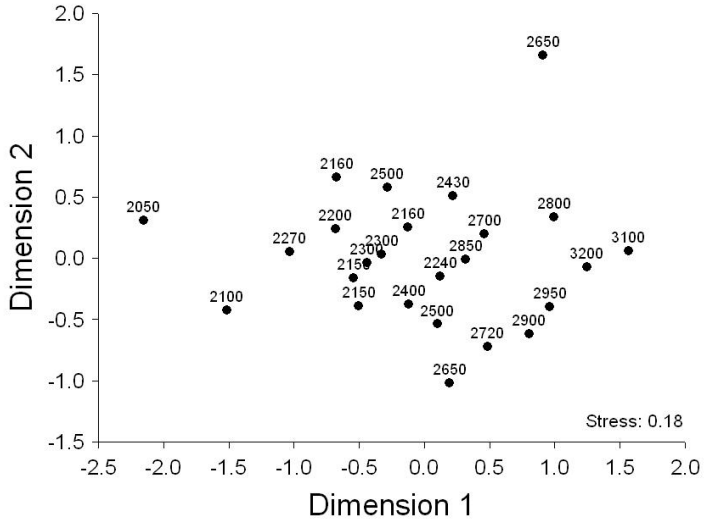

Fig. 11. NMDS plot based on Bray-Curtis Similarities for Lepidoptera assemblages sampled at different altitudes (indicated by numbers next to data points).

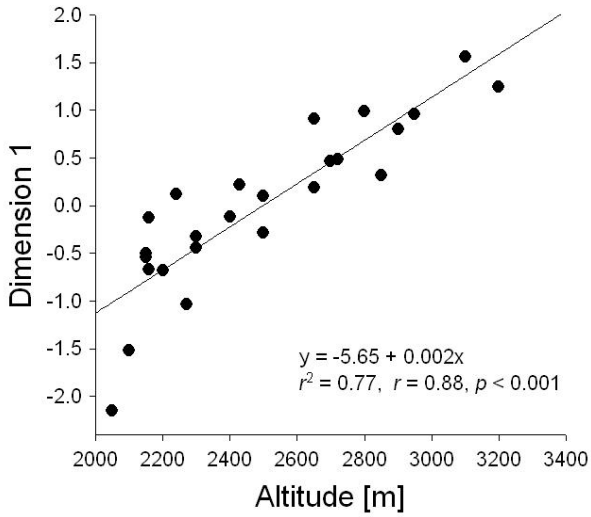

Fig. 12. Relationship between Dimension 1 values extracted from a NMDS ordination based on Bray-Curtis similarities for Lepidoptera communities (see Fig. 11) and altitude described by a linear regression model.

Similarity of Lepidoptera declined with increasing altitudinal distance between sampling sites (Spearman matrix rank correlation: *Rho* = 0.53, $p < 0.001$; Fig. 13a) and was positively related to similarity of plant composition (*Rho* = 0.50, $p < 0.001$; Fig. 13b).

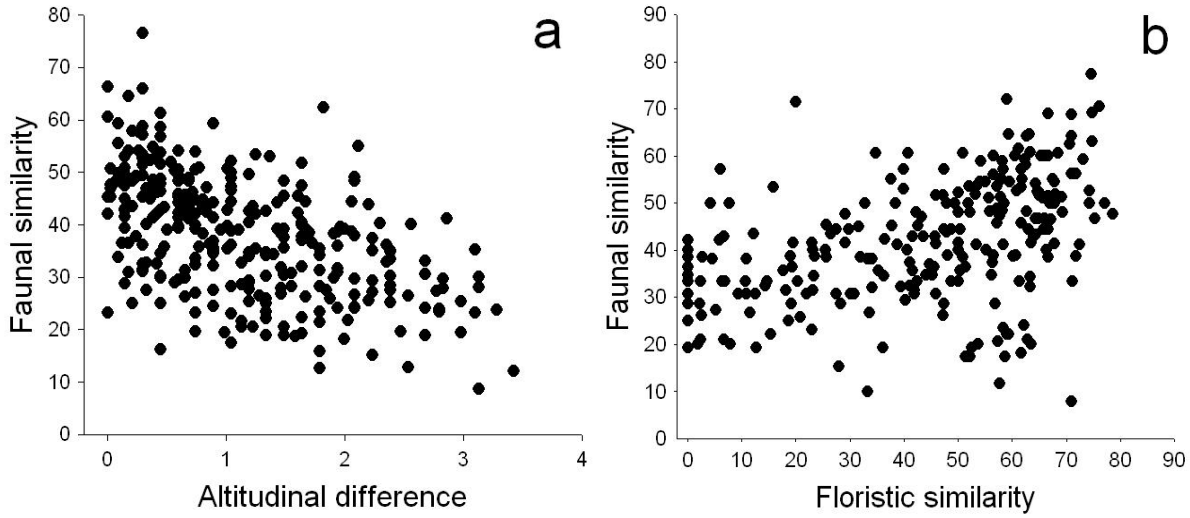

Fig. 13. Relationship between (Bray-Curtis) similarity of Lepidoptera communities and altitudinal differences between compared sites (a) and similarity of plant species composition (b).

Altitudinal change of species richness of Lepidoptera with different larval host plant specificity

A total of 18 monophagous species, 24 oligophagous species and 29 polyphagous species were found (not including exclusively nocturnal, migratory and two unidentified species). All three groups show a similar pattern of continuously declining richness with increasing altitude as indicated by nearly identical inclination coefficients (k = 0.003) and very similar r^2 values (Fig. 14).

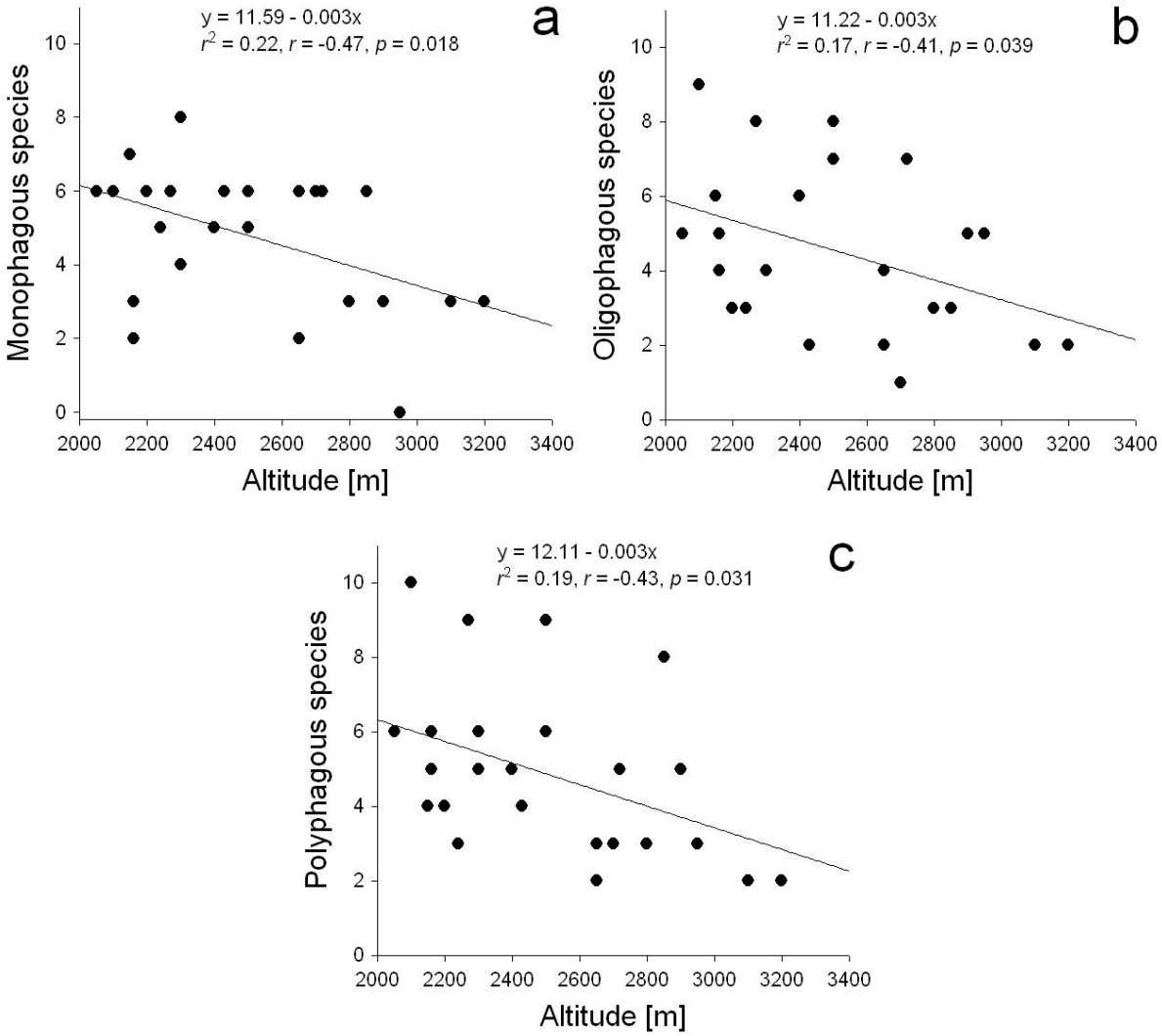

Fig. 14. Change of species richness across the altitudinal gradient described by linear regressions for Lepidoptera species groups with different larval hostplant specificity: monophagous (a), oligophagous (b) and polyphagous species (c).

Discussion

Species richness and abundance

The estimated sampling completeness indicates that the majority of diurnal Lepidoptera occurring above the timberline on Mount Schrankogel was recorded during our study in 2009. The total of 41 butterfly species found above 2,000 m at Mt. Schrankogel was remarkably high, considering that for instance only 48 butterfly species occur above 2,000 m in the entire area of the Swiss Alps (compare Figure at p. 38 in SBN 1987).

While various studies on changes of insect species richness across elevational gradients reported a mid-elevation peak of species diversity (Janzen et al. 1976; Holloway 1987; Hammond 1990; Holloway et al. 1990; Schulze 2000; Pyrcz & Wojtusiak 2002; see also article on “mid-domain effect” by Colwell et al. 2004), others found a decline of species richness with increasing altitude (Lawton et al. 1987; Wolda 1987; Brühl et al. 1999; Axmacher et al. 2004) or no prominent change in species diversity over a wide range of different elevations (Brehm 2002; Brehm & Fiedler 2003). The elevation of highest species richness appears to be determined by ecological interactions, latitude, disturbance and not least sampling regimes (McCoy 1990). Long-term sampling regimes are more likely to show a peak at lower altitudes whereas short-term regimes often show a mid-elevation peak of species richness. Further human disturbance can affect elevational patterns of diversity, because disturbance often occurs more frequently at lower elevations (McCoy 1990). Also in our study disturbance due to cattle grazing decreased from the lowest towards higher altitudes.

Our data shows a significant decline of species richness with increasing altitude above the timberline. Above the timberline a general decrease of ectothermal species with increasing altitude can be expected, particularly because the climate is already harsh at the lowest altitudes sampled during this study at around 2,000 m and is getting increasingly worse for insects towards the summit of Mt. Schrankogel. Our data indicate a more or less linear decline of Lepidoptera species with increasing

altitude. Only at the nival zone species richness appeared to stabilize and for every transect between 2,950 and 3,200m 9 species were recorded.

In contrast to species richness, abundance of Lepidoptera only showed a weak (but none-significant) trend of decline towards higher elevations. Furthermore, variance of weather conditions did not significantly affect the number of counted Lepidoptera per transect. This may not only be caused by the fact that all transect runs were conducted during mostly optimal weather conditions supporting a high flight activity of diurnal Lepidoptera. That variance of cloudiness and wind speed did not proof to significantly affect the abundance could also be the result of a high robustness of high-alpine Lepidoptera against often harsh weather conditions at higher elevations.

The diversity of resources is an important measurement for the number of species on the next higher trophic level. Therefore, landscapes inhabiting a high diversity of resources can facilitate a higher number of individuals and consequently a high number of species (*More Individuals – Hypothesis*, Srivastava & Lawton 1998; Hurlbert 2004). In our study at Mount Schrankogel resource diversity declined continuously towards higher altitude as indicated by the decrease of plant diversity. Although Lepidoptera species richness was positively related to plant richness, a stronger relationship was found between Lepidoptera species richness and Lepidoptera abundance across the elevational gradient. This provides strong support for this *More-Individuals-Hypothesis.*

The *Productivity Hypothesis* assumes that plant growth is limited by the available energy which is determined by e.g. temperature. The decrease of nectar availability and vegetation cover with increasing altitude in this study indicate a decrease of resource availability with increasing altitude, and hence, a decrease of net primary production, which is an accurate predictor of species richness (Williams et al. 2004). However, already Rausher (1979) demonstrated that habitats including a high richness of larval food plants may be rarely used by Lepidoptera, when there is a lack of adult nectar plants (Murphy 1983). Therefore, a high Lepidoptera species richness is not necessarily related to a dense plant cover; nectar availability is at least as important as larval food resources. In our study, nectar producing plants declined with altitude. In the upper alpine zone nectar producing plants visited by Lepidoptera

only occur in low densities, while grasses, mosses and lichens predominate the patchy ”vegetation cover”. This situation could favor the occurrence of species at higher altitudes which do not require food sources as adults, consequently often characterized by a non-functional reduced proboscis and short life times. However, only few species found in higher areas (> 2700m) at Mount Schrankogel were species with reduced proboscis (e.g. the arctiids *Grammia quenseli, Parasemia plantaginis, Setina aurita*; see Appendix B). In our study, both variables vegetation cover and nectar availability proved to be highly related to Lepidoptera species richness, at least in univariate tests. However, when residuals of Lepidoptera richness on altitude were used, only Lepidoptera abundance remained as significant predictor variable. Therefore, our results may favor the *More-Individuals Hypothesis.*

However, the habitat variable vegetation cover may not be a reliable indicator for resource availability. Increasing altitude affects growth rates, morphology, phenology, nutrient composition, concentrations of secondary and defensive compounds, and extent of flowering and seed production of plants utilized by Lepidoptera. Although insects can respond by changing their food consumption, food conversion efficiency and growth rates (Margraf et al. 2003; Hodkinson 2005), the reduced quality of exploited resources can decrease fecundity towards higher altitudes. For example, egg production in *Colias* (Pieridae) butterflies at high elevations can drop to the half of the amount of eggs produced by females at lower elevations (Kingsolver 1983; Hodkinson 2005). Furthermore, a decline of resource availability due to a shorter vegetation period at higher elevations can reduce the time available for oviposition.

Beside climatic and habitat variables, the decline of available area towards high altitudes, which can cause a decrease of niches and of opportunities for speciation, potentially diminish biodiversity at high latitudes (Gorelick 2008). Corresponding to analytic geometry, a conical mountain, like Schrankogel, should show a linear decrease of available area and consequently of species number with altitude (Gorelick 2008).

Species composition

Altitude does not only affect species richness but also the species composition of insect communities (Whittaker 1952; Hodkinson 2005). Our results demonstrate that also Lepidoptera species composition did not change abruptly but continuously across the elevational gradient at Mount Schrankogel. Altitude can be the key variable for explaining changes of Lepidoptera species composition across elevational gradients, while other variables such as vegetation structure are only weakly related to changes of species composition (Axmacher 2003), although vegetation structure can have a prominent effect on the species richness of herbivorous insects (Wettstein & Schmid 1999). In contrast, in our study changes in species composition of Lepidoptera was highly correlated with changes in plant species composition, although a slightly stronger altitude was indicated for altitude. The high importance of altitude as explanatory variable is certainly due to its role as "surrogate variable" integrating a large number of different parameters, which itself are continuously changing across elevational gradients such as climate variables (particularly temperature) and plant composition (at least above the treeline).

The structure of Lepidoptera composition can also vary between identical elevations when study sites are located on different mountain sides (Shapiro 1975). Exposition changes the elevational climate gradient and therefore affects the altitudinal distribution of the entire vegetation, which has important consequences for herbivores insects such as Lepidoptera. In this study all study sites were located on the south and south-west flanks of Mount Schrankogel (except the lowest transect at 2,050, which was situated on the eastern side of the mountain). For this reason, exposition did not affect species composition in our study.

Hostplant specificity vs. altitude

Species richness of Lepidoptera in different altitudes appears to be predominantly determined by climate factors, hostplant richness and habitat diversity. The contribution of these factors may lead to a differentiation between habitat specialist and habitat generalist Lepidoptera (Menéndez 2007). In the past scientists assumed an increase of polyphagous alpine Lepidoptera with increasing altitude, without

providing clear evidence. The spatial heterogeneity hypothesis postulates that structurally complex habitats will support more species than simple habitats because they offer a greater diversity of microhabitats, hence a broader resource base and more resources to partition (Pianka 1966). In this study, we tested the hypothesis that a decline of niches towards higher altitudes caused by a decreasing heterogeneity of the vegetation cover leads to a more prominent decrease of monophagous (specialists) compared to oligophagous and polypahous species (generalists) with increasing altitude. However, our data indicate that species richness decreased similarily along the elevational gradient even when analyzed separately for Lepidoptera with different larval hostplant specificity. In contrast, a study on Microlepidoptera (feeding on Rosaceae) in west Austria reported an increase of specialists with increasing altitude (Huemer 1988).

Species richness of specialist butterflies depends on the availability of adequate hostplants. However, above the timberline perhaps abiotic variables, particularly climatic factors (e.g. duration of snow cover, temperature), are getting increasingly important for shaping Lepidoptera communities. It is of high importance to be perfectly adapted to these harsh conditions. For instance 10% of the Swiss butterflies are restricted to tallus slopes, rocks or large stones (SBN 1987). Hence, their occurrences depend predominantly on abiotic habitat structures, but not on specific hostplants. The heat radiation of the stones causes a quicker acting of butterflies utilizing this microhabitat than of those bathing on vegetation. Furthermore, stones heated up the whole day radiate heat to the surrounded plants which has a positive effect on the nocturnal feeding caterpillars and increases the vegetation period by more than one month, and sunbathing and relaxing on stones is less dangerous for adult butterflies than on plants (crab-spiders). Additionally, several caterpillars are able to overwinter und pupate under save rocks (SBN 1987). Butterfly species with such adaptations observed in this study at Mt. Schrankogel were *E. pluto*, *E. meolans, E. montana* and *Erebia gorge*.

Effects of climate change on alpine insects

Because species show specific responses to changes of environmental variables, it is reasonable to assume that climate change will affect the temporal and spatial

association between species interacting at different trophic levels (Harrington et al. 1999). Interactions that involve different trophic groups, such as plant-herbivore interactions probably suffer the largest mismatch (Harrington et al. 1999; Menéndez 2007). Temperature represents the dominant abiotic variable affecting herbivorous insects because it directly affects mortality, development and abundance (Bale et al. 2002). Pauli et al. (2007) reported a change in plant species richness and plant composition related to temperature changes over a decade between an altitude of 2,900 and 3,200m asl. at Mt. Schrankogel. This vegetational shift may additionally affect herbivore communities.

Climatic change also affects Lepidoptera communities (Dennis 1993; Gutierrez 1997). For example, in Europe and Northern America butterfly species shifted their ranges to the north and to higher elevations because of global warming (Parmesan 1996; Wilson et al. 2005; Menéndez 2007). The response of montane insects to climate change, particularly rising temperature, can vary significantly among species, depending on characteristics of their life history. Some species will expand their altitudinal ranges, others are likely to contract their vertical distribution (Hodkinson 2005). Herbivores such as Lepidoptera species utilizing plants with different survival strategies and growth forms will be differentially affected by climate warming (Bale et al. 2003).

There are still many challenges in monitoring and predicting climate change impacts on biodiversity (Bale et al. 2002). Studies documenting the vertical distribution of Lepidoptera across elevational gradients in temperate regions are rare but provide the basis for such prognoses on the impacts of climate change. Our quantitative data on species richness and composition of Lepidoptera communities at Mount Schrankogel could be used for evaluating effects of climate change on alpine insects when a regular monitoring scheme would be implemented at Mount Schrankogel.

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Appendix A:

Habitat features of the 25 sampled transects, including transect code (numbers behind the letters represent the altitude), replicate number, survey date, start and end time of the transect survey, cloudiness, wind force, nectar availability, inclination, signs of pasturing (for classification of the later 5 variables see Method section), vegetation cover, open ground cover and rock cover. Numbers printed in bold and italics indicate the mean of the 3 replicates of each transect.

Transect code	Replicate number	Date	Start	End	Cloudiness (in eighths)	Wind force	Nectar availability	Inclination	Vegetation cover (%)	Open ground cover (%)	Rock cover (%)	Pasturing
N2050	1	21/07/2009	13:00	13:20	1/8	1	2	2	70	1	29	1
	2	24/07/2009	10:20	10:40	2/8	1	3	2	70	1	29	1
	3	27/07/2009	12:20	12:40	0	1	2	2	75	2	23	1
					0.13	***1.00***	***2.33***	***2.00***	***71.67***	***1.33***	***27.00***	***1.00***
N2100	1	16/07/2009	16:10	16:30	6/8	1	3	2	60	0	40	1
	2	24/07/2009	11:30	11:50	5/8	1	3	2	60	0	40	1
	3	27/07/2009	13:45	14:05	0	1	3	2	70	2	28	1
					0.46	***1.00***	***3.00***	***2.00***	***63.33***	***0.67***	***36.00***	***1.00***
B2150	1	18/06/2009	16:35	16:55	5/8	1	1	1	70	0	30	1
	2	02/07/2009	13:40	14:00	6/8	2	2	1	65	0	35	2
	3	23/07/2009	16:00	16:20	6/8	3	4	1	70	1	29	1
					0.71	***2.00***	***2.33***	***1.00***	***68.33***	***0.33***	***31.33***	***1.33***
C2150	1	18/06/2009	16:00	16:20	4/8	1	1	2	65	0	35	1
	2	02/07/2009	12:45	13:05	4/8	1	2	2	70	1	29	1
	3	22/07/2009	15:30	15:50	6/8	0	4	2	70	0	30	1
					0.58	***0.67***	***2.33***	***2.00***	***68.33***	***0.33***	***31.33***	***1.00***
A2160	1	18/06/2009	10:40	11:00	0	2	1	3	20	0	80	0
	2	08/07/2009	16:20	16:40	6/8	2	2	3	60	0	40	0
	3	01/08/2009	16:20	16:40	6/8	1	3	3	65	0	35	1
					0.50	***1.67***	***2.00***	***3.00***	***48.33***	***0.00***	***51.67***	***0.33***
B2160	1	18/06/2009	11:25	11:45	0	3	2	2	50	0	50	0
	2	09/07/2009	15:00	15:20	7/8	1	2	2	50	2	48	1
	3	27/07/2009	14:45	15:05	0	2	3	2	65	1	34	1
					0.29	***2.00***	***2.33***	***2.00***	***55.00***	***1.00***	***44.00***	***0.67***
B2200	1	18/06/2009	12:45	13:05	2/8	2	1	3	90	0	10	1
	2	04/07/2009	10:00	10:30	6/8	1	3	3	70	2	28	1
	3	22/07/2009	10:20	10:40	6/8	2	4	3	85	5	10	1
					0.58	***1.67***	***2.67***	***3.00***	***81.67***	***2.33***	***16.00***	***1.00***

B2240	1	18/06/2009	15:15	15:40	4/8	1	2	3	60	0	40	1
	2	02/07/2009	11:45	12:05	3/8	1	2	3	65	1	34	0
	3	22/07/2009	14:20	14:40	7/8	3	4	3	70	0	30	1
					0.58	***1.67***	***2.67***	***3.00***	***65.00***	***0.33***	***34.67***	***0.67***
A2270	1	14/07/2009	16:30	16:50	6/8	2	4	4	85	2	13	0
	2	24/07/2009	13:00	13:20	6/8	3	4	4	85	0	15	0
	3	27/07/2009	15:45	16:05	0	1	5	4	90	1	9	0
					0.50	***2.00***	***4.33***	***4.00***	***86.67***	***1.00***	***12.33***	***0.00***
A2300	1	18/06/2009	13:50	14:10	2/8	2	2	3	80	1	20	1
	2	02/07/2009	10:00	10:20	1/8	1	2	3	70	1	29	0
	3	22/07/2009	11:30	11:50	1/8	1	4	3	70	1	29	1
					0.17	***1.33***	***2.67***	***3.00***	***73.33***	***1.00***	***26.00***	***0.67***
B2300	1	17/06/2009	16:45	17:05	1/8	1	2	4	80	3	20	1
	2	02/07/2009	10:55	11:15	2/8	0	2	4	82	3	15	0
	3	22/07/2009	13:00	13:20	6/8	1	4	4	70	1	29	1
					0.38	***0.67***	***2.67***	***4***	***77.33***	***2.33***	***21.33***	***0.67***
C2400	1	17/06/2009	15:35	15:55	0	4	1	4	85	0	15	1
	2	04/07/2009	11:20	11:40	5/8	3	3	4	85	2	13	0
	3	23/07/2009	14:50	15:10	5/8	5	4	4	85	1	14	1
					0.42	***4.00***	***2.67***	***4***	***85.00***	***1.00***	***14.00***	***0.67***
A2430	1	17/06/2009	14:40	15:00	0	4	1	2	75	0	35	0
	2	04/07/2009	12:10	12:30	5/8	2	2	2	65	0	35	0
	3	23/07/2009	13:55	14:15	4/8	5	3	2	55	0	45	0
					0.38	***3.67***	***2.00***	***2.00***	***65.00***	***0.00***	***38.33***	***0.00***
B2500	1	30/06/2009	11:00	11:20	5/8	1	1	4	70	0	30	0
	2	04/07/2009	13:15	13:35	5/8	3	2	4	65	0	35	0
	3	01/08/2009	14:40	15:00	5/8	4	4	4	85	0	15	0
					0.63	***2.67***	***2.33***	***4.00***	***73.33***	***0.00***	***26.67***	***0.00***
C2500	1	09/07/2009	11:20	11:40	6/8	1	1	2	30	0	70	1
	2	23/07/2009	12:40	13:00	2/8	4	3	2	35	0	75	1
	3	29/07/2009	10:10	10:30	0	1	3	2	30	0	70	1
					0.33	***2.00***	***2.33***	***2.00***	***31.67***	***0.00***	***71.67***	***1.00***
A2650	1	01/07/2009	14:20	14:40	6/8	1	0	4	2	0	98	0
	2	23/07/2009	11:30	11:50	2/8	3	1	4	5	0	95	0
	3	01/08/2009	13:30	13:50	4/8	2	1	4	5	0	95	0
					0.50	***2.00***	***0.67***	***4.00***	***4.00***	***0.00***	***96.00***	***0.00***
C2650	1	14/07/2009	14:15	14:35	4/8	1	2	5	65	5	30	0
	2	23/07/2009	10:30	10:50	2/8	2	3	5	65	5	30	0
	3	01/08/2009	10:30	10:50	2/8	0	3	5	60	1	39	0
					0.33	***1.00***	***2.67***	***5.00***	***63.33***	***3.67***	***33.00***	***0.00***

B2700	1	30/06/2009	13:10	13:30	7/8	1	0	2	30	0	70	0
	2	14/07/2009	11:25	11:45	3/8	1	2	2	50	0	50	1
	3	01/08/2009	11:30	11:50	3/8	1	2	2	50	1	49	1
					0.54	***1.00***	***1.33***	***2.00***	***43.33***	***0.33***	***56.33***	***0.67***
C2720	1	01/07/2009	10:40	11:00	3/8	1	1	4	70	5	25	0
	2	14/07/2009	12:15	12:35	3/8	3	2	4	60	5	35	1
	3	01/08/2009	12:30	12:50	5/8	2	3	4	70	2	28	1
					0.46	***2.00***	***2.00***	***4.00***	***66.67***	***4.00***	***29.33***	***0.67***
C2800	1	01/07/2009	11:50	12:10	6/8	1	1	2	50	5	45	1
	2	16/07/2009	10:30	10:50	1/8	2	2	2	45	5	50	1
	3	31/07/2009	13:55	14:15	7/8	2	2	2	40	1	59	1
					0.58	***1.67***	***1.67***	***2.00***	***45.00***	***3.67***	***51.33***	***1.00***
A2850	1	16/07/2009	12:00	12:20	3/8	2	2	3	70	1	29	0
	2	29/07/2009	12:30	12:50	0	2	3	3	75	2	23	1
	3	31/07/2009	10:00	10:20	5/8	2	3	3	75	1	24	1
					0.33	***2.00***	***2.67***	***3.00***	***73.33***	***1.33***	***25.33***	***0.67***
C2900	1	16/07/2009	13:00	13:20	5/8	2	1	4	25	20	55	0
	2	29/07/2009	13:45	14:05	0	2	2	4	20	10	70	0
	3	31/07/2009	13:15	13:35	7/8	3	2	4	25	5	70	1
					0.50	***2.33***	***1.67***	***4.00***	***23.33***	***11.67***	***65.00***	***0.33***
A2950	1	16/07/2009	14:00	14:20	6/8	2	1	4	5	5	90	0
	2	29/07/2009	14:30	14:50	0	4	1	4	8	2	90	0
	3	30/07/2009	14:00	14:20	7/8	4	1	4	5	2	93	0
					0.54	***3.33***	***1.00***	***4.00***	***6.00***	***3.00***	***91.00***	***0.00***
N3100	1	29/07/2009	15:45	16:05	1/8	2	0	4	5	5	90	0
	2	30/07/2009	12:30	12:50	6/8	2	1	4	2	3	95	0
	3	31/07/2009	11:10	11:30	6/8	2	1	4	1	2	97	0
					0.54	***2.00***	***0.67***	***4.00***	***2.67***	***3.33***	***94.00***	***0.00***
N3200	1	29/07/2009	16:35	16:55	1/8	1	0	4	1	4	95	0
	2	30/07/2009	11:30	11:50	5/8	2	0	4	1	1	98	0
	3	31/07/2009	12:00	12:20	6/8	3	0	4	1	2	97	0
					0.50	***2.00***	***0.00***	***4.00***	***1.00***	***2.33***	***96.67***	***0.00***

Appendix B

List of all species recorded indicating larval host plant specificity, ability to feed on nectar and daily activity. Furthermore, the total number of specimens counted at each of the 25 transect sites (columns) is provided for all species.

Family	Species	Larval host plant specificity[1]	Nectarivorous[2]	Activity[3]	N2050	N2100	B2150	C2150	A2160	B2160	B2200	B2240	A2270	A2300	B2300	C2400	A2430	B2500	C2500	A2650	C2650	B2700	C2720	C2800	A2850	C2900	A2950	N3100	N3200	Total
Hesperiidae	*Carterocephalus palaemon*	O	yes	d	3																									**3**
Hesperiidae	*Pyrgus warrenensis*	M	yes	d			1														1									**2**
Hesperiidae	*Pyrgus serratulae*	M	yes	d	1			1			1	1			2	1	1					1	1	2	1					**13**
Hesperiidae	*Pyrgus andromedae*	O	yes	d			1			1	1					3		1	2		2					1				**12**
Hesperiidae	*Pyrgus cacaliae*	M	yes	d			4	3			3	1		1			1	1	5		5	2	1		1			1		**29**
Hesperiidae	*Pyrgus malvoides*	O	yes	d	1	2																								**3**
Lycaenidae	*Cupido minimus*	M	yes	d			1				1		1	1			3													**7**
Lycaenidae	*Plebejus orbitulus*	O	yes	d		1	1	2	2				3		1	3			2											**15**
Lycaenidae	*Plebejus optilete*	M	yes	d	2	1																								**3**
Lycaenidae	*Plebejus glandon*	M	yes	d										2		2														**4**
Lycaenidae	*Polyommatus semiargus*	M	yes	d				3																						**3**
Nymphalidae	*Aglais urticae*	M	yes	d		5	1	4	2	1	1	10	3	6	3	1	1	3	5	2	3	2	6	3	8	6	13	12	10	**111**
Nymphalidae	*Boloria pales*	P	yes	d	2	1	4	2	2	3	1	2	6	1	4	1	1	1	5		9	3	7	1	4	1	1		1	**63**
Nymphalidae	*Boloria napaea*	P	yes	d									2			1	3	1	1											**8**
Nymphalidae	*Boloria euphrosyne*	M	yes	d	1	3							1																	**5**
Nymphalidae	*Boloria thore*	M	yes	d	4																									**4**
Nymphalidae	*Coenonympha gardetta*	O	yes	d	1	6	4	3	1				1	4	1				4											**25**
Nymphalidae	*Erebia nivalis*	M	yes	d													2		2	2				1	1			2	3	**13**
Nymphalidae	*Erebia pandrose*	O	yes	d		2	4	4	2	3	1	3	1	5	4	8	7	5	7		1	3	2	5	6	3	1			**77**
Nymphalidae	*Erebia eriphyle*	P	yes	d	4		2	2					7						2						1					**18**
Nymphalidae	*Erebia medusa*	O	yes	d		5																	1							**6**
Nymphalidae	*Erebia pharte*	P	yes	d	18	3				2	2		6	2	2				2											**37**
Nymphalidae	*Erebia euryale*	P	yes	d	9	3				1																				**13**
Nymphalidae	*Erebia gorge*	O	yes	d				1								2							1			6	2			**12**
Nymphalidae	*Erebia pluto*	O	yes	d																						2		13	4	**19**
Nymphalidae	*Erebia montana*	O	yes	d																					1					**1**
Nymphalidae	*Erebia epiphron*	P	yes	d														2												**2**
Nymphalidae	*Erebia meolans*	O	yes	d																							2			**2**
Nymphalidae	*Euphydryas aurinia glaciegenita*	M	yes	d			1							1		1			1		16		3							**23**
Nymphalidae	*Euphydryas cynthia*	P	yes	d												1		1								2				**4**
Nymphalidae	*Inachis io*	M	yes	d						1			1					2			1	1	2		3	4			2	**17**
Nymphalidae	*Lasiommata petropolitana*	O	yes	d		2																								**2**
Nymphalidae	*Vanessa cardui*	P	yes	d,m	8	2	8	6	3	6	4	9	3	9	9	4	6	5	3	3	4	2	7	1	8	7	12	5	4	**138**
Papilionidae	*Papilio machaon*	O	yes	d															1											**1**
Papilionidae	*Parnassius phoebus*	P	yes	d									2	1					3		1				1					**8**

Pieridae	*Colias palaeno*	M	yes	d	5	3		1			2			1															**12**
Pieridae	*Colias phicomone*	O	yes	d									2					2												**4**
Pieridae	*Pieris bryoniae*	O	yes	d	2																									**2**
Pieridae	*Pieris rapae*	O	yes	d	1	1	2	2	1	2			1							1										**11**
Pieridae	*Pieris brassicae*	O	yes	d								2																		**2**
Pieridae	*Pontia callidice*	O	yes	d		1	3	1		1	1	2	1	1	2	1		1			1		1	10	1	1	2	2	2	**35**
Arctiidae	*Diacrisiasannio*	P	no	d	1	3																								**4**
Arctiidae	*Grammia quenseli*	P	no	d																				1						**1**
Arctiidae	*Parasemia plantaginis*	P	no	d																		1								**1**
Arctiidae	*Setina aurita*	P	no	d																						2				**2**
Geometridae	*Colostygia kollariaria*	M	yes	n				2			1		1	1	1															**6**
Geometridae	*Ematurga atomaria*	P	yes	d		3	1		1																					**5**
Geometridae	*Entephria caesiata*	P	yes	d	1	1																								**2**
Geometridae	*Epirrhoe molluginata*	M	yes	d		1																								**1**
Geometridae	*Glacies burmanni*	P	yes	d																						2				**2**
Geometridae	*Glacies alpinata*	P	yes	d		1					7		4	1	4	1			4	2										**24**
Geometridae	*Glacies canaliculata*	P	yes	d															1	1		1	3		1					**7**
Geometridae	*Glacies noricana*	P	yes	d															1			2		2	1					**6**
Geometridae	*Nebula nebulata*	M	yes	n				1	1				6																	**8**
Geometridae	*Psodos quadrifarius*	P	yes	d				2	6	1	9	1	12	6	5	3	2	1	3											**51**
Geometridae	*Pygmaena fusca*	P	yes	d															1						1					**2**
Geometridae	*Rheumaptera subhastata*	M	yes	d		4	5	3			1	3	1	1	2															**20**
Geometridae	*Sciadia tenebraria*	P	yes	d					2																		3			**5**
Geometridae	*Scopula ternata*	O	yes	n		2																								**2**
Hepialidae	*Hepialus humuli*	P	no	n									1																	**1**
Noctuidae	*Autographa gamma*	P	yes	d,m	2	2	1		1			2			3			3			2	1	1	1	1		1			**21**
Noctuidae	*Heliothis peltigera*	P	yes	d,m			1																							**1**
Noctuidae	*Syngrapha hochenwarthi*	P	yes	d									1					1												**2**
Pterophoridae	*Merrifieldia leucodactyla*	P	yes	n	1																									**1**
Pyralidae	*Asarta aethiopella*	M	yes	d														1	2		2	2	3			2				**12**
Pyralidae	*Catastia marginea*	O	yes	d														1												**1**
Pyralidae	*Catoptria petrificella*	P	yes	d		2			1				2																	**5**
Pyralidae	*Catoptria radiella*	P	yes	d						1																				**1**
Pyralidae	*Catoptria furcatella*	P	yes	d																			1			1				**2**
Pyralidae	*Crambus monochromella*	O	yes	d									1										5							**6**
Pyralidae	*Crambus pascuella*	P	yes	d		3																								**3**
Pyralidae	*Crambus lathoniellus*	O	yes	d		1																								**1**
Pyralidae	*Eudonia vallesialis*	O	no	n																		1		1		1	1	1	1	**6**
Pyralidae	*Gesneria centuriella*	P	?	n				1																						**1**
Pyralidae	*Metaxmeste phrygialis*	P	yes	d					1			2			1						1				1					**6**
Pyralidae	*Metaxmeste schrankiana*	O	yes	d						3								1	1				2	2						**9**
Pyralidae	*Nomophila noctuella*	P	yes	n,m														2				1		1						**4**
Pyralidae	*Udea murinalis*	O	yes	d										1																**1**
Pyralidae	*Udea uliginosalis*	M	yes	d	2		8	7	2	2	1	4	5	1	3	1	1	13	2			2			1					**55**
Pyralidae	*Udea rhododendronalis*	O	yes	d											1				5	1	9		12							**28**
Zygaenidae	*Zygaena exulans*	P	yes	d		1	1	1					4		2	2	2	3					2		1	1		2	2	**24**
Gelechiidae	*Pleurota bicostella*	O	no	n											1															**1**

Tortricidae	*Clepsis steineriana*	P	?	n	1						1																	**2**
Tortricidae	*Celypha cespitana*	P	?	n					1																				**1**
Psychidae	*Ptilocephala plumifera*	P	no	d													1												**1**
	Spec 1		?	n							1																		**1**
	Spec 2		?	d								1											1						**2**
SUM					**70**	**65**	**54**	**52**	**29**	**28**	**39**	**43**	**79**	**46**	**51**	**36**	**31**	**51**	**65**	**12**	**58**	**24**	**63**	**31**	**43**	**40**	**37**	**41**	**29**	**1117**

[1]: Larval host plant specificity: M = Monophagous, O = Oligophagous, P = Polyphagous

[2]: Nectarivorous species: yes or no (or no information was found)

[3]: Activity: d = diurnal, n = nocturnal, m = migratory

Appendix C

Results of linear regressions of Dimension 1 and Dimension 2 scores extracted from an NMDS analysis based on Bray-Curtis similarities of Lepidoptera communities sampled across an elevational gradient (see Fig. 11) on various habitat variables. Results remaining significant after Bonferroni correlation are printed bold.

Parameter	r^2	***R***	***p***	**linear equation**
Dimension 1				
Altitude	**0.77**	**0.88**	**< 0.001**	**y = 2497.2 + 341.04x**
Vegetation cover	**0.47**	**-0.69**	**< 0.001**	**y = 53.71 - 21.56x**
Inclination	0.18	0.43	0.033	y = 3.03 + 0.48x
Open ground	0.15	0.38	0.060	y = 1.76 + 1.08x
Rock cover	**0.44**	**0.67**	**< 0.001**	**y = 44.81 + 20.46x**
Pasturing	0.26	-0.51	0.009	y = 0.53 - 0.25x
Nectar availability	**0.52**	**0.72**	**< 0.001**	**y = 3.88 + 0.75x**

Dimension 2				
Altitude	0.01	-0.11	0.590	y = 0.46 - 0.0002x
Vegetation cover	0.08	-0.29	0.167	y = 0.31 - 0.01x
Inclination	0.10	-0.32	0.115	y = 0.55 - 0.18x
Open ground	0.18	-0.42	0.037	y = 0.16 - 0.09x
Rock cover	0.12	0.34	0.097	y = -0.31 + 0.01x
Pasturing	0.00	-0.03	0.901	y = 0.02 - 0.03x
Nectar availability	0.06	0.25	0.221	y = -0.60 + 0.15x

Curriculum Vitae

Persönliche Angaben

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1988 – 1992	Volksschule Schüttdorf/Zell am See
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