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Caterpillar communities on *Chusquea* sp. (Poaceae) in the Andes of southern Ecuador

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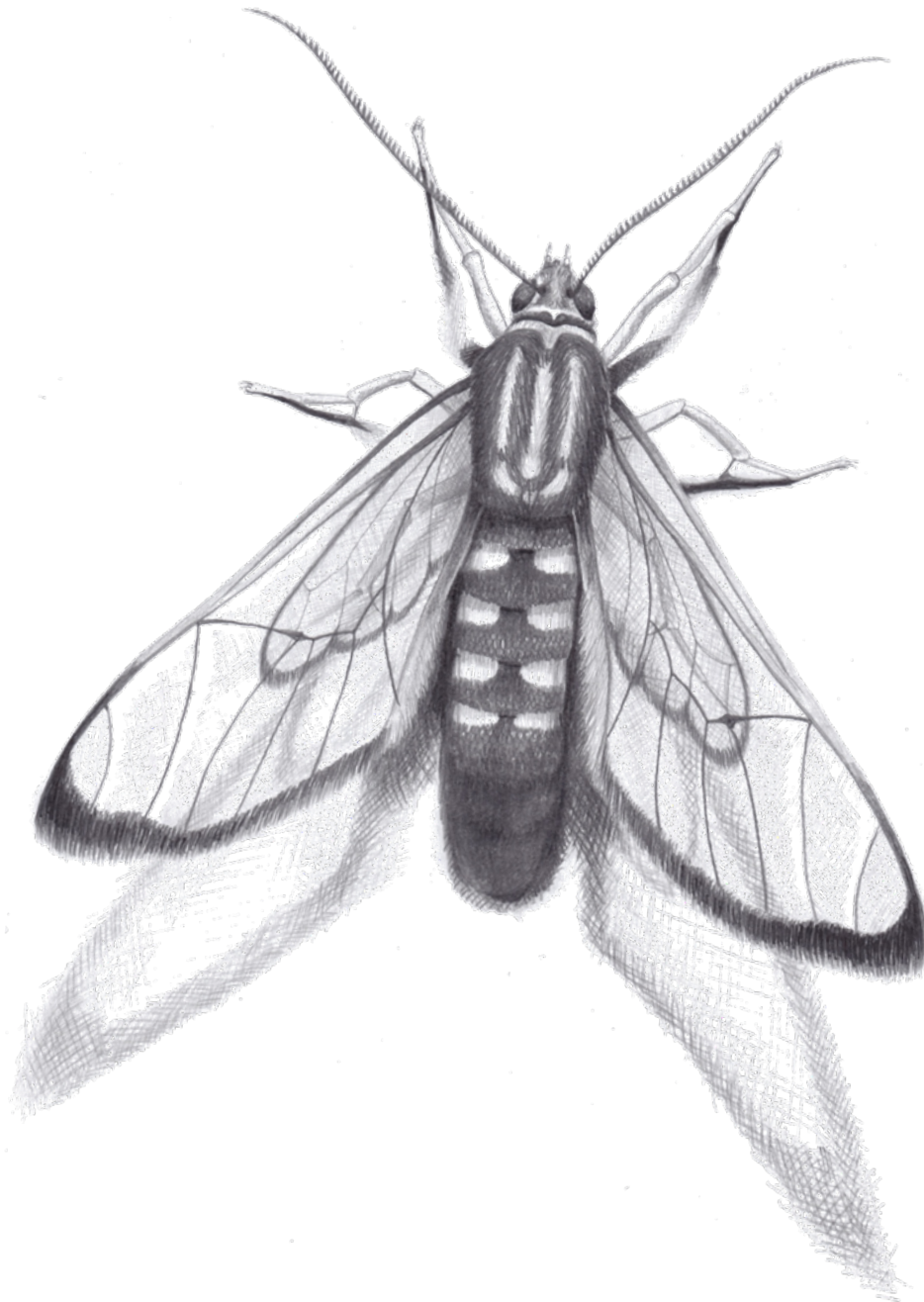## Magistra der Naturwissenschaften (Mag.rer.nat.)

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Caterpillar communities on *Chusquea* sp. (Poaceae) in the Andes of southern Ecuador

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Adult of *Cosmosoma* sp. illustration by L. Lehner. Larvae of this genus were for the first time observed feeding on Poaceae.

Abstract

Chusquea (Bambusoideae) is an abundant and widely distributed plant genus in the Andes and may therefore serve as a potentially important host to a variety of phytophagous insects. To date, little is known about its associated herbivores. Caterpillar communities on various shrubs in the lower mountain forest zone of South Ecuador have been extensively studied and were found to be highly diverse. Cloud forests have been poorly studied, but are assumed to harbor an exceptionally species rich community due to their specific ecological features, such as enhanced precipitation and dense epiphyllic growth. For this reason, species diversity, taxonomic composition, and feeding guild structure of Lepidopteran larvae communities on *Chusquea* sp. were compared between a lower mountain forest (2000m a.s.l.) and a cloud forest (3000m a.s.l.). Caterpillars were collected by the beating method, subjected to feeding trials, and reared (whenever possible) to adulthood in the laboratory. Deceased caterpillars were identified by use of DNA barcoding. Altogether 392 individuals belonging to 193 species in 12 families were recorded, of which Geometridae, Noctuidae, Erebidae and Nymphalidae were the most abundant. Approximately 50% of individuals were herbivorous, 25% non-herbivorous and 25% were switchers (i.e. young larvae feed on dead foliage or epiphytic growth and older ones on fresh foliage). Species diversity as measured by Shannon's entropy was very high and exceeded values reported for communities affiliated with other plant species in this area. Beta diversity between the two forest types was very high with only eight shared species. Dominance structure in the present assemblage was unusually low with a Berger-Parker index of only 0.04. The proportion of singletons (66%), on the other hand, was very high compared to other studies. Caterpillar communities differed in terms of taxonomic composition and feeding guild structure between the two habitats. Notably, herbivorous taxa were more abundant at higher elevations, while non-herbivores showed higher densities at lower altitude.

Deutsche Zusammenfassung

Chusquea (Bambusoideae) ist eine weitverbreitete und sehr häufige Bambuspflanze in den Anden und stellt somit eine gut verfügbare potenzielle Nahrungsressource für phytophage Insekten dar. Dennoch ist bisher noch sehr wenig über Herbivorengesellschaften bekannt, welche diese Pflanze nutzen. Eine hohe Diversität von Raupengemeinschaften im Bergregenwald Südecuadors wurde bereits an anderen Pflanzenfamilien nachgewiesen. Über Herbivorengesellschaften in dem ebenfalls im Untersuchungsgebiet gelegenen Nebelwald hingegen ist noch wenig bekannt, wobei gerade diesem Waldtyp eine besondere Artenvielfalt nachgesagt wird, die sich vermutlich durch strukturelle Eigenheiten des Waldes, wie z.B. vermehrten Niederschlag und dichten Ephiphyllenbewuchs, ergibt. Aus diesem Grund wurden die Artenvielfalt, taxonomische Zusammensetzung und Struktur der Nahrungsgilden von Raupengemeinschaften an *Chusquea* zwischen dem Bergregenwald (2000m ü.d.M) und dem Nebelwald (3000m ü.d.M.) in den Anden Südecuadors miteinander verglichen. Raupen wurden mittels der Klopfmethode gesammelt, im Labor einem Fraßversuch unterzogen und anschließend bis zum Adulttier großgezogen. Verstorbene Raupen wurden mittels DNA-Barcoding bestimmt. Insgesamt wurden 392 Individuen von 193 Arten in 12 Familien gesammelt, wobei die meisten Arten den Geometriden, Noctuiden, Erebiden und Nymphaliden angehörten. Ungefähr 50% der Individuen waren Herbivore, 25% Nicht-Herbivore und 25% Wechsler (d.h. Jungraupen fressen totes Laub oder

Epiphylle, ältere Raupen frisches Laub). Die Diversität der Gemeinschaften, gemessen als Shannon-Index, war unerwartet hoch und übertraf die Werte bisherig besammelter Gemeischaften auf anderen Pflanzenarten bei weitem. Die Beta-Diversität war mit nur acht gemeinsamen Arten zwischen den beiden Waldtypen sehr hoch. Die Dominanz einer Art in den Gemeinschaften war ungewöhnlich niedrig mit einem Berger-Parker Index von nur 0.04. Der Anteil von Arten, die nur einmal vertreten waren, den sogenannten „Singletons", war mit 66% höher als in anderen Studien. Weiters unterschieden sich die Raupengemeinschaften in Hinsicht auf taxonomische Zusammensetzung und Nahrungsgilden-Struktur auffällig voneinander. Auffallend war der deutlich höhere Anteil herbivorer Raupen im Nebelwald im Gegensatz zu den Nicht-Herbivoren, welche im Bergregenwald häufiger waren.

Keywords: Caterpillar communities, *Chusquea* sp., elevational gradient, tropical mountain forest, feeding guilds, species diversity

Introduction

Altitudinal gradients in tropical forests combine an enormous range of climatic environments with high habitat heterogeneity due to variance in aspect and shape of mountain slopes. This results in a mosaic-like environment harboring panoply of structurally complex habitat types at small spatial scales, which in turn provide more different niches than homogenous environments do (Tews 2004). Thus, the tropical Andes, due to the prevailing steep elevational gradients and the strong topographic variation on the one hand and the rooting of their foothills in species-rich Amazonian rainforest on the other, are considered a hotspot of global biodiversity for vascular plants and vertebrates (Myers 2000). Whether less conspicuous groups of organisms such as insects are equally diverse in this region has been assessed to a lesser extent by now. Available evidence from a few Lepidopteran clades, such as Nymphalidae (Pyrcz et al. 2009) or Geometridae (Brehm et al. 2005), however, indicates that also for these the Andean mountain forest zone ranks top with regard to species density.

The global distribution of vascular plant diversity is far better known than is the distribution of any animal taxon except for birds (Barthlott et al. 2005; Jetz & Rahbek 2002). Therefore, the idea has been advanced to infer insect species richness from plant species richness, assuming robust ratios in the extent of host-plant specificity to prevail (Hamilton et al. 2010; Basset et al. 2012). Predicting insect diversity on the basis of plant diversity is, however, still hampered by the fact that there are too many factors influencing the occurrence of herbivorous insects (Lewinsohn & Roslin 2008) and that documentation of host affiliations in the tropics remains scant. However, findings reported by Novotny et al. (2006) show that tree species of comparable phylogenetic distribution along a latitudinal gradient harbor similar herbivore species numbers, which thus indicates a positive correlation between plant diversity and herbivore diversity. This suggests that the Andean mountain forests are likely to be a diversity hotspot for herbivorous insects as they are for plants. Indeed, first local assessments of herbivorous Lepidopteran larvae in the Ecuadorian Andes, conducted in the north of the country by Dyer et al. (e.g. 2007) and in the south by Bodner et al. (2012), confirmed a very high richness. Besides high local species richness of Lepidoptera also a high species turnover within small spatial scales has been revealed (e.g. Brehm et al. 2003a, Fiedler et al. 2008, Novotny et al. 2005).

One of the main focus genera to unravel factors generating and maintaining Lepidopteran biodiversity in the tropical Andes so far has been *Eois* (Geometridae; Brehm et al. 2011), the larvae of which predominantly feed on *Piper* (Piperaceae). Differences in caterpillar communities were shown both between different species of *Piper* at one elevational level (Bodner et al. 2012), as well as along an elevational gradient (Rodriguez et al. 2010). How specialized tropical herbivores really are still is debated (Dyer et al. 2007; Novotny et al. 2002), but the results for *Piper* species showed clearly that most associated herbivore assemblages are dominated by host specialists. *Piper* is chemically defended and its secondary compounds vary from species to species, which heavily influences the herbivore community it harbors. An ecological study thus requires a suitable plant taxon which grows all along an environmental gradient and does not vary too severely in traits, such as chemical composition of secondary compounds which may influence host plant choice of Lepidoptera.

A less well studied plant group in tropical elevational gradients that would fulfill the above requirements are the Poaceae. Poaceae are hardly ever chemically defended and thus do not exert a strong selective force mediated by secondary metabolites upon their consumers (Tscharntke & Greiler 1995). Graminivorous Lepidoptera are hardly ever specialized on one single grass species (Nakasuji 1987) and their host selection is rather mediated by leaf toughness and nutrient content. Thus representatives of the Poaceae were chosen in this study to be compared among sites across a larger elevational range. In the tropical mountain forest of southern Ecuador, where this study was conducted, Poaceae are frequently represented by bamboos, of which the genus *Chusquea* is among the most abundant. *Chusquea* is a very diverse genus which typically occurs in high elevations, especially in cloud forests, where it is an important constituent part of the plant community (Homeier et al. 2008).

Cloud forests or elfin forests grow in a narrow elevational zone characterized by significantly elevated levels of precipitation, to high portions in the form of occult or horizontal precipitation, i.e. water from the clouds is condensing on the trees' surface wherefrom it trips down (Stadtmüller 1987). Cloud forests are usually characterized by a range of physiognomic features (e.g. high proportion of biomass occurring as epiphytes, dwarf trees with sclerophyllic leaves, etc.) which are thought to favor higher diversity and greater endemism than adjacent ecosystems (Hamilton 1995; Williams-Linera 2002). In contrast, the lower mountain rain forest grows in a broader altitudinal belt and so covers in total a larger area, which might be taken into consideration in terms of the species area relationship (Rahbek 1997). A further important aspect, especially for ectothermic insects, is the average annual temperature difference of 6.3°C between the two sites as a consequence of the lapse rate. Decreasing temperature decelerates growth rates and development of insect larvae and impairs flight performance of adults (Hodkinson 2005). This raises the question whether the cloud forest would support a similarly diverse Lepidopteran fauna as has already been proven for the lower mountain forests (e.g. Bodner et al. 2012; Brehm et al. 2003b; Fiedler et al. 2008; Hilt et al. 2006).

A further interesting aspect which has received only little attention so far is the high portion (up to 80%) of 'non-herbivores' among caterpillars retrieved from Andean mountain forest shrubs (Bodner 2011). The percentage of non-herbivores varied significantly between plant families and less so between plant genera, though the underlying reasons are not clear yet.

The actual diet of non-herbivores can vary from epiphyllic fungi, lichens, algae, or mosses to leaf litter. These food resources can be expected to be largely independent of the phorophyte plant species. Plants with high numbers of non-herbivorous caterpillars associated usually have complex growth architecture, where leaf litter may get easily caught in the foliage, and large leaves which provide more area for epiphyllic vegetation. *Chusquea*, in comparison, has a simple growth form and small leaves, which are both traits that typically do not promote the provisioning of resources for non-herbivores. This leads to the question whether *Chusquea* bamboos support the existence of non-herbivorous caterpillars, and if so, whether the same non-herbivore species can be found as on other plant families from the same region.

In this study, for the first time ever bamboo-feeding caterpillar communities were systematically assessed in a tropical mountain forest at two distinct elevations. The following research questions were addressed:

1. How many caterpillar species use *Chusquea* as nutrient resource in an Andean mountain forest?
2. How does the systematic composition (families) of the assemblages look like?
3. How far do the communities differ between lower mountain and cloud forest with regard to density, species richness and feeding guild composition?
4. Do non-herbivorous caterpillars use *Chusquea* at all, and if so, to what extent?

Methods

Study area

The study area is located in the Eastern Cordillera of the Andes in southern Ecuador in the province Zamora-Chinchipe. Samples were partly assembled in the Podocarpus National park and partly in the Reserva Biológica San Francisco (RBSF), an adjacent privately owned nature reserve. Sampling was performed in two different forest types within this area, ca. 17km apart from another. The forest type in the lower altitudes is defined as evergreen lower mountain forest, which is adjacent to the Estación Científica San Francisco (3°58' S, 79°05' W) at 1800-2100m a.s.l. (termed RBSF hereafter). Canopy height is about 25m with occasional emergents up to 35m; understory is comprised of megaphyllous shrubs and herbs, such as Piperaceae, Heliconiaceae, Araceae and Cyclanthaceae. Understory is not very dense and epiphytes from families such as Ericaceae or Orchidaceae are not very common. Disturbances such as landslides and wildfires form differently sized gaps which are characterized by a particular pioneer flora consisting of grasses, bushes (especially a number of Asteraceae species like *Baccharis* or *Ageratina*) and also *Chusquea* bamboos. Mean annual air temperature is 14.9°C, mean annual precipitation 2176mm, and mean horizontal precipitation 121mm. The forest type in the higher altitude is defined as evergreen cloud forest at 2900-3000m a.s.l. in Cajanuma (4°06' S, 79°10' W), which is part of the Podocarpus National Park. Here trees only grow up to 6-8m and are the last ones beneath the timberline. Trees are characterized by a small stunted growth with diagonal stems, which are densely covered with epiphytic mosses and vascular plants such Bromeliaceae and Orchidaceae. Understory is comprised of shrubs such as Melastomataceae or Cunoniaceae and impenetrable *Chusquea* thickets. Forest ground is covered by terrestrial

bromeliads and a distinct bryophyte flora. Disturbing events are rarer in the cloud forest. Mean annual air temperature is 8.6°C, mean annual precipitation 4743mm, and mean horizontal precipitation amounts to 1958mm. Further information on vegetation and climate of both areas can be found in Homeier et al. (2008), Bendix et al. (2008) and Röderstein et al. (2005).

Focal plants

Caterpillars were collected from *Chusquea* sp. which is one of the largest genera in the Bambusoideae (Poaceae) with 134 described species (Clever 2013). *Chusquea* primarily grows in higher elevations and can be found throughout the Andes from Colombia to Chile (Clark 1989). New species are still being described on a regular basis, especially from the high Andes (Clark 1996, 2007). In Ecuador, about 30 species have so far been recorded, three of which are growing in the study area (*C. falcate, C. scandens* and *C. neurophylla*; Clark et al. 2007; Homeier & Werner 2007). *Chusquea* is a taxonomically difficult genus and the three occurring species could not be reliably identified for the purpose of this study. This is not assumed to be a problem because the main factors which influence host plant choice of grass-feeding caterpillars (e.g. scarcity of toxic secondary compounds, high silicate content, and prominent leaf toughness) are considered to be approximately equal in all three species (Nakasuji 1987; Tscharntke & Greiler 1995). At lower sites in the study region, as around RBSF, bamboos behave as pioneer plants and are comparatively rare in mature forest. At higher altitudes, as in Cajanuma, bamboos are a pervasive part of the plant community (Homeier et al. 2008). In the study region, *Chusquea* species are climbing bamboos and as such easily distinguishable from other bamboo genera. Its vines grow up to 40m in length and reach into the forest canopy, where they produce their main leaf mass. In RBSF, *Chusquea* is ubiquitous in small gaps along little creeks and ravines as well as in sites with a more open canopy, such as successional vegetation on regenerating landslides (Beck et al. 2008).

Data collection

Caterpillars were collected from February to April 2011 by the well-established beating method (Bodner et al. 2010). Single vines (creeping or hanging down from trees) of *Chusquea* sp. were beaten with a stick and caterpillars falling down were collected manually from a white spring-steel collecting sheet (Ø 72cm). Per sample between 1 and 3 vines (length approx. 200-400 cm) were beaten. Sampling sites laid a minimum of 10m apart and their location (whether inside the forest or outside) was additionally recorded. Sampled leaf area was recorded by counting the branch nodes of the bamboo vines which were classified according to estimated leaf area. Leaf area was estimated by counting the leaves of reference nodes classified in 5 different size categories. The mean leaf area of each node size class was determined by calculating the area of 100 scanned leaves by use of the software ImageJ 1.47 (Rasband 1997-2012). Class 1: ≈25 leaves per node to $115cm^2$; 2: ≈70 leaves to $322cm^2$; 3: ≈100 leaves to $469 cm^2$; 4: ≈200 leaves to $920 cm^2$ and class 5: ≈300 leaves to $1380cm^2$.

Collected caterpillars were reared to adulthood in order to ease identification and gain information about their feeding habits. Caterpillars were held separately in small transparent plastic boxes (≈250 cm^3) lined with tissue paper. Containers were checked

regularly, and old or decaying food was replaced if necessary. Since earlier studies (Bodner et al. 2012) indicated a high proportion of non-herbivorous moth taxa in the study area (i.e. caterpillars feeding on dead plant materials or grazing on epiphytic or epiphyllic lichens or mosses), feeding trails were performed with fresh as well as dead leaves. Feeding guilds were classified as (i) herbivores (feeding on fresh leaves), (ii) non-herbivores (feeding on leaf litter, or grazing on lichens, fungi and/or algae) and (iii) switchers (switching from a non-herbivore diet in early instars to leaf herbivory in later stages). Caterpillars were documented by digital photography (Nikon D70s equipped with a Sigma 105mm F2.8 EX DG macro lens) on the day of collection. Deceased animals were stored in 70% ethanol at -20°C.

Successfully reared moths and butterflies were identified using available taxonomic literature (Piñas Rubio 2004; Dyer et al. 2013; Janzen et al. 2009) and photo documentations from earlier collection campaigns provided by Gunnar Brehm (University of Jena, Germany). Deceased larvae and pupae were identified by DNA barcoding using the established 658bp fragment from the mitochondrial cytochrome oxidase subunit I (COI) gene. The advantages of using genetic methods for identification are (i) relatively accurate species delimitation in the absence of established taxonomic literature, (ii) the potential to perform comparisons with all sequences generated by the iBol project (Ratnasingham et al. 2007) and (iii) comparison with other reference sequences gained locally in the RBSF and Cajanuma area. DNA extraction, COI amplification and sequence reaction was performed with standard protocols as outlined in Strutzenberger et al. (2010). The primer pair LepF (5′-ATTCAACCAATCATAAAGATATTGG-3′) /LepR (5′-TAAACTTCTGGATGTCCAAAAAATCA-3′) was described to be a universal primer for Lepidoptera and thus chosen for all samples (Hajibabaei et al. 2005).

Raw sequence data was processed using DNAStar Lasergene SeqMan Pro Ver. 9.1. For species delimitation pairwise Kimura-2-paramater distances (Kimura 1980) were calculated with MEGA version 5 (Tamura et al. 2011). In compliance with Hebert et al. (2003), the sequence divergence threshold for species boundaries was set at 3%. This threshold has generally proven to work well with tropical Lepidoptera (Janzen et al. 2011).

Data analysis

Alpha diversity of caterpillar assemblages associated with *Chusquea* bamboos was assessed using the bias-corrected version of the exponential Shannon entropy calculated with the SPADE software (Chao & Shen 2010). This diversity measure is recommended when species-rich communities are likely to be severely undersampled (Beck & Schwanghart 2010). Expected species numbers at a common large sample sizes were extrapolated from an individual-based species accumulation curve (Colwell et al. 2012) using the software EstimateS V.9 (Colwell 2013). Significance of the observed differences in proportions of feeding guilds between the two forest types was tested by a Chi-square test. Generalized linear models (GLMs) were used to test for differences between low- and high-elevation sampling areas with regard to individual and species numbers as well as caterpillar guild densities per bamboo sampling unit. Surveyed leaf area was included in GLMs as covariate. These statistical tests were performed using the software Statistica 7.1.

Results

Caterpillar community composition

A total of 149 samples, with at least one caterpillar, were taken, 103 in the RBSF ($\approx$277m^2 cumulative leaf area) and 36 in Cajanuma ($\approx$207m^2 cumulative leaf area). The moderate difference in surveyed leaf area, as opposed to the larger difference in sample numbers, reflects the higher foliage density of *Chusquea* bamboos in elfin forest. Of the total number of 398 encountered caterpillars, 36 (8%) were excluded from subsequent statistical analyses. Omitted individuals were either clearly identified as strays from nearby plants with no functional relationship to bamboos as nutrient resource, or they could not be confidently assigned to any feeding guild. The remaining data set contained 362 individuals, belonging to 193 species in 12 families (Fig. 1). Hereof 215 individuals from 120 species were collected in the RBSF area, and 147 individuals from 81 species in Cajanuma (more details see Appendix Table A1 and A2). 49 of the 362 collected specimens could be identified by classical taxonomic means while the 313 remaining individuals were identified through DNA barcodes. 31 caterpillars - mainly Nymphalidae-Satyrinae and Erebidae-Ctenuchini (well known as typical grass feeders) - could be successfully reared to the imago, while the rest died prematurely due to parasitoid infestation (8%) by flies or wasps or of uncertain causes. Especially non-herbivores (27%) and switchers (25%) are difficult to rear because too little is known about their dietary requirements.
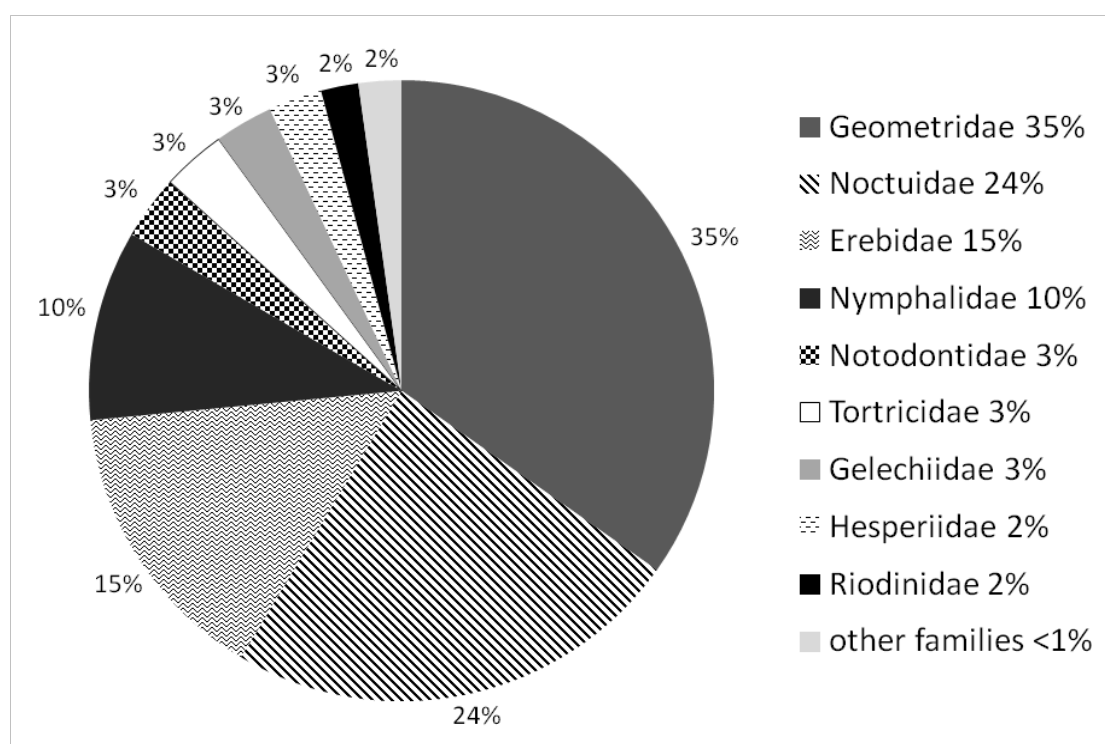
Fig. 1: Relative contribution of Lepidopteran families to caterpillar assemblages sampled from *Chusquea* bamboos in two areas in the Andes of Southern Ecuador. Proportions refer to individuals (not species; n=362), pooled across elevations and functional guild affiliations. Taxa pooled in the "other families" group were represented with less than 5 individuals and comprised representatives of the families Lasiocampidae, Megalopygidae and Elachistidae.

A total of 12 Lepidopteran families were recorded across both forest types, eight of which were found at lower altitude (RBSF). In order from most to least abundant, these were: Geometridae, Noctuidae, Erebidae, Nymphalidae, Tortricidae, Hesperiidae, Gelechiidae and Riodinidae. 10 families were recorded at the higher altitude (Cajanuma): Geometridae, Noctuidae, Nymphalidae, Tortricidae, Elachistidae, Erebidae, Hesperiidae, Notodontidae, Lasiocampidae and Megalopygidae.

Six families were common to both sites (Fig. 2), two were exclusive to the RBSF, and four were found only in Cajanuma. Families that were particular to one habitat or the other were generally only represented by fewer than five species. Of the shared families, the Erebidae are the only clade that differed significantly with regard to habitat with respect to the bamboo caterpillar samples. Erebidae are a very extensive family, which was recently redefined on the grounds of DNA sequence analyses, and is now split into 18 subfamilies, many of which differ tremendously in their ecological traits (Zahiri et al. 2012; Wagner et al. 2011). In Cajanuma, the family was only represented by 5 individuals of the Arctiinae subfamily (tiger moths), while in the RBSF two additional subfamilies were encountered: the Boletobiinae (fungus moths: 15 individuals, 5 species) and the Herminiinae (litter moths: 9 individuals, 5 species).
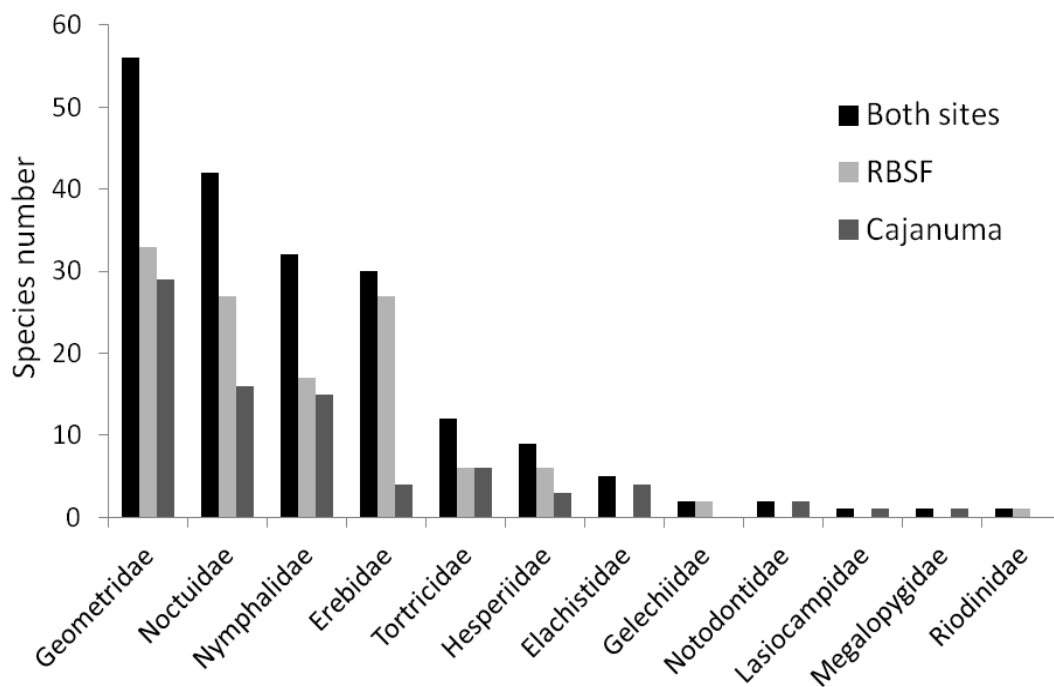
Fig. 2: Observed species numbers of caterpillars per family. Note that only eight species in three families were common to both sites.

Altogether I recognized 193 species of the order Lepidoptera represented among the caterpillars sampled from *Chusquea* which use live or dead foliage of this bamboo, or fungi or algae growing there, as food resource. None of the species exceeded 3% of the pairwise distance in COI sequences. Species diversity expressed as Shannon's entropy was higher in the lower mountain forest (164.3) compared to the elfin forest (115.5). Shannon's entropy for all herbivores together yielded 64.1, for herbivores in RBSF 70.4 and in Cajanuma 26.8. Analyses of extrapolated species numbers (Colwell et al. 2012) likewise revealed a higher

expected species richness for the RBSF (182.8 ± 29.6) than for Cajanuma (154.5 ± 40.0). Based on the overlap of the 95% confidence intervals between both extrapolations, however, the difference only just marginally reached significance. Of the 193 caterpillar species observed on *Chusquea* bamboos, only eight (4%) were encountered at both altitudes. This indicates a very high turn-over between the two habitats, which is all the more noteworthy since they are only separated by an aerial distance of about 17km, yet segregated by about 1000m elevation.

The Berger-Parker index calculated for the whole community only yielded a value of 0.0404, which together with the high fraction (66%) of singleton species indicates a very evenly structured caterpillar community.
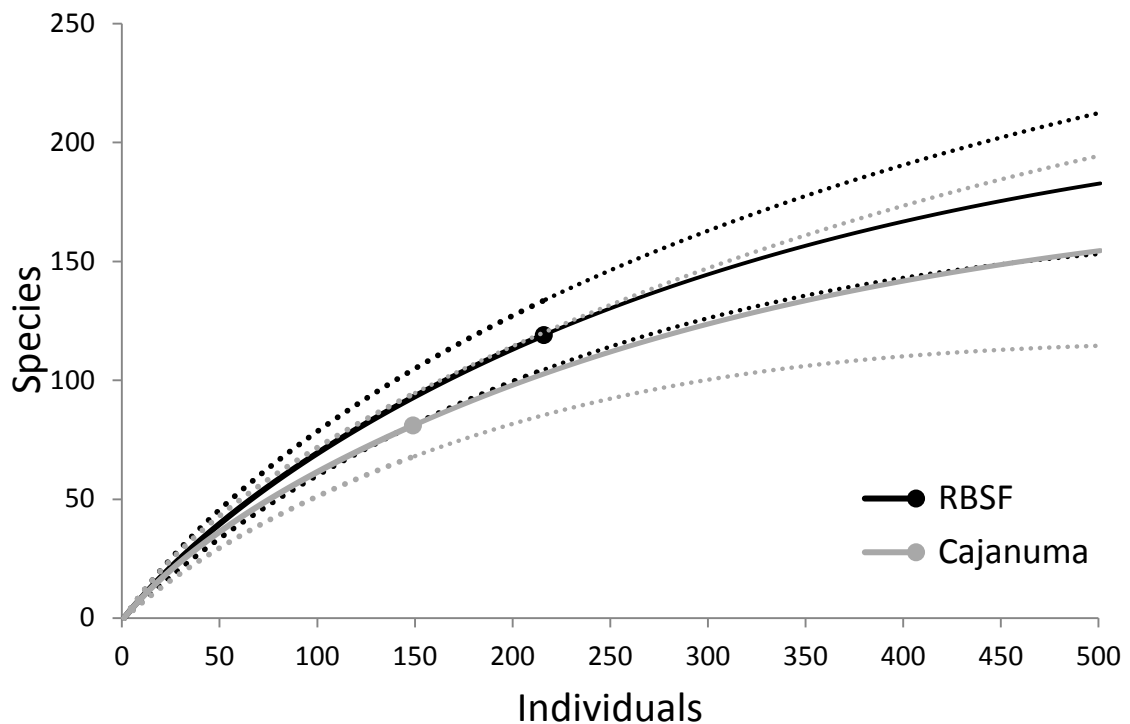

Fig. 3: Extrapolated, individual-based species accumulation curves of all bamboo-associated caterpillars with 95% confidence intervals. Dots mark the extent of observed data. Rarefaction to 147 individuals yields a species richness of 81 and 93.8 for Cajanuma and the RBSF, respectively. Extrapolation to 500 individuals indicates an expected richness of 154.5 (Cajanuma) and 182.8 species (RBSF).

With an average density of 3.3 (± 0.19 SE) individuals per sample, caterpillars were found to be significantly more abundant on *Chusquea* bamboos in Cajanuma compared to the RBSF with only 2.4 (± 0.11; $F_{1,136} = 17.04$, $p<0.001$; see Fig. 4A). A similar pattern was apparent with regard to the density of species with 2.6 (± 0.17) and 2.2 (± 0.09) species per sample for Cajanuma and the RBSF, respectively ($F_{1, 136} = 4.58$, $p<0.05$; see Fig. 4B). In both cases, available leaf area had a strong and positive ($\beta=0.38$) influence (individuals: $F_{1, 136} = 21.9$, $p<0.001$; species: $F_{1, 136} = 167.79$, $p<0.001$).
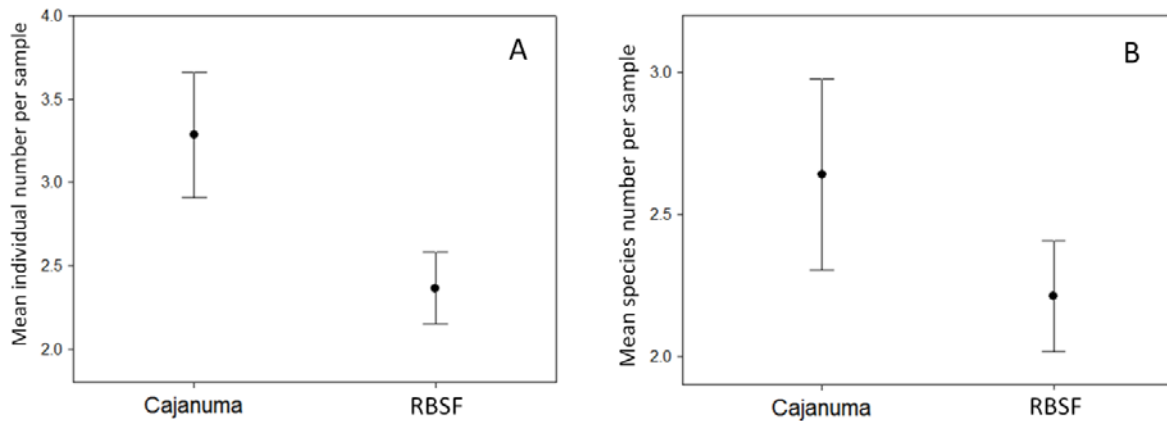
Fig. 4: Average number of caterpillar individuals (A: $F_{1,136} =17.04$, $p< 0.001$) and species (B: $F_{1, 136} =4.58$, $p< 0.05$) per beating sample from *Chusquea* bamboos, with forest site as categorical predictor and the leaf area per sample as covariate. Whiskers represent 95% confidence intervals.

Feeding guilds

With regard to feeding guilds only 48% of all caterpillars were true herbivores, but they were distributed among all families mentioned above except for the Riodinidae, which were represented by only one non-herbivorous epiphyll-feeding species (*Sarota* sp.). Non-herbivorous caterpillars were found among four families (Geometridae, Noctuidae, Erebidae and Riodinidae), while switchers were exclusive to Ennominae, a subfamily of Geometridae (Fig. 5). Across all feeding guilds some species sampled from *Chusquea* bamboos had also been encountered in previous studies on different plant taxa and are thus not specifically associated with the bamboos. Herbivores shared 6 species of three families (Erebidae, Noctuidae and Tortricidae) with Asteraceae. The non-herbivores shared 19 species of four families (Noctuidae, Erebidae, Geometridae and Riodinidae; previously encountered on one or more of the following plant families: Asteraceae, Bignoniaceae, Chloranthaceae, Malvaceae, Meliaceae, Piperaceae). And the switchers (12 species of Geometridae) had also been encountered on one or more plant families mentioned above (more detailed information see Appendix Table A1 and A2).
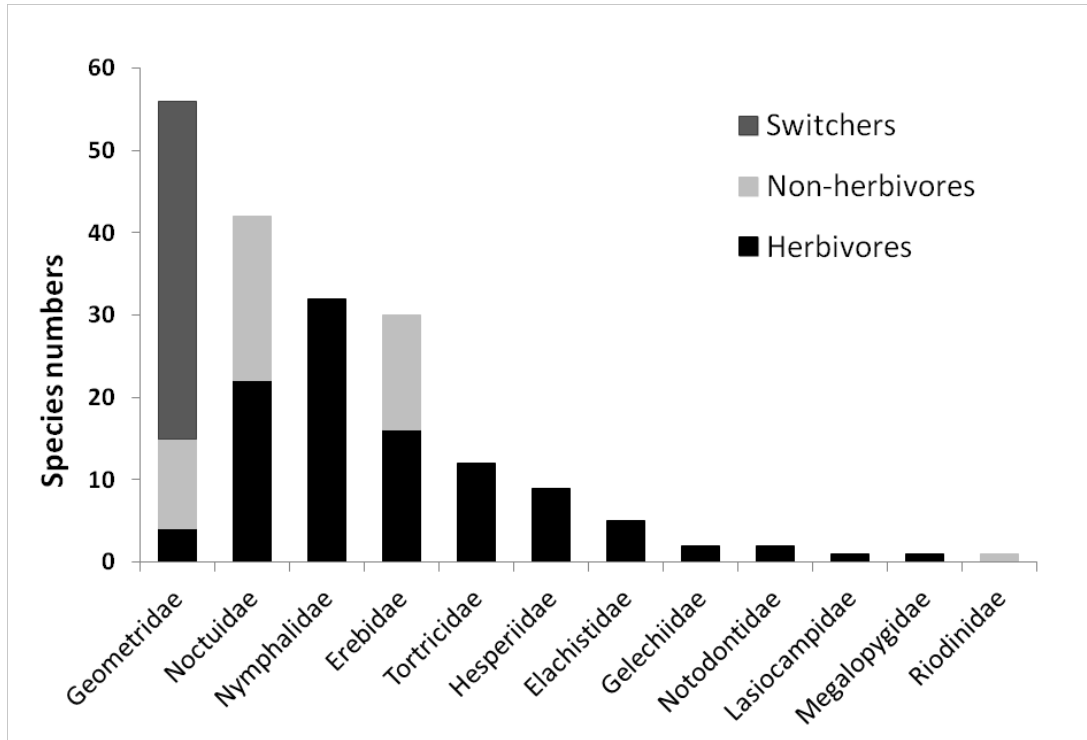
Fig. 5: Taxonomic distribution of the caterpillar feeding guilds observed on *Chusquea* bamboos across Lepidopteran families.

Statistical tests showed a significant difference in the composition of feeding guilds between *Chusquea* bamboos at RBSF and Cajanuma. While switchers occurred in roughly equal proportions, herbivorous larvae were much more abundant in the elfin forest than non-herbivorous ones. In the RBSF, herbivores and non-herbivores were fairly evenly distributed.
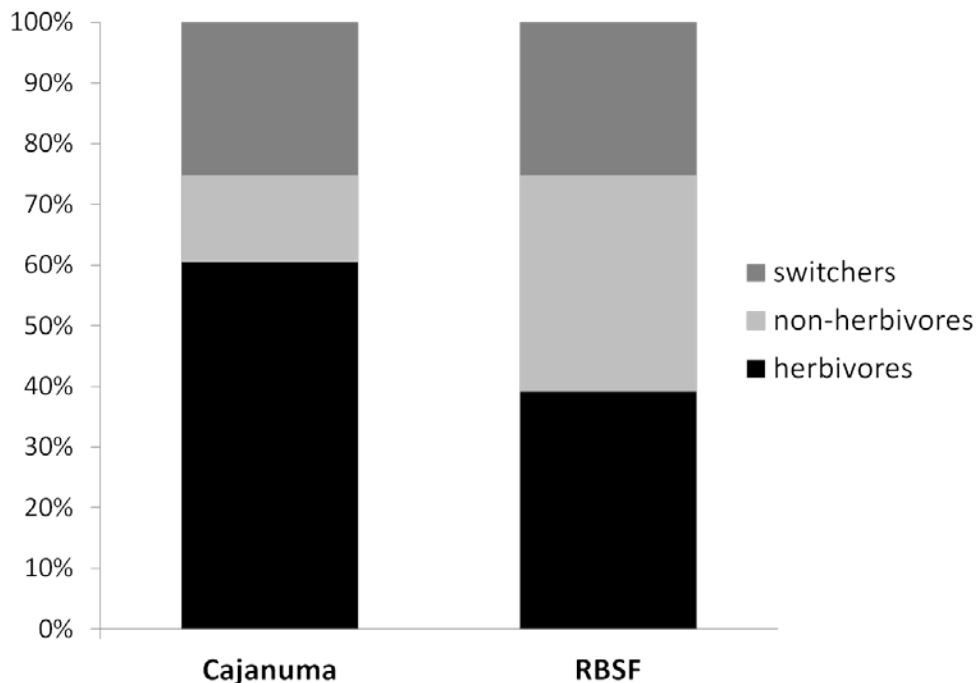
Fig. 6: Proportions of caterpillar individuals allocated to feeding guilds in the two forest types ($\chi^2 2df = 23.37$; p= <0.001). A total of 147 individuals in Cajanuma and 215 individuals in RBSF were recorded

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A comparison of caterpillar abundance per feeding guild and sample indicated herbivores to be significantly more abundant in Cajanuma (GLM: $F_{1, 136} = 15.32$; $p < 0.001$), while non-herbivores tended to be more numerous in the RBSF ($F_{1, 136} = 4.48$; $p = 0.03$). Abundance of switchers did not differ significantly between these two sites ($F_{1, 136} = 2.85$; $p = 0.09$). By comparing the overall difference of the feeding guild distribution per sample these results revealed a significant difference between the two forest types. In RBSF the three feeding guilds were more evenly distributed per sample, while in Cajanuma the share of herbivores per sample was higher than that of switchers and even much higher than non-herbivores (Fig. 7). Further analyses showed significant more non-herbivores in samples taken inside the forest than outside (GLM: $F_{(1, 136)} = 7.11$; $p < 0.005$). Leaf area was again significantly ($F_{3, 134} = 114.34$; $p < 0.001$) and positively ($\beta = 0.38$) related to caterpillar abundances per sample.
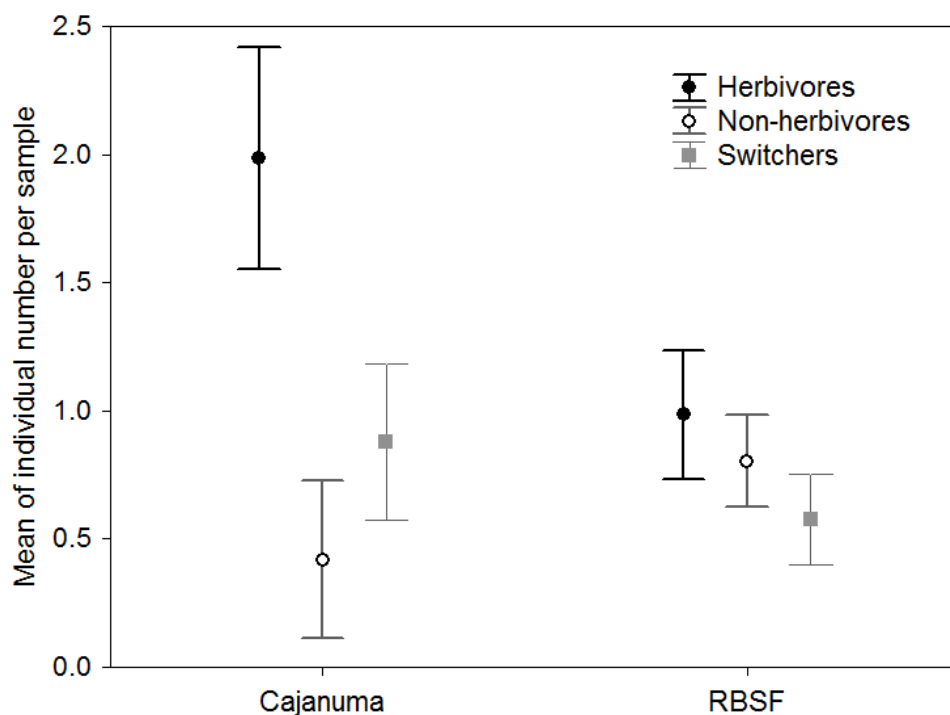
Fig. 7: Mean number of caterpillar individuals per sample from *Chusquea* bamboos for the two forest types, allocated into the three feeding guilds. Analysis by a generalized linear model revealed a significant difference ($F_{3, 134} = 8.93$; $p < 0.001$) between RBSF and Cajanuma.

Discussion

The results of this study revealed an unexpectedly high diversity of caterpillar species using *Chusquea* as food resource. Furthermore, species turnover between the two forest types was high with only eight shared species between the two sample sites. The community of the cloud forest was surprisingly diverse and structurally different in comparison to the assemblage of the lower mountain forest, suggesting that the cloud forest actually harbors a distinct "cloud forest community" of bamboo-feeding Lepidoptera. Overall, non-herbivorous and food-switching caterpillars made up half of the total community in the present study, and at the lower elevation these unusual feeders even accounted for the majority. Feeding guild structure in both forest types differed considerably from one another. While the

switchers (exclusively Geometridae) occurred in equal shares in both forest types, the proportion of herbivores was significantly larger in the cloud forest and that of non-herbivores larger in the lower mountain forest.

Considering only herbivorous taxa, Shannon's entropy for *Chusquea* caterpillars was 70.35 and thus nearly twice as high compared to other plant species in the same area, where the highest value found so far was 33.97 for caterpillars feeding on *Ageratina dendroides* (Asteraceae) (Bodner et al. 2012). Other quantitative studies of focal plants conducted in Papua New Guinea (Novotny et al. 2003) also revealed values far below those that I observed on *Chusquea* (*Piper umbellatum*: 25.73; *P. aduncum*: 8.05). Furthermore, species abundance distribution differed noticeably from other studies, where communities were often found to be dominated by a single species constituting 30-50% of total abundance (Novotny et al. 2002b; Miller et al. 2003). In the present study the most abundant species only made up 4% of the community total, which was very low compared to the dominance pattern of communities reported from other host plants in the same study area in South Ecuador (e.g. *Ageratina dendroides:* 90%, or the median of several *Piper* species: 40%; Bodner et *al.* 2012). A second difference is the high number of singleton species (66%) compared to other studies, while typically reported values vary around 45% (Morse et al. 1988; Novotny et al. 2000; Basset et al. 1991). Low dominance here indicates the absence of any specialized "core species" to predictably feed on *Chusquea* bamboos. Pronophiline Satyrinae, which are known to be very diverse in the Andes and closely associated with Poaceae (Pyrcz et al. 2009), were expected to clearly dominate the caterpillar community on *Chusquea*. Instead many pronophiline species were found, but only in one or two individuals each. A study dealing with adult butterflies (80% hereof were Satyrinae) in the same area also revealed a high number of rare species, however there were one or two dominant species (Kling 2000).

Fecundity of diurnally active butterflies is known to decrease with altitude (Hodkinson 2005) i.a. because lower temperatures shorten the viable time span for oviposition in these sunlight dependent insects. Together with their tendency to lay eggs singly (DeVries 1987) this may explain small population sizes to prevail amongst tropical montane butterflies. A further possible explanation for the overall low caterpillar densities observed on *Chusquea* bamboos may be found in the relatively dry conditions during the sampling period (T. Peters, unpublished climate data). M.-O. Adams (personal communication) also recorded lower insect densities during this time compared to previous studies, and he noted a significant increase in overall arthropod abundance with the normalization of weather conditions in 2011/12. A general decline in butterfly and moth populations due to unusually dry conditions in the year 2011 might therefore also explain the unexpectedly high percentage of singletons.

The majority of herbivore genera associated with *Chusquea* were grass specialists like *Pedaliodes* (Nymphalidae), *Dalla* (Hesperiidae), *Xenomigia* (Notodontidae), or *Praina* (Noctuidae). But I also found a high diversity of polyphagous herbivores such as Erebidae (e.g. *Sphecosoma* sp., *Zatrephes* sp.), Geometridae (e.g. *Pero* sp.) and Noctuidae (e.g. *Orthodes* sp., *Hampsonodes* sp.). This might indicate that *Chusquea* is a palatable host plant for many polyphagous species. However, high silica content and poverty of nutrients is not optimal for insufficiently adapted caterpillars. Therefore, even if such polyphagous species are obviously able to utilize *Chusquea* foliage as larval food, they may not be able to reach high densities in bamboo stands.

The expected pattern of declining abundance and species richness with increasing altitude (Hodkinson 2005; see also Beck et al. 2011 for adult moths in the same study region) was only partly supported by the present results. Using Shannon's entropy, caterpillar diversity was indeed lower in the cloud forest but the density of individuals as well as species per sampling unit was significantly higher. These results support the hypothesis of Hamilton (1995) that cloud forests form a distinct system with an own, highly diverse community. For graminivorous communities the high abundance of *Chusquea* in the cloud forest provides a huge resource while these bamboos only rarely (and transiently) occur in high densities at lower elevations. Consequently, higher caterpillar densities may be better explained by differences in the predominance of bamboo between both forest types rather than by increasing altitude and its accompanying climate features alone. Also the large species turnover between the two forest types could be explained this way.

Familial composition differed markedly between the two forest types. Of a total of 12 recorded families both forest types only had six families in common (Geometridae, Noctuidae, Erebidae, Nymphalidae, Hesperiidae and Tortricidae), while four families occurred exclusively in the cloud forest (Elachistidae, Notodontidae, Lasiocampidae and Megalopygidae) and two families were restricted to the lower mountain forest (Gelechiidae and Riodinidae). In Cajanuma two families, the Geometridae and Noctuidae dominated the community, while in RBSF three families, the Geometridae, Erebidae and Noctuidae did. The high proportion of Geometridae observed in this context was rather unexpected because larvae in this moth family typically do not feed on grass (Robinson et al. 2010). However Geometridae in the Andes are as species rich as nowhere else in the world (Brehm et al. 2005), so one might expect novel host plant affiliations to be uncovered. Moreover, most of the Geometridae collected from *Chusquea* were non-herbivores or switchers which explains their abundant occurrence on bamboo. Only representatives of one genus of Geometridae, namely *Pero*, which was found in 8 individuals (all of the same species), indeed fed on fresh bamboo leaves. Since elsewhere species in the genus *Pero* are known to be quite polyphagous (Janzen & Hallwachs 2009), this extension towards bamboo feeding was not too surprising. A closely related species (*Pero maculicosta*) was also found in the sampling area feeding on Myricaceae (Bodner et al. 2011). The rather large number of representatives of the genus *Eupithecia* in my samples from *Chusquea* bamboos remains inexplicable thus far. *Eupithecia* larvae feed predominantly on flowers of developing seeds, and none is known to feed on grass foliage. Indeed, all 19 *Eupithecia* larvae that I observed on bamboo fed on dead foliage, which is still remarkable.

A further conspicuous change in community structure was the decline of Erebidae, which constituted the second most abundant family in the RBSF, represented by three subfamilies (Arctiinae, Herminiinae and Boletobiinae), while in the cloud forest only few individuals from the subfamily Arctiinae occurred. Herminiinae and Boletobiinae are both non-herbivorous groups which were, together with Riodininae, exclusive to the lower elevations. An elevational decline of some groups of Arctiinae was already observed from light trap samples and might be caused by their insufficient adaptation to higher elevations (Fiedler et al. 2008, Beck et al. 2011).

Some typical grass feeding taxa such as Elachistidae, Gelechiidae, Tortricidae and Hesperiidae were also less frequent than expected. Surprisingly not even one individual of the superfamiliy Pyraloidea was found on *Chusquea* although many representatives typically feed on Poaceae and they also were proven to be quite species rich and especially abundant in the study area, recorded by light trapping up to 2700m a.s.l. (Süßenbach 2003). However,

the most abundant pyraloid group at higher elevations were the Scopariinae, which usually do not feed on Poaceae. Other pyraloid clades which are known to feed Poaceae and also reached high elevations in the study region typically are stem borers as larvae (Süßenbach 2003), and these were not covered by sampling in my study. The low representation of Hesperiidae in my samples was less surprising because only ca. 20 species of Hesperiidae (Piñas 2006) are known from higher elevations in Ecuador, suggesting that they might be generally rare at higher altitudes in the mountain forest zone. *Xenomigia* (Notodontidae) is a widely distributed genus, which often occurs at high elevations and typically feeds on *Chusquea* (Miller 2009, Dyer et al. 2013). Indeed I only found these in the cloud forest, but quite abundantly with 12 individuals of 2 species.

High proportions of non-herbivorous and food switching caterpillars among the communities associated with different plant species were for the first time found in another study of caterpillar communities on various shrub species in the same region (Bodner 2011). Interestingly, in his study the percentage of non-herbivores varied considerably among plant species, although these insects are not in a direct trophic relationship with the plant itself. Different traits of plant architecture (such as growth form, leaf size) might play a role here, since such traits could drive the abundance and structure of epiphyllic growth which in turn is expected to influence the non-herbivorous fraction of caterpillar communities. Microclimatic differences (e.g. in temperature and humidity) associated with the surrounding habitat, however, are likely to be stronger determinants. Bodner (2011) postulated that such climatic factors may influence the growth of epiphylls and the toughness of dead leaves, as well as the rate of fungal growth on dead leaves, which is known to alter their nutritional value. Hence any correlation between a focal plant species and its associated non-herbivore caterpillar community is more likely to be related to the habitat in which the plant species preferentially grows, rather than a function of the plant traits itself. Indeed, a comparison of *Chusquea* plants growing in more open habitat to sites beneath a closed canopy cover indicated a distinctly higher abundance of non-herbivores at forest sites, corroborating microclimatic conditions as an important factor. *Chusquea* would be well suited to further examine such potential habitat effects on the non-herbivorous fraction of caterpillar communities more closely because this plant grows both inside the forest and in more open habitats. At any rate, my study confirms that also on bamboos in the Andean mountain forest zone, like on a variety of other understory shrubs, non-herbivores make up a sizeable fraction of the caterpillar community. Since epiphyllic mosses and lichens do not occur on the rather short-lived foliage of *Chusquea* bamboos, these non-herbivores can be assumed to be primarily detritivores, i.e. they either feed on dead bamboo foliage or on other dead organic matter trapped between the bamboo leaves. In lepidopteran caterpillars, detritivory and mycophagy are tightly linked to each other. It can often not be differentiated clearly whether the decaying plant matter or rather the associated fungal growth serve as the main nutrient source (Rawlings 1983).

Feeding guild structure in the two forest types differed considerably from each other. A trend of decreasing numbers of non-herbivorous caterpillars with increasing altitude has recently been observed (F. Bodner, personal communication) and is further corroborated by the present data. In this case, an explanation based on resource availability for larvae alone is not plausible because the cloud forest provides leaf litter, epiphyllic growth and high humidity in much the same way as the lower mountain forest. However, the declining temperature might constrain non-herbivorous species not due to larval diet, but more as a consequence of characteristics of their respective adult stages. The largest groups of non-

herbivores are Noctuidae, Erebidae and Geometridae. While adult Geometridae are known to have a number of adaptations to higher elevations, such as better flight performance at lower temperatures, these are largely lacking in Noctuoidea (Casey et al. 1982). Consequently the imagines of important non-herbivore taxa might not be able to colonize higher elevations, leading to a lower overall proportion of this dietary guild at the cloud forest site.

This study confirmed *Chusquea* to be an important resource for Lepidopteran communities, which likely applies for many regions within the Andes. Species accumulation was highly unsaturated, resulting in the highest figures ever recorded of species diversity of caterpillars associated with a particular tropical focal plant taxon. Furthermore, *Chusquea* may serve as an important model for further community studies and other ecological research due to its wide distribution and its unexpected value as resource for a wide variety of Lepidoptera species across numerous families.

Acknowledgments

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Appendix

Table A1: Individual (N) and species number (Spec.) of caterpillars sampled from *Chusquea* bamboos per family, segregated into the three feeding guilds as used for analyses. Herbivores - caterpillar fed on living bamboo foliage; non-herbivores: caterpillar fed on dead leaves or related resources (i.e. basically detritivores and/or fungal feeders); switchers: young larvae fed on detritus, older larvae on living foliage.

Family	Herbivores		Non-herbivores		Switchers		Total count	
	N	Spec.	N	Spec.	N	Spec.	N	Spec.
Elachistidae	5	5	-	-	-	-	5	5
Erebidae	26	16	28	14	-	-	54	30
Gelechiidae	11	2	-	-	-	-	11	2
Geometridae	11	4	24	11	91	40	126	55
Hesperiidae	10	9	-	-	-	-	10	9
Lasiocampidae	1	1	-	-	-	-	1	1
Megalopygidae	2	1	-	-	-	-	2	1
Noctuidae	47	22	39	20	-	-	86	42
Notodontidae	12	2	-	-	-	-	12	2
Nymphalidae	36	32	-	-	-	-	36	32
Riodinidae	-	-	7	1	-	-	7	1
Tortricidae	12	12	-	-	-	-	12	12

Table A2: List of all 201 caterpillar species found on *Chusquea* bamboos, including 9 tourist species. Specific epithets give informal codes, apart from described species that could be identified to true species level. Species for which COI subunit 1 sequences exist are marked with *. **Other plant**= caterpillars has also been found on other plants within the same area; **N**= individual number. **Feeding guild**= herbivores (herb.), non-herbivores (non-herb.), switchers, and tourist species. **Site**= caterpillars found at Cajanuma (Caj.), Reserva Biológica San Francisco (RBSF), or at both sites.

Family	Subfamily	Tribe	Genus	Species	Other plant	N	feeding guild	Site
Elachistidae	-	-	-	elac122*		1	herb.	Caj.
Elachistidae	-	-	-	elac155*		1	herb.	Caj.
Elachistidae	-	-	-	elac231*		1	herb.	Caj.
Elachistidae	-	-	-	elac287*		1	herb.	Caj.
Elachistidae	-	-	-	elac94*		1	tourist	Caj.
Erebidae	Arctiinae	Arctiini	*Leucanopsis*	*luridioides*		4	herb.	both
Erebidae	Arctiinae	Arctiini	*Argyroides*	cten03		2	herb.	RBSF
Erebidae	Arctiinae	Arctiini	*Delphyre*	*tetilla*		1	herb.	RBSF
Erebidae	Arctiinae	Arctiini	*Napata*	cten74*		4	herb.	RBSF
Erebidae	Arctiinae	Arctiini	*Sphecosoma*	cten32*		1	herb.	RBSF
Erebidae	Arctiinae	Arctiini	-	cten u06*		1	herb.	Caj.
Erebidae	Arctiinae	Arctiini	-	cten u15		1	herb.	RBSF
Erebidae	Arctiinae	Arctiini	*Cosmosoma*	cten08		3	herb.	RBSF
Erebidae	Arctiinae	Arctiini	-	cten10		1	herb.	Caj.
Erebidae	Arctiinae	Arctiini	-	cten18		1	herb.	RBSF
Erebidae	Arctiinae	Arctiini	-	cten203*		2	herb.	RBSF
Erebidae	Arctiinae	Arctiini	-	cten309*		1	herb.	RBSF
Erebidae	Arctiinae	Arctiini	*Ischnocampa*	isch166*		1	herb.	Caj.
Erebidae	Arctiinae	Arctiini	*Ischnocampa*	*mamona**	x	3	herb.	RBSF
Erebidae	Arctiinae	Arctiini	*Zatrephes*	zat30*	x	1	herb.	RBSF
Erebidae	Arctiinae	Lithosiini	*Agylla*	lit1*	x	1	non-herb.	RBSF
Erebidae	Arctiinae	Lithosiini	*Agylla*	lit19*	x	1	non-herb.	RBSF
Erebidae	Boletobiinae	-	-	fun197*		2	non-herb.	RBSF
Erebidae	Boletobiinae	-	-	fun200*		3	non-herb.	RBSF
Erebidae	Boletobiinae	-	-	fun22*		2	non-herb.	RBSF
Erebidae	Boletobiinae	-	-	fun25*		3	non-herb.	RBSF
Erebidae	Boletobiinae	-	-	fun33*		5	non-herb.	RBSF
Erebidae	Eulepidotinae	-	*Antiblemma*	anti17*		1	tourist	RBSF
Erebidae	Herminiinae	-	*Lascoria*	las169*		3	non-herb.	RBSF
Erebidae	Herminiinae	-	-	her12*	x	1	non-herb.	RBSF
Erebidae	Herminiinae	-	-	her13*	x	2	non-herb.	RBSF
Erebidae	Herminiinae	-	-	her40*	x	2	non-herb.	RBSF
Erebidae	Herminiinae	-	-	her45*	x	1	non-herb.	RBSF
Erebidae	Hypeninae	-	*Hypena*	hyp84*		1	tourist	RBSF
Erebidae	Hypeninae	-	-	hyp48		1	tourist	RBSF
Erebidae	-	-	-	E312*		1	herb.	RBSF
Erebidae	-	-	-	sco175*	x	1	non-herb.	RBSF
Erebidae	-	-	-	sco78*		1	non-herb.	RBSF
Gelechiidae	Gelechiinae	-	-	gel168*		8	tourist	RBSF
Gelechiidae	-	-	-	gel31*		1	herb.	RBSF

Family	Subfamily	Tribe	Genus	Species	Other plant	N	feeding guild	Site
Gelechiidae	-	-	-	gel77*		2	herb.	RBSF
Geometridae	Ennominae	Azelinini	*Pero*	pero15*		8	herb.	RBSF
Geometridae	Ennominae	Boarmiini	*Iridopsis*	AH08EcPe*	x	2	switcher	RBSF
Geometridae	Ennominae	Boarmiini	*Physocleora*	AH06Ec*	x	2	switcher	RBSF
Geometridae	Ennominae	Boarmiini	*Physocleora*	*bella*		1	switcher	RBSF
Geometridae	Ennominae	Boarmiini	*Physocleora*	boa235*		1	switcher	Caj.
Geometridae	Ennominae	Boarmiini	-	boa102*		1	Switcher	RBSF
Geometridae	Ennominae	Boarmiini	-	boa139*		1	switcher	Caj.
Geometridae	Ennominae	Nacophorini	*Ischnopteris*	*brehmi**	x	1	switcher	RBSF
Geometridae	Ennominae	Nacophorini	*Rucana*	ruc51*		1	switcher	RBSF
Geometridae	Ennominae	Nacophorini	-	nac124*		5	switcher	both
Geometridae	Ennominae	Nephodiini	*Astyochia*	*marginea**	x	2	non-herb.	RBSF
Geometridae	Ennominae	Nephodiini	*Nephodia*	AH01Ec*		1	switcher	RBSF
Geometridae	Ennominae	Nephodiini	*Nephodia*	*astyochides*		1	switcher	RBSF
Geometridae	Ennominae	Nephodiini	*Nephodia*	*astyochides* GB02Ec*	x	4	switcher	RBSF
Geometridae	Ennominae	Nephodiini	*Nephodia*	nep232*		1	switcher	Caj.
Geometridae	Ennominae	Nephodiini	*Patalene*	pat100*		3	switcher	both
Geometridae	Ennominae	Nephodiini	*Patalene*	pat113*		1	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Cirsodes*	*acuminata* AH09Pe*		1	herb.	Caj.
Geometridae	Ennominae	Ourapterygini	*Eusarca*	eus127*	x	6	switcher	both
Geometridae	Ennominae	Ourapterygini	*Eusarca*	eus129*		7	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Eusarca*	eus252*		2	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	AH15Ec*	x	16	switcher	both
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	AH18Ec*		4	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	geo184*		1	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	geo186sf*		1	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	geo188sf*		1	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	iso137*		2	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	iso237*	x	1	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	*iso255**		3	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	iso269*		1	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Isochromodes*	iso283*		1	switcher	Caj.
Geometridae	Ennominae	Ourapterygini	*Mesedra*	GB05Ec*	x	7	switcher	both
Geometridae	Ennominae	Ourapterygini	*Mesedra*	mes11		1	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	*Mesedra*	mes207*		2	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	*Oxydia*	*platypterata* AH02Ec*		1	tourist	RBSF
Geometridae	Ennominae	Ourapterygini	-	geo183*		1	switcher	RBSF
Geometridae	Ennominae	Ourapterygini	-	geo264*		1	herb.	Caj.
Geometridae	Ennominae	Ourapterygini	-	geo138*		1	switcher	Caj.
Geometridae	Ennominae	Palyadini	*Opisthoxia*	opis99*		1	tourist	RBSF
Geometridae	Ennominae	-	-	geo02		1	switcher	RBSF
Geometridae	Ennominae	-	-			1	switcher	Caj.
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	AH27Ec*	x	7	non-herb.	both
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	*duena* AH01Ec*		1	non-herb.	RBSF

Family	Subfamily	Tribe	Genus	Species	Other plant	N	feeding guild	Site
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	eup101*		1	non-herb.	RBSF
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	eup147*	x	2	non-herb.	Caj.
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	eup159*		1	non-herb.	Caj.
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	eup162*		1	non-herb.	Caj.
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	eup165*		1	non-herb.	Caj.
Geometridae	Larentiinae	Eupitheciini	*Eupithecia*	eup282*		5	non-herb.	Caj.
Geometridae	Larentiinae	-	*Erateina*	radiata*		1	tourist	RBSF
Geometridae	Larentiinae	-	-	eup u01		1	tourist	Caj.
Geometridae	Larentiinae	-	-	eup u14		1	non-herb.	RBSF
Geometridae	Larentiinae	-	-	geo108*		1	non-herb.	RBSF
Geometridae	-	-	-	geo u08		1	switcher	RBSF
Geometridae	-	-	-	geo u09		1	switcher	RBSF
Geometridae	-	-	-	geo u12		1	switcher	RBSF
Geometridae	-	-	-	geo118*		1	switcher	Caj.
Geometridae	-	-	-	geo36*		1	tourist	RBSF
Geometridae	-	-	-	geo42*		2	herb.	Caj.
Geometridae	-	-	-	geou117		1	switcher	Caj.
Hesperiidae	Heteropterinae	-	*Dalla*	hes123*		2	herb.	Caj.
Hesperiidae	Heteropterinae	-	*Dalla*	*ibhara**		1	herb.	RBSF
Hesperiidae	Hesperiinae	-	*Lychnuchus*	hes07		1	herb.	RBSF
Hesperiidae	-	-	-	hes143*		1	herb.	Caj.
Hesperiidae	-	-	-	hes72*		2	herb.	RBSF
Hesperiidae	-	-	-	hes11		1	herb.	RBSF
Hesperiidae	-	-	-	hes223*		1	herb.	Caj.
Hesperiidae	-	-	-	hes62		1	herb.	RBSF
Hesperiidae	-	-	-	hes89		1	herb.	RBSF
Lasiocampidae	-	-	-	las142*		1	herb.	Caj.
Megalopygidae	-	-	-	meg117*		2	herb.	Caj.
Noctuidae	Eustrotiinae	-	-	E141*		1	herb.	Caj.
Noctuidae	Eustrotiinae	-	-	E195*		2	herb.	RBSF
Noctuidae	Eustrotiinae	-	-	E204*		1	herb.	RBSF
Noctuidae	Eustrotiinae	-	-	E271*		1	herb.	Caj.
Noctuidae	Noctuinae	Apameini	-	apa3*	x	2	herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	*Elaphria*	ela157*		1	non-herb.	Caj.
Noctuidae	Noctuinae	Elaphriini	*Elaphria*	ela198*	x	2	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	*Elaphria*	ela4*		2	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	*Gonodes*	ela13*		1	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	*Gonodes*	ela20*	x	2	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	*Gonodes*	ela34*	x	3	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	-	ela u10		1	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	-	ela121*		3	non-herb.	Caj.
Noctuidae	Noctuinae	Elaphriini	-	ela163*		1	non-herb.	Caj.
Noctuidae	Noctuinae	Elaphriini	-	ela194*		2	non-herb.	RBSF
Noctuidae	Noctuinae	Elaphriini	-	ela196*		6	non-herb.	both
Noctuidae	Noctuinae	Elaphriini	-	ela206*		1	non-herb.	RBSF

Family	Subfamily	Tribe	Genus	Species	Other plant	N	feeding guild	Site
Noctuidae	Noctuinae	Elaphriini	-	ela217*		1	non-herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	*Eriopyga*	eri178*	x	1	non-herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	*Eriopyga*	eri307*	x	1	non-herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	*Lacinipolia*	eri281*		2	herb.	Caj.
Noctuidae	Noctuinae	Eriopygini	*Orthodes*	eri135		1	herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	*Orthodes*	eri291		1	herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	-	eri112*		2	herb.	Caj.
Noctuidae	Noctuinae	Eriopygini	-	eri151*		2	herb.	Caj.
Noctuidae	Noctuinae	Eriopygini	-	eri156*		1	non-herb.	Caj.
Noctuidae	Noctuinae	Eriopygini	-	eri2*	x	6	non-herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	-	eri201*	x	2	non-herb.	RBSF
Noctuidae	Noctuinae	Eriopygini	-	eri222*		1	herb.	Caj.
Noctuidae	Noctuinae	Eriopygini	-	eri82*		1	non-herb.	RBSF
Noctuidae	Noctuinae	Hadenini	*Chabuta*	had23*		2	herb.	RBSF
Noctuidae	Noctuinae	Hadenini	*Hampsonodes*	had64*		1	herb.	RBSF
Noctuidae	Noctuinae	Hadenini	*Lepteria?*	had 27		1	herb.	RBSF
Noctuidae	Noctuinae	Hadenini	*Trichorthosia*	*diapera**		2	herb.	RBSF
Noctuidae	Noctuinae	Hadenini	-	had116*		2	herb.	Caj.
Noctuidae	Noctuinae	Hadenini	-	had161*		1	herb.	Caj.
Noctuidae	Noctuinae	Hadenini	-	had190*		2	herb.	RBSF
Noctuidae	Noctuinae	Hadenini	-	had210*	x	1	herb.	RBSF
Noctuidae	Noctuinae	Hadenini	-	had214*		1	herb.	RBSF
Noctuidae	Noctuinae	Noctuini	*Praina*	noc136*		14	herb.	Caj.
Noctuidae	Noctuinae	-	-	noc140*		5	herb.	Caj.
Noctuidae	-	-	-	noc197		1	non-herb.	RBSF
Notodontidae	Dioptinae	Dioptini	*Xenomigia*	not238*		7	herb.	Caj.
Notodontidae	Dioptinae	Dioptini	*Xenomigia*	not275*		5	herb.	Caj.
Nymphalidae	Morphinae	Morphini	*Antirrhea*	*adoptiva**		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Corades*	*cistene**		3	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Corades*	cor85*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Eretris*	*calisto*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Eretris*	ere11*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Eretris*	*fuscus*		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Lymanopoda*	lym224		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	*manis*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	*montagna*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped s13		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped128*		3	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped144*		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped241*		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped257*		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped42*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped52*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped68*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	ped75*		1	herb.	RBSF

Family	Subfamily	Tribe	Genus	Species	Other plant	N	feeding guild	Site
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	*phasa*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	*pisona*		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Pedaliodes*	*poesia*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pronophila*	*thelebe**		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Pronophila*	*unifasciata*		2	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	*Steremnia*	*pronophila*		1	herb.	Caj.
Nymphalidae	Satyrinae	Pronophilini	*Steroma*	*superba*		1	herb.	RBSF
Nymphalidae	Satyrinae	Pronophilini	-	pro74		1	herb.	Caj.
Nymphalidae	Satyrinae	Euptychiini	*Forsterinaria*	*neonympha**		1	herb.	RBSF
Nymphalidae	Satyrinae	Erebiini	*Manerebia*	man240*		1	herb.	Caj.
Nymphalidae	Satyrinae	-	-	sat224*		1	herb.	Caj.
Nymphalidae	Satyrinae	-	-	sat251*		1	herb.	Caj.
Nymphalidae	-	-	-	nymph120*		1	herb.	Caj.
Nymphalidae	-	-	-	ped119*		1	herb.	Caj.
Riodinidae	Riodininae	Helicopini	*Sarota*	sar35*	x	7	non-herb.	RBSF
Tortricidae	-	-	-	tor u16		1	herb.	RBSF
Tortricidae	-	-	-	tor05		3	herb.	Caj.
Tortricidae	-	-	-	tor152*		1	herb.	Caj.
Tortricidae	-	-	-	tor167*		1	herb.	RBSF
Tortricidae	-	-	-	tor185*	x	1	herb.	RBSF
Tortricidae	-	-	-	tor253*		1	herb.	Caj.
Tortricidae	-	-	-	tor258*		1	herb.	Caj.
Tortricidae	-	-	-	tor265*	x	1	herb.	Caj.
Tortricidae	-	-	-	tor289*		1	herb.	Caj.
Tortricidae	-	-	-	tor3		1	herb.	RBSF
Tortricidae	-	-	-	tor44*		1	herb.	RBSF
Tortricidae	-	-	-	tor98*		1	herb.	RBSF

Curriculum Vitae

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1991-1995:   Primary school in Salzburg, Austria

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