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Caterpillar communities on shrubs in the montane forest
zone of southern Ecuador

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Caterpillar communities on shrubs
in the montane forest zone
of southern Ecuador



Phyle versatile (Geometridae)

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1. Abstract

Caterpillar communities were studied on 16 shrub species from the family Asteraceae and the genus *Piper* (Piperaceae) in the Andean montane rainforest zone of southern Ecuador. The applied sampling methodology was evaluated and found well suited for sampling of caterpillars, especially with focus on resampling.

During standardized sampling, a total of 18890 specimens were collected in 11 field surveys between August 2007 and June 2009. Overall, samples were dominated by gregarious early instars and egg clutches of *Altinote dicaeus albofasciata* (Nymphalidae) on *Erato polymnioides* (Asteraceae). Those and all other such groups and egg clutches were down-weighted for analyses to their cubic root to balance against their overrepresentation in the data set. Trophic associations of caterpillars were confirmed by feeding trials. A substantial fraction of more than 22% of the encountered caterpillars (and up to 80% on individual shrub species) was found not to be trophically linked to the living biomass of the shrubs themselves (“non-herbivores”), but rather feed on dead leaves and epiphylls. Abundance of non-herbivores differed strongly between the two studied plant families, but was very similar on different shrub species within these families. Abundance of herbivorous caterpillars, to the contrary, differed hardly between plant families, but varied strongly between individual plant species. Herbivores were almost entirely comprised of ectophagous folivores, while florivores (2.3%) and semi-endophagous folivores (leaf rollers and tiers; 6.0%) were unexpectedly rare.

Absolute species richness of herbivorous caterpillars was high, with a total of 191 Lepidoptera species on the studied 16 shrub species, but varied up to 40fold between individual plant species. Rarefied species numbers were more similar among plant species, but still showed a 15fold difference between the most species rich and most species poor community. Communities on *Piper* species were characterized by low effective species numbers (measured as exponential Shannon entropy) and high dominance of one or two species of the Geometridae genus *Eois*. *E. polymnioides* featured a similar structure dominated by *A. dicaeus albofasciata*. Communities on the other two Asteraceae (*Ageratina dendroides* and *Baccharis latifolia*), to the contrary, were found to have high effective species numbers and low dominance. In conclusion, while *Piper* species and *E. polymnioides* feature caterpillar communities defined by small, predictable sets of core herbivores, these defining sets do not exist for the other two of the studied Asteraceae species. Communities on *Piper* were also more specialized, with 62.8% of the caterpillar species considered monophagous at plant species level, than on Asteraceae with only 11.6% monophagous species. The observed

diversity patterns point mainly to shaping by (chemical) plant-herbivore-defense, while geographic range and local abundance of host plants appear to have only limited and varying influence on the associated caterpillar communities.

2. Zusammenfassung

Die Raupengemeinschaften auf 16 Straucharten aus der Familie Asteraceae und der Gattung *Piper* (Piperaceae) im Bergregenwald in den Anden Südecuadors wurden untersucht. Die angewandte Sammelmethode erwies sich im Zuge einer Evaluierung als gut geeignet für das Sammeln von Raupen auf Sträuchern, insbesondere im Hinblick auf zeitliche Replikation der Aufnahmen an denselben Strauchindividuen.

Im Rahmen von 11 standardisierten Aufnahmezyklen zwischen August 2007 und Juni 2009 wurden 18890 präimaginale Schmetterlingsindividuen erfasst. Insgesamt wurden die erhobenen Daten stark von gregären Jungrauen und Eigelegen einer Tagfalterart, *Altinote dicaeus albofasciata* (Nymphalidae), auf der Asteraceae *Erato polymnioides* dominiert. Diese und alle weiteren Raupengruppen und Eigelege wurden für die Analysen herabgewichtet und durch ihre dritte Wurzel ersetzt, da sie im Verhältnis zum Gesamtdatensatz stark überrepräsentiert waren. Die trophische Beziehung zur Wirtspflanze wurde durch Fraßexperimente überprüft. Hierbei stellte sich heraus, dass sich ein beträchtlicher Anteil von über 22% der Individuen (und bis zu 80% auf einzelnen Straucharten) nicht von der lebenden Biomasse des Strauches ernährt, auf dem die Raupe gefunden wurde, sondern von Totlaub, Flechten und Epiphyllen („Nicht-Herbivore“). Die Abundanz von Nicht-Herbivoren unterschied sich stark zwischen den Strauchfamilien, war jedoch auf Sträuchern unterschiedlicher Arten innerhalb der Familien weitestgehend konstant. Die Abundanz von herbivoren Lepidopteren waren dagegen im Mittel auf beiden Strauchfamilien sehr ähnlich, wies aber starke Unterschiede zwischen den einzelnen Straucharten auf. Herbivore Raupen waren zum weit überwiegenden Teil ektophage Folivore, während Florivore (2,3%) und semi-endophage Folivore (in Blattrollen, -tüten oder Gespinsten; 6,0%) selten waren.

Der Gesamtartenreichtum herbivorer Lepidopteren war mit 191 Arten auf 16 untersuchten Straucharten hoch, variierte aber zwischen einzelnen Straucharten bis zu 40fach. Nach Anwendung einer Rarefaction-Analyse verringerten sich diese Unterschiede erheblich, die Differenz der Artenzahl zwischen artenreichster und artenärmster Gemeinschaft lag jedoch immer noch beim 15fachen. Charakteristisch für Artengemeinschaften auf *Piper* waren eine niedrige effektive Artenzahl (gemessen als exponentielle Shannon-Entropie) und hohe Dominanz durch Arten der Geometridengattung *Eois*. Bei den Asteraceenarten wies die Raupengemeinschaft auf *E. polymnioides* mit *A. dicaeus albofasciata* als dominanter Art eine ähnliche Struktur auf, wohingegen die Gemeinschaften auf den übrigen beiden Asteraceenarten (*Ageratina dendroides* und *Baccharis latifolia*) von hoher effektiver Artenzahl und niedrigen Dominanzwerten geprägt waren. Daraus lässt sich ableiten, dass Raupengemeinschaften auf *Piper*-Arten und *E. polymnioides* von einem kleinen, vorhersagbaren Set an Kernarten definiert werden, während solche Kerngemeinschaften auf den verbleibenden beiden Asteraceenarten fehlen. Gemeinschaften auf *Piper* wiesen außerdem mit 62,8% als monophag eingestuften Schmetterlingsarten einen höheren Grad an Spezialisierung auf als auf Asteraceen mit 11,6% monophagen Schmetterlingsarten. Die beobachteten Diversitätsmuster deuten am ehesten auf einen formenden Einfluss durch (chemische) Herbivorenabwehr hin, während Größe des Verbreitungsgebiets und lokale Häufigkeit der Pflanzenarten eher eine untergeordnete Rolle für die assoziierten Raupengemeinschaften zu spielen scheint.

3. List of manuscripts with statement of personal contribution

Chapter 5: Feasibility of a combined sampling approach for studying caterpillar assemblages – a case study from shrubs in the Andean montane forest zone.

F. Bodner, S. Mahal, M. Reuter & K. Fiedler

Published as

Bodner, F., Mahal, S., Reuter, M. & Fiedler, K. (2010) Feasibility of a combined sampling approach for studying caterpillar assemblages – a case study from shrubs in the Andean montane forest zone. *The Journal of Research on the Lepidoptera*, **43**: 27–35.

Personal contribution:

- Planning of the experiment under supervision of Konrad Fiedler
- Fieldwork for two of the four presented sub-experiments
- Supervision of fieldwork for the two other presented sub-experiments
- Data analysis under supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 6: Abundance and guild structure of caterpillars (Lepidoptera) on shrubs in the montane forest zone in southern Ecuador. (prepared for submission to *Biotropica*)

F. Bodner, G. Brehm & K. Fiedler

Personal contribution:

- Co-planning and design of surveys
- Field- and labwork (collecting, rearing and documenting the samples)
- Data preparation and analysis und supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 7: Species richness and host specificity among caterpillar communities on shrubs in the Andes of southern Ecuador. (prepared for submission to *Ecological Entomology*)

F. Bodner, P. Strutzenberger, G. Brehm & K. Fiedler

Personal contribution:

- Co-planning and design of surveys
- Field- and labwork (collecting, rearing and documenting of the samples)
- Preliminary species identification
- Data preparation and analysis und supervision of Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

4. Introduction

The trophic association between plants and insect herbivores is one of the most prevalent ecological interactions in terrestrial ecosystems on Earth. Food webs consisting of herbivorous insects and their host plants contain a major part of terrestrial biodiversity (Price 2002). Understanding their basic function and structure is central for many scientific questions ranging from estimations of the total number of species on Earth (e.g. Hamilton et al. 2010) to predicting their vulnerability to climate change and habitat loss (Koh et al. 2004). However, despite their fundamental role, data on host-herbivore interactions has long been scarce. This is especially true for the tropics (Basset 1992), where both insect herbivores and their host plants are most diverse – but where still today for the largest fraction of taxonomically recognized herbivore species no single host plant record has ever been published in the scientific literature. Data on plant secondary metabolites, which are central to understanding plant-herbivore interactions, are equally scarce. Secondary plant metabolites provide a challenge for the physiology of any plant-feeding insect and may be an important factor in high host-specificity as evident e.g. in many species of Lepidoptera, although however other herbivore taxa are notably more generalistic (Novotny et al. 2002a).

Early attempts to quantify diversity and host specificity of tropical herbivore communities have led to the famous – and famously exaggerated – estimations of global biodiversity in the range of 30 (Erwin 1982) or even 50 (Erwin 1988) million species. As data and understanding of herbivore-host interactions have improved, these extrapolations have been gradually scaled back to between 2.5 and 8.5 (Hamilton et al. 2010) million tropical arthropod species. While plant-herbivore interactions have come more strongly into focus of ecological investigation in the last decade (Novotny & Basset 2005), studies dealing with them in detail are still comparatively few. Furthermore, they often arrive at contradicting conclusions. For example, while earlier studies had found high levels of randomness in tropical herbivore communities on trees sampled by insecticidal knockdown methods (e.g. Floren & Linsenmair 1998), Novotny et al. (2002b) characterized them as “predictably simple” in that they were dominated by few abundant specialists with little spatial and temporal variability, concluding from studies based on extensive hand collection surveys. The situation is similar regarding the question whether tropical herbivore communities are more specialized than their temperate counterparts, one of the main hypotheses proposed as a reason for high tropical insect diversity (Lewinsohn & Roslin 2008). Novotny et al. (2006) concluded that tropical herbivorous insects are no more specialized than in temperate-zone communities, whereas Dyer et al. (2007) observed significantly higher specialization in

tropical communities. Recently, Rodríguez-Castañeda et al. (2010) have shown from two Neotropical sites that community patterns of host plant use also change with elevation, adding yet another dimension of complexity.

While many of the contradicting results may well be explained by differences in sampling method (e.g. fogging vs. hand collection), region (e.g. South America vs. Southeast Asia), targeted taxa (e.g. all herbivorous insects vs. immature Lepidoptera), or elevational level of study sites, what they all show is that the available data is currently too scarce to arrive at convincing, generally accepted conclusions.



Fig. 4.1: Estación Científica San Francisco (ECSF) and surrounding habitats in southern Ecuador.

The aim of this doctoral thesis was to shed light on the diversity, host specificity and guild structure of communities of preimaginal Lepidoptera on shrubs in the montane forest zone in southern Ecuador. Of particular interest were the abundance and diversity – and differences thereof – of caterpillar communities on different plant species, the host specificity

of herbivorous caterpillars in these communities, and the overall contrast between communities associated with common shrub species in two phylogenetically distant plant families. Target plant species were three species of Asteraceae that grow in heavily disturbed areas, as opposed to 13 species of *Piper* shrubs (Piperaceae) that thrive inside the closed mountain rain forest. Shrubs, rather than trees, were selected as targets for this study, as they (1) are represented with several abundant species in both natural and disturbed habitats, (2) are easily accessible, (3) can be thoroughly sampled with non-invasive techniques, (4) have a simpler and more homogenous structure and (5) are likely to harbor somewhat less diverse communities than trees (Lawton 1983), rendering them more suitable for a thesis project.



Fig. 4.2: Studied habitats in the Reserva Biológica San Francisco. Left: heavily disturbed habitat along a canal with a *Baccharis latifolia* shrub in the foreground. Right: closed forest.

Additionally, caterpillar guild structure, which was originally expected to be only a minor topic, turned into a main focus of the study as it became clear during early steps of my field work that a substantial fraction of caterpillars living on the studied shrub species were indeed feeding on lichens, epiphylls, or dead leaves, rather than on the living biomass of the shrubs.

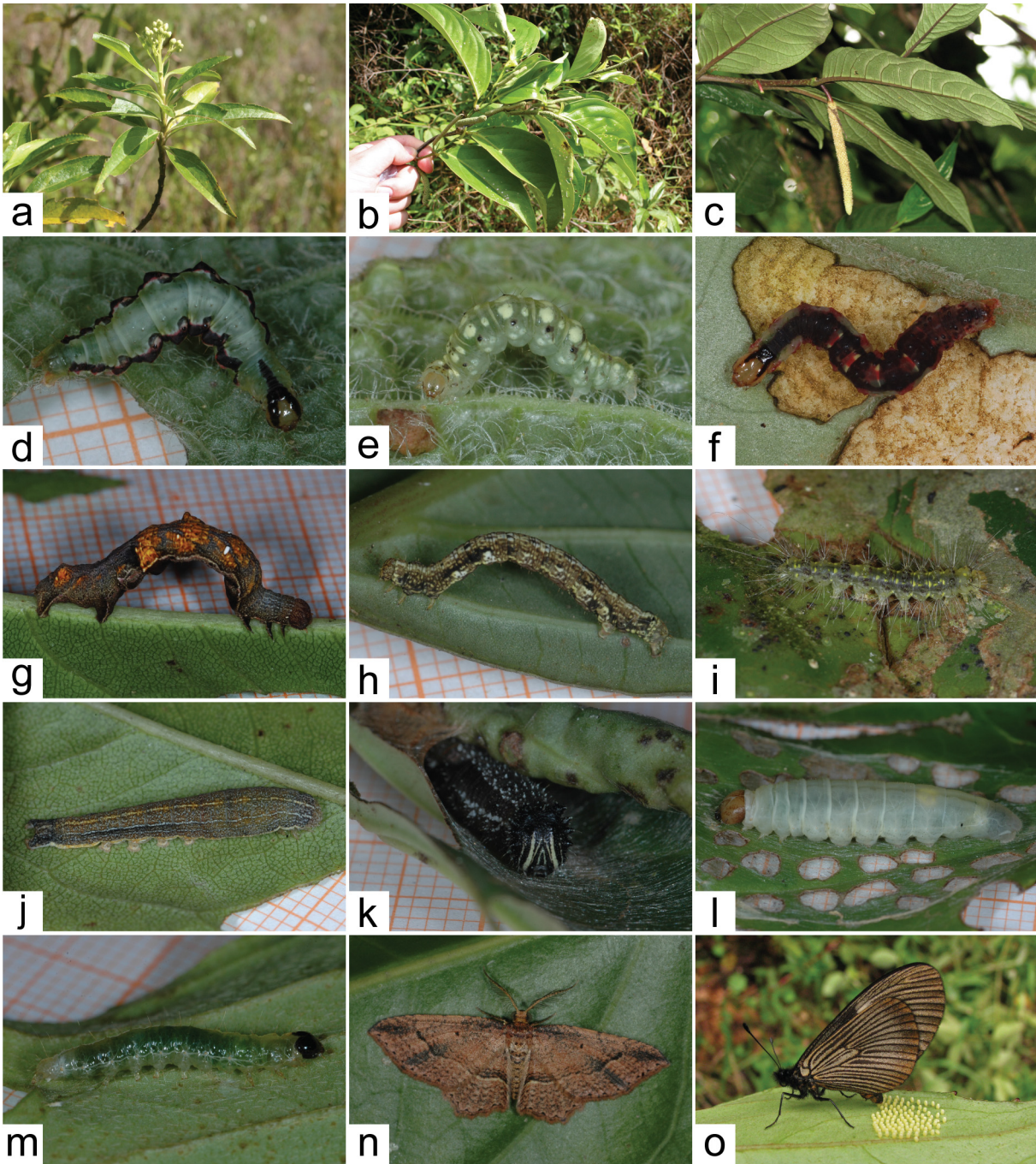


Fig. 4.3: Selected shrubs, caterpillars and adult Lepidoptera from this study. **a:** *Baccharis latifolia*, **b:** *Piper carpunya*, **c:** *Piper densiciliatum*, **d:** *Eois angulata* (E032), **e:** *Eois* sp. nr. *olivacea* (E060), **f:** *Eois* sp. nr. *goodmanii* (L14), **g:** *Cirsodes* sp. nr. *acuminata* (G294), **h:** *Physocleora* sp. (d-h: Geometridae), **i:** *Illice* sp. (Erebidae: Arctiinae), **j:** *Hypnotype placens* (L46; Noctuidae: Cucullinae), **k:** *Memphis pseudiphis* (L52; Nymphalidae), **l:** *Quadrus* sp. (L38; Hesperiiidae), **m:** *Blepharomastix* sp. (L3; Crambidae), **n:** *Eois* sp. nr. *encina* (G412; Geometridae), **o:** *Altinote dicaeus albofasciata* (L51; Nymphalidae). Codes in parentheses correspond to those in Table A1 (Appendix) for herbivorous Lepidoptera. *Physocleora* sp. and *Illice* sp. are members of the “non-herbivorous” guild.

Lepidoptera are one of the most important groups of insect herbivores, with currently about 160,000 species described (Kristensen et al. 2007). They can reach high abundance in herbivore samples (Novotny et al. 2006) and include many agricultural and forestry pests. Moreover, despite the many and large gaps remaining there is no other rich insect group for which a comparable body of evidence exists with regard to host plant affiliations and distributional data.

The study area selected, the Reserva Biológica San Francisco (Fig. 4.4) adjacent to the Podocarpus National Park in southern Ecuador, has been the focus of intense interdisciplinary ecological research for more than a decade (Beck et al. 2008). In the course of these studies, the region had been identified as a global hotspot of moth diversity (Brehm et al. 2005). Thus, the question as to how this tremendous species diversity as observed in light-trap samples of moths can be related to their early stages feeding on plants in an outstandingly rich flora (Homeier & Werner 2007) achieved particular relevance.

Specifically, the aims of my study were:

- (a) to assess the caterpillar assemblages with a non-invasive methodology – Chapter 5
- (b) to obtain insight into the taxonomic and guild structure of caterpillar communities – Chapter 6
- (c) to examine the diversity and host specificity of herbivorous caterpillar communities on the plant species level – Chapter 7

With these steps, this thesis aims to contribute to unraveling dimensions of complexity that underlie the mega-diverse Lepidoptera fauna of equatorial Andean mountain forests – the most species rich moth communities known thus far globally.

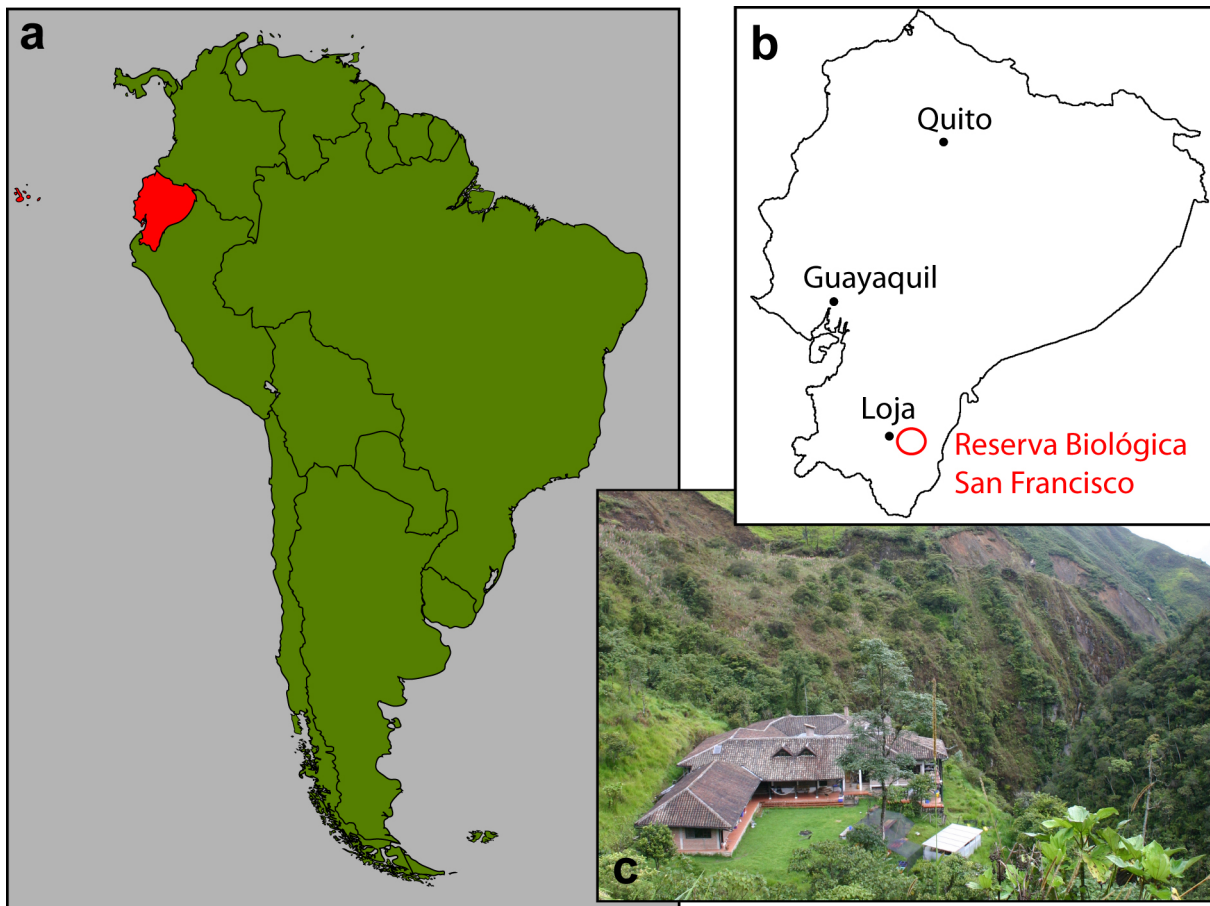


Fig. 4.4: Location of Ecuador in South America (a) and the study area in the south of Ecuador (b) around the Estación Científica San Francisco (c).

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5. Feasibility of a combined sampling approach for studying caterpillar assemblages – a case study from shrubs in the Andean montane forest zone

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Abstract

We analyzed the suitability of a combined sampling approach – consisting of visual search and branch-beating – for quantifying tropical caterpillar communities. Surveys were conducted in the Ecuadorian montane forest zone, with two shrub species from the genus *Piper* serving as focal targets. We sampled 160 shrubs in the course of four experiments following a standardized sampling protocol. Subsequently each shrub was completely defoliated accompanied by an intensive leaf-by-leaf search, in an effort to extract as close to 100% of all present caterpillars as possible. We analyzed the resulting dataset with regard to completeness, taxonomical bias, and influences of daytime, complexity of shrub structure, or experience of the researcher. The standardized sampling protocol extracted between 50.6% and 71.6% of the caterpillars present on a shrub. A minor taxonomic bias of the sampling protocol was observed, but appears to be of a simple and predictable nature, and is therefore easy to account for. We did not find any significant influences of daytime. Structure and size of shrubs had a strong influence on sampling results with small and simply structured shrubs being sampled most completely, large and complex shrubs most incompletely in our dataset. Researcher experience did not appear to have an influence on the sampling efficiency or taxonomic composition of samples obtained when we compared caterpillars obtained by standardized sampling with those collected by exhaustive leaf-by-leaf search. Comparison of caterpillar sizes revealed however, that inexperienced field assistants tended to overlook large fractions of the smallest caterpillars entirely. We conclude that our standardized combined

sampling approach is fairly suitable for studies concerning caterpillar communities, especially when resampling of the same shrub individuals is desired.

Keywords

Lepidoptera, *Piper*, beating tray, visual search, sampling efficiency

Introduction

Herbivorous insects are a major fraction of all life on earth (e.g. Price 2002). Their diversity and ecological roles have become a focus of many studies in the last decades. Lepidoptera are one of the largest taxa among this group, with currently approximately 155,000 species described (Pogue 2009). While sampling of adults has been performed in largely identical ways for several decades, standardized sampling of their larvae is less common. Especially in the tropics, where Lepidoptera are both especially diverse and particularly poorly studied, investigation of caterpillar communities and their ecology are still in a very early stage. Projects dealing with caterpillars employ a variety of collection methods such as canopy fogging (e.g. Floren & Linsenmair 2001), complete destructive sampling (e.g. Rodríguez-Castañeda et al. 2010), visual searching (e.g. Novotny et al. 2002), or branch beating (e.g. Mody & Linsenmair 2004). Canopy fogging (Adis et al. 1998) has been widely used to study canopy arthropods, however caterpillars appear to be surprisingly rare in such samples (e.g. Basset 1991, Floren & Linsenmair 2001) and are probably highly underrepresented. Also, with many fogging protocols, only dead specimens are retrieved, making evaluation of their ecological roles impossible. Complete destructive sampling can be expected to yield highly complete samples and allows for feeding trials, but obviously renders resampling of the same plant individual impossible.

Visual search and branch beating are both classic, low-tech, none-invasive sampling techniques for caterpillars. Visual search allows for the recovery of well attached or concealed feeding individuals, and additionally offers the possibility to record behavioral information. Branch beating can on the other hand be expected to be more effective in the recovery of small individuals. Both methods retrieve living caterpillars and therefore allow for successive feeding trials and rearing. However, both methods are only suitable for shrubs, treelets and lower tree branches due to their limitations based on the reach of the field researcher.

We here present a combination of visual search and branch beating as standardized sampling protocol with temporal replications for immature Lepidoptera on shrubs and address various questions concerning the suitability and applicability of this sampling approach for studying caterpillar communities. In particular we aim at testing the following specific hypotheses:

- (1) Samples obtained by our combined standardized protocol retrieve the majority of individuals, but are nevertheless incomplete.
- (2) Sampling efficiency is higher on shrubs with simpler structure (i.e.: fewer, larger, hairless leaves).
- (3) Samples obtained by our protocol are unbiased with regard to higher taxa, feeding guilds, or size of caterpillars.
- (4) Sampling efficiency of the combined standardized protocol is independent of shrub size.
- (5) Sampling efficiency and composition of samples does not differ between collections taken during day and nighttime.
- (6) Samples collected by operators with and without sampling experience are comparable in terms of efficiency and composition.

Methods

Study area

The study was conducted in southern Ecuador (province Zamora-Chinchipec), in the Reserva Biológica San Francisco (RBSF). This is a privately owned nature reserve adjacent to Podocarpus National Park which since 2007 forms part of the UNESCO biosphere reserve “Podocarpus-El Condor“. The study area is located on the eastern slope of the Andes, where intensive ecological research has been conducted since 1997 (Beck et al. 2008a). Caterpillars for the present study were sampled between 1800 and 2000m above sea level, in proximity to the Estación Científica San Francisco (3°58' S, 79°05' W). We collected data in May 2008, December 2008, February to July 2009, and October 2009.

The RBSF area is covered by nearly pristine montane rain forest (Beck et al. 2008b; Homeier et al. 2008). Its moth fauna has been studied intensively since 1999 by light-trapping, offering insight into patterns of moth diversity and community structure at the level of adult stages (e.g. Brehm & Fiedler 2003, Brehm et al. 2003, Fiedler et al. 2008, Hilt &

Fiedler 2008). In addition, life-histories and larval host plant affiliations of geometrid moths have been studied (Brehm 2003, Bodner et al. 2010).

Study organisms

We chose two species of *Piper* for experiments. Neither of them could be formally identified yet, and they are therefore referred to with their tentative names “*Piper* sp. I” and “*Piper* sp. III” (Fig. 5.1). Both species have been shown to harbor a substantial caterpillar community (F. Bodner, unpublished observations), dominated by species belonging to the geometrid genus *Eois*. While both *Piper* species exhibit a shrub-like growth form with maximum sizes usually around 2-3 m (sp. I) and 2-5 m (sp. III), they differ notably in structure and complexity. *Piper* sp. I has many small twigs with many rather small leaves (average leaf size \pm SD: 38.4 ± 5.5 cm²). The undersides of the leaves are covered with thin, short hairs, especially along the leaf venation. *Piper* sp. III has a more simple structure with fewer small twigs. The leaves are larger, tougher, smooth and hairless (average leaf size \pm SD: 128.4 ± 33.7 cm²). Our sampling considered all ectophagous and semi-endophagous caterpillars of any lepidopteran family. Only stem borers and leaf miners were not searched for. Eggs and pupae of Lepidoptera were also recorded, but not included in statistical analyses.

Sampling design

The standardized sampling protocol employed in this study usually consisted of two stages. First shrubs were visually searched for lepidopteran immatures. Afterwards shrubs were beaten over a beating tray, made of 1 m² of white cloth mounted on the frame of an umbrella drop net, to shake further caterpillars off the shrub. This two-staged procedure was chosen to extract a maximum of lepidopteran immatures present on the shrub. Beating usually only retrieves caterpillars, especially those species which more readily drop off the shrub when disturbed or attacked. Visual searching also yields at least a part of the eggs and pupae present as well as those caterpillars which cling tightly to the branches or live as concealed feeders in leaf rolls, webs or alike. During both stages sampling effort was standardized by estimated shrub volume.

Four different experiments were carried out in the course of this study (Table 5.1) to analyze effects of researcher experience, sampling approach, plant species, and time of day when sampling was conducted.



Fig. 5.1: The two focal shrub species (a: *Piper* sp. I; b: *Piper* sp. III) and some of the caterpillar species (c: *Eois* sp. nr. *odatis*, d: species from the *Eois olivacea* complex, e: unidentified noctuid) from this study.

Standardization

We used estimated shrub volume for standardization of sampling effort. From practical reasons sampling effort was not increased linearly with shrub volume, but in steps measured as sampling effort factor (SEF). When tailoring the SEF to shrub size classes, we allowed for a larger range of shrub volumes in the higher categories, whereas for smaller shrubs a more fine grained class division was accepted. This aimed at avoiding excessive sampling effort at the upper end of the range of shrub sizes covered, or unacceptably low effort at the lower end of the size spectrum. This procedure was also implemented to balance against expected higher sampling efficiency for larger shrubs. We expected higher efficiency on larger shrubs because more leaf area can be visually searched simultaneously and more shrub volume can be accessed by individual beats. The SEF increased in the following fashion: 2 for a shrub volume of $\frac{1}{6} \text{ m}^3$, 3 for $\frac{1}{4} \text{ m}^3$ of shrub volume, 4 for $\frac{1}{2} \text{ m}^3$ of shrub volume and +1 for every further $\frac{1}{2} \text{ m}^3$ of shrub volume. For intermediate volumes SEF was adjusted to the nearest 0.5 for calculation of visual search effort only (see below).

Table 5.1: List of experiments conducted to assess the feasibility of our sampling approach as a means of characterizing caterpillar assemblages of shrubs in the montane forest zone of southern Ecuador. Following the standardized sampling protocol, the number of remaining caterpillars present was evaluated by total defoliation of each shrub individual (Table 5.2).

Experiment	carried out by	standardized sampling	shrub species	sampling time	number of shrubs
P1	experienced researcher	beating	<i>Piper</i> sp. I	day only	37
P2	experienced researcher	searching and beating	<i>Piper</i> sp. I	day only	29
P3/I	inexperienced field assistants	searching and beating	<i>Piper</i> sp. I	day and night	50
P3/III	inexperienced field assistants	searching and beating	<i>Piper</i> sp. III	day and night	44

Field work

We selected well accessible shrubs in the forest, mainly along paths, in various sizes from about 0.05 m³ to about 2 m³ volume to assess possible size effects on the efficiency of the employed sampling methods. The field sampling consisted of the following stages:

1. Estimation of shrub volume by rough measurement.
2. Spreading of white sheets of cloth around and below the plant. If necessary surrounding undergrowth was cut down to allow for smoothing of sheets.
3. Visual search of the entire target plant for lepidopteran immatures for 1 × SEF minutes (first stage of standardized sampling).
4. Beating on shrub 1 × SEF times over beating tray which was held underneath the plant (second stage of standardized sampling).
5. Checking of sheets on the ground for caterpillars that had dropped off during search or beating, but had not been caught on the beating tray.
6. Complete leaf-by-leaf defoliation of the entire shrub during which every leaf was checked individually on both sides for lepidopteran immatures.

The first two experiments (P1 and P2) were performed by the first author who has years of experience in collecting and rearing lepidopteran caterpillars (Bodner et al. 2010).

The other two experiments were carried out by undergraduate students without previous experience with the sampling procedure of the experiments. We chose this setup to allow for analysis of effects of previous recorder experience or training on the completeness and comparability of samples obtained.

Lab work and analysis

All caterpillars were photographed in the lab on scaled paper to allow for length measurement. All leaves of every sampled shrub were dried in an oven at 45°C for 72 hours and then weighed as a measure of available foliar biomass. For analysis, we coded caterpillars found during the two stages of the standardized protocol (stages 3 and 4) as $cat_{(ss)}$, those found outside of the standardized sampling protocol (stages 5 and 6) as $cat_{(es)}$ for exhaustive sampling. We calculated sampling efficiency as $\frac{cat_{(ss)}}{cat_{(ss)} + cat_{(es)}}$ for every experiment.

Caterpillars were sorted by higher taxonomic levels (genus *Eois*, other Geometridae, other Macrolepidoptera, ‘microlepidoptera’) and feeding guild affiliation. True herbivores which feed on living *Piper* foliage were contrasted to non-herbivores (viz. feeding on epiphylls, lichens, mosses, or dead plant material). Data were analyzed by evaluation of contingency tables and ANOVAs calculated in Statistica 7.1 (StatSoft 2005).

Results

In total we collected 734 caterpillars from 160 shrubs (total volume: 87.9 m³, total dry leaf mass: 5.19 kg) in the course of the four experiments reported in this study. Of these, 400 were obtained by means of the standardized sampling approach ($cat_{(ss)}$), the remaining 334 were collected from sheets on the ground or during complete leaf-by-leaf defoliation of the shrubs ($cat_{(es)}$). The collected samples consisted mainly of members of the geometrid genus *Eois* (75.4% on *Piper* sp. I, 36.8% on *Piper* sp. III), other geometrid species (8.5% on *Piper* sp. I, 28.4% on *Piper* sp. III) and Noctuoidea (10.5% on *Piper* sp. I, 16.8% on *Piper* sp. III). While most caterpillars, especially the dominant genus *Eois*, were true herbivores (75.5%), a large fraction, notably consisting of other Geometridae and Noctuoidea, belonged to species feeding on dead leaves, lichens and other epiphylls (22.9%), as shown by extensive rearing trials (F. Bodner, unpublished observations). The remaining 1.6% of caterpillars could not be reliably assigned to either guild and were excluded from all analyses based on feeding guild

affiliation. We additionally found 174 eggs and 16 pupae of Lepidoptera, but did not include them in statistical analysis as they were not the focus of the study and their samples can be expected to be far too incomplete even from exhaustive search to allow for any meaningful analysis.

The overall sampling efficiency was 54.5% for all four experiments and 56.4% for those three applying our combined sampling protocol. It ranged from 48.9% to 56.2% on *Piper* sp. I and was therefore similar for the three experiments dealing with this particular shrub species. The two experiments on this shrub species applying our combined sampling protocol (P2 and P3/I) retrieved the majority of caterpillars (50.6% and 56.2%), but only by a very narrow margin (Table 5.2). Sampling of shrub species *Piper* sp. III (experiment P3/III) was more effective with a yield of 71.6%. This was significantly higher ($\text{Chi}^2_{(\text{DF}=1)} = 6.51$, $p < 0.011$) than in experiment P3/I, which was performed on *Piper* sp. I under otherwise identical conditions. Comparison of $\text{cat}_{(\text{ss})}$ and $\text{cat}_{(\text{es})}$ on higher taxonomical levels revealed a significant bias in two of the experiments (P1 and P2), but not so in the remaining two (Table 5.3). The same applies to analyses based on feeding guilds. Detailed inspection of the data shows that in both cases most of the effect was due to the genus *Eois* being underrepresented in $\text{cat}_{(\text{ss})}$. When comparing $\text{cat}_{(\text{ss})}$ and $\text{cat}_{(\text{es})}$ with regard to caterpillar lengths, an overall bias of the standardized sampling protocol towards larger caterpillars becomes evident (Table 5.4). Separate analyses of all experiments confirmed this effect only for P2 (Table 5.4, Fig. 5.2).

Table 5.2: Caterpillars obtained as $\text{cat}_{(\text{ss})}$ and $\text{cat}_{(\text{es})}$ in the different experiments. Mean number of caterpillars per shrub \pm standard deviation are given for both $\text{cat}_{(\text{ss})}$ and $\text{cat}_{(\text{es})}$ for every experiment.

Experiment	$\text{cat}_{(\text{ss})}$	Mean \pm SD	$\text{cat}_{(\text{es})}$	Mean \pm SD	Efficiency
P1	91	2.46 \pm 2.28	95	2.57 \pm 6.47	48.9%
P2	123	4.24 \pm 3.67	120	4.14 \pm 4.54	50.6%
P3/I	118	2.36 \pm 1.72	92	1.84 \pm 1.71	56.2%
P3/III	68	1.55 \pm 1.25	27	0.61 \pm 0.95	71.6%
total	400	2.50 \pm 2.39	334	2.09 \pm 3.96	54.5%

Table 5.3: Comparison of $cat_{(ss)}$ and $cat_{(es)}$ on basis of higher taxa (genus *Eois*, other Geometridae, other Macrolepidoptera, ‘microlepidoptera’) and feeding guilds (herbivores, non-herbivores) by means of Pearson’s Chi².

Experiment	Taxa		Guilds	
	Chi ² (DF = 3)	p	Chi ² (DF = 1)	p
P1	24.20	< 0.00003	21.27	< 0.00001
P2	8.88	< 0.031	8.01	< 0.005
P3/I	2.14	> 0.54	1.71	> 0.19
P3/III	6.01	> 0.11	1.04	> 0.30

Table 5.4: Results of ANOVAs comparing caterpillar lengths of $cat_{(ss)}$ and $cat_{(es)}$ for all experiments (Fig. 5.2). DF: degrees of freedom.

Experiment	DF Model	DF Residual	F	p
all	1	729	15.66	< 0.0001
P1	1	183	0.43	> 0.51
P2	1	240	20.11	< 0.0001
P3/I	1	207	2.16	> 0.14
P3/III	1	93	0.97	> 0.32

To analyze possible effects of shrub size on sampling efficiency, we combined all available data from the experiments on *Piper* sp. I (P1, P2 and P3/I) and assigned all shrubs to size categories by their dry leaf mass. We chose class borders in a fashion to distribute total dry leaf mass of shrubs over all categories as evenly as possible. Intermediate shrubs which did not clearly fall into one category were assigned to the one with lower total number of caterpillars. To rule out chance effects of category delimitations on the results, we performed this calculation three times, accepting 6, 7 and 8 categories, respectively. In all three cases correlation analyses of the overall sampling efficiency within each category versus the mean dry leaf mass of all its shrubs showed a significantly negative effect of shrub size on sampling efficiency (Table 5.5, Fig. 5.3).

We set up contingency tables to address the question whether samples collected during day and night differ in efficiency and composition. No significant effects of collection time were observed for either sampling efficiency or sample composition on levels of higher taxa or feeding guilds (Chi²(DF=1) < 6.68, p > 0.06).

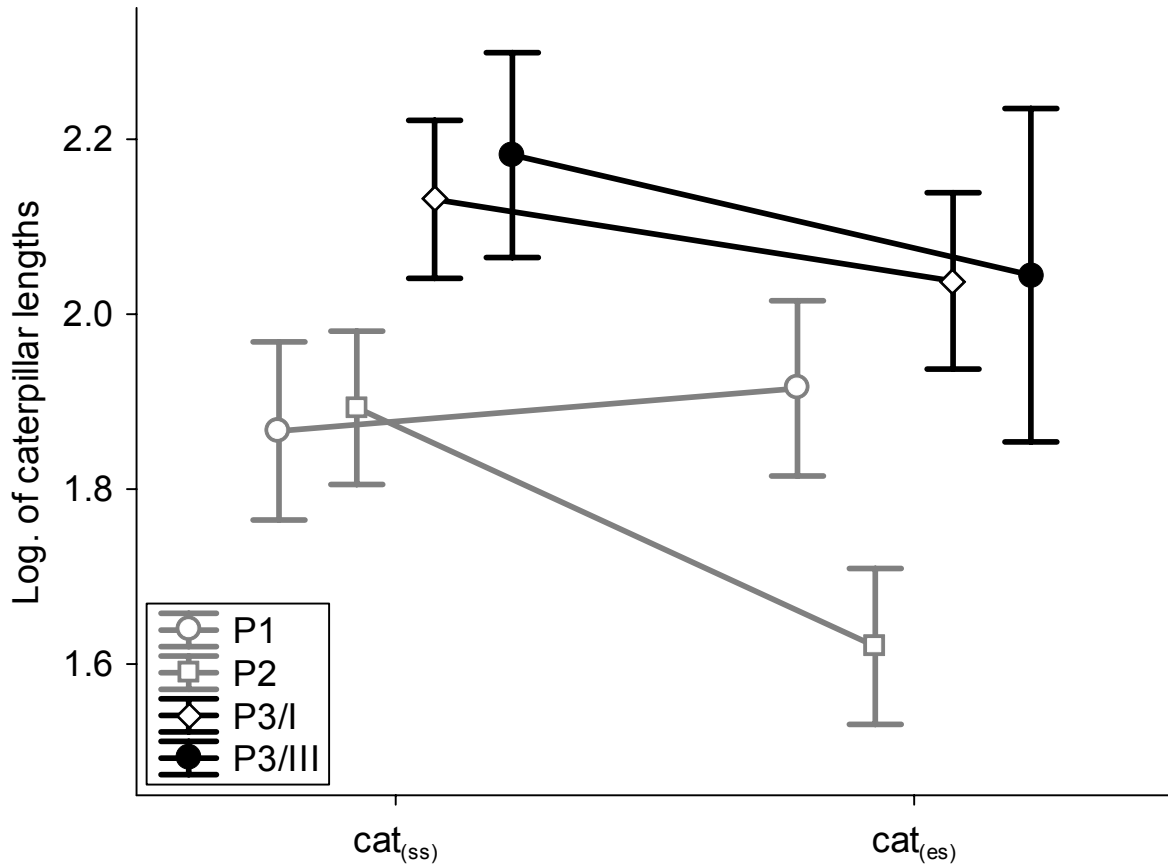


Fig. 5.2: Average caterpillar lengths (log transformed) retrieved during the four experiments, segregated into those sampled by the standardized protocol ($cat_{(ss)}$) or during complete defoliation ($cat_{(es)}$). Whiskers are 95% confidence intervals. Grey: experiments by experienced researcher, black: experiments by field assistants. Empty symbols: *Piper* sp. I; filled symbols: *Piper* sp. III. Significance of experiment \times sampling group interaction (two-way ANOVA): $F_{(4, 723)} = 5.5249$, $p = 0.00022$.

Comparison of experiments P2 and P3/I with regard to the effect of recorder experience on sampling results did not reveal significant differences in sampling efficiency, or taxon or guild composition. This was true both for $cat_{(ss)}$ and for the whole dataset ($cat_{(ss)} + cat_{(es)}$) ($p \geq 0.27$). However, average size of caterpillars obtained in total was significantly smaller ($F_{(1, 436)} = 54.244$, $p < 0.0001$) when gathered by an experienced researcher (mean \pm S.D. = 6.55 ± 3.30 mm) as compared to data collected by inexperienced field assistants (8.87 ± 3.91 mm; Fig. 5.4).

Table 5.5: Correlations of sampling efficiency with mean foliar dry weight of shrubs per category for combined data from experiments with *Piper* sp. I (P1, P2 and P3/I), split into 6 (Q6; Fig. 5.3), 7 (Q7) and 8 (Q8) categories, respectively.

	r	r ²	t	p
Q6	-0.9421	0.8875	5.617	0.0049
Q7	-0.8565	0.7336	3.710	0.0138
Q8	-0.7373	0.5436	2.673	0.0369

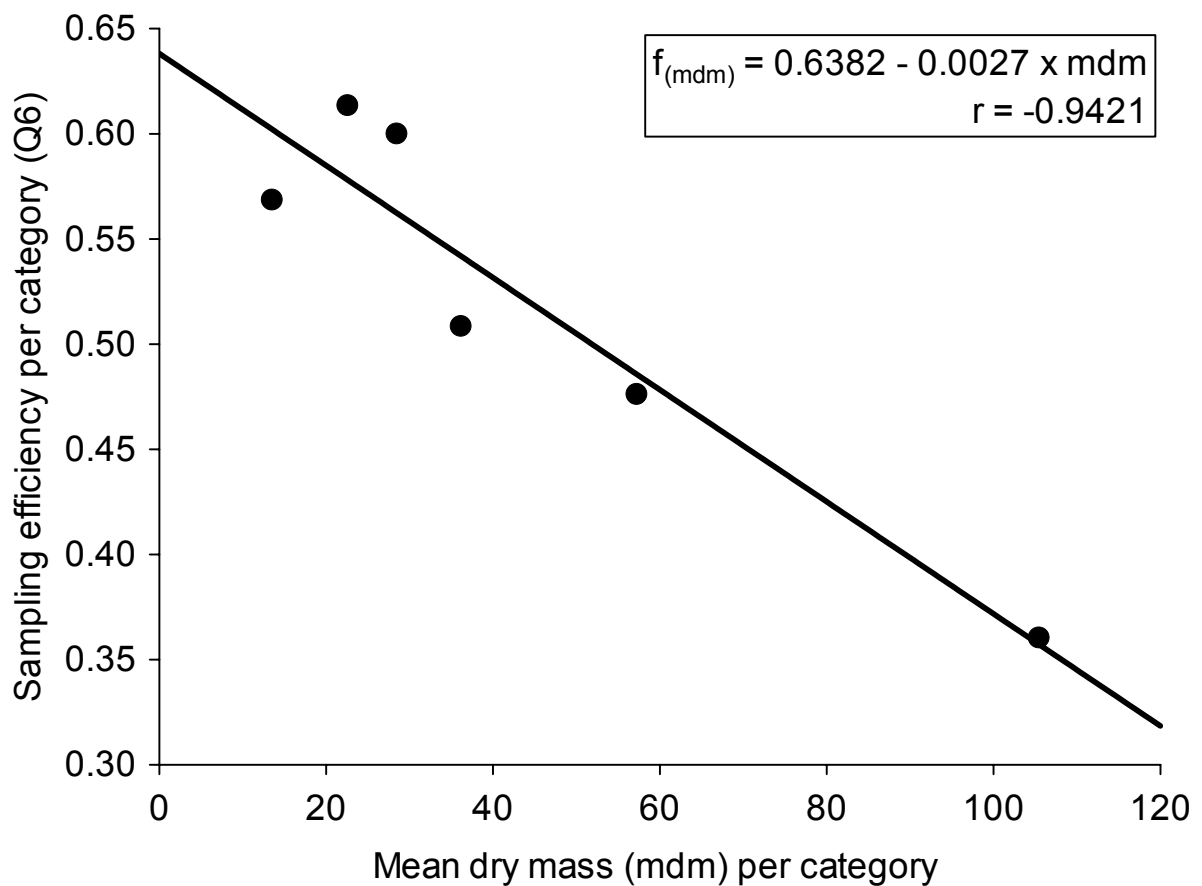


Fig. 5.3: Relationship between sampling efficiency quotient and mean dry mass of shrubs for combined data of experiments P1, P2 and P3/I (*Piper* sp. I) split into six shrub size classes (statistical evaluation see Table 5.5). Regression line fitted by ordinary least squares regression.

Discussion

Even though studies of caterpillar populations and assemblages frequently make use of both branch-beating (e.g.: Yela & Lawton 1997, Mody & Linsenmair 2004, Markó et al. 2006) and visual searching / hand collecting (e.g. Novotny et al. 2006, Dyer et al. 2007) methods, studies that try to quantitatively assess their overall efficiency and possible biases are strikingly rare. Sampling of two species of *Piper* shrubs in the montane forest zone of southern Ecuador turned out to retrieve only slightly more than 50% of the caterpillars that were present on shrubs of *Piper* sp. I. Considering that especially some very small caterpillars will likely have been overlooked even during our high intensity leaf-by-leaf search, the real efficiency can probably be expected to be a bit lower and may be below 50% even for the combined sampling protocol. In the light of these results our hypothesis (1) that sampling retrieves the majority of caterpillars on a shrub can at best be cautiously accepted. Efficiency of sampling on simpler structured *Piper* sp. III was significantly higher, as predicted by hypothesis (2). More detailed analysis revealed that the increase in overall efficiency on this shrub species was almost entirely due to visual search. The fraction of caterpillars recovered by beating was also slightly higher, even though the fraction of caterpillars still remaining on the shrub at this stage is smaller, revealing that beating efficiency has also increased notably. While higher search efficiency is probably due to lower availability of hiding places and less visual distraction of the researcher, higher beating efficiency is likely due to the smoother leaf surface of *Piper* sp. III offering a less strong foothold to caterpillars.

Comparison of cat(ss) and cat(es) on higher taxonomical levels revealed a significant bias in two of the experiments, especially in P1 where only sampling by beating was performed. In both cases the bias was almost entirely due to caterpillars from the genus *Eois* being underrepresented in cat(ss). *Eois* species are small-sized and usually very specialized herbivores. The limited data presently available indicates that many species may even be limited to a single host plant species (e.g. Dyer et al. 2010, Strutzenberger et al. 2010). This could explain their reluctance to drop off the plant, since they are unlikely to find a suitable host plant again. Such a behavior would render them underrepresented in samples acquired by beating. Identification of the individual caterpillar specimens did not indicate any entirely new *Eois* species that would have been acquired only by subsequent defoliation (even though species accumulation of *Eois* in the study area is far from being complete: Strutzenberger et al. 2011). Consequently, although hypothesis (3) has to be discarded, the sampling bias is of a predictable nature and in a small range that appears to be acceptable, since no herbivore species were overlooked.

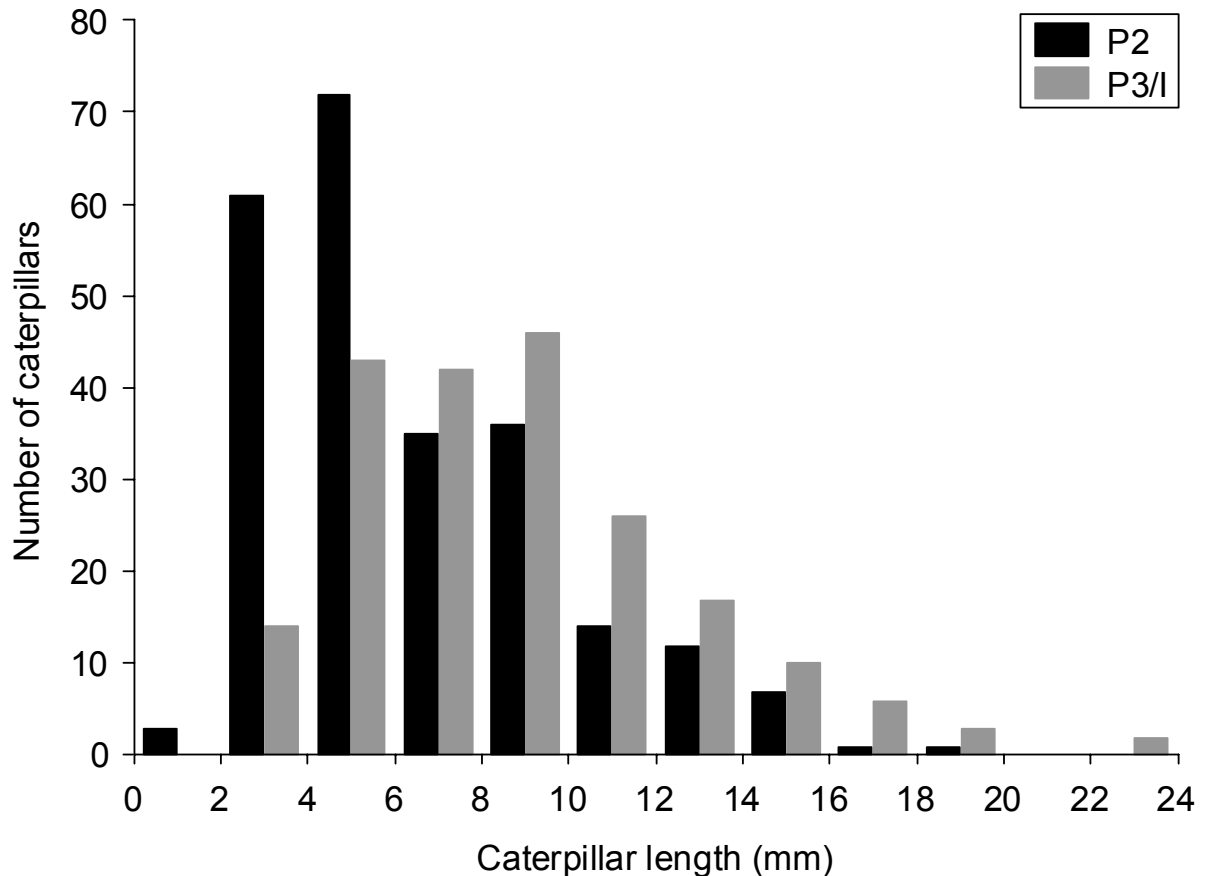


Fig. 5.4: Frequency distributions of caterpillar lengths for experiments P2 (performed by an experienced observer, red bars) and P3/I (performed by inexperienced field assistants, blue bars) on *Piper* sp. I. Mean sizes of retrieved caterpillars differed significantly (see text). Note the difference between the experiments in the three lowest size classes.

Caterpillar assemblages on larger shrubs were sampled less completely as compared to small shrubs, falsifying hypothesis (4). We had not increased sampling effort in linear fashion with shrub size since we had expected higher per-effort-efficiency for larger shrubs, i.e. more shrub biomass can be sampled by a single beat or searched visually by turning one branch. Evidently this expected effect has either been overestimated or canceled out at least partly by other effects. One possible negative size dependent influence is e.g. loss of recorder focus when visually searching larger numbers of leaves simultaneously. Beating efficiency on the other hand could be negatively influenced e.g. by tighter packing of branches and leaves, resulting in caterpillars shaken off from one leaf to land on another instead of the beating tray.

Samples taken under otherwise identical conditions during day and night did not significantly differ in any aspect, confirming hypothesis (5). This indicates that there is no reason to assume substantial day-to-night migrations of caterpillars on the sampled shrubs.

Therefore caterpillar assemblages sampled during daytime should not be biased, e.g. due to missing nocturnal species. This confirms that the standardized sampling protocol is suitable for assessments irrespective of the time of day. However, we do not expect this to be necessarily true for other plant species, where diurnal migration of caterpillars might play a more important role (see e.g. Huogue 1993).

Samples gathered by inexperienced field assistants did not significantly differ on a taxonomical basis from those taken by an experienced researcher and are therefore comparable and can be combined for analysis. Sampling efficiency was even calculated to be slightly higher for inexperienced assistants. This appears surprising at first glance, since one would suspect that experience in searching for caterpillars increases the number of caterpillars found during the same time during visual search at least. Closer examination of the size distribution of caterpillars collected during the experiments P2 and P3/I reveals, however, that the average size of all caterpillars (cat(ss) and cat(es) combined) was significantly larger on shrubs sampled by recorders without previous experience. This indicates that a larger fraction of small caterpillars was overlooked by inexperienced field assistants even during intensive leaf-by-leaf search. This also offers an explanation why the average number of caterpillars per shrub in both cat(ss) and even more so in cat(es) is lowest in experiment P3/I of the three experiments dealing with the plant species *Piper* sp. I. This leads to the conclusion that the efficiency of P3/I is particularly overestimated by the raw numbers and that the real efficiency is probably considerably lower for inexperienced field assistants as compared to experienced researchers.

Conclusions

We conclude that the two-staged sampling protocol presented in this study retrieved about half of the caterpillars which were in fact present on the sampled *Piper* shrubs. While a taxonomic bias existed against well attached host plant specialists, this bias was smaller than with beating alone and of a predictable nature. Overall sampling efficiency was only slightly increased by adding visual search to beating, possibly because the slight shaking of the shrub, which is unavoidable during search, caused caterpillars to hold on more tightly. However, besides the reduction in taxonomic bias, visual search also allows for the gathering of at least some part of the eggs, cocoons and pupae that would be completely overlooked by beating alone. Moreover, observations during visual research have the potential to yield information on behavior and functional connections between caterpillars and plants that are lost after

beating. This includes the ability to distinguish between gregarious and solitary caterpillars. Sampling intensity has to be chosen in consideration of necessary sampling efficiency, but also with consideration of the size range of shrubs to be studied, lest sampling effort becomes unreasonably small or large at either end of the range. Linear increase of sampling effort might however lead to more homogenous sampling efficiency across shrub sizes.

Overall we consider the presented two-stage sampling protocol to be fairly suitable for studying caterpillar communities on shrubs, especially when resampling of the same shrub individuals in a time series is desired. At the same time the method is minimally invasive, since only the caterpillars present on the shrub at that time are affected and non-target animals can be freed again immediately.

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6. Abundance and Guild Structure of Caterpillars (Lepidoptera) on Shrubs in the Montane Forest Zone in Southern Ecuador

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Abstract

We investigated caterpillar communities on 16 shrub species in the families Piperaceae and Asteraceae in the montane forest zone of southern Ecuador. For each plant species, 7 to 24 (total: 194) replicate individuals were surveyed for lepidopteran immatures every six weeks during two field campaigns of in total 16 months in the years 2007 to 2009. More than 18,000 lepidopteran early instars from at least 17 families were recorded and their feeding habits confirmed by subsequent rearing. Samples were dominated by gregarious *Altinote dicaeus albofasciata* (Nymphalidae) larvae on *Erato polymnioides* (Asteraceae). After down-weighting of gregarious early instars, Geometridae were the prevalent Lepidoptera family, accounting for 62% of all caterpillars encountered. Caterpillars that do not feed on living tissues of the sampled shrub species (termed ‘non-herbivores’) made up a considerable fraction of caterpillar counts on some shrub species (up to 80%). Approximately two thirds of the caterpillars were ectophagous leaf feeders. Overall mean herbivore abundance per shrub volume differed hardly between Asteraceae and Piperaceae, indicating that both families are equally suited for consumption by caterpillars. Yet, caterpillar densities varied strongly even between closely related shrub species. This variation was largely restricted to true herbivores. Concealed feeders (in leaf rolls or folds, 6.0% of records) and flower feeders (2.3%, Asteraceae only) were unexpectedly rare.

Keywords

Herbivores, feeding guilds, non-herbivorous larvae, tropical mountain forest, Asteraceae, Piperaceae

Introduction

Interactions of herbivores and their host plants are of profound ecological interest. Herbivorous insects comprise an important fraction of global biodiversity (Price 2002). Just like their hosts, they are especially diverse in the tropics. Their ecological importance may even be higher in the Neotropics as opposed to other tropical realms, since large herbivorous mammals are virtually absent here (Cristoffer & Peres 2003).

Herbivorous insects and their degree of host specialization have been at the very center of the debate on the magnitude of the total number of species on Earth (e.g. Erwin 1982, Basset et al. 1996, Ødegaard 2000, Hamilton et al. 2010). This debate is tightly linked with ongoing discussions about the mechanisms behind their enormous diversity in tropical regions (e.g. Novotny et al. 2006, as opposed to: Dyer et al. 2007).

Within the herbivorous arthropods, the species-rich Lepidoptera (moths and butterflies) form an important insect order. Caterpillars were reported to be only minor contributors to, or almost absent from, arthropod communities on tropical trees in canopy fogging studies of the 1980s and 1990s (e.g. Basset 1991, Floren & Linsenmair 2001). During the last decade, however, they have emerged as key group in studies on tropical herbivore communities. Novotny et al. (2006) found immature Lepidoptera to outrank any other taxon in their large dataset on herbivores from tropical forests in Papua New Guinea and temperate forests in central Europe. The discrepancy between those findings may result from a shift in sampling methods from insecticidal fogging to hand collecting, which appears to be a more suitable approach for caterpillars.

While the analysis of species-rich insect herbivore communities in tropical moist forests has made substantial progress in recent years (Novotny & Basset 2005), available studies are partially biased with regard to the target regions, plant functional types, and approaches. (1) Most data on food webs between tropical plants and their herbivorous arthropods still stem from lowland sites. Montane forests have received less attention (but see Miller & Dyer 2009), despite their, in parts, enormous species diversity. (2) Similarly, most studies, especially those applying fogging methods, focused on the canopy fauna of trees (e.g.

Basset 1991, Floren & Linsenmair 2001), while understory shrubs (e.g. Rodríguez-Castañeda et al. 2010) were less commonly studied. (3) Also, while recent studies employ feeding trials to identify ‘tourist species’ (Novotny & Basset 2000), the occurrence of ‘unusual’ feeding habits among Lepidoptera (e.g. Powell et al. 1999) appears to have received less consideration.

We here present results on caterpillar communities of woody shrubs from a tropical montane rain forest in southern Ecuador. The study area, the Reserva Biológica San Francisco (RBSF), has been the target of extensive interdisciplinary ecological studies during the last decade (Beck et al. 2008a), including analyses of moth communities along altitudinal and succession gradients (Fiedler et al. 2008). These studies identified the region as a global hotspot of geometrid diversity (Brehm et al. 2005). For a still small, but ever growing fraction of moths also their functional relationships towards host plants become elucidated (Brehm 2003, Bodner et al. 2010a, Strutzenberger et al. 2010). Against this background this paper aims at testing the following hypotheses:

- (a) Density of caterpillars is more similar on shrub species within one family than between families.
- (b) Density of herbivorous caterpillars is lower on shrubs of the family Piperaceae than on those of the family Asteraceae, since plants in the genus *Piper* are known to be often chemically well defended (Bernard et al. 1995, Dyer & Palmer 2004).
- (c) Caterpillar communities on all shrubs generally consist of herbivores which are trophically directly associated with living tissues of the shrub itself.

Methods

Study area

Data were collected in the Reserva Biológica San Francisco (RBSF), a privately owned nature reserve adjacent to Podocarpus National Park in southern Ecuador (province Zamora-Chinche). The study area, located on the eastern slope of the Andes, has been the target of intensive ecological research since 1997 (Beck et al. 2008a). Caterpillar sampling was performed between 1800 and 2100m above sea level, in proximity to the Estación Científica San Francisco (3°58' S, 79°05' W). Sampling periods were from August 2007 to March 2008 and from December 2008 to June 2009.

RBSF is mostly covered by nearly pristine montane rain forest (Beck et al. 2008b; Homeier et al. 2008). Its moth fauna has been studied intensively since 1999 by light-trapping, offering insight into patterns of moth diversity and community structure at the level of adult stages (e.g. Brehm & Fiedler 2003, Brehm et al. 2003, Fiedler et. al. 2008, Hilt & Fiedler 2008).

Study organisms

We chose representatives of two plant families for investigation, to compare community patterns of associated caterpillars across a habitat disturbance gradient. In both cases the major criteria for selection of target species were shrub-like growth form, availability of a sufficient number of replicate individuals, and their accessibility. For the open, disturbed areas, three species from different genera of the family Asteraceae were selected. These three species (*Ageratina dendroides*, *Baccharis latifolia* and *Erato polymnioides*) are highly abundant in open and disturbed habitats in the RBSF (Beck et al. 2008c). While *B. latifolia* is confined to the more heavily disturbed open areas, *A. dendroides* and *E. polymnioides* were also, though rarely, encountered in disturbed forest habitats. To balance against the lower number of suitable species within Asteraceae in open habitats, about twice as many (21 to 24) individuals per species were sampled as compared to the Piperaceae species (7-12).

For investigation of caterpillar communities within the closed-canopy forest, 13 species of *Piper* (Piperaceae) were selected. *Piper* is the single most species rich (Homeier & Werner 2007) and abundant (own observations; see also Homeier et al. 2008) genus of understory shrubs (but including also some larger trees) in the RBSF. In the study area the majority of *Piper* species preferentially grow in moist areas like ravine forests, while comparatively few occur in ridge forest (own observations; see also Homeier et al. 2008). *Piper* species are the major host plants of the diverse and abundant geometrid genus *Eois* which alone comprises about 10% of geometrid moth individuals attracted to light traps in the study area (Brehm et al. 2005, in press).

Species identification of *Piper* is difficult even for specialists. Their taxonomy and systematics have undergone major changes in recent years (Jaramillo & Manos 2001, Wanke et al. 2007, Smith et al. 2008). So far, 6 of the 13 species from this study have been formally identified, with the remaining species being tentatively referred to by morphospecies numbers (Table 6.1). The only *Piper* species regularly encountered in heavily disturbed, open or half-open areas in the RBSF was *P. carpunya*. The remaining 12 species were confined to closed forest of various succession stages.

Table 6.1: Totals of recorded Lepidoptera immatures (caterpillar groups and egg clutches down-weighted to their cubic root) of different feeding guilds for the 16 shrub species of this study. Cumulative volume: the sum of the volume estimates of all sampled shrubs over all sampling events. **n:** number of shrub individuals.

Shrub species	n	Non-herbivores	Flori-vores	Ecto-phagous folivores	Semi-endo-phagous folivores	Cumulative volume (m ³)
<i>Ageratina dendroides</i> (Spreng.) R.M.King & H.Rob.	21	49	38	65	25	161.57
<i>Baccharis latifolia</i> (Ruiz & Pav.) Pers.	21	47.6	51	679.5	110	201.92
<i>Erato polymnioides</i> DC.	24	49	13	591.4	15	119.38
<i>Piper arboreum</i> Aubl.	10	68	-	57.5	6	47.78
<i>Piper carpunya</i> Ruiz & Pav.	7	40	-	309	4	29.98
<i>Piper densiciliatum</i> Yunck.	10	22.8	-	18	8	14.36
<i>Piper obliquum</i> Ruiz & Pav.	10	30.5	-	61.0	1	31.59
<i>Piper perareolatum</i> C. DC.	10	54	-	123.0	10	47.84
<i>Piper subscutatum</i> C. DC.	10	99	-	11	16	80.55
<i>Piper</i> sp. I	11	134.8	-	581	11	96.78
<i>Piper</i> sp. III	10	117.4	-	176.4	21	80.11
<i>Piper</i> sp. V	10	87.1	-	112	4	62.53
<i>Piper</i> sp. VIII	12	63.2	-	19	6	48.24
<i>Piper</i> sp. IX	9	40	-	47	9	33.23
<i>Piper</i> sp. XII	8	19	-	150	7.6	19.82
<i>Piper</i> sp. XV	11	57	-	6	6	37.98

In total we surveyed 194 shrub individuals from 16 species (Table 6.1). Not all of them were sampled throughout the entire study. Some died off or were destroyed by falling trees or flooding, while others were only selected later in the project to replace losses.

All immatures of any Lepidoptera family encountered during sampling were collected. The only exceptions were leaf miners, which were rare and require much effort to rear at high losses (own observations), and stem borers, which cannot be sampled without destroying the target plant, making resampling impossible.

Field and lab work

Lepidopteran preimaginal stages (mainly caterpillars, but also eggs or pupae if these were found) were collected by means of a two staged sampling approach. This consisted of first visually screening the target shrub and secondly beating the shrub with a wooden stick over a white sheet of 1x1 m². For details on the applied methodology see Bodner et al. (2010b). Plant beating (e.g. Southwood & Henderson 2000, Leather 2005) is a simple, yet efficient and non-invasive technique for the sampling of insects on shrubs and low branches. It yields unharmed specimens suitable for feeding trials, while also keeping damage to the plant to a minimum, allowing for multiple resampling efforts at the same plant individuals. Sampling effort was standardized by an estimation of the shrub's crown volume. This estimation was obtained for every shrub individual just before each sampling event. For statistical analysis, estimates were later corrected by means of a calibration curve of visual estimations vs. more exact measurements.

All collected specimens were subsequently reared in the lab in plastic boxes lined with damp paper towels to provide constant high air humidity. Caterpillars that did not immediately accept leaves or flowers of the shrub they originated from were first additionally offered dead leaves, foliose lichens and leaves covered with epiphyllic lichens and algae. If those were not accepted either, leaves from various other plants growing either in the close vicinity of the target shrub or known to be accepted by many generalist caterpillar species were offered as alternative. Caterpillars were kept in the lab until death or emergence of either the adult moth or parasitoids.

Data analysis

Caterpillars were assigned to four feeding guilds based on field and lab observations. Individuals for which no observations were available (e.g. due to early death or immediate pupation) were assigned to feeding guilds based on observations of conspecifics. If assignment to a feeding guild was not possible, caterpillars were scored as strays and discarded from further analyses.

Feeding guilds consisted of (a) ectophagous folivores, (b) semi-endophagous folivores (i.e. feeding inside a rolled or folded leaf), and (c) florivores. These three were combined to the guild of "herbivores" (i.e. those that directly feed on living biomass of their host shrub) for most analyses.

Caterpillars that were observed to feed on dead leaves, foliose lichens, or epiphyllic lichens, mosses or algae were assigned to the guild of (d) "non-herbivores". This term was

chosen to emphasize the lack of direct trophic interaction between the caterpillar and the living biomass of the target shrub. Some caterpillars were found to feed on dead leaves, foliose lichens or epiphylls in their early instars, but switched to feeding on living plant tissue in latter instars. In statistical analysis these were treated as herbivores on all shrub species where this switch in trophic connection could be confirmed. This was done to reflect their ecological role, as caterpillars take up far more biomass in later than in early instars.

Egg clutches and caterpillar groups were counted, but their individual numbers were subsequently down-weighted to their cubic root. The reasoning for this was (a) their overrepresentation: egg clutches and large larval groups are comparatively easy to find, while solitary early instars are far more cryptic; and (b) raw numbers were overstating their apparent ecological importance. For example, in the case of *Altinote dicaeus albofasciata* mortality of early instars is excessive and later instars did not nearly show up at comparable relative abundances in the dataset (own observations). Down-weighting to cubic root transformed the average values for egg clutches and caterpillar groups of *A. dicaeus*, the most prominent case of gregarious caterpillars, to values similar to counts of remaining caterpillars at early post-gregarious instars of the same species.

For variance based statistical analyses, caterpillar counts and shrub volumes were log and root transformed to improve normality and subsequently standardized to a mean of zero and a variance of one. Cumulative volume (the sum of volume estimates at all sampling events for every shrub, Table 6.1) was used as covariate in these analyses to account for the obvious effect of a shrub's size on its total number of caterpillars. We then calculated one-way and two-way ANCOVAs to analyze differences in caterpillar densities on shrub species and family level. All analyses were performed using Statistica 7.1 (StatSoft Inc. 2005), except for calculation of Fisher's *z* as a measure of effect size, which was performed by use of the online Meta-Analysis Calculator (Lyons & Morris 2010).

Results

In total, 18,890 preimaginal specimens of Lepidoptera (8,929 caterpillars, 9,885 eggs, and 76 pupae) were collected in the course of this study. Of these, 477 (2.5%; equivalent to 7.5% of the dataset after down-weighting of gregarious immatures) were excluded from the dataset since no trophic links to the target shrubs or their epiphylls could be established with sufficient certainty. In all likelihood these larvae or pupae were strays from nearby plants. The majority (13,739) of the remaining data set was made up of caterpillar groups (109 groups

with 4,692 individuals) and egg clutches (43 clutches with 9,047 eggs) of gregarious *Altinote dicaeus albofasciata* on *Erato polymnioides*. After down-weighting of groups, the dataset comprised 92.6% caterpillars, 6.7% eggs and 0.6% pupae. All subsequent analyses are based on these standardized counts.

Composition of caterpillar communities at the Lepidopteran family level showed pronounced differences (Pearson's $\chi^2_{9df} = 1173.76$, $p < 0.00001$; only families with > 10 individuals) when comparing sampled shrubs of Asteraceae and Piperaceae (Fig. 6.1). While Geometridae were the most prominent group on both plant families, their contribution to the total community was far greater on Piperaceae. Shrubs of the genus *Piper* are known to be the host plant for many representatives of the speciose and abundant geometrid genus *Eois*. This was confirmed in this study, where *Eois* contributed 60.2% of standardized counts on *Piper* shrubs. *A. dicaeus* still made up the second largest fraction to the Asteraceae caterpillar communities after down-weighting and accounted for 76.7% of the dataset on *E. polymnioides* (97.3% before down-weighting).

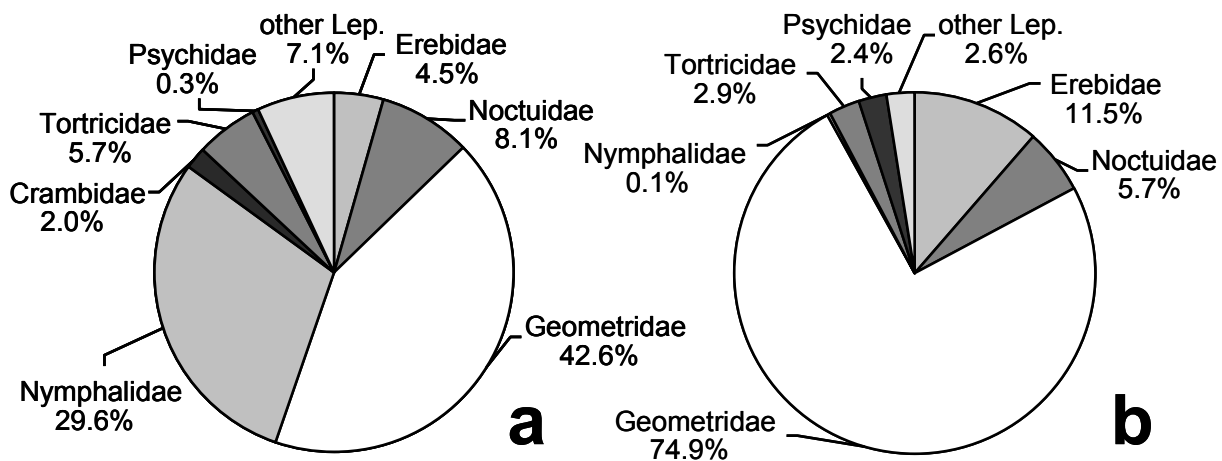


Fig. 6.1: Relative fractions of Lepidoptera families on all shrubs of Asteraceae (a) and Piperaceae (b). Nymphalidae on Asteraceae consists entirely of gregarious *Altinote dicaeus* caterpillars and egg clutches. ‘Other Lep.’ contains representatives of the Apatelodidae, Hesperidae, Limacodidae, Lycaenidae, Megalopygidae, Pterophoridae, Riodinidae, Thyrididae and specimens tentatively identified as Bucculatricidae and Gelechiidae, as well as a number of unidentified specimens.

In total, non-herbivores made up for 22.5% of the standardized dataset, with a maximum of up to 80% on individual plant species (e.g. *P. subscutatum*). Herbivores consisted mainly of ectophagous folivores (67.3% of the whole dataset) and some (6.0%) semi-endophagous folivores (i.e. feeding in leaf rolls or folds). Florivores were only encountered on Asteraceae and contributed a mere 2.3% to the dataset (Table 6.1). A further

1.9% of caterpillars were found to feed on epiphylls and foliose lichens in their early instars, but switched to feeding on leaves in later instars.

Total caterpillar counts per shrub volume differed strongly between individual plant species, especially within the genus *Piper* (Figs. 6.2, 6.3), but did not vary significantly between the two plant families ($p > 0.41$) in one-way ANCOVA. When caterpillar communities were split into herbivore and non-herbivore guilds (Fig. 6.4) and analyzed in two-way ANCOVA with guild and shrub family as independent variables and cumulative shrub volume as covariate, both categorical predictors achieved significant values. Feeding guild had the more powerful influence, but shrub family also was clearly significant (Table 6.2; Fig. 6.5). In total, this statistical model explained 48.2% of the variation in standardized caterpillar counts.

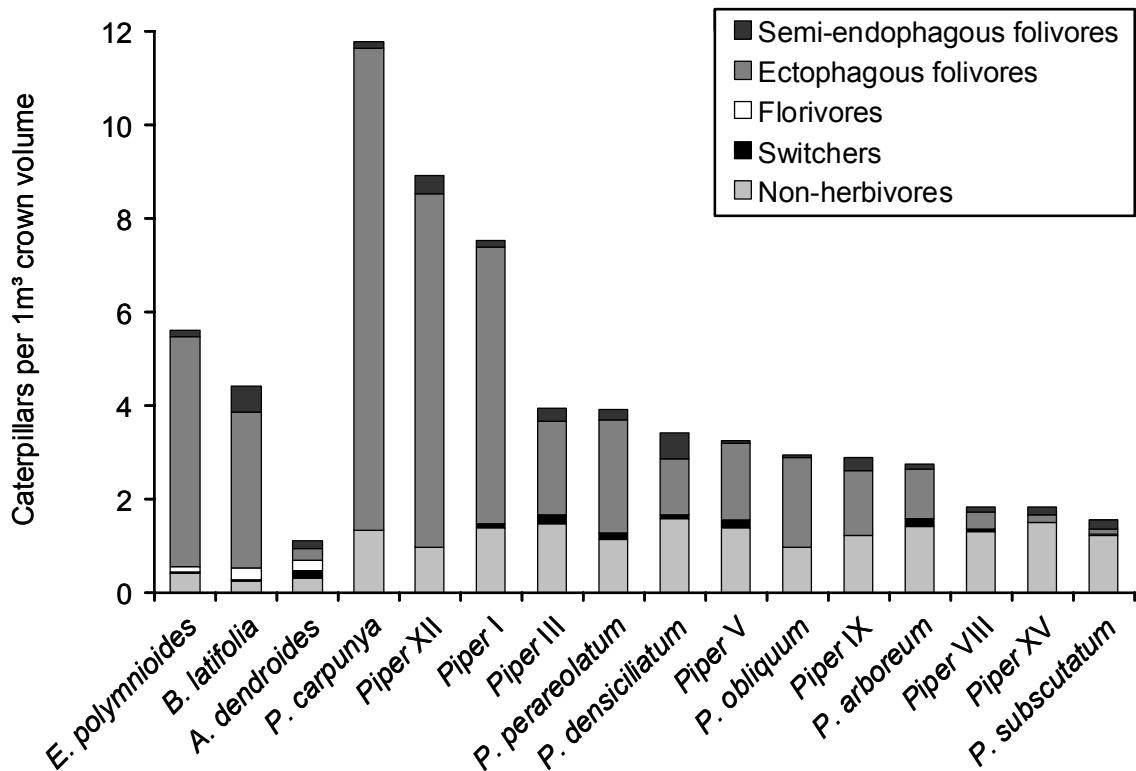


Fig. 6.2: Average caterpillar counts per m³ shrub volume for the different shrub species, split into feeding guilds (Table 6.1).

When analyzing the explanatory value of shrub family and shrub species (separately for Asteraceae and Piperaceae) for the abundance of both main guilds, density of herbivores

was best explained by shrub species, and density of non-herbivores only by shrub family (Table 6.3). While shrub family was also moderately significant when used to explain variation in herbivores, the effect was much smaller than on non-herbivores. Non-herbivore densities increased more strongly with shrub volume on Piperaceae (effect size: $z = 0.861$) than on Asteraceae ($z = 0.571$). For herbivore densities, the effect was intermediate and more similar between the families (Piperaceae: $z = 0.818$; Asteraceae: $z = 0.686$).

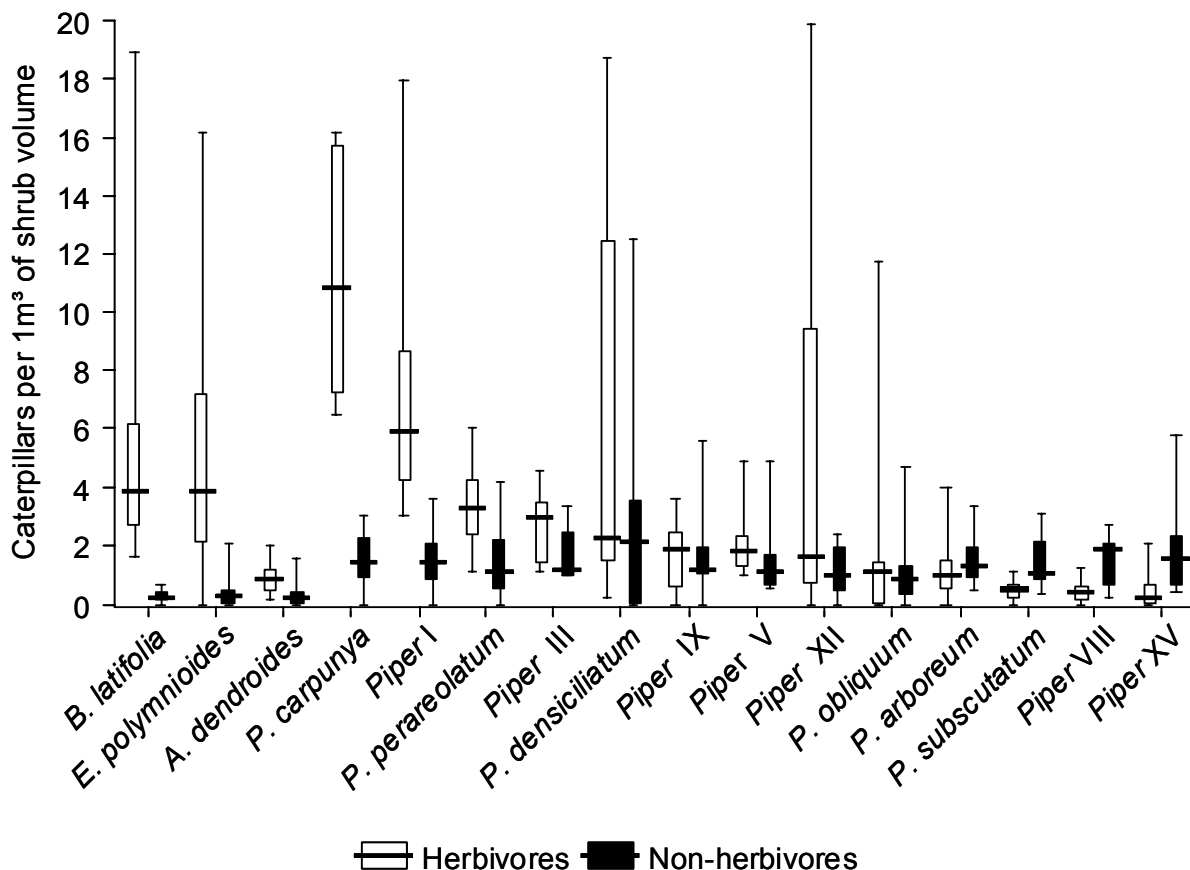


Fig. 6.3: Density (caterpillars per m³ shrub volume) of herbivorous (open) and non-herbivorous (filled) caterpillars on the sampled shrub species. Squares – median values, boxes – quartiles of each series. Whiskers – total range of values.

Discussion

The studied shrub species in the two families Piperaceae and Asteraceae harbored a rich and abundant caterpillar fauna. The large fraction of Geometridae among the caterpillar communities of both shrub families matches well with the high abundance of geometrid adults in Andean mountain forests (Brehm et al. 2005, Beck et al. 2011, personal observations). The genus *Eois* reaches high densities in forest sites around 2000 m elevation (Brehm & Fiedler

2005), where shrubs of the genus *Piper*, the larval host plant of many of its species (e.g. Dyer & Palmer 2004; Strutzenberger et al. 2010), abound (personal observation). *Eois* immatures contributed the majority (60.2%) to the Lepidopteran fauna on *Piper* observed in this study, matching with their reported dominance in *Piper* herbivore communities from other studies (e.g. Connahs et al. 2009, Rodríguez-Castañeda et al. 2010). On Asteraceae, the dominant geometrid was *Microxydia* sp. near *ruficomma* on *Baccharis latifolia* (17.8% of communities on Asteraceae, 34.8% on *B. latifolia*) followed by *Melanolophia reducta meridiana* and *Sabulodes thermidora*.

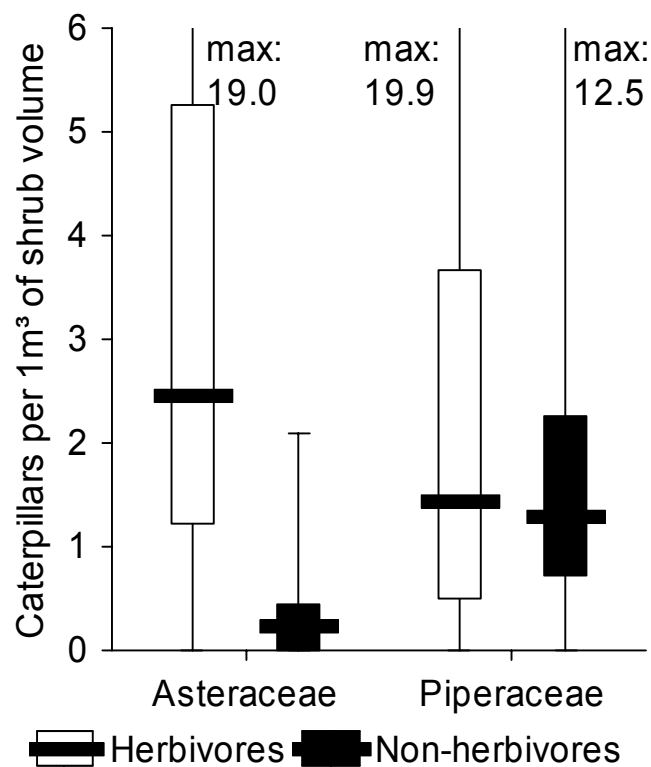


Fig. 6.4: Density (caterpillars per m³ shrub volume) of herbivorous (open) and non-herbivorous (filled) caterpillars for both sampled shrub families. Bars – median values, boxes – quartiles of each series. Whiskers – total range of values.

In contrast, the comparatively small fraction of Noctuoidea (Noctuidae and Erebidae sensu Zahiri et al. 2011) in the samples was less expected. This superfamily is very diverse and abundant globally as well as in the study area (personal observations, see Hilt & Fiedler 2005 for Erebidae: Arctiinae). Noctuidae on *Piper* were entirely, and Erebidae on both plant families to a very large part, members of the non-herbivorous guild. We suppose that chemical defenses render the studied *Piper* species undesirable hosts for many herbivores

apart from *Eois*. Methodological artifacts (e.g. a bias to increased representation of loopers in beating samples) can largely be ruled out. The two-staged sampling approach retrieved the majority of caterpillars on shrubs, as shown by complete destructive sampling in a number of test cases, and did not appear to have any substantial taxonomic biases (Bodner et al. 2010b). Similarly, we can rule out daily migration of caterpillars between feeding and resting places (e.g. Hogue 1993), since comparisons of day- and night-sampling on two *Piper* species did not indicate any pronounced day-to-night cycle in any taxa (Bodner et al. 2010b).

Table 6.2: Results of two way ANCOVAs for density of caterpillars across feeding guilds (herbivores vs. non-herbivores) and shrub families with cumulative shrub volume as covariate. **DF:** Degrees of Freedom. **MS:** mean of squares. **R²_{adj}** of total model: 0.482.

Effect	DF	MS	F	p
Constant	1	1.22	2.55	0.1108
Cumulative volume	1	102.57	214.17	< 0.0001
Shrub family	1	6.57	13.71	0.0002
Guild	1	56.74	118.47	< 0.0001
Shrub family × Guild	1	36.98	77.21	< 0.0001
Error	383	0.48		

Guild structure and abundance of caterpillar communities on different shrub species turned out to vary strongly, especially within the genus *Piper*. Three *Piper* species (*carpunya*, “I”, “XII”) had far higher herbivore densities than the others. In contrast, *Piper subscutatum*, “VIII” and “XV” were surprisingly rarely attacked by herbivorous caterpillars. Within the Asteraceae, *B. latifolia* and *E. polymnioides* had much higher herbivore densities than *A. dendroides*. The latter species belongs to the tribe Eupatorieae, many members of which are known to be defended by pyrrolizidine alkaloids (e.g. Hartmann 1998), offering a possible explanation for this observation. Overall, shrub species identity turned out to be a very important factor for herbivore caterpillar densities on individual shrubs, while the overall difference between shrub families in this regard was low. Thus, our hypothesis (a) of rather homogeneous herbivore loads among co-existing shrubs of the same plant family, with differences occurring mainly between shrub families, must be discarded.

Table 6.3: Results of one way ANCOVAs for density of non-herbivores and herbivores explained by shrub species (*Asteraceae* and *Piper* analyzed separately) and shrub families, with cumulative shrub volume as covariate. **DF**: degrees of freedom. **MS**: mean of squares.

Model	Predictor	DF	MS	F	p
Non-herbivores by shrub spp. (<i>Piper</i>)	Shrub volume	1	40.73	107.57	< 0.0001
	Shrub spp.	12	0.23	0.61	0.83
Non-herbivores by shrub spp. (<i>Asteraceae</i>)	Shrub volume	1	11.43	22.51	< 0.0001
	Shrub spp.	2	0.21	0.42	0.66
Non-herbivores by shrub family	Shrub volume	1	77.94	184.82	< 0.0001
	Shrub family	1	62.24	147.59	< 0.0001
Herbivores by shrub spp. (<i>Piper</i>)	Shrub volume	1	24.19	94.85	< 0.0001
	Shrub spp.	12	4.30	16.85	< 0.0001
Herbivores by shrub spp. (<i>Asteraceae</i>)	Shrub volume	1	11.34	34.02	< 0.0001
	Shrub spp.	2	10.44	31.30	< 0.0001
Herbivores by shrub family	Shrub volume	1	54.06	84.09	< 0.0001
	Shrub family	1	4.24	6.59	0.0110

Overall herbivore density across species was not much higher in the *Asteraceae* as compared to the *Piperaceae*. The weak observed differences between shrub families indicate that both were on average rather similarly suited for herbivores, contrary to hypothesis (b), while individual shrub species within the families differed strongly in their suitability for the guild of herbivores. We expect these pronounced differences to be rooted in species specific anti-herbivore-defense, probably based on chemical barriers provided by secondary plant metabolites (see also Bernard et al. 1995, Dyer & Palmer 2004 for anti-herbivore-defense in *Piper*).

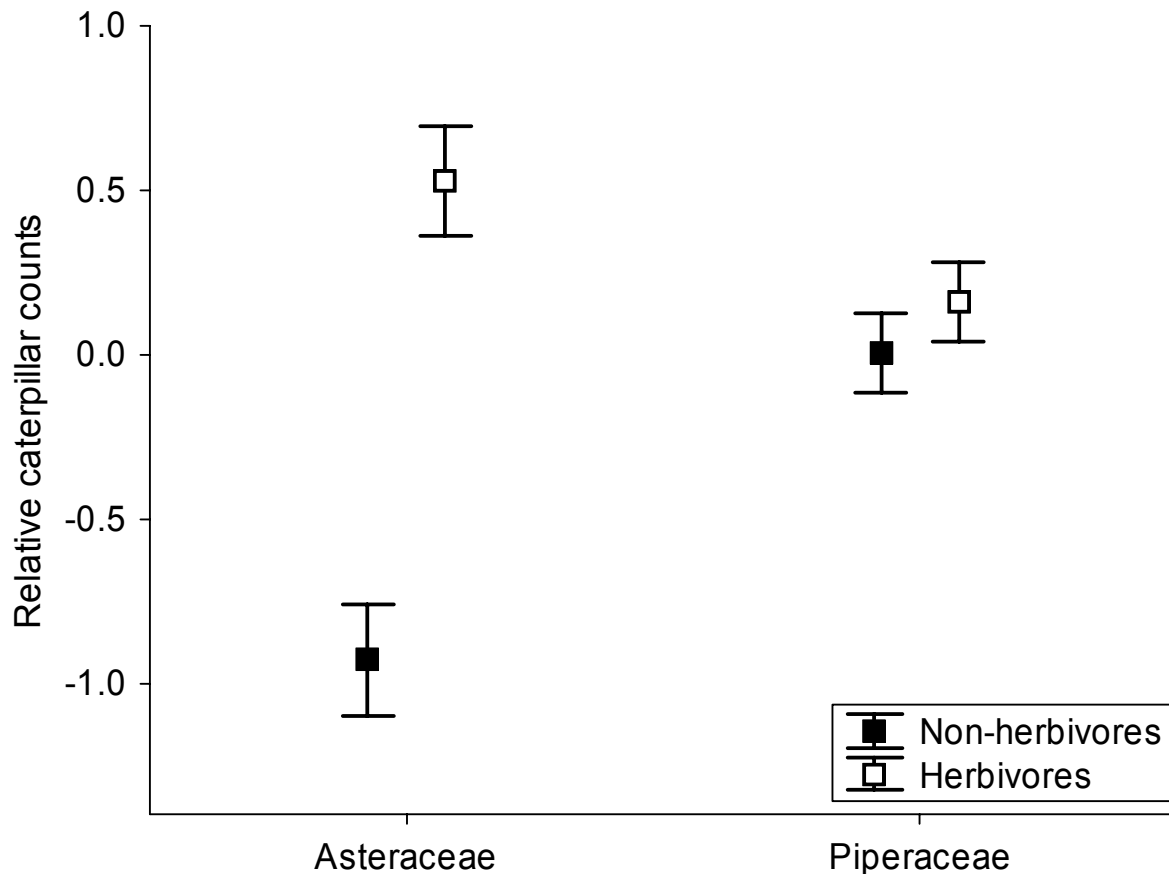


Fig. 6.5: Results of two-way ANCOVA of feeding guilds (herbivore vs. non-herbivore) and shrub family as predictors for caterpillar counts with cumulative shrub volume as covariate (Table 6.2). Analysis was based on cumulative data for all resamplings per shrub individual. Caterpillar counts were log transformed and standardized for this analysis.

The lack of explanatory value of “shrub species” as a categorical predictor for non-herbivorous caterpillars leads us to conclude that plant species traits (including chemical properties) are of minor importance for the suitability of a shrub to this caterpillar guild. Considering their life history this is hardly surprising, since their habitat preferences should overlap with conditions that are favorable for their resources. *Piper* shrubs in the closed forest displayed higher levels of epiphyllic lichen cover than Asteraceae in disturbed habitats (personal observation). This could either result from higher leaf turnover rates in the studied Asteraceae or be related to micro-climate conditions within the forest that might be more favorable for epiphyllic lichens. Forest habitats feature higher levels of air humidity and moistness of leaf surfaces due to shading by trees. These conditions result in higher coverage by most types of epiphylls, although not necessarily of epiphyllic lichens (Lücking 2008). Additionally, moist conditions in closed forest keep dead leaves soft, which appears to be advantageous for consumption by detritivorous caterpillars (personal observation). The

apparent preference of non-herbivore caterpillars for Piperaceae over Asteraceae observed in this study could therefore also be interpreted as preference for forest over open habitats. Shrub volume had a stronger influence on the densities of non-herbivores on Piperaceae than on Asteraceae, while its influence on herbivores was more similar on both families. This further emphasizes the differential suitability of these two plant families for the non-herbivore guild. *Piper* shrubs in closed forest are generally well suited sites, and their epiphyll resource supply is mainly limited by their volume and architecture. Asteraceae in open habitats are less favorable sites for non-herbivores due to their microclimate conditions, and they provide fewer epiphyll resources even on larger shrubs. Their suitability for this caterpillar guild would therefore be expected to depend more on small scale differences related to their individual growth site and micro-climate conditions than on shrub size.

Florivorous caterpillars played a surprisingly minor role. They contributed merely 5.9% of standardized counts on Asteraceae and were completely absent on *Piper* (Table 6.1). This was unexpected since several of the *Piper* shrub species of this study are in flower almost all year round, providing a constant potential resource. Yet, few cases of obligate flower-feeders were observed (e.g. the lycaenid *Rhanna arria* on *B. latifolia*). The geometrid genus *Eupithecia* whose caterpillars are often florivorous (e.g. McGuffin 1958, Mironov 2003) is particularly species-rich and abundant in the study area (Brehm & Fiedler 2005). Many *Eupithecia* feed on plants in the family Asteraceae, and this also applies to *Eupithecia* species in the study area (Brehm 2003). The low incidence of flower feeders in our caterpillar samples from montane forest therefore merits further attention. For example, these caterpillars could be more seasonal in appearance, or their coverage would require a sampling scheme more targeted to inflorescences.

The most unexpected result of this study was the high fraction of caterpillars which are not directly trophically linked to the shrub they inhabit. Their contribution of 22.5% to the whole dataset and up to 80% on individual shrub species clearly falsifies hypothesis (c) and begs further investigation into their ecological role. We could not find any reports of a similarly large fraction of non-herbivores in caterpillar communities in the literature. While studies on arthropod communities and food webs often include guilds that would be included in our non-herbivorous guild (e.g. Novotny et al. 2010), these do not usually include substantial numbers of Lepidoptera immatures. However, this might be explained by the difficulties in rearing such non-herbivores to adulthood in captivity. In our samples raising non-herbivores and thereby confirming their dietary links and taxonomic identities required many replicate attempts to adjust rearing conditions and proper food supply. In similar studies on *Piper*-herbivore interactions in northern Ecuador, Noctuoidea larvae suffered from

exceptionally high mortality (Genoveva Rodríguez-Castañeda, personal communication). In our study caterpillars of this superfamily sampled on *Piper* were exclusively (Noctuidae) or almost exclusively (Erebidae) found to belong to the non-herbivorous guild. Hence, if this trophic association was neglected in other studies and caterpillars were instead only offered green leaves from the plant species where they had been collected on, this would explain their high mortality. Moreover, such larvae may have been excluded as ‘tourists’ in some published studies after feeding trials with green leaves had been unsuccessful. It remains to be tested if the high fraction of non-herbivores as observed in our study is a specific feature of montane tropical forest (characterized by a very high abundance of lichens and other epiphylls), or whether targeted searching would reveal similar fractions in tropical lowland forest as well. Dyer & Letourneau (2007) reported lichen cover to be higher on *Piper cenocladum* plants with ant mutualists than on plants without ants in lowland Costa Rican forest. Since ants will most likely remove eggs and caterpillars of all Lepidoptera, regardless of their trophic association, this observation could also, at least partly, result from the removal of lichenivorous caterpillars.

Further, our finding on the high abundance of non-herbivore caterpillars might have importance for attempts to estimate total herbivore diversity on the basis of specificity in the affiliation with plants from which caterpillars have been gathered. Complete species identifications of the non-herbivorous caterpillars from our study are not yet available, but first estimates indicate that their species numbers outrank herbivore species by a factor of 2-4 on most, if not all *Piper* species in our study. At the same time, the large majority of them appear to have little or no specialization with regard to the shrub species they are living on. This would severely impact estimates of specialization levels, if those species were treated as normal herbivores, emphasizing the importance of performing extensive feeding trials. Our findings also highlight one problem of insecticidal knock-down sampling (Adis et al. 1998) after which feeding trials are often no more possible. Not only is there the problem of tourist species (Novotny & Basset 2000), which contributed a small but still noteworthy fraction to our samples, but also the potentially much larger issue of unexpected trophic associations. It might be misleading to attribute caterpillars obtained by fogging per se to the guild of herbivores associated with the tree or shrub of collection, even if they are abundant and regularly encountered, as long as no functional link to the source plant could be established.

An even more intriguing idea comes to mind when considering that caterpillar frass may increase nutrient circulation (Frost & Hunter 2004) while on the other hand removal of epiphyllic lichens and algae from the leaf surface may have positive effects on the plant’s photosynthesis. Thus, a substantial fraction of the caterpillars observed in this study might

indeed be considered plant mutualists, rather than antagonists, a role not usually associated with the larval stages of Lepidoptera.

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7. Species richness and host specificity among caterpillar communities on shrubs in the Andes of southern Ecuador

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Abstract

Caterpillar communities on 16 species of abundant shrubs from the family Asteraceae and the genus *Piper* (Piperaceae) were sampled in open and forest habitats in the Andean montane forest zone of southern Ecuador between August 2007 and May 2009. Trophic affiliations of caterpillars to the host plants were confirmed in feeding trials. Overall species richness of truly herbivorous caterpillars was high (191 species across all plants), but varied strongly between communities associated with different plant species (2-96 lepidopteran species per shrub species). Communities on *Piper* species were characterized by low effective species numbers and high dominance of one or two species of the Geometridae genus *Eois*. Low species number and high dominance also applied to latex-bearing *Erato polymnioides*, whereas communities on two other Asteraceae species were far more diverse and less strongly shaped by a few dominant species. The observed diversity patterns fit well to the concept that anti-herbivore defenses of plants are the major factors regulating associated insect communities. Local abundance and geographic range of host plants appear to have less influence. Lepidopteran species feeding on Asteraceae were found to be more generalistic than those feeding on *Piper* species. We conclude that caterpillar communities on most, but not all, studied plant species are defined by a small number of predictable dominant species, which usually are narrow host specialists. This pattern was more distinct on *Piper* shrubs in forest understory, whereas Asteraceae in disturbed habitats had more open caterpillar communities.

Keywords

Asteraceae, diversity, dominance, host specificity, insect herbivores, Lepidoptera, Piperaceae, plant defense, tropical montane forest

Introduction

Tropical insect herbivore communities on plants remain in the focus of ecological research (Novotny & Basset 2005). Their diversity, specificity and community structure have been investigated at a couple of sites in a few countries around the world with varying scales and focus (e.g. Diniz & Morais 1997, Dyer et al. 2007, Janzen & Hallwachs 2011, Novotny et al. 2002, Skippari et al. 2009). Among the topics of particular interest are explaining the underlying mechanisms of the overall high diversity of tropical insects (Novotny et al. 2006), the total extent of their diversity (Hamilton et al. 2010) and their vulnerability to habitat loss (Koh et al. 2004). However, those studies are still comparatively few and they often arrived at contradicting conclusions. For example, Novotny et al. (2002) characterized tropical herbivore communities on trees as “predictably simple” in that they were dominated by few abundant specialists with little spatial and temporal variability, while previous studies had emphasized high levels of randomness (e.g. Floren & Linsenmair 1998). On the matter of host specialization, Novotny et al. (2006) concluded that tropical herbivorous insects are no more specialized than in temperate-zone communities, whereas Dyer et al. (2007) observed significantly higher specialization in tropical communities. Rodríguez-Castañeda et al. (2010) have recently shown that patterns of host plant use may change with elevation, adding yet another dimension of complexity.

Further investigations into this field are obviously required to reveal the patterns and processes that shape herbivore-host plant interactions. In particular, data from additional regions and plant taxa may be the cue to resolve conflicting conclusions and improve our understanding of mechanisms that drive herbivore communities on individual plant species in the tropics.

We here present results from a study on communities of herbivorous caterpillars on shrubs in a tropical montane rainforest in southern Ecuador. Herbivore communities on shrubs are assumed to be somewhat less species rich than those on trees (Lawton 1983), which are more commonly the focus of investigations into tropical host-herbivore interactions.

Specifically, we studied the caterpillar communities of 16 abundant shrub species from the families Asteraceae and Piperaceae. In this paper we address the following questions:

- (1) Does observed or effective species richness of herbivorous caterpillars differ between communities on Asteraceae and those on Piperaceae?
- (2) Is the number of observed caterpillar species on a shrub species correlated with the local abundance of the shrub species?
- (3) Does host specificity of herbivores differ between Piperaceae and Asteraceae?
- (4) Do communities on Asteraceae and Piperaceae differ with regard to their dominance structure?
- (5) Are the studied caterpillar communities “predictably simple” in their structure, as suggested by Novotny et al. (2002)?

Methods

Study area

We studied caterpillar communities in the Reserva Biológica San Francisco (RBSF), a nature reserve adjacent to Podocarpus National Park in southern Ecuador (province Zamora-Chinchipe), located on the eastern slope of the Andes. This area has been the target of intensive ecological research since 1997 (Beck et al. 2008a), including studies on moth communities along elevational and disturbance gradients (e.g. Brehm & Fiedler 2003, Fiedler et al. 2008, Hilt & Fiedler 2008). It has been identified as a global diversity hotspot of moths (Brehm et al. 2005). RBSF is mostly covered by nearly pristine montane rain forest and by various types of succession vegetation of different ages after anthropogenic interventions (Beck et al. 2008b, Beck et al. 2008c, Homeier et al. 2008).

Caterpillars were sampled in forest and neighboring open habitats between 1800 and 2050m above sea level, in proximity to the Estación Científica San Francisco (3°58' S, 79°05' W). Sampling periods lasted from August 2007 to March 2008 and from December 2008 to June 2009.

Study organisms

For investigation we chose shrub species from two plant families, to contrast patterns of associated caterpillar communities across a steep gradient of habitat disturbance. In both families the major criteria for selection of target species were shrub-like growth form, availability of a sufficient number of replicate individuals, and their accessibility. In open, disturbed areas, three species from different genera of the family Asteraceae were selected. These three species (*Ageratina dendroides*, *Baccharis latifolia* and *Erato polymnioides*) are highly abundant in open and disturbed habitats in the RBSF (Beck et al. 2008b). While *B. latifolia* grows almost exclusively in more heavily disturbed open areas, *A. dendroides* and *E. polymnioides* are also found in disturbed forest habitats. No other Asteraceae shrubs were even nearly as common to be included in this study.

For investigation of caterpillar communities within closed-canopy forest we selected 13 species of *Piper* (Piperaceae). *Piper* is the most species rich (Homeier & Werner 2007) and abundant (own observations; see also Homeier et al. 2008) genus of understory shrubs (but including also some larger trees) in the RBSF. Most *Piper* species in the study area prefer moist areas in ravine forests, while comparatively few occur in ridge forest (own observations; see also Homeier et al. 2008). *Piper* species are the major host plants of the diverse and abundant geometrid genus *Eois*. This genus alone comprises about 10% of geometrid moth individuals attracted to light traps in the study area (Brehm et al. 2005, Brehm et al. in press), and the evolutionary biology of *Eois* has been the subject of recent studies (Strutzenberger et al. 2010, Strutzenberger & Fiedler 2011).

Taxonomy of *Piper* is still poorly resolved (Jaramillo & Manos 2001). To the present, 6 of the 13 species from this study have been formally identified, while the remaining species are tentatively referred to by morphospecies numbers. The only *Piper* species often encountered in heavily disturbed, open or half-open areas in the RBSF was *P. carpunya*. The other 12 species were confined to closed forest of various succession stages. The 13 studied *Piper* species comprised all representatives of the genus that were reasonably common along forest trails between 1800 and 2050m elevation. Four to five further species were inspected during initial surveys, but were too rare to warrant further quantitative study of their associated caterpillar faunas. In total 30 species of *Piper* are currently known from RBSF (Homeier & Werner 2007).

We surveyed a total of 194 individuals from these 16 plant species. Of Asteraceae in open habitats, 21 to 24 shrub individuals were sampled per species, Piperaceae species were sampled with 7-12 individuals each. To estimate the abundance of our target shrub species we performed a preliminary inventory along the trail system in RBSF before the onset of

herbivore sampling. While these counts were far from complete we accept them to largely reflect the relative abundances of targeted shrubs in the area.

Caterpillar sampling was performed every six weeks resulting in a total of eleven temporal replicates per shrub. Not all shrub individuals were sampled throughout the entire study. Some died off or were destroyed by falling trees or flooding, while others were only selected later in the project to replace losses. All immatures of any Lepidoptera family encountered during sampling were collected. The only exceptions were leaf miners and stem borers. Miners were rarely encountered and require much effort to rear at high losses (own observations). Stem borers cannot be sampled without destroying the target plant, which would have rendered resampling impossible.

Field collections and lab rearing

We collected lepidopteran preimaginal stages (mainly caterpillars, but also eggs or pupae if these were found) by means of a two staged sampling approach. This consisted of first visually searching the target shrub and secondly beating the shrub with a wooden stick over a white sheet of 1x1 m². For both stages sampling effort was standardized by an estimation of the shrub's crown volume. For details on sampling methodology see Bodner et al. (2010b).

All collected specimens were stored in plastic boxes and their exact sampling data (shrub individual, sampling stage, etc.) noted. They were subsequently reared in the lab in plastic boxes lined with damp paper towels to provide constant high air humidity. Caterpillars that did not immediately accept leaves or flowers of the shrub they originated from were first additionally offered dead leaves, foliose lichens and epiphyllic lichens and algae. If those were not accepted either, leaves from various other plants growing either in the close vicinity of the target shrub or known to be accepted by many polyphagous caterpillar species were offered as alternative. Caterpillars were kept in the lab until death or emergence of either the adult moth or parasitoids.

Sorting and identification

All lepidopteran herbivores encountered on the shrub species were carefully sorted to morphospecies level through a multi-stage process. Species delimitation and identification was based on an integrative taxonomy approach (Schlick-Steiner et al. 2010) using a combination of adult morphology, caterpillar morphology, and DNA-barcoding. Specimens that we managed to rear to adults were identified by comparison with photographs, with

published literature, or identified by taxonomic experts. Identification of the remaining specimens was first attempted by comparison of photographs of the caterpillars with those of caterpillars that had developed into adults. If this was not possible larvae were matched to adults by DNA barcodes provided that the specimens were still suitable for DNA extraction. The use of DNA sequences for identification of immature stages is well established (Ahrens et al. 2007, Miller et al. 2005, Pfenninger et al. 2007, Strutzenberger et al. 2011, Webb et al. 2006). The barcoding region (Hebert et al. 2003) of the mitochondrial cytochrome-oxidase subunit I (COI) gene was sequenced using primers LepF/LepR (Hebert et al. 2003), for details on DNA extraction, PCR amplification and DNA sequencing see Strutzenberger et al. (2011). We aligned our sequences with 1,993 reference sequences generated by the iBOL project (www.boldsystems.org) from adult Geometridae and Erebidae: Arctiinae collected at the RBSF (G. Brehm, unpublished data). Species identification and delimitation was assisted by neighbor joining (NJ) trees. Trees were calculated with MEGA version 4.3 (Tamura et al. 2007) using the Kimura-2-parameter distance model (Kimura 1980). Sequences with a pairwise distance of less than 3% were considered conspecific. In total 409 barcodes were generated from both unidentified immatures and adult reference specimens. Genbank accession numbers of sequences generated in this study are indicated in Table A2 (Appendix). Samples where no remains suitable for barcoding were available (e.g. if parasitoids had destroyed all caterpillar tissues or if the caterpillars had died and their carcasses decayed unnoticed) had to be discarded from all analyses. For the present study, only caterpillars belonging to species that were confirmed to feed on living plant tissue of the target shrubs were considered, viz. all caterpillars that turned out to feed on epiphylls, foliose lichens, dead plant material or for which no trophic association could be established were excluded.

Data analysis

Egg and larval numbers in large clutches and caterpillar groups were down-weighted to their cubic root. The reasoning for this was (a) their overrepresentation: egg clutches and large larval groups are comparatively easy to find, while solitary early instars are far more cryptic; and (b) raw numbers were overstating their apparent ecological importance. For example, in the case of *Altinote dicaeus albofasciata* (Nymphalidae), mortality of early instars was excessive and later instars did not nearly show up at comparable relative abundances in the dataset (own observations). Down-weighting to cubic root transformed the average values for egg clutches and caterpillar groups of *A. dicaeus albofasciata*, the most prominent case of gregarious caterpillars, to similar values as counts of survivors at early post-gregarious instars of the same species.

Field data were organized as lepidopteran species \times plant species matrices which formed the basis of all statistical analyses. To assess herbivore species richness per plant species we calculated Coleman rarefaction curves, species accumulation curves and the species richness estimators ICE (Colwell 2009) plus the abundance based versions of first, second, and third order Jackknife estimators. We subsequently selected the species richness estimator most suitable for this range of coverage according to Brose & Martinez (2004). This procedure was only changed for *Piper* sp. VIII, as, due to data structure, first and second order Jackknife estimators returned meaningless values lower than observed species richness and were therefore ignored. Dominance was calculated as Berger-Parker indices – i.e. the contribution of the most abundant species to the dataset (first order dominance). We also calculated modifications to additionally include the second and third most abundant caterpillar species per shrub (second and third order dominance). To additionally account for differences in the sampled crown volume per species, we re-scaled the x-axis of the Coleman rarefaction curves for every shrub species by its average crown volume. This correction factor was also used in correlation analyses. As replicate units we treated the collected samples, comprised of all herbivore specimens collected from one plant individual during one sampling event. We consider those samples to be sufficiently independent from those taken from the same plant six weeks earlier or later, as our sampling removed the majority of caterpillars (Bodner et al. 2010b) from the shrubs and almost all overlooked caterpillars would have completed their development before the next sampling event (own observations).

As a measure of herbivore diversity we calculated the bias corrected version of the exponential Shannon entropy with the program Spade (Chao & Shen 2009). For this purpose, we aggregated all available samples for each of the studied shrub species into one list. Herbivore diversity measures for shrub species with small sample sizes (< 50 caterpillars) must be treated with caution. All other standard statistical procedures, such as correlation analyses, were performed with the software Statistica 7.1 (Statsoft 2005).

For analysis of the possible influence of plant geographic range on herbivore diversities we extracted data on plant distribution from the online database of the Missouri Botanical Garden (<http://www.tropicos.org/>). We exported available records for those plant species we were able to identify to species level into Google Earth (Google Inc. 2010) and counted the number of occupied $1 \times 1^\circ$ grids as a rough measure of species distribution areas.

To evaluate the degree of host specificity for every caterpillar species, we combined data from this study, own unpublished observations, and host plant affiliation data from Brehm (2003), Bodner et al. (2010a), Dyer et al. (2010), and Robinson et al. (2010). Caterpillar species were then grouped by their host plant range on both plant family and plant

species level. Following Fiedler (1998), we distinguished monophagous (reported from only one plant family / species), oligophagous (reported from 2 or 3 plant families / species) and polyphagous (reported from four or more plant families / species). We restricted this analysis to Macrolepidoptera, as data on microlepidopterans from Ecuador is too scarce. Further, we excluded all herbivore species that could not be identified at least to genus level, to allow for a minimum of comparability with literature data. Finally, we excluded all herbivore species for which we could not obtain at least four records (sum of own specimens plus records from further sources), as this is the minimum number where a species could theoretically rank as polyphagous using the aforementioned definition.

Results

In total, 18,890 preimaginal specimens of Lepidoptera (8,929 caterpillars, 9,885 eggs, and 76 pupae) were collected in the course of this study. Of these, 477 (2.5%) were excluded as likely strays, since no trophic connection with the target shrubs or their epiphylls could be established. Another 1396 (7.4%) were found to feed on epiphyllous or epiphytic lichens, algae, or detritus. These were also excluded from analysis since they did not qualify as herbivores of the target shrub species in a functional sense. Caterpillars that feed on detritus or epiphylls in their early instars, but switch to living plant tissue of the target shrub species in their later instars, were retained in the dataset. Finally, another 295 caterpillars – mostly microlepidoptera and very early instars of Geometridae and Noctuidae – were excluded as they could not be reliably assigned to a (morpho)-species.

The largest part of the remaining dataset (16,722 individuals) comprised caterpillar groups (109 groups with 4,692 individuals; down-weighted to 261.5) and egg clutches (43 clutches with 9,047 eggs; down-weighted to 251.4) of gregarious *Altinote dicaeus albofasciata* (Nymphalidae: Acraeini) on *Erato polymnioides*. After down-weighting of groups and egg clutches, Nymphalidae were the second most prominent family in the dataset (16.1%) following Geometridae (70.1%). The majority of Geometridae were members of the genus *Eois* on *Piper* shrubs (47.2% of entire dataset), a moth genus known to be largely comprised of specialist herbivores of Piperaceae (Dyer et al. 2010, Strutzenberger et al. 2010).

Four of the surveyed *Piper* species (*densiciliatum*, *subscutatum*, VIII, XV) yielded less than 50 herbivorous caterpillars each and were consequently excluded from some of the analyses and subsequent discussion, as these low numbers may cause erratic behavior of diversity estimators and indices.

A total of 191 different herbivorous caterpillar species were encountered during this study (see Table A1 in Appendix for a full list). On individual plant species their number ranged from only 2 on *Piper carpunya* to 96 on *Baccharis latifolia*. While observed herbivore species richness on *Piper* species averaged at 9.5 and never exceeded 18, herbivore richness was far larger on all studied Asteraceae species with a minimum of 40 (Fig. 7.1, Table 7.1). On Asteraceae species, exponential Shannon entropy of herbivores (which can be regarded as a measure of the effective number of species: Jost 2006) ranged from 2.79 to 33.97. On Piperaceae species, exponential Shannon entropies of herbivores ranged from 1.07 to 9.11 with an average of 5.58. After exclusion of the four most scarcely populated *Piper* species, which ranked highest in exponential Shannon entropy, the maximum value was reduced to 7.15, and the average to 4.44.

Table 7.1: Herbivore species richness and diversity values for the studied shrub species. Rarefied species are based on a shrub volume of 29.89 m³; no values are available for *Piper densiciliatum* and XII, as total sampled shrub volume was below this value. Shrub species with less than 50 caterpillars found in total are shaded in grey; here any diversity estimates are hardly informative. Total species number according to third (a), second (b) or first (c) order abundance based Jackknife estimator. d: no additional species predicted by estimators.

	Species	Indi- viduals	exp. Shannon entropy	Rarefied species	Estimated total species	Coverage (%)	Total shrub volume (m ³)
<i>A. dendroides</i>	40	112	33.97	13.9	85.5 ^a	46.8	161.57
<i>B. latifolia</i>	96	791.3	19.96	36.8	182.8 ^a	52.5	201.92
<i>E. polymnioides</i>	43	611.4	2.79	17.5	105.8 ^a	40.6	119.38
<i>P. arboreum</i>	11	61.5	7.15	9.5	14.0 ^c	78.8	47.78
<i>P. carpunya</i>	2	313	1.07	2.0	2.0 ^d	100	29.98
<i>P. densiciliatum</i>	8	22	9.11	-	25.11 ^a	31.9	14.36
<i>P. obliquum</i>	6	62	3.87	5.9	7.0 ^c	85.9	31.59
<i>P. perareolatum</i>	10	128	2.71	8.2	21.8 ^a	45.9	47.84
<i>P. subscutatum</i>	8	24	7.34	4.8	16.5 ^a	48.5	80.55
<i>Piper</i> I	18	541	5.14	10.7	36.9 ^a	48.7	96.78
<i>Piper</i> III	17	195.4	6.24	11.1	43.7 ^a	38.9	80.11
<i>Piper</i> V	14	108	6.22	10.1	26.8 ^a	52.2	62.53
<i>Piper</i> VIII	8	21	7.70	6.8	9.0 ^c	89.4	48.24
<i>Piper</i> IX	9	54	4.16	8.5	24.3 ^a	37.0	33.23
<i>Piper</i> XII	7	151.6	3.44	-	9.0 ^b	77.9	19.82
<i>Piper</i> XV	6	11	8.44	5.1	16.3 ^a	36.7	37.98

On most studied shrub species, estimated total caterpillar species richness was far higher than observed species numbers. Besides the community on *Piper carpunya*, that estimators predicted to be covered entirely by our samples, only the communities on four further shrub species (*Piper arboreum*, *obliquum*, VIII, and XII) were estimated to be more than 53% complete. Mean coverage was 57.0% overall (Asteraceae: 46.6%; Piper: 59.4%).

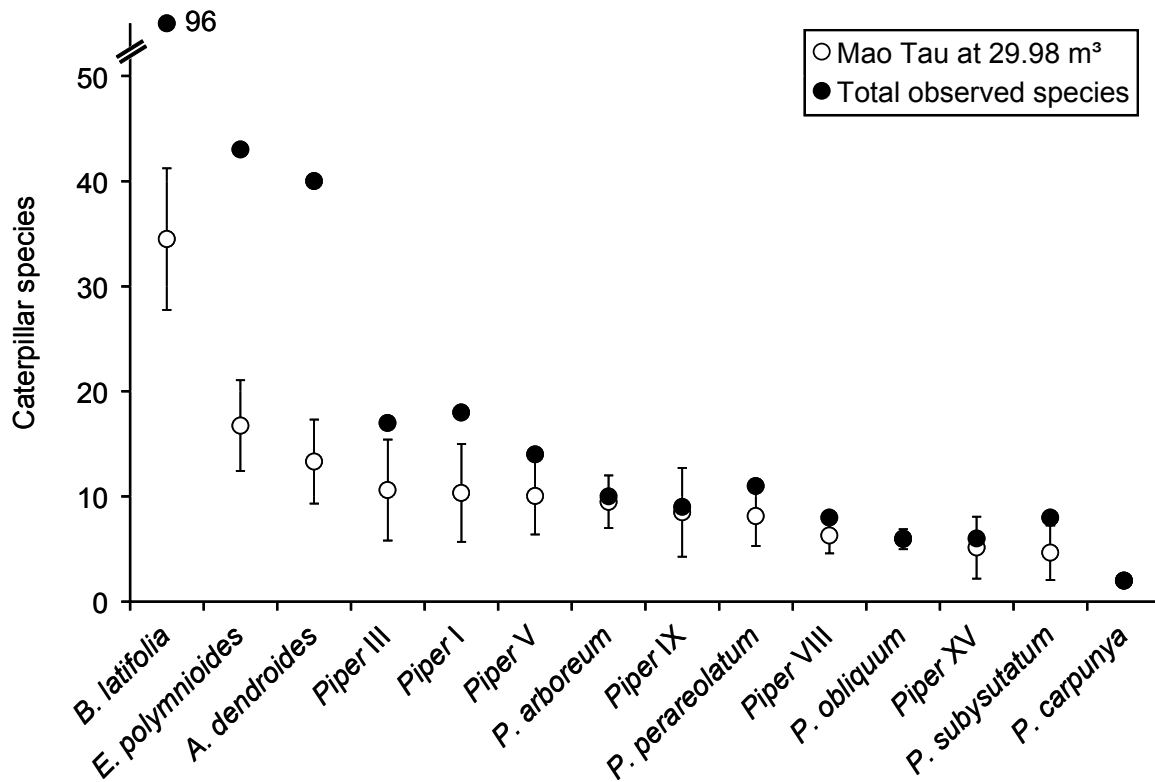


Fig. 7.1: Mao Tau species accumulation values at 29.98m³ of sampled shrub volume (empty circles) with 95% confidence intervals (whiskers), and total observed species numbers (filled circles) for all shrub species with 29.98 m³ or more total sampled shrub volume.

Inspection of species accumulation curves confirms these results and yields further insights. The curve of *B. latifolia* starts off steeply and runs well above all others (Fig. 7.2 top), again emphasizing the far higher diversity of caterpillar communities on this shrub species as compared to all others covered in this study. The curves of most *Piper* species also feature a steep increase at the start (Fig. 7.2 bottom), but flatten off notably faster than those of *A. dendroides* and *E. polymnioides* (with the exception of *Piper densiciliatum*, see below), which soon overtake them. This means that a comparatively more substantial fraction of the caterpillar fauna of *Piper* shrubs is covered with a limited number of samples, while samples

from *A. dendroides* and *E. polymnioides* continue to accumulate species. On most shrub species the curves display the usual shape (e.g. Xuan Mao et al. 2005) and are still far from approaching their asymptote. However, for some shrub species the geometry of the curves is notably different. The curves of *Piper carpunya*, *obliquum* and XII flatten much stronger than in all other plant species, indicating that the caterpillar inventory is close to completion. In contrast, the curve of *Piper densiciliatum* increases steeply in an almost linear fashion with no sign of saturation.

We correlated the abundance of shrub species with their numbers of caterpillar species. These analyses were restricted to shrubs from the genus *Piper*, to avoid taxonomic bias. Absolute numbers of observed species correlated notably ($r^2 = 0.572$, $p = 0.003$) with total sampled shrub volume of the specific plant species. Estimated total caterpillar numbers correlated moderately with shrub abundance ($r^2 = 0.395$, $p = 0.021$). Correlations based on rarefaction to the largest common total shrub volume for the 12 (excluding *Piper densiciliatum*) and 11 (excluding *Piper densiciliatum* and XII) best sampled shrub species yielded similar trends, but no significant results ($r^2 \leq 0.355$, $p \geq 0.053$). Even weaker relationships were found between shrub abundance and exponential Shannon entropy values ($r^2 \leq 0.203$, $p \geq 0.223$; calculated only for the nine *Piper* species with more than 50 caterpillar specimens).

Host plant specificity was evaluated for those 76 macrolepidopteran species that were identified at least to genus level and had at least 4 records associated with them (Fig. 7.3). Overall, specificity of these herbivores on the level of attacked host plant families differed distinctly between the sets of species associated with the two studied plant families. While 48.8% of the caterpillar species found on Asteraceae are only known to feed on plants of this family, 74.4% of caterpillar species on Piperaceae were scored as monophagous on plant family level. This difference in host plant specificity became even more distinct when considered on plant species level: On Asteraceae only 11.6% of the caterpillar species were monophagous and 53.5% were polyphagous, whereas on Piperaceae the fractions were 62.8% monophagous and 25.6% polyphagous, respectively.

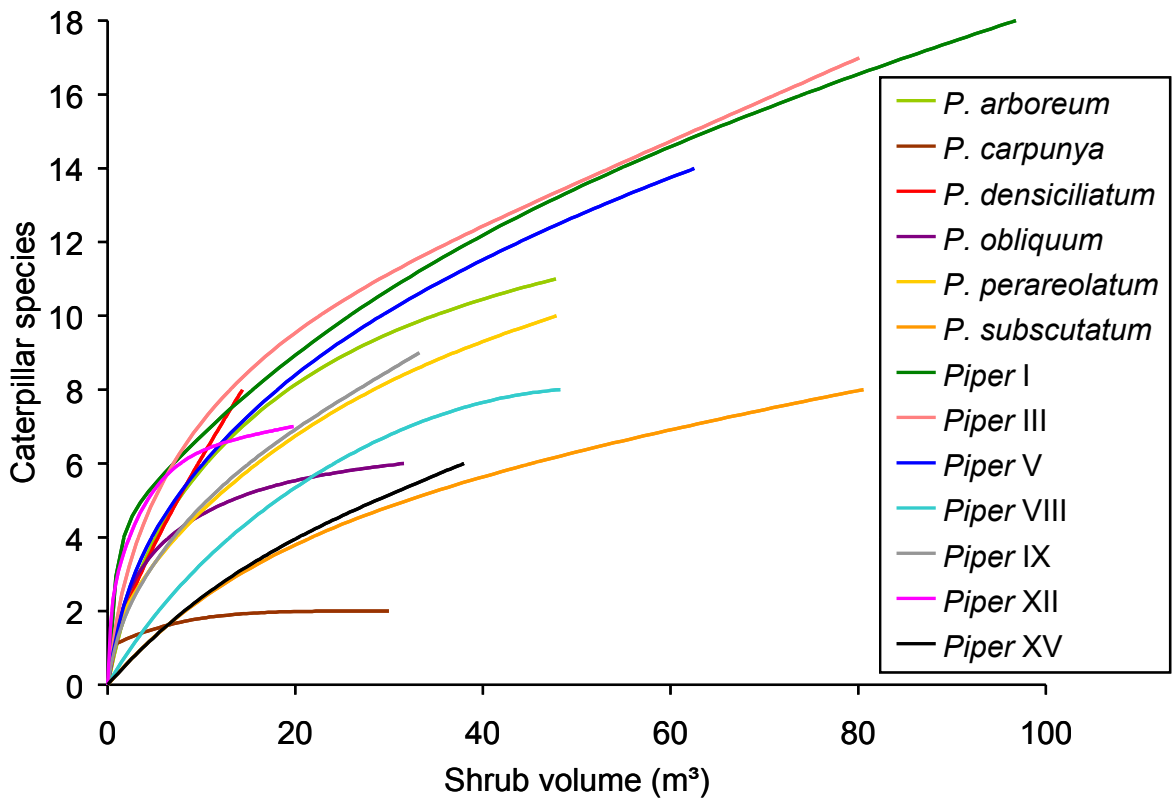
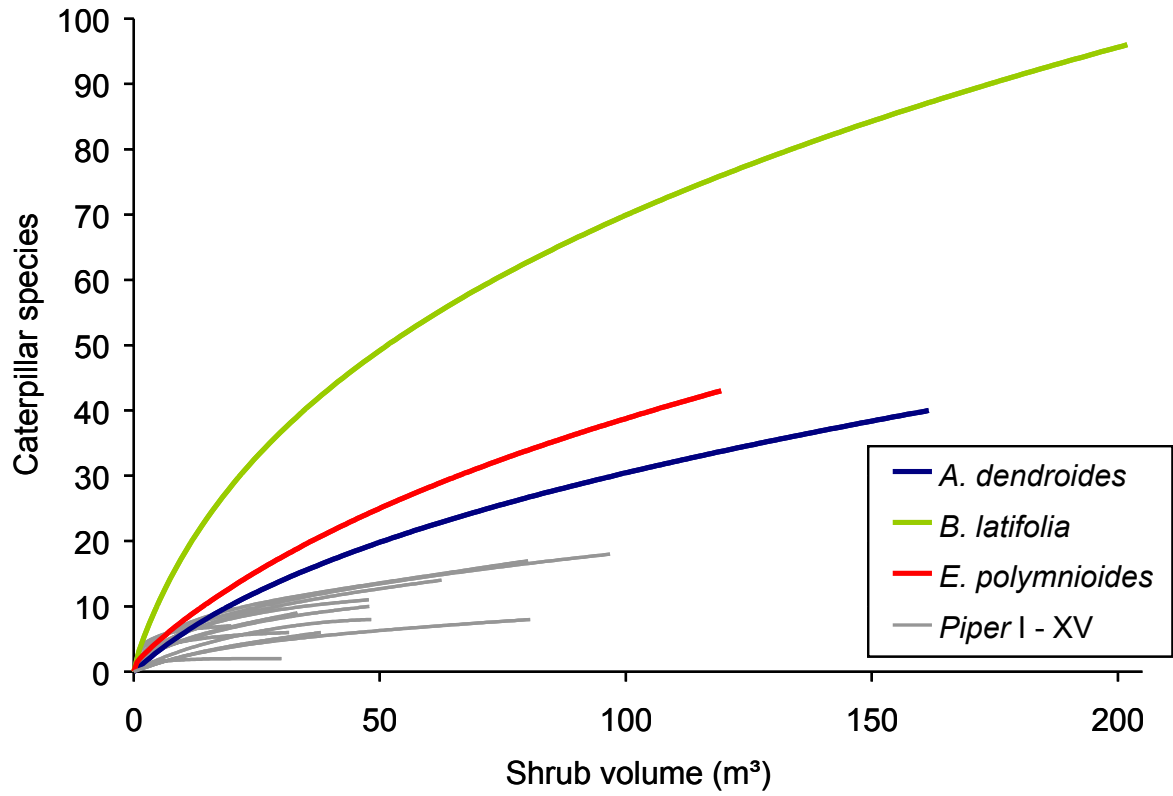


Fig. 7.2: Coleman rarefaction curves for all shrub species with Asteraceae highlighted in color (top) and only for *Piper* spp. (bottom).

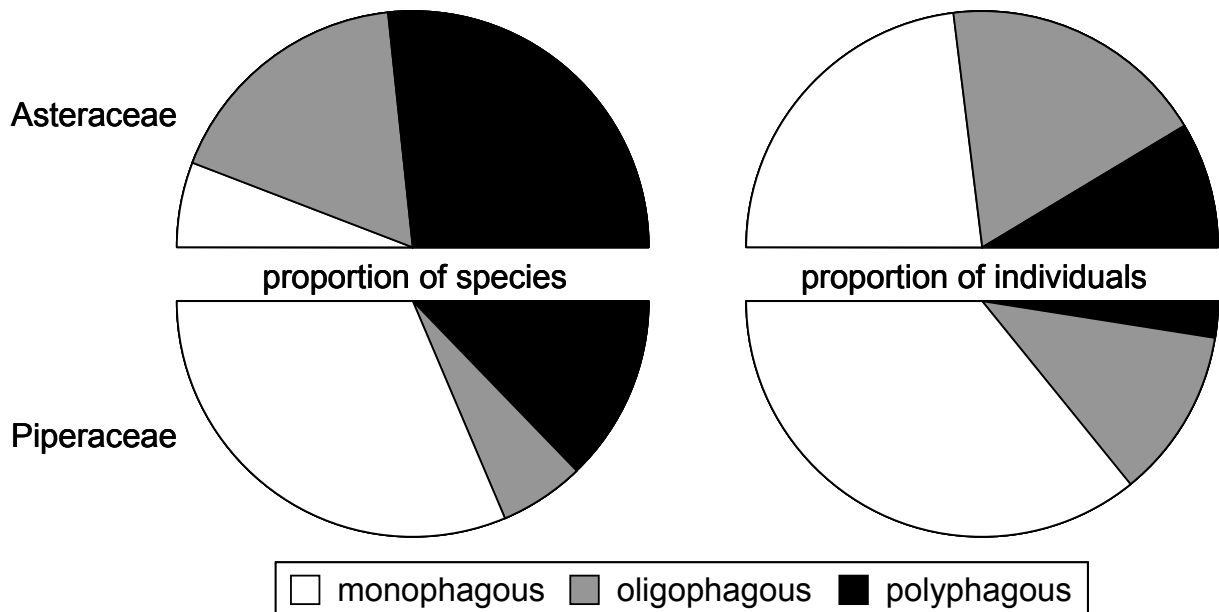


Fig. 7.3: Proportion of species (left) and individuals belonging to species (right) considered as poly- (black), oligo- (grey), and monophagous (white) at plant species level on Asteraceae (top) versus *Piper* species (bottom).

Berger-Parker dominance indices ranged from 0.170 (0.348 for top three species) on *A. dendroides* to 0.987 (1.000 for top two species, as only two were found) on *Piper carpunya* (Fig. 7.4). The median value for dominance was 0.450 for all shrub species, and did not differ much between Asteraceae (0.426; range: 0.170 – 0.839) and *Piper* species (0.475; range: 0.320 – 0.987). However, while all three dominance values on *E. polymnioides* ranked high, values for the other two Asteraceae were notably lower. *A. dendroides* returned the lowest values for all three indices, while *B. latifolia* was intermediate for top one species and third and second lowest for top two and three, respectively. The highest dominance values were those on *Piper carpunya*, where the most abundant caterpillar species alone already achieved higher dominance (0.987) than the top three on any other of the shrub species. As with *E. polymnioides*, the contribution of the second most abundant caterpillar species was already minute. Most other *Piper* species also reached high dominance values of > 0.7 for the three most abundant caterpillar species, but their dominance values increased in a more stepwise fashion.

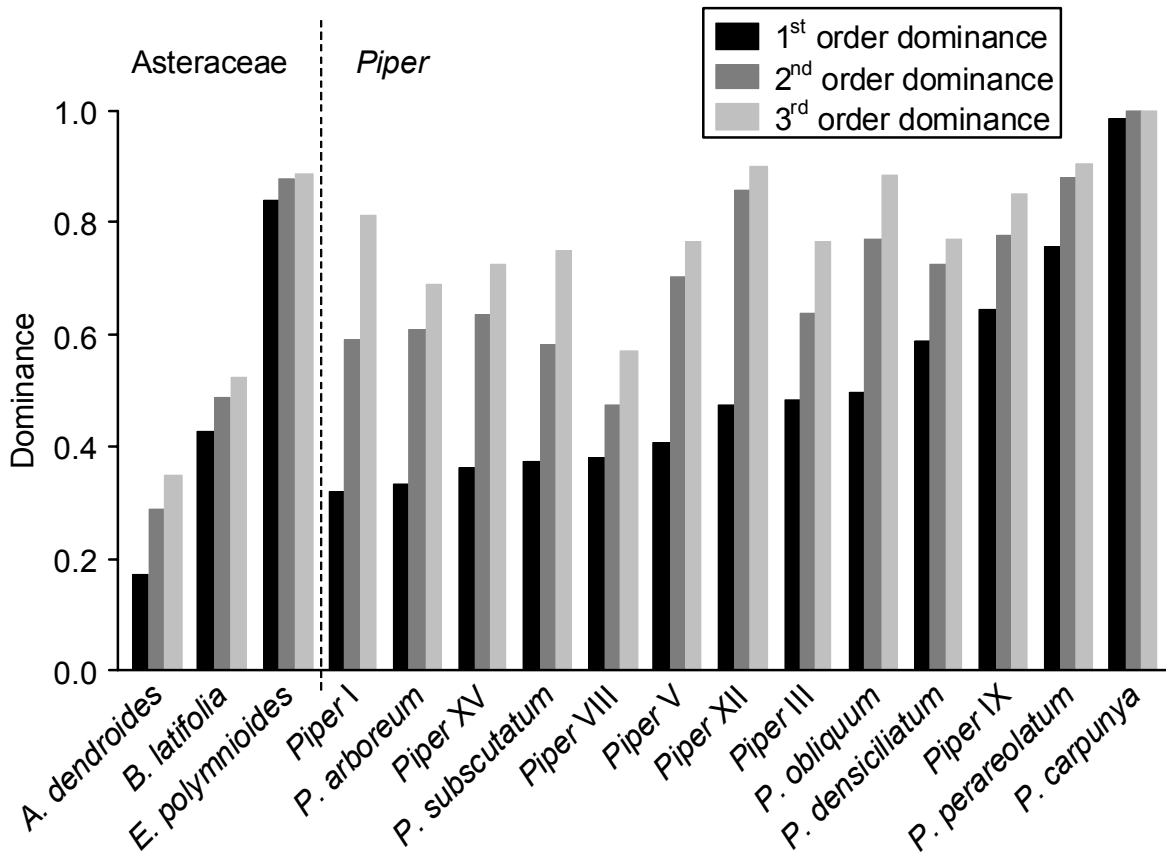


Fig. 7.4: First (black), second (dark grey) and third (light grey) order dominance values of herbivores for all sampled shrub species. Shrub species sorted first by family, then by first order dominance.

Discussion

We found the studied shrub species to overall harbor a rich and abundant caterpillar fauna and further sampling would likely still increase those numbers substantially. However, despite similar architecture and being exposed to a mega-diverse lepidopteran fauna (Brehm et al. 2005), some plant species were populated by considerably fewer different caterpillar species than others. Most noteworthy is the more than 40fold difference in observed and estimated caterpillar richness between the poorest community on *Piper carpunya* and the most species rich community on *B. latifolia*. Although some of these differences diminish when controlling for shrub volume and sampling effort (Fig. 7.1), there still remains a more than 15fold difference in rarified species numbers. These findings highlight both the importance of controlling for differences in sampled biomass when studying herbivore communities and the pitfalls of using “plant species \times average number of herbivore species” for diversity extrapolations.

Caterpillar communities on asteracean shrubs were notably more diverse than on *Piper* shrubs. All three Asteraceae ranked higher than any *Piper* species in total number of both observed and predicted species. This rank order persisted after rarefaction to largest common total sampled shrub volume, although the differences between *A. dendroides* and *E. polymnioides* and the highest ranking *Piper* species vanished almost entirely and only *B. latifolia* retained a clear lead. Inspection of the shape of the species rarefaction curves also confirmed the higher herbivore richness on all three Asteraceae, as curves continue to ascend in a more steady way than even the most herbivore-rich *Piper* species. We expect that these observed diversity patterns are the consequence of a variety of factors. Some studies have reported a positive correlation between the extent of a plant's geographic range and the species richness of its associated herbivores (Lewinsohn et al. 2005). We therefore plotted rarefied herbivore species richness against plant distribution area (Fig. 7.5). The scarce data basis (three Asteraceae species, five *Piper* species with assigned names and sufficient data for analysis) did not allow for statistical analysis, but two different patterns are visible in the diagram. Species richness of caterpillar communities on Asteraceae appears to be positively influenced by plant geographic range, whereas no such trend is visible in *Piper* species. We tentatively conclude that plant geographic range has only limited influence on herbivore diversity in our samples – if at all – and that such influence is not consistent between different host taxa. Correlation of local abundance of shrub species with rarefied species richness of their herbivores showed a notable positive trend, but was not significant. Consequently we currently consider this factor to also be only of limited importance.

Chemical defense properties of plant species strongly affect their herbivores, although not much is currently known on how they influence associated herbivore communities as a whole (Lewinsohn et al. 2005). Unfortunately there is hardly any data available on the toxicity of the plant species of this study for herbivorous insects. *Ageratina* is a member of the Eupatorieae, many of which produce pyrrolizidine alkaloids (Rizk 1991). Some *Ageratina* species are toxic to mammals (Fuller & McClintock 1986), while others contain non-toxic pyrrolizidine alkaloids (Lang et al. 2001). *Baccharis latifolia* essential oils were tested for insecticidal activity against disease vectors (Chantraine et al. 1998, Laurent et al. 1997) with little success. *Erato polymnioides*, like other species from this genus (Moran & Funk 2006), produces milky latex which likely acts as anti-herbivore defense (Agrawal & Konno 2009). *Piper* species are known to be generally well defended against herbivores (Dyer & Palmer 2004), however specific data for the species of our study are mostly lacking. Bernard et al. (1995) found that extracts from most of 14 tested Neotropical *Piper* species, including *P. obliquum*, significantly reduced growth rate and increased mortality when added to the diet of European corn borers (*Ostrinia nubilalis*). Despite the lack of species-specific information,

the general trend to be inferred from these phytochemical studies matches with the observed species richness of the individual herbivore communities: the likely well defended *Piper* rank lowest, followed by latex-bearing *E. polymnioides* and the putative pyrrolizidine alkaloid plant *A. dendroides*, and all are greatly surpassed by *B. latifolia*. Data on the chemical defense properties of these plant species would be necessary to further test this conclusion.

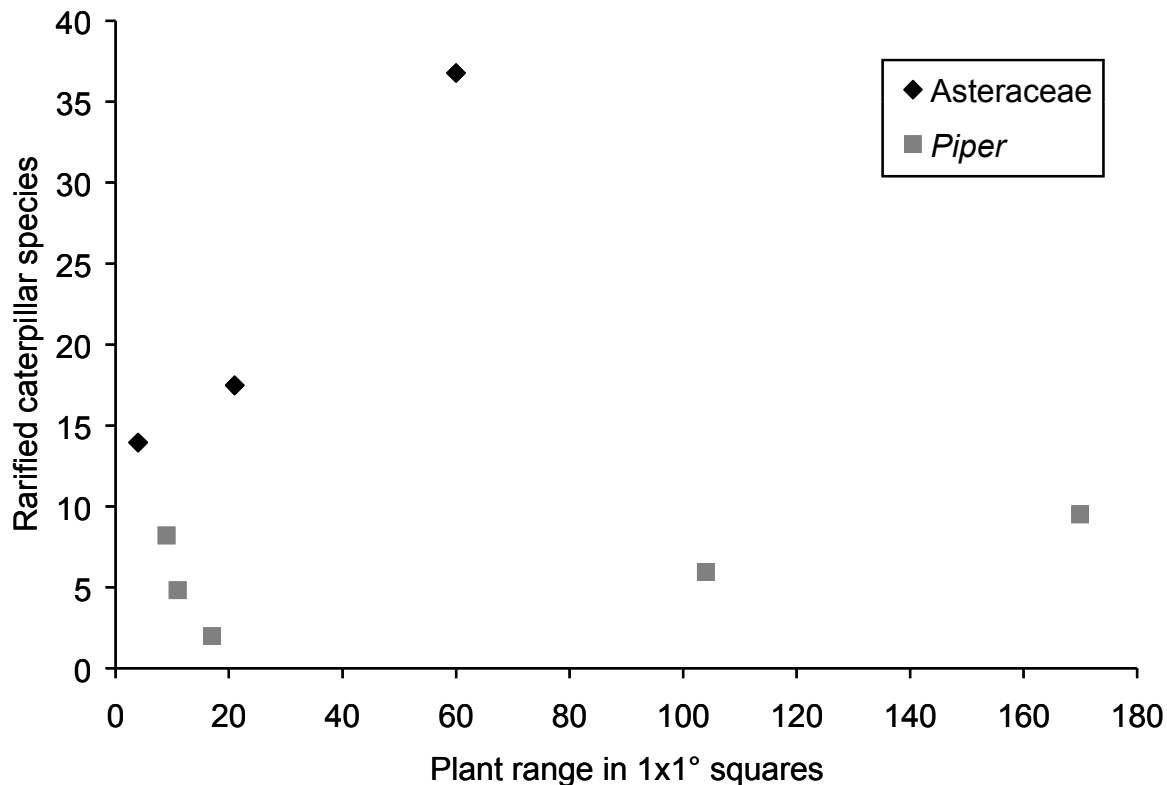


Fig. 7.5: Rarified species richness of herbivore communities plotted against an estimate of the geographic range of the host plant species (obtained by counting 1x1° map squares occupied with records from the Missouri Botanical Garden database). Only plant species that were identified to species level and with a sampled volume of > 29.98 m³ (rarefaction threshold) are included. Black diamonds: Asteraceae; grey squares: *Piper* spp.

Comparison of exponential Shannon entropy, i.e. the effective number of species in a community, and dominance values added notably to the insights from species accumulation curves. In terms of effective species numbers, *A. dendroides* and *B. latifolia* retain their clear lead over all *Piper* species with sufficiently large data sets for comparison. The high Shannon value for *A. dendroides*, which reaches close to the total number of observed species, shows that there is no small subset of core herbivores of *A. dendroides* that would define its community. This is also confirmed by the low dominance values and the low number of

herbivore individuals on this shrub. Instead, *A. dendroides* harbors a substantial number of caterpillar species, each one rarely encountered. *E. polymnioides*, to the contrary, scores far lower in exponential Shannon entropy, while dominance values are far higher. With an effective species number of only 2.8, it ranks in the lower end of the range occupied by the *Piper* species. This indicates that, unlike on the other two Asteraceae and notably similar to most *Piper* species, the community on *E. polymnioides* is defined by a very small number of specialist herbivores. We attribute this to its latex production rendering it an undesirable host plant for generalists. In this respect, *E. polymnioides* is similar to the chemically well defended *Piper* species, although it is evidently edible to a substantial number of both specialists and generalists. The most prominent caterpillar species on *E. polymnioides* was the gregarious *A. dicaeus albofasciata*.

Piper species with sufficient data for detailed analysis featured low effective species numbers between 1.1 and 7.2. High levels of dominance with the three most abundant species usually accounting for around 80% of the communities also indicate that their herbivore communities are defined by a small set of core species. Inspection of raw data for these nine *Piper* species revealed that those three most abundant caterpillar species were almost always *Eois* species, with few other taxa in third places. Only one non-*Eois* scored as second rank herbivore, namely on *P. carpunya* where only one *Eois* species was found. Most caterpillar observations on *Piper* spp. beyond the few dominant species resulted from accumulation of generalists that likely utilize *Piper* only as minor host plants, or very rare species. Further sampling effort would likely increase their numbers, as suggested by unsaturated species accumulation curves and estimates of sampling coverage. To identify the core communities, on the other hand, in most cases a notably lower sampling effort would have sufficed. Rarified species numbers for 30 m³ of sampled shrub volume already surpassed effective species numbers for all shrub species with sufficient data with the only exception of *A. dendroides*.

Within the genus *Piper* the highest values for exponential Shannon entropy were obtained for *Piper densiciliatum* and XV. We excluded both from quantitative comparisons due to very small sample sizes, and they both featured a high fraction of singleton herbivores (6 of 8, and 4 of 6 species, respectively). High proportions of singletons, a common feature of tropical herbivore communities, can pose problems for the study of host-herbivore interactions (Novotny & Basset 2000). It is often hard to establish whether a plant-insect association supported by only a single record is (a) the consequence of rarity of the herbivore, (b) represents a marginal association of a herbivore otherwise specialized on a different set of host plants, (c) an extremely polyphagous species feeding on so many plant species that it is hardly ever found twice on the same one, or (d) a tourist specimen. The latter possibility can

be ruled out by our extensive feeding trials, although even then the possibility still persists that a confirmed trophic association occurs but exceptionally in nature.

Novotny et al. (2003) reported on caterpillar communities from three *Piper* species in comparison with records from further 68 species of other woody plants from Papua New Guinea. The median of dominance values reported here (0.450) is close to that of 0.48 in Novotny et al. (2003). Equally, dominance values for our *Piper* species lie in a similar range as those reported for one native (*P. macropiper*) and two introduced (*P. aduncum* and *P. umbellatum*) *Piper* in the same study, although none rank as low as the 0.09 reported for the introduced *Piper umbellatum*. We also calculated bias-corrected exponential Shannon entropies from their data. Values for the two introduced *Piper* species (*P. aduncum*: 8.054, *P. umbellatum*: 25.728) ranked above all of our *Piper* species with the exception of *P. densiciliatum* and XV, both of which we excluded from our analysis due to their small data sets. The native New Guinean *P. macropiper* ranked even lower than most of our species (1.684).

Novotny et al. (2002) reported caterpillar samples from rain forest trees in Papua New Guinea as dominated by few specialized species with little variation in assemblage structure and concluded that herbivore communities were “predictably simple”. This characterization also applies to the most of the caterpillar communities on shrubs reported here. However, communities on *A. dendroides* and *B. latifolia* notably divert from this characterization. *B. latifolia* has one moderately dominant caterpillar herbivore (*Microxydia* sp. nr. *ruficomma*, Geometridae), but beyond this there exists a rich and abundant caterpillar community on that shrub. In contrast, communities on *A. dendroides* entirely lack any moderately dominant species, but are composed of a substantial number of rare, unpredictable species.

The number of caterpillar species per plant species was moderately correlated with the plant’s abundance in the study area. However, this relationship became ever more obscured the better sampling effects in the data were controlled for. Hence, even though a shrub species’ abundance may have some influence on the species richness of its associated herbivores (Marquis & Braker 1994), this does not appear to be a strong driver in the herbivore communities of this study.

Vanin et al. (2008) reported “remarkably narrow feeding preferences” for *Piper* herbivores from both field and lab data. Similarly, host plant specificity of caterpillar species found on *Piper* plants in this study was pronouncedly higher than of those found on

Asteraceae. This was especially clear on the level of utilized plant species. Increased specificity was also visible for plant families, although almost half of the lepidopteran species found on Asteraceae were scored as monophagous at this level. Host plant data for Neotropical caterpillars – even after exclusion of particularly poorly studied microlepidoptera – is extremely incomplete, so conclusions remain tentative. Furthermore, although data from a number of sources is included, the majority of records used in this analysis stems from this study and therefore has an inherent bias towards the two studied plant families. However, considering as our study includes 13 *Piper* species and only 3 asteracean species, bias in this dataset would rather be expected to overemphasize specificity on the asteracean side. Hence, the discovery a disproportionately high fraction of specialist feeders on *Piper* bears some weight. The likely explanation is stronger and diverse chemical defense in *Piper* species (Bernard et al. 1995) as compared to Asteraceae, rendering them less suitable to generalist feeders and promoting the evolution of specialists (Strutzenberger et al. 2010, Strutzenberger & Fiedler 2011).

Connahs et al. (2009) studied geographic variation in host plant utilization by *Eois* species for various Neotropical sites. They concluded that *Eois* species in Ecuador utilize on average two *Piper* species as host plants, with a 95% confidence interval of approx. 1.7 to 2.2 (measured from their diagram). This is notably higher than our average of 1.2 *Piper* species utilized per *Eois* species. We assume that these differences are at least partly due to the larger size of their data set. Additionally the much larger elevational range covered in Connahs et al. (2009) may play a role, as *Eois* diet breadth is known to change with altitude (Rodríguez-Castañeda et al. 2010). Irrespective of these minor differences, all these lines of evidence support the notion that *Piper* species generally support herbivorous caterpillar communities of comparatively low diversity and characterized by high host specificity.

Altogether we conclude that the studied shrub species harbor a rich and abundant caterpillar fauna, which however differs strongly and in various ways between individual plant taxa. Certain plant species in the genus *Piper* were hardly colonized by herbivorous insects at all. The abundance and the geographic range of the plant species modulate the local diversity of their affiliated herbivores, but overall chemical anti-herbivore defense appears to be the most important factor. Hence, edibility of individual plant species must be taken into account when attempts are made to up-scale from herbivore communities of plant species to entire vegetation units. As in other studies from tropical lowland forest most communities harbored only few dominant and therefore functionally relevant caterpillar species – usually specialists – that define them. Hence, caterpillar communities on shrubs in the montane forest

zone of the Andes can be considered “predictably simple” in the sense of Novotny et al. (2002), although clear exceptions exist. The differences in specificity of herbivore communities of common shrubs in different habitats might indicate that with the ongoing loss of natural tropical mountain forests also the diversity of plant-herbivore interactions will be affected (Koh et al. 2004), at the cost of highly specific interactions that prevail amongst forest understory shrubs.

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8. Synopsis

The results of this thesis revealed many interesting facets and some novel insights into the structure, diversity and guild composition of caterpillar communities on shrubs in a biodiversity hotspot in the Andes of southern Ecuador.

Evaluation of the employed standardized sampling method, consisting of a visual searching and a branch beating stage (Chapter 5), proved its suitability for studying caterpillar communities. The combined sampling approach retrieved a large portion of the caterpillars present on the sampled shrub with little taxonomic bias. Counts of caterpillars remaining on the shrubs after, or shaken off the shrub during sampling indicated a sampling efficiency above 50% for shrubs with complex architecture and more than 70% on shrubs with simple architecture. However, these numbers are probably slight overestimations, as caterpillar size distributions showed that some fraction of the smallest caterpillars was likely overlooked even during intensive examination of shrubs after standardized sampling.

The chosen combination of visual search and beating allowed for observations on behavior of caterpillars located during the first sampling stage (including distinction between gregarious and solitary caterpillars). As a non-invasive sampling method this approach also allowed for multiple re-samplings of the same plant individuals and retrieved unharmed specimens that could be further studied, e.g. in feeding trials for verification of their trophic association. The sample method was also shown to be suitable for application by untrained field assistants as sample composition on level of higher taxa and feeding guilds did not differ significantly from samples taken by an experienced researcher.

Analysis of caterpillar communities with regard to their abundance and guild structure (Chapter 6) revealed striking differences between shrub families (Asteraceae, Piperaceae) and species. A surprisingly large fraction of more than 22% of caterpillars turned out not to be directly trophically linked to the living biomass of the shrub itself. To emphasize this lacking trophic connection these caterpillars were here referred to as “non-herbivores”. These non-herbivores feed on dead leaves, foliose or epiphyllic lichen, algae and, in some few cases, on epiphytic or epiphyllic mosses. No account of similarly high numbers of non-herbivorous caterpillars was found in extensive literature surveys. It remains an open question, whether their prominence is a unique feature of lichen-rich perhumid tropical montane forests, or whether targeted searching and adapted feeding trials would reveal similar numbers at other

study sites (e.g. in tropical humid lowland forest). Specimens identified as strays (“tourists”) from surrounding vegetation – a well known problem in studies on diverse tropical insect communities (e.g. Novotny & Basset 2000) – contributed a small, but still noteworthy fraction.

Abundance patterns in the non-herbivore guild differed strikingly from those of herbivore caterpillars. Abundance of true herbivores was, on average, quite similar between shrub families, but varied strongly across individual plant species, with some *Piper* species hardly colonized by herbivorous caterpillars at all. Abundance of non-herbivores, in contrast, was much higher on Piperaceae than on Asteraceae, but showed only minor variation among species within either family. This is likely an effect of habitat and microclimate in that higher air humidity around *Piper* shrubs in closed forests results in higher coverage of leaves with epiphylls. In addition, the more long-lived leaves of *Piper* shrubs may acquire a higher epiphyll load during their lifespan, which would support a more substantial non-herbivore caterpillar fraction. Herbivorous caterpillars were remarkably homogenous with regard to their guild affiliation, as the vast majority of them were ectophagous folivores. Only a minor fraction were semi-endophagous folivores (mostly leaf rollers and tiers), while florivores were rare and observed exclusively on Asteraceae.

Additionally, the pronounced differences in herbivore loads between different shrub species from the genus *Piper* show that even congeneric plant species with similar architecture and growing at neighboring sites are not necessarily comparable in terms of their herbivore communities. This is an important factor that has to be taken into account when planning studies on insect herbivores, or when attempting to extrapolate from field studies on selected plants to the ecosystem level.

Species richness, diversity and dominance structure of the true herbivore fraction of the caterpillars were covered in the final part of this study (Chapter 7). Overall species richness was high, with 191 herbivorous caterpillar species recorded on the 16 shrub species of this study. Raw species numbers varied strongly between plant species, with a more than 40fold difference between the most species rich (on *Baccharis latifolia*, Asteraceae) and the most species poor community (on *Piper carpunya*). While most of these differences were strongly attenuated after rarefaction to the largest shared shrub volume, the difference between the richest and poorest shrub species in terms of associated herbivore richness was still more than 15fold. Herbivore communities on Asteraceae were generally more species rich than those on *Piper* shrubs. Community diversity (calculated as exponential Shannon index, a measure of effective number of species in a community; Jost 2006) was similar on most *Piper*

species, with most values between 3 and 7. Only those communities with low sample sizes ranked notably higher, but this is likely be a sampling effect. Two of the Asteraceae species (*Ageratina dendroides* and *B. latifolia*) featured much larger effective species numbers of 34 and 20, respectively. The third representative of the Asteraceae, *Erato polymnioides*, featured a low effective species number similar to those of most studied *Piper* species, as its community was strongly dominated by gregarious early instars of one single species, *Altinote dicaeus albofasciata* (Nymphalidae). The data featured a notable, though not significant trend for local abundance of shrub species positively influencing the species richness of the hosted caterpillar community, as suggested by Marquis & Braker (1994). Also a tendency for shrubs with wider distribution to support more species rich herbivore communities (e.g. Kelly & Southwood 1999) was observed in Asteraceae, but not in Piperaceae. However, the most influential factor governing species richness of herbivore communities is expected to be plant (chemical) herbivore defense. While data on plant chemistry is unfortunately not available for the species studied here – as for the vast majority of tropical plants – observed species richness patterns appear to point in this direction. Lowest species numbers were observed on often chemically well defended (Bernard et al. 1995, Dyer & Palmer 2004) *Piper* species, followed by communities on *Ageratina dendroides*, a member of the Eupatorieae, which often feature pyrrolizidine-alkaloids (Rizk 1991), and *Erato polymnioides*, a latex producing species (Moran & Funk 2006). The plant species with the highest number of herbivore species in this study, *Baccharis latifolia*, is also the only one for which no indication was found hinting at any kind of noteworthy anti-herbivore defense.

Dominance values for caterpillar communities (calculated as modified Berger-Parker indices) varied more strongly and more consistently between Asteraceae species than between *Piper* species. While first order dominance also varied strongly between *Piper* species and was on average very similar to the values found on Asteraceae, second and third order dominance (i.e. cumulating the dominance of the two or three most common species, respectively) was notably more similar between *Piper* species and on average also higher than on Asteraceae. The two most dominant caterpillar species accounted for 58% or more of the communities on 12 of the 13 *Piper* species.

These results regarding community structure mostly support the conclusion of Novotny et al. (2002) that herbivore communities on individual tropical plant species are usually predictably simple, in that they are dominated by few abundant specialists. However, they also show notable examples to the contrary, especially in the case of Asteraceae shrubs that grow in more disturbed habitat conditions.

Regarding the question of host specialization, our results lean more towards those of Dyer et al. (2007) than Novotny et al. (2006), as at least on *Piper* shrubs high degrees of specialization were observed. However, the notably lower degree of host specialization on Asteraceae shrubs – which would likely decrease even further if more species of this family were studied – also clearly showed that results strongly depend on the selected plant taxa. The large fraction of highly specialized caterpillars on *Piper* mainly consisted of representatives of one single species-rich clade, the geometrid genus *Eois*. They were the dominant herbivores on almost all *Piper* species covered in this study, as was also reported in other studies on Neotropical *Piper* herbivores (Connahs et al. 2009, Rodríguez-Castañeda et al. 2010). These moths are known to be highly host specific and largely confined to host plants from the family Piperaceae, with which they likely have undergone a long history of co-evolution (Strutzenberger & Fiedler 2011). Most observed *Eois* species were only recorded on a single species of *Piper*, despite the fact that all but the rarest *Piper* species that occur in the studied habitats were covered in this study. Such high specialization also renders these species particularly vulnerable to the threat of co-extinction if their host species are lost (Koh et al. 2004), a factor of particular importance in the Andes of Ecuador, which suffer from one of the highest deforestation rates in the world (Mosandl et al. 2008). Further details on phylogenetic patterns of their host plant use have recently been revealed in a case study co-authored by the author of this thesis (Strutzenberger et al. 2010).

These results offer an insight into the ecology of host-herbivore interactions in a megadiverse region in southern Ecuador. They are a first step to fill a gap between surveys of communities of adult moths and of vascular plants, which have been performed in the study area over the last decade, and improve our general understanding of the connection between both. Thereby, they also form an important contribution to baseline data for upcoming modeling studies on the impact of ongoing climate change and habitat destruction on this ecosystem.

Despite this progress, however, much remains to be done. Further topics to be investigated in the coming years will be: (1) identifying patterns of beta diversity and community overlap amongst Andean herbivorous insects at various scales, (2) studying the ecological role and diversity patterns of the non-herbivorous guild that turned out to be unexpectedly rich, (3) increasing the coverage of plant taxa, and (4) expanding the elevational range to study effects of altitude on diversity and structure of caterpillar communities. Overall, this study provides a first step from documenting and understanding the species

richness and diversity of herbivorous insects in a biodiversity hotspot to their interactive diversities (Ings et al. 2009) relative to host-plants.

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10. Curriculum vitae

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1988 - 1992 Primary school in Pressath, Germany.

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2002 - 2005 Study of Biology at the University of Bayreuth, Germany.

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11. Appendix

Table A1: Lepidoptera species × plant species matrix of herbivorous Lepidoptera collected on 16 shrub species from 2007 to 2009 in the Reserva Biológica San Francisco with abundance classes as follows: not found (-), found once (**I**), 2 to 5 individuals (**II**), 6 to 15 individuals (**III**), 16 to 50 individuals (**IV**), 51 or more individuals (**V**). Names in parentheses are tribes. Species codes follow Hilt (2005) for Erebidae: Arctiinae (beginning with **A**), Brehm et al. (2005) for Geometridae (**G**) with exception of *Eois* species, where those of Strutzenberger et al. (2011) are given if applicable (**E**). For all species not covered in these publications or not reliably assignable to those taxa, new species codes were assigned (**L**). Codes for *Eois* species according to Brehm et al. (2005) are listed in Strutzenberger et al. (2011). For references see chapter 7. **indet.**: unidentified family / genus; **sp.**: unidentified species; **sp. nr.**: closely resembles described species, but likely not conspecific (higher taxa only marked **nr.**); **cf.**: preliminary identification of higher taxon.

Family Genus / (Tribe)	Species	Species code	<i>A. dendroides</i>	<i>B. latifolia</i>	<i>E. polymnioides</i>	<i>P. arboreum</i>	<i>P. carpanya</i>	<i>P. densiciliatum</i>	<i>P. obliquum</i>	<i>P. perareolatum</i>	<i>P. subscutatum</i>	<i>Piper I</i>	<i>Piper III</i>	<i>Piper V</i>	<i>Piper VIII</i>	<i>Piper IX</i>	<i>Piper XII</i>	<i>Piper XV</i>
Apateledidae																		
indet.	sp.	L1	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	-
Bucculatricidae																		
indet.	sp.	L114	-	IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crambidae																		
<i>Aethiophysa</i>	sp.	L2	-	IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Blepharomastix</i>	sp.	L3	II	II	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pleuroptya</i>	sp.	L4	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L5	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L6	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erebidae																		
<i>Amastus</i>	<i>aconia</i>	A1	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Amastus</i>	<i>coccinator</i>	A7	II	II	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bertholdia</i>	<i>griseopalpis</i>	A71	-	-	II	-	-	-	-	-	-	I	-	-	II	-	-	I
<i>Dysschema</i>	<i>semirufa</i>	A84	-	-	IV	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Melese</i>	<i>nebulosa</i>	A203	-	-	II	II	-	-	II	I	I	II	-	II	-	-	-	II
<i>Pelochyta</i>	sp. nr. <i>lystra</i>	A49	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pelochyta</i>	sp.	A214	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I
<i>Phaegoptera</i>	sp.	L7	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L8	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
Gelechiidae																		
indet.	sp.	L9	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geometridae																		
<i>Apiciopsis</i>	sp.	G2168	-	II	I	-	-	-	-	-	-	-	-	I	-	-	-	-
<i>Bonatea</i>	<i>viridilinea</i>	G76	-	II	II	-	-	-	-	-	-	-	I	I	-	-	-	-
<i>Bryoptera</i>	sp. nr. <i>friaria</i>	G268	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cargolia</i>	sp.	L10	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Charca</i>	sp.	G307	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chloropteryx</i>	<i>opalaria</i>	G358	II	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cirsodes</i>	sp. nr. <i>acuminata</i>	G294	-	II	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyclophora</i>	<i>acutaria</i>	G29	III	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eois</i>	<i>angulata</i>	E032	-	-	-	-	-	-	-	II	-	-	I	-	-	-	-	-

Family Genus / (Tribe)	Species	Species code	<i>A. dendroides</i>	<i>B. latifolia</i>	<i>E. polynioides</i>	<i>P. arboreum</i>	<i>P. carponya</i>	<i>P. densiciliatum</i>	<i>P. obliquum</i>	<i>P. perareolatum</i>	<i>P. subscutatum</i>	<i>Piper I</i>	<i>Piper III</i>	<i>Piper V</i>	<i>Piper VIII</i>	<i>Piper IX</i>	<i>Piper XII</i>	<i>Piper XV</i>
<i>Eois</i>	<i>basaliata</i>	G401	-	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-
<i>Eois</i>	<i>encina</i> ^a	E049	-	-	-	-	-	-	-	-	-	-	V	-	-	-	-	-
<i>Eois</i>	<i>mediostrigata</i>	G413	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>catana</i>	E062	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>encina</i>	G412	-	-	-	-	V	-	-	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>fuscosa</i>	E039	-	-	-	II	-	-	-	-	-	-	IV	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>golosata</i>	G374	-	-	-	-	-	-	-	-	-	-	-	-	-	III	-	-
<i>Eois</i>	sp. nr. <i>goodmanii</i>	E052	-	-	-	IV	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>goodmanii</i>	E055	-	-	-	-	-	-	-	-	-	-	III	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>goodmanii</i>	L12	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>goodmanii</i>	L13	-	-	-	IV	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>goodmanii</i>	L14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	V	-
<i>Eois</i>	sp. nr. <i>goodmanii</i>	L15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	II	-
<i>Eois</i>	sp. nr. <i>ignefumata</i>	E080	-	-	-	-	-	-	II	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>muscosa</i>	E056	-	-	-	-	-	-	-	-	-	-	-	-	II	-	-	-
<i>Eois</i>	sp. nr. <i>muscosa</i>	L16	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>nigrosticta</i>	L17	-	-	-	-	-	-	-	-	-	-	-	II	-	-	-	-
<i>Eois</i>	sp. nr. <i>nigrosticta</i>	L21	-	-	-	-	-	III	-	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>odatis</i>	E030	-	-	-	-	-	-	-	-	-	V	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>olivacea</i>	E058	-	-	-	-	-	-	-	-	-	-	IV	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>olivacea</i>	E059	-	-	-	-	-	-	-	-	-	V	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>olivacea</i>	E060	-	-	-	-	-	-	-	V	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>olivacea</i>	L19	-	-	-	-	-	-	-	-	-	-	-	IV	-	-	-	-
<i>Eois</i>	sp. nr. <i>olivaria</i>	E075	-	-	-	-	-	-	-	III	-	-	-	-	-	-	-	-
<i>Eois</i>	sp. nr. <i>pallidicosta</i>	E050	-	-	-	-	-	-	-	-	-	-	-	-	-	-	III	-
<i>Eois</i>	sp. nr. <i>pallidicosta</i>	E090	-	-	-	-	-	-	-	-	-	-	-	-	-	-	V	-
<i>Eois</i>	sp. nr. <i>planetaria</i>	E019	-	-	-	I	-	-	-	-	-	-	-	-	-	-	II	-
<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	-	-	-	-	-	-	-	-	-	V	-	III	-	I	-	-
<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	-	-	-	-	-	-	-	-	-	V	-	-	III	-	-	-
<i>Eois</i>	sp. nr. <i>tegularia</i>	E111	-	-	-	-	-	-	-	-	-	-	-	-	-	IV	-	-
<i>Eois</i>	sp. nr. <i>tegularia</i>	L18	-	-	-	-	-	-	-	-	-	-	-	-	-	II	-	-
<i>Eois</i>	sp.	E026	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-
<i>Eois</i>	sp.	E029	-	-	-	-	-	-	-	-	-	-	-	IV	-	-	-	-
<i>Eois</i>	sp.	E077	-	-	-	-	-	-	IV	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp.	E093	-	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-
<i>Eois</i>	sp.	G2117	-	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-
<i>Eois</i>	sp.	G2126	-	-	-	-	-	-	III	-	-	-	-	-	-	-	-	-
<i>Eois</i>	sp.	L11	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
<i>Eois</i>	sp.	L20	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-
<i>Eupithecia</i>	<i>bullata</i>	G705	II	III	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	<i>higa</i>	G677	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp. nr. <i>penicilla</i>	G561	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp.	L22	-	III	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp.	L23	II	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp.	L24	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-

Family Genus / (Tribe)	Species	Species code	<i>A. dendroides</i>	<i>B. latifolia</i>	<i>E. polynioides</i>	<i>P. arboreum</i>	<i>P. carponya</i>	<i>P. densiciliatum</i>	<i>P. obliquum</i>	<i>P. perareolatum</i>	<i>P. subscutatum</i>	<i>Piper I</i>	<i>Piper III</i>	<i>Piper V</i>	<i>Piper VIII</i>	<i>Piper IX</i>	<i>Piper XII</i>	<i>Piper XV</i>
<i>Eupithecia</i>	sp.	L25	II	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp.	L26	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp.	L27	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eupithecia</i>	sp.	L28	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Glena</i>	sp. nr. <i>juga</i>	G265	II	III	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hygrochroma</i>	sp. nr. <i>olivinaria</i>	G939	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Iridopsis</i>	<i>litharia</i>	G263	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Iridopsis</i>	<i>scolanocala</i>	G259	II	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Iridopsis</i>	<i>subnigrata</i>	G262	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Iridopsis</i>	sp. nr. <i>litharia</i>	L29	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ischnopteris</i>	<i>brehmi</i>	G308	-	II	III	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ischnopteris</i>	sp.	G1104	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	-
<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	IV	III	II	II	-	-	-	II	I	-	III	III	-	-	-	-
<i>Isochromodes</i>	sp. nr. <i>polvoreata</i>	G1124	-	I	-	-	-	-	-	-	-	-	I	-	-	-	-	-
<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	II	IV	I	I	-	-	-	-	II	-	-	-	-	-	-	-
<i>Melinodes</i>	<i>detersaria</i>	G160	-	II	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mesedra</i>	sp. nr. <i>confinis</i>	G178	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mesedra</i>	sp.	G180	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microxydia</i>	sp. nr. <i>ruficoma</i>	G695	-	V	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mychonia</i>	<i>violacea</i>	G921	II	III	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	III	-	-	II	-	I	-	II	-	III	III	II	II	-	-	-
<i>Nephodia</i>	sp. nr. <i>organa</i>	G204	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-
<i>Oxydia</i>	<i>geminata</i>	G60	-	II	II	-	-	-	-	-	-	-	-	-	-	-	I	-
<i>Oxydia</i>	<i>scriptipennaria</i>	G72	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxydia</i>	<i>trychiata</i>	G58	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxydia</i>	sp.	L30	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxydia</i>	sp.	L31	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pero</i>	<i>homodoxa</i>	G249	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Perusia</i>	<i>praecisaria</i>	G812	I	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Phyle</i>	<i>versatile</i>	G326	-	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Physocleora</i>	sp. nr. <i>accessilinea</i>	G280	-	III	II	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Physocleora</i>	sp. nr. <i>curvifera</i>	G905	-	-	II	II	-	-	-	-	-	I	-	-	-	-	-	-
<i>Physocleora</i>	sp. nr. <i>warreni</i>	G1123	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Physocleora</i>	sp.	L32	-	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sabulodes</i>	<i>caberata oberthuri</i>	G93	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sabulodes</i>	<i>colombiata</i>	G2034	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sabulodes</i>	<i>thermidora</i>	G125	I	IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Semiothisa</i>	<i>regressa</i>	G319	-	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Synchlora</i>	<i>dependens</i>	G611	-	III	I	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L33	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L34	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L35	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L36	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L37	-	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-

Family Genus / (Tribe)	Species	Species code	<i>A. dendroides</i>	<i>B. latifolia</i>	<i>E. polynnioides</i>	<i>P. arboreum</i>	<i>P. carpunya</i>	<i>P. densiciliatum</i>	<i>P. obliquum</i>	<i>P. perareolatum</i>	<i>P. subscutatum</i>	<i>Piper I</i>	<i>Piper III</i>	<i>Piper V</i>	<i>Piper VIII</i>	<i>Piper IX</i>	<i>Piper XII</i>	<i>Piper XV</i>
Hesperiidae																		
<i>Quadrus</i>	sp.	L38	-	-	-	-	-	-	-	-	-	-	III	-	-	-	-	-
indet.	sp.	L39	-	-	-	-	-	-	-	-	II	-	-	-	-	-	-	-
Limacodidae																		
indet.	sp.	L40	-	-	-	-	-	-	-	-	-	-	-	-	II	-	-	-
Lycaenidae																		
<i>Rhamma</i>	<i>arria</i>	L41	I	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L42	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L43	I	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Megalopygidae																		
indet.	sp.	L44	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Noctuidae																		
<i>Ctenoplusia</i>	<i>oxygramma</i>	L45	-	IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hypnotype</i>	<i>placens</i>	L46	-	IV	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spodoptera</i>	<i>eridania</i>	L47	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L48	-	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L49	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L50	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nymphalidae																		
<i>Altinote</i>	<i>dicaeus albofasciata</i>	L51	-	-	V	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Memphis</i>	<i>pseudiphis</i>	L52	-	-	-	I	-	-	-	-	-	I	-	-	-	-	-	-
Pterophoridae																		
cf. <i>Hellinsia</i>	sp.	L53	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Platyptilia</i>	<i>thyellopa</i>	L54	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thyrididae																		
indet.	sp.	L55	-	-	-	II	-	-	-	-	-	-	II	-	-	-	-	-
Tortricidae																		
nr. <i>Amorbia</i>	sp.	L56	II	II	-	-	-	-	-	I	-	-	-	-	-	-	-	-
<i>Anacrusis</i>	sp.	L57	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	-
<i>Anopinella</i>	sp.	L58	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nr. <i>Archipimima</i>	sp.	L59	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	I	II	I	-	-	-	-	I	-	-	-	-	-	-	-	I
<i>Argyrotaenia</i>	sp. nr. <i>subchordillerae</i>	L64	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Argyrotaenia</i>	sp.	L60	-	I	-	-	-	-	-	-	-	-	-	-	-	I	-	-
<i>Argyrotaenia</i>	sp.	L61	I	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Argyrotaenia</i>	sp.	L63	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nr. <i>Holoptygma</i>	sp.	L65	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nr. <i>Netechma</i>	sp.	L66	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
nr. <i>Romanaria</i>	sp.	L67	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
cf. <i>Seticosta</i>	sp.	L68	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sisurcana</i>	sp. nr. <i>fasciana</i>	L70	-	-	-	-	II	I	-	-	I	-	-	-	-	-	-	-
<i>Sisurcana</i>	sp. nr. <i>sanguinoventer</i>	L69	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sisurcana</i>	sp. nr. <i>topina</i>	L72	-	-	-	-	-	II	-	-	-	-	-	-	-	-	-	-
<i>Sisurcana</i>	sp. nr. <i>triangulifera</i>	L73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I
<i>Sisurcana</i>	sp.	L71	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Family Genus / (Tribe)	Species	Species code	<i>A. dendroides</i>	<i>B. latifolia</i>	<i>E. polynnioides</i>	<i>P. arboreum</i>	<i>P. carponya</i>	<i>P. densiciliatum</i>	<i>P. obliquum</i>	<i>P. perareolatum</i>	<i>P. subscutatum</i>	<i>Piper I</i>	<i>Piper III</i>	<i>Piper V</i>	<i>Piper VIII</i>	<i>Piper IX</i>	<i>Piper XII</i>	<i>Piper XV</i>
(Euliini)	sp.	L74	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
(Euliini)	sp.	L75	-	-	I	-	-	-	I	-	-	-	-	II	I	I	-	-
(cf. Euliini)	sp.	L76	-	-	-	-	-	-	-	-	-	I	-	-	II	-	-	-
(Polyorthini)	sp.	L77	-	-	-	-	-	-	-	-	-	II	-	-	II	II	-	-
(Sparganothini)	sp.	L78	I	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L79	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L80	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L81	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
indet.	sp.	L82	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L83	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L84	-	III	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L85	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L86	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-
indet.	sp.	L87	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L88	-	I	-	-	-	-	-	II	III	-	-	-	-	-	III	II
indet.	sp.	L89	-	I	-	-	-	-	-	-	-	-	I	-	-	-	-	-
indet.	sp.	L90	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L91	-	-	-	-	-	I	-	-	-	-	-	-	-	I	-	-
indet.	sp.	L92	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-
indet.	sp.	L93	-	I	-	-	-	-	-	I	-	I	-	-	-	-	-	-
indet.	sp.	L94	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L95	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
indet.	sp.	L96	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L97	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L98	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L99	-	-	II	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L100	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-
Lep. indet.																		
indet.	sp.	L101	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L102	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L103	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
indet.	sp.	L104	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L105	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L106	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
indet.	sp.	L107	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L108	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L109	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L110	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L111	-	-	-	-	-	-	-	-	-	-	-	-	-	I	-	-
indet.	sp.	L112	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
indet.	sp.	L113	I	II	-	-	-	-	-	-	-	-	-	-	-	-	-	-

a: Listed in Strutzenberger et al. (2011) as *Eois* sp. nr. *encina* 412 sensu Brehm et al. (2005), but likely conspecific with *E. encina* 378 sensu Brehm et al. (2005).

b: Likely a species complex consisting of several closely related species.

Table A2: List of Genbank accession numbers for all CO1 sequences used for species assignment in this study. Species codes follow Hilt (2005) for Erebidae: Arctiinae (beginning with **A**), Brehm et al. (2005) for Geometridae (**G**) with exception of *Eois* species, where those of Strutzenberger et al. (2011) are given if applicable (**E**). For all species not covered in these publications or not reliably assignable to those taxa, new species codes were assigned (**L**). Codes for *Eois* species according to Brehm et al. (2005) are listed in Strutzenberger et al. (2011). **indet.**: unidentified family / genus; **sp.**: unidentified species; **sp. nr.**: closely resembles described species, but likely not conspecific (higher taxa only marked **nr.**); **cf.**: preliminary identification of higher taxon.

Family	Genus / (Tribe)	Species	Species code	Genbank accession number
Apatelodidae	indet.	sp.	L1	JF729818
Crambidae	<i>Aethiophysa</i>	sp.	L2	JF729511
Crambidae	<i>Aethiophysa</i>	sp.	L2	JF729690
Crambidae	<i>Blepharomastix</i>	sp.	L3	JF729521
Crambidae	<i>Blepharomastix</i>	sp.	L3	JF729654
Crambidae	indet.	sp.	L5	JF729524
Crambidae	indet.	sp.	L6	JF729753
Crambidae	<i>Pleuroptya</i>	sp.	L4	JF729513
Erebidae	<i>Amastus</i>	<i>aconia</i>	A1	JF729593
Erebidae	<i>Amastus</i>	<i>coccinator</i>	A7	JF729884
Erebidae	<i>Amastus</i>	<i>coccinator</i>	A7	JF729885
Erebidae	<i>Amastus</i>	<i>coccinator</i>	A7	JF729903
Erebidae	<i>Bertholdia</i>	<i>griseopalpis</i>	A71	JF729776
Erebidae	<i>Bertholdia</i>	<i>griseopalpis</i>	A71	JF729851
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729619
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729621
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729632
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729637
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729820
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729849
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729874
Erebidae	<i>Melese</i>	<i>nebulosa</i>	A203	JF729883
Erebidae	<i>Pelochyta</i>	sp. nr. <i>lystra</i>	A49	JF729858
Gelechiidae	indet.	sp.	L9	JF729824
Geometridae	<i>Apiciopsis</i>	sp.	G2168	JF729622
Geometridae	<i>Apiciopsis</i>	sp.	G2168	JF729800
Geometridae	<i>Bonatea</i>	<i>viridilinea</i>	G76	JF729606
Geometridae	<i>Bonatea</i>	<i>viridilinea</i>	G76	JF729659
Geometridae	<i>Charca</i>	sp.	G307	JF729579
Geometridae	<i>Chloropteryx</i>	<i>opalaria</i>	G358	JF729882
Geometridae	<i>Cyclophora</i>	<i>acutaria</i>	G29	JF729638
Geometridae	<i>Eois</i>	<i>basaliata</i>	G401	JF729774
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729501
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729605
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729653
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729674
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729736
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729749
Geometridae	<i>Eois</i>	<i>encina</i> ^a	E049	JF729757
Geometridae	<i>Eois</i>	<i>mediostrigata</i>	G413	JF729848
Geometridae	<i>Eois</i>	sp. nr. <i>encina</i>	G412	JF729616
Geometridae	<i>Eois</i>	sp. nr. <i>fucosa</i>	E039	JF729627
Geometridae	<i>Eois</i>	sp. nr. <i>fucosa</i>	E039	JF729667
Geometridae	<i>Eois</i>	sp. nr. <i>fucosa</i>	E039	JF729703
Geometridae	<i>Eois</i>	sp. nr. <i>fucosa</i>	E039	JF729900
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	E052	JF729499
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	E052	JF729614
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	E052	JF729826

Family	Genus / (Tribe)	Species	Species code	Genbank accession number
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	E052	JF729828
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	E055	JF729612
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	L13	JF729742
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	L13	JF729867
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	L14	JF729495
Geometridae	<i>Eois</i>	sp. nr. <i>goodmanii</i>	L14	JF729620
Geometridae	<i>Eois</i>	sp. nr. <i>muscosa</i>	E056	JF729734
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729493
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729502
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729665
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729668
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729671
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729673
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729684
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729699
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729704
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729706
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729710
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729711
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729714
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729720
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729731
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729739
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729752
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729766
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729771
Geometridae	<i>Eois</i>	sp. nr. <i>odatis</i>	E030	JF729832
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E058	JF729663
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E058	JF729678
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E059	JF729623
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E059	JF729683
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E059	JF729717
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E059	JF729738
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	E060	JF729639
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	L19	JF729650
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	L19	JF729670
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	L19	JF729725
Geometridae	<i>Eois</i>	sp. nr. <i>olivacea</i>	L19	JF729730
Geometridae	<i>Eois</i>	sp. nr. <i>olivaria</i>	E075	JF729611
Geometridae	<i>Eois</i>	sp. nr. <i>pallidicosta</i>	E050	JF729591
Geometridae	<i>Eois</i>	sp. nr. <i>pallidicosta</i>	E050	JF729853
Geometridae	<i>Eois</i>	sp. nr. <i>pallidicosta</i>	E090	JF729494
Geometridae	<i>Eois</i>	sp. nr. <i>pallidicosta</i>	E090	JF729754
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729492
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729497
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729503
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729504
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729505
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729517
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729617
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729677
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729693
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729694
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729700
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729702
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729705
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729709

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Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729712
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729715
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729716
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729718
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729722
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729723
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729732
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729733
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729735
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729740
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729746
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729747
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729763
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729769
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729770
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729773
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729822
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E031	JF729831
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729491
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729496
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729498
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729500
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729516
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729518
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729519
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729573
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729590
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729626
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729672
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729685
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729691
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729692
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729697
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729698
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729708
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729719
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729721
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729724
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729726
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729728
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729729
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729741
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729743
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729750
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729751
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729772
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729792
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729804
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729810
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729834
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729836
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729837
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729847
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E067	JF729866
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E111	JF729523
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E111	JF729529
Geometridae	<i>Eois</i>	sp. nr. <i>tegularia</i>	E111	JF729607

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Geometridae	<i>Eois</i>	sp.	E026	JF729795
Geometridae	<i>Eois</i>	sp.	E029	JF729656
Geometridae	<i>Eois</i>	sp.	E029	JF729681
Geometridae	<i>Eois</i>	sp.	E029	JF729696
Geometridae	<i>Eois</i>	sp.	E029	JF729713
Geometridae	<i>Eois</i>	sp.	E029	JF729727
Geometridae	<i>Eois</i>	sp.	E029	JF729737
Geometridae	<i>Eois</i>	sp.	E029	JF729744
Geometridae	<i>Eois</i>	sp.	E029	JF729745
Geometridae	<i>Eois</i>	sp.	E029	JF729764
Geometridae	<i>Eois</i>	sp.	E029	JF729815
Geometridae	<i>Eois</i>	sp.	E029	JF729835
Geometridae	<i>Eois</i>	sp.	E029	JF729842
Geometridae	<i>Eois</i>	sp.	E029	JF729872
Geometridae	<i>Eois</i>	sp.	E077	JF729864
Geometridae	<i>Eois</i>	sp.	E093	JF729701
Geometridae	<i>Eois</i>	sp.	E093	JF729791
Geometridae	<i>Eois</i>	sp.	G2117	JF729525
Geometridae	<i>Eois</i>	sp.	G2117	JF729860
Geometridae	<i>Eois</i>	sp.	L20	JF729520
Geometridae	<i>Eupithecia</i>	<i>bullata</i>	G705	JF729509
Geometridae	<i>Eupithecia</i>	<i>bullata</i>	G705	JF729551
Geometridae	<i>Eupithecia</i>	<i>bullata</i>	G705	JF729564
Geometridae	<i>Eupithecia</i>	<i>bullata</i>	G705	JF729575
Geometridae	<i>Eupithecia</i>	<i>bullata</i>	G705	JF729707
Geometridae	<i>Eupithecia</i>	<i>bullata</i>	G705	JF729838
Geometridae	<i>Eupithecia</i>	<i>higa</i>	G677	JF729538
Geometridae	<i>Eupithecia</i>	sp. nr. <i>penicilla</i>	G561	JF729546
Geometridae	<i>Eupithecia</i>	sp. nr. <i>penicilla</i>	G561	JF729563
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729531
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729532
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729539
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729545
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729556
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729652
Geometridae	<i>Eupithecia</i>	sp.	L22	JF729873
Geometridae	<i>Eupithecia</i>	sp.	L23	JF729558
Geometridae	<i>Eupithecia</i>	sp.	L24	JF729876
Geometridae	<i>Eupithecia</i>	sp.	L25	JF729561
Geometridae	<i>Eupithecia</i>	sp.	L25	JF729861
Geometridae	<i>Eupithecia</i>	sp.	L26	JF729544
Geometridae	<i>Eupithecia</i>	sp.	L26	JF729552
Geometridae	<i>Eupithecia</i>	sp.	L26	JF729555
Geometridae	<i>Eupithecia</i>	sp.	L27	JF729646
Geometridae	<i>Eupithecia</i>	sp.	L28	JF729537
Geometridae	<i>Eupithecia</i>	sp.	L28	JF729559
Geometridae	<i>Glena</i>	sp. nr. <i>juga</i>	G265	JF729586
Geometridae	<i>Glena</i>	sp. nr. <i>juga</i>	G265	JF729695
Geometridae	<i>Glena</i>	sp. nr. <i>juga</i>	G265	JF729817
Geometridae	<i>Iridopsis</i>	<i>scolancala</i>	G259	JF729687
Geometridae	<i>Iridopsis</i>	<i>scolancala</i>	G259	JF729868
Geometridae	<i>Iridopsis</i>	<i>scolancala</i>	G259	JF729890
Geometridae	<i>Ischnopteris</i>	<i>brehmi</i>	G308	JF729588
Geometridae	<i>Ischnopteris</i>	<i>brehmi</i>	G308	JF729594
Geometridae	<i>Ischnopteris</i>	<i>brehmi</i>	G308	JF729595
Geometridae	<i>Ischnopteris</i>	<i>brehmi</i>	G308	JF729662
Geometridae	<i>Ischnopteris</i>	<i>brehmi</i>	G308	JF729765

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Geometridae	<i>Ischnopteris</i>	sp.	G1104	JF729578
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729584
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729615
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729635
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729642
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729682
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729778
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729780
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729782
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729783
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729846
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729886
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729887
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729888
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729889
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729891
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729892
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729893
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729894
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729895
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729896
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729897
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729898
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729901
Geometridae	<i>Isochromodes</i>	sp. nr. <i>extimaria</i> ^b	G112	JF729902
Geometridae	<i>Isochromodes</i>	sp. nr. <i>polvoreata</i>	G1124	JF729644
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729577
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729592
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729624
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729689
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729781
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729801
Geometridae	<i>Melanolophia</i>	<i>reducta meridiana</i>	G269	JF729814
Geometridae	<i>Mesedra</i>	sp. nr. <i>confinis</i>	G178	JF729825
Geometridae	<i>Microxydia</i>	sp. nr. <i>ruficomma</i>	G695	JF729676
Geometridae	<i>Mychonia</i>	<i>violacea</i>	G921	JF729583
Geometridae	<i>Mychonia</i>	<i>violacea</i>	G921	JF729657
Geometridae	<i>Mychonia</i>	<i>violacea</i>	G921	JF729768
Geometridae	<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	JF729628
Geometridae	<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	JF729658
Geometridae	<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	JF729680
Geometridae	<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	JF729688
Geometridae	<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	JF729788
Geometridae	<i>Nephodia</i>	sp. nr. <i>astyochiodes</i>	G299	JF729797
Geometridae	<i>Nephodia</i>	sp. nr. <i>organa</i>	G204	JF729854
Geometridae	<i>Oxydia</i>	<i>geminata</i>	G60	JF729585
Geometridae	<i>Oxydia</i>	<i>geminata</i>	G60	JF729636
Geometridae	<i>Oxydia</i>	<i>geminata</i>	G60	JF729643
Geometridae	<i>Oxydia</i>	<i>geminata</i>	G60	JF729679
Geometridae	<i>Oxydia</i>	<i>geminata</i>	G60	JF729840
Geometridae	<i>Oxydia</i>	<i>scriptipennaria</i>	G72	JF729869
Geometridae	<i>Oxydia</i>	<i>trychiata</i>	G58	JF729813
Geometridae	<i>Perusia</i>	<i>praecisaria</i>	G812	JF729880
Geometridae	Phyle	<i>versatile</i>	G326	JF729640
Geometridae	<i>Physocleora</i>	sp. nr. <i>accessilinea</i>	G280	JF729576
Geometridae	<i>Physocleora</i>	sp. nr. <i>curvifera</i>	G905	JF729603
Geometridae	<i>Physocleora</i>	sp.	L32	JF729634

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Geometridae	<i>Sabulodes</i>	<i>caberata oberthuri</i>	G93	JF729601
Geometridae	<i>Sabulodes</i>	<i>caberata oberthuri</i>	G93	JF729602
Geometridae	<i>Sabulodes</i>	<i>caberata oberthuri</i>	G93	JF729604
Geometridae	<i>Sabulodes</i>	<i>caberata oberthuri</i>	G93	JF729609
Geometridae	<i>Sabulodes</i>	<i>caberata oberthuri</i>	G93	JF729863
Geometridae	<i>Sabulodes</i>	<i>colombiata</i>	G2034	JF729827
Geometridae	<i>Sabulodes</i>	<i>thermidora</i>	G125	JF729598
Geometridae	<i>Sabulodes</i>	<i>thermidora</i>	G125	JF729777
Geometridae	indet.	sp.	L36	JF729844
Geometridae	indet.	sp.	L36	JF729845
Hesperiidae	<i>Quadrus</i>	sp.	L38	JF729580
Hesperiidae	<i>Quadrus</i>	sp.	L38	JF729600
Hesperiidae	<i>Quadrus</i>	sp.	L38	JF729760
Hesperiidae	<i>Quadrus</i>	sp.	L38	JF729802
Hesperiidae	indet.	sp.	L39	JF729587
Hesperiidae	indet.	sp.	L39	JF729871
Lycaenidae	<i>Rhamma</i>	<i>arria</i>	L41	JF729610
Lycaenidae	<i>Rhamma</i>	<i>arria</i>	L41	JF729645
Lycaenidae	<i>Rhamma</i>	<i>arria</i>	L41	JF729878
Lycaenidae	indet.	sp.	L42	JF729843
Lycaenidae	indet.	sp.	L43	JF729881
Noctuidae	<i>Ctenoplusia</i>	<i>oxygramma</i>	L45	JF729666
Noctuidae	<i>Hypnotype</i>	<i>placens</i>	L46	JF729599
Noctuidae	<i>Hypnotype</i>	<i>placens</i>	L46	JF729625
Noctuidae	<i>Spodoptera</i>	<i>eridania</i>	L47	JF729596
Noctuidae	indet.	sp.	L49	JF729631
Noctuidae	indet.	sp.	L49	JF729648
Noctuidae	indet.	sp.	L49	JF729651
Noctuidae	indet.	sp.	L50	JF729597
Nymphalidae	<i>Memphis</i>	<i>pseudiphis</i>	L52	JF729581
Nymphalidae	<i>Memphis</i>	<i>pseudiphis</i>	L52	JF729589
Pterophoridae	cf. <i>Hellinsia</i>	sp.	L53	JF729553
Pterophoridae	cf. <i>Hellinsia</i>	sp.	L53	JF729669
Pterophoridae	<i>Platyptilia</i>	<i>thyellopa</i>	L54	JF729533
Pterophoridae	<i>Platyptilia</i>	<i>thyellopa</i>	L54	JF729641
Thyrididae	indet.	sp.	L55	JF729655
Thyrididae	indet.	sp.	L55	JF729660
Thyrididae	indet.	sp.	L55	JF729661
Thyrididae	indet.	sp.	L55	JF729862
Tortricidae	<i>Anacrusis</i>	sp.	L57	JF729543
Tortricidae	<i>Anopinella</i>	sp.	L58	JF729536
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	JF729508
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	JF729572
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	JF729767
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	JF729811
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	JF729856
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>artocopa</i>	L62	JF729859
Tortricidae	<i>Argyrotaenia</i>	sp.	L60	JF729540
Tortricidae	<i>Argyrotaenia</i>	sp.	L60	JF729649
Tortricidae	<i>Argyrotaenia</i>	sp.	L61	JF729528
Tortricidae	<i>Argyrotaenia</i>	sp.	L61	JF729562
Tortricidae	<i>Argyrotaenia</i>	sp.	L63	JF729550
Tortricidae	<i>Argyrotaenia</i>	sp.	L63	JF729566
Tortricidae	<i>Argyrotaenia</i>	sp. nr. <i>subchordillerae</i>	L64	JF729560
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>fasciana</i>	L70	JF729554
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>fasciana</i>	L70	JF729629
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>fasciana</i>	L70	JF729755

Family	Genus / (Tribe)	Species	Species code	Genbank accession number
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>fasciana</i>	L70	JF729875
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>fasciana</i>	L70	JF729879
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>sanguiniventer</i>	L69	JF729549
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>topina</i>	L72	JF729535
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>topina</i>	L72	JF729542
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>topina</i>	L72	JF729557
Tortricidae	<i>Sisurcana</i>	sp. nr. <i>triangulifera</i>	L73	JF729565
Tortricidae	<i>Sisurcana</i>	sp.	L69	JF729515
Tortricidae	<i>Sisurcana</i>	sp.	L71	JF729530
Tortricidae	<i>Sisurcana</i>	sp.	L71	JF729809
Tortricidae	nr. <i>Amorbia</i>	sp.	L56	JF729510
Tortricidae	nr. <i>Amorbia</i>	sp.	L56	JF729608
Tortricidae	nr. <i>Amorbia</i>	sp.	L56	JF729756
Tortricidae	nr. <i>Amorbia</i>	sp.	L56	JF729758
Tortricidae	nr. <i>Amorbia</i>	sp.	L56	JF729806
Tortricidae	nr. <i>Archipimima</i>	sp.	L59	JF729522
Tortricidae	nr. <i>Archipimima</i>	sp.	L59	JF729823
Tortricidae	nr. <i>Holoptygma</i>	sp.	L65	JF729507
Tortricidae	nr. <i>Netechma</i>	sp.	L66	JF729570
Tortricidae	nr. <i>Netechma</i>	sp.	L66	JF729829
Tortricidae	nr. <i>Romanaria</i>	sp.	L67	JF729574
Tortricidae	(Euliini)	sp.	L74	JF729547
Tortricidae	(Euliini)	sp.	L75	JF729548
Tortricidae	(Euliini)	sp.	L75	JF729569
Tortricidae	(Euliini)	sp.	L75	JF729571
Tortricidae	(Euliini)	sp.	L75	JF729789
Tortricidae	(cf. Euliini)	sp.	L76	JF729541
Tortricidae	(cf. Euliini)	sp.	L76	JF729613
Tortricidae	(Polyorthini)	sp.	L77	JF729514
Tortricidae	(Polyorthini)	sp.	L77	JF729534
Tortricidae	(Polyorthini)	sp.	L77	JF729796
Tortricidae	(Polyorthini)	sp.	L77	JF729799
Tortricidae	(Polyorthini)	sp.	L77	JF729877
Tortricidae	(Sparganothini)	sp.	L78	JF729526
Tortricidae	(Sparganothini)	sp.	L78	JF729807
Tortricidae	indet.	sp.	L79	JF729798
Tortricidae	indet.	sp.	L81	JF729568
Tortricidae	indet.	sp.	L87	JF729686
Tortricidae	indet.	sp.	L88	JF729506
Tortricidae	indet.	sp.	L88	JF729527
Tortricidae	indet.	sp.	L88	JF729582
Tortricidae	indet.	sp.	L88	JF729748
Tortricidae	indet.	sp.	L88	JF729762
Tortricidae	indet.	sp.	L88	JF729779
Tortricidae	indet.	sp.	L88	JF729803
Tortricidae	indet.	sp.	L88	JF729805
Tortricidae	indet.	sp.	L88	JF729865
Tortricidae	indet.	sp.	L89	JF729512
Tortricidae	indet.	sp.	L90	JF729784
Tortricidae	indet.	sp.	L91	JF729786
Tortricidae	indet.	sp.	L91	JF729794
Tortricidae	indet.	sp.	L92	JF729785
Tortricidae	indet.	sp.	L93	JF729675
Tortricidae	indet.	sp.	L93	JF729808
Tortricidae	indet.	sp.	L93	JF729857
Tortricidae	indet.	sp.	L94	JF729647
Tortricidae	indet.	sp.	L95	JF729630

Family	Genus / (Tribe)	Species	Species code	Genbank accession number
Tortricidae	indet.	sp.	L96	JF729793
Tortricidae	indet.	sp.	L96	JF729841
Tortricidae	indet.	sp.	L97	JF729819
Tortricidae	indet.	sp.	L98	JF729775
Tortricidae	indet.	sp.	L99	JF729761
Tortricidae	indet.	sp.	L99	JF729899
Tortricidae	indet.	sp.	L100	JF729833
Lepidoptera indet.	indet.	sp.	L103	JF729633
Lepidoptera indet.	indet.	sp.	L104	JF729759
Lepidoptera indet.	indet.	sp.	L105	JF729830
Lepidoptera indet.	indet.	sp.	L107	JF729850
Lepidoptera indet.	indet.	sp.	L108	JF729852
Lepidoptera indet.	indet.	sp.	L109	JF729790
Lepidoptera indet.	indet.	sp.	L110	JF729567
Lepidoptera indet.	indet.	sp.	L111	JF729664
Lepidoptera indet.	indet.	sp.	L112	JF729618
Lepidoptera indet.	indet.	sp.	L112	JF729839
Lepidoptera indet.	indet.	sp.	L112	JF729870
Lepidoptera indet.	indet.	sp.	L113	JF729812

a: Listed in Strutzenberger et al. (2011) as *Eois* sp. nr. *encina* 412 sensu Brehm et al. (2005), but likely conspecific with *E. encina* 378 sensu Brehm et al. (2005).

b: Likely a species complex consisting of several closely related species.