

DISSERTATION

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Herbivore communities and folivory under different re-
forestation regimes in the montane rainforest zone of
southern Ecuador

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**Herbivore communities and folivory
under different reforestation regimes
in the montane rainforest zone of
southern Ecuador**



Frontpiece:

Reserva Biológica San Francisco, Ecuador & Sphingid caterpillar near Misahualli, Ecuador

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List of manuscripts with statement of personal contribution

Chapter 2: *Abundance patterns of arthropod dietary guilds across different forms of targeted reforestation in Southern Ecuador.*

M.-O. Adams & K. Fiedler

(prepared for submission to *Biotropica*)

Personal contribution:

- Co-planning and design of surveys
- Field- and lab work (collection, rearing and documentation of samples, taxonomic identification)
- Data analysis in collaboration with Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 3: *Reforestation in the Ecuadorian Andes: Can they help sustain local arthropod diversity?*

M.-O. Adams & K. Fiedler

(prepared for submission to *Biodiversity Conservation*)

Personal contribution:

- Co-planning and design of surveys
- Field- and lab work (collection, rearing and documentation of samples, taxonomic identification)
- Data analysis in collaboration with Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

Chapter 4: *Insect folivory as a function of tree species and surrounding habitat – A case study on targeted reforestation in the Andes of southern Ecuador.*

M.-O. Adams & K. Fiedler

(prepared for submission to *Forest Ecology and Management*)

Personal contribution:

- Co-planning and design of surveys
- Field- and lab work (documentation of sample leaves, supervision of image post-processing)
- Data analysis in collaboration with Konrad Fiedler
- Literature survey, preparation of figures, drafting and co-writing of the manuscript

General abstract

Based on experimental reforestations in the montane rainforest zone of southern Ecuador, we investigated patterns of arthropod abundance, community composition, and the extent of insect folivory as a function of surrounding habitat and host tree species. We focused on native tree species of potential silvicultural interest (i.e. Meliaceae: *Cedrela montana*, Malvaceae: *Heliocarpus americanus*, and Bignoniaceae: *Tabebuia chrysantha*) and compared young reforestations established within locally characteristic anthropogenic habitat types (i.e. abandoned pasture, successional shrub vegetation, and a plantation of exotic *Pinus patula*) with treelets from the regeneration stock of adjacent near-natural rainforest. While the main focus was on phytophagous taxa (i.e. Coleoptera, Hemiptera and juvenile Lepidoptera), we also surveyed key predator guilds (i.e. Coleoptera and Araneae). Furthermore, unusually dry weather conditions during the initial surveys allowed a preliminary appraisal of the impact of drought on insect communities in the study region.

Overall arthropod abundance was relatively low with the exception of three host-specific Hemipteran species which occurred in high densities on reforestation sites. Habitat-specific patterns of herbivore abundance were for the most part similar across taxonomic orders: The highest densities were observed in near natural forest, followed by reforestations beneath *P. patula*, on pasture sites, and among secondary shrub vegetation, respectively. Predatory Coleoptera showed a similar response as phytophagous taxa, while spider density varied relatively little between habitats. Among reforestations, habitat structure (e.g. canopy- or ground-cover) and its effect on microclimate, rather than plant species diversity emerged as the primary determinant of the observed patterns. Host tree specific abundances varied significantly as a function of habitat, and in near-natural forest phytophagous taxa tended to be most abundant on *H. americanus*. Beneath *P. patula*, on the other hand, densities were highest on saplings of *T. chrysantha*. Drought was associated with a marked decline in abundance across taxonomic orders, but populations appeared to recover with the advent of more benign climatic conditions. Araneae and phytophagous Lepidoptera larvae, however, showed signs of delayed recuperation.

Insect diversity was relatively high on treelets growing in near-natural forest (i.e. phytophagous Coleoptera: 167 observed species; predatory Coleoptera: 90 spp., phyto. Hemiptera: 126 spp., and phyto. Lepidoptera: 101 spp.). By comparison, treelets on reforestation sites typically harbored only about half as many species and considerably less among secondary shrub vegetation. As such, insect species richness across habitats roughly mirrors the pattern already observed for abundance. Among host tree species, communities associated with *H. americanus* tended to be more diverse, which may have been related to more complex plant architecture. With regard to species composition, the relative impact of habitat and host

species varied widely between taxonomic orders. Coleoptera were influenced primarily by habitat. As such, phytophagous beetles formed distinct communities depending on the presence of canopy cover (i.e. pasture sites vs. pine plantation / near-natural forest). By contrast, predatory taxa showed little overlap between the assemblages in near-natural forest and those found among reforestation sites. For Hemiptera and Lepidoptera, community composition was predominantly a function of tree species, which is in agreement with typically greater host specificity among these insect orders. Tree-level α -diversity and species turnover between individual sample trees contributed most to overall diversity, which may have been a result of small-scale heterogeneity in topography and soil conditions throughout the study region. Although there was a trend towards overall lower species richness during drought months, salient patterns in species composition seemed to have remained largely unaffected. Contrary to initial expectations, overall leaf area loss was relatively low, but on average higher in near-natural forest (~ 7% of leaf area per tree and survey) compared to saplings on reforestation sites (4-6%), thus reflecting the habitat-specific patterns in herbivore abundance and biodiversity described above. Also unexpected, host-specific folivory did not correspond to the assumed growth-defense trade-off between pioneer and successional species. Instead, leaf damage was highest for the mid-successional *T. chrysantha*, followed by the pioneer *H. americanus* and the likewise successional *C. montana*. Apparently, *H. americanus* is more strongly protected than originally thought, and the observed pattern would therefore seem to follow an underlying gradient in phytochemical defense. Foraging activity of leaf-cutting ants (*Acromyrmex* sp.) was largely restricted to saplings of *T. chrysantha* growing on more open habitat (i.e. pasture and shrub sites), presumably due to higher ground-level temperature during the day. In general, herbivore pressure was highest at the onset of the dry period and seemed to decline in the course of the season.

Allgemeine Zusammenfassung

Ziel der vorliegenden Arbeit war es, Populationsgröße und Artenzusammensetzung von Arthropodengemeinschaften in Abhängigkeit von Baumart und umgebendem Habitat innerhalb experimenteller Wiederaufforstungsflächen in der Bergregenwaldzone Süd-Ecuadors zu untersuchen, sowie den durch Insekten verursachten Fraßschaden zu quantifizieren. Der Fokus der Studie lag auf drei autochthonen Baumarten von potentiell forstwirtschaftlichem Interesse (Meliaceae: *Cedrela montana*, Malvaceae: *Heliocarpus americanus* und Bignoniaceae: *Tabebuia chrysantha*), welche auf für die Region charakteristischen Landnutzungsflächen angepflanzt wurden (d.h. aufgegebenes Weideland, von Büschen und Adlerfarn dominierte Sukzessionsflächen, sowie eine *Pinus patula* Plantage). Angepflanzte Bäumchen wurden mit artgleichen Individuen aus dem Regenerationsbestand des angrenzenden, naturnahen Bergregenwalds verglichen. Neben den phytophagen Gruppen (d.h. Coleoptera, Hemiptera und juvenile Lepidoptera) als Schwerpunkt der Studie wurden auch prädatorische Taxa erfasst (d.h. Coleoptera and Araneae). Ungewöhnlich trockene Wetterbedingungen während der ersten Phase der Feldaufnahmen ermöglichten überdies eine grobe Einschätzung der Auswirkung von Dürre auf Arthropodengemeinschaften im Untersuchungsgebiet.

Im Allgemeinen war die Arthropodendichte vergleichsweise gering mit Ausnahme dreier wirtsspezifischer Hemipteren, welche mitunter in großer Zahl auf Wiederaufforstungsflächen angetroffen wurden. Die untersuchten Herbivorengruppen zeigten weitestgehend ähnliche habitatsabhängige Muster. Die höchste Dichte wurde jeweils in naturnahem Wald beobachtet, gefolgt von Pflanzungen unter *P. Patula*, auf Weideland und schließlich auf Sukzessionsflächen. Dieses Muster war auch unter prädatorischen Coleoptera erkennbar, wohingegen die Spinnendichte nur relativ geringfügig zwischen den Habitaten variierte. In Bezug auf die Arthropodendichte in Wiederbewaldungsflächen waren die beobachteten Muster offenbar hauptsächlich abhängig von strukturellen Habitatsparametern (z.B. Kronenschluss oder Bodenbedeckung) und deren Einfluss auf das lokale Mikroklima; pflanzlicher Artenreichtum hingegen spielte nur eine untergeordnete Rolle. Die Häufigkeit phytophager Insekten auf einzelnen Baumarten war ebenfalls eine Funktion der Umgebung. In naturnahem Wald zeichnete sich *H. americanus* durch die höchste Herbivorendichte aus, unter *P. Patula* hingegen *T. chrysantha*. Vermutlich in Folge einer ausgeprägten Trockenheit und unabhängig von taxonomischer Ordnung war die Arthropodendichte während der ersten Feldphase relativ gering verglichen mit späteren Aufnahmen. In diesem Zusammenhang zeigten Spinnen und phytophage Raupen Zeichen einer langsameren Erholung nach der Dürreperiode.

Auf Probebäumen im naturnahen Wald war der Artenreichtum phytophager and prädatorischer Insekten relative hoch (phytophage Coleoptera: 167 erfasste Arten; prädatorische

Coleoptera: 90 spp., phyto. Hemiptera: 126 spp., and phyto. Lepidptera: 101 spp.). Im Vergleich dazu wiesen Bäume auf Wiederaufforstungsflächen nur etwa halb so viele Spezies auf und jene auf sekundären Strauchflächen sogar noch weniger. Somit entsprachen die habitatsabhängige Unterschiede in Artenreichtum weitestgehend den bereits für Abundanz beobachteten Mustern. Im Vergleich zu den zwei anderen Baumarten wurden im Allgemeinen mehr Species auf *H. americanus* gefunden, was vermutlich mit einer komplexeren Wuchsform zusammenhing. Hinsichtlich der Artenzusammensetzung gab es auffällige Unterschiede zwischen den untersuchten Insektenordnungen in Bezug auf den relativen Einfluss von Habitat und Baumart. Coleoptera-Gemeinschaften waren vor allem eine Funktion der Umgebung. Mit Hinblick auf phytophage Arten zeigte sich eine gewisse Konvergenz in der Artenzusammensetzung zwischen Flächen mit geschlossenem Kronendach (d.h. Kiefernplantage und natur-naher Wald), aber deutliche Unterschiede zwischen diesen und offenem Weideland. Unter den prädatorischen Käfern hingegen gab es charakteristische Waldgemeinschaften, die jedoch nur geringe Ähnlichkeit zu jenen in Wiederaufforstungsflächen aufwiesen. Im Gegensatz zu Käfern, waren Hemipteren und Raupen-Gesellschaften vorwiegend von der Baumspezies geprägt, was durch eine oftmals stärkere Wirtsspezifität dieser Ordnungen erklärbar ist. Der Hauptteil der Gesamtdiversität ergab sich aus der α -Komponente sowie aus der Varianz zwischen einzelnen Probebäumen, was vermutlich eine Folge kleinräumiger Heterogenität in Topographie und Bodenqualität des Untersuchungsgebiets war. Obwohl es Anzeichen geringeren Artenreichtums während der Dürreperiode gab, scheint es zu keiner grundlegenden Verschiebung im Artenspektrum gekommen zu sein.

Entgegen anfänglicher Erwartungen war der Fraßschaden auf Wiederaufforstungsflächen (4-6% der Blattfläche pro Baum und Aufnahme) im Durchschnitt geringer als im naturnahen Wald (~ 7%). Damit spiegelt das Ausmaß an durch Insekten verursachtem Blattfraß die oben beschriebenen Muster hinsichtlich Abundanz und Artenreichtum in den einzelnen Habitaten wieder. Ebenfalls unerwartet zeigte die Sukzessionsart *T. chrysantha* das höchste Maß an Fraßschaden, gefolgt von *H. americanus* (Pionier) und *C. montana* (Sukzession). Entgegen des anfänglich vermuteten Wachstums-Verteidigungs-Tradeoff zwischen Pionier- und Sukzessionsarten, scheint *H. americanus* über eine effizientere Verteidigung zu verfügen als ursprünglich erwartet. Somit würde dem beobachteten Muster ein Gradienten in der Stärke der phytochemischen Verteidigung zugrundeliegen. Blattschneiderameisen (*Acromyrmex* sp.) kamen fast ausschließlich auf offenen Flächen vor (d.h. Weideland und sekundäre Strauchvegetation), was vermutlich mit höheren Temperaturen in Bodennähe in Zusammenhang steht. Auch zeigten die Ameisen eine starke Präferenz für *T. chrysantha*, wo sie zum Teil erheblichen Schaden verursachen konnten. Im Allgemeinen war der Fraßdruck am Beginn der Trockenperiode am höchsten und nahm im Laufe der Saison bis zum Einsetzen der Regenzeit ab.

CHAPTER 1

Introduction

The loss of forest cover poses a central threat to the conservation of global biodiversity as well as the continued provision of vital ecosystem services (Coe *et al.*, 2013; Laurance *et al.*, 2014). Estimates of deforestation rates typically represent a combined average of decreases in forested areas due to anthropogenic activity or natural causes, and increases of forest cover due to natural regeneration and artificial reforestation.

Annual losses caused by timber harvest and agricultural expansion are highest in tropical countries (FAO, 2010; Hansen *et al.*, 2013), many of which harbor global hotspots of biodiversity (Myers *et al.*, 2000; Fonseca, 2009; Pimm *et al.*, 2014). Neotropical ecosystems – especially along the Andean slopes – count among the most species-rich habitats worldwide (Myers *et al.*, 2000; Barthlott *et al.*, 2007; Pimm *et al.*, 2014), but also among the most threatened by ongoing land cover change and fragmentation. Over the past decade, South America showed the greatest net loss of forest cover (~ 4.0 million hectares/year between 2000 and 2010; FAO, 2010), with the highest relative rate of deforestation observed in Ecuador (-1.89%; FAO, 2010). At the present rate of progression, associated extinction rates are expected to reach up to 67 species per year – with the highest values notably predicted for Ecuador (Koopowitz *et al.*, 1994). In response, the respective governments have made an effort to revise or abandon policies that actively promote forest clearance and to preserve existing forests (e.g. Costa Rica: Brockett & Gottfried, 2002; Brazil: Bauch *et al.*, 2009). Nonetheless, population growth, socio-economic forces and often unsustainable management practice continue to drive land cover conversion (Laurance *et al.*, 2014). Throughout Latin America, the need for viable pasture land remains one of the main drivers of forest conversion, as many farmers and low-income smallholders rely on extensive cattle ranching as part of their livelihood (Wassenaar *et al.*, 2007). Particularly among highland pastures, the period of effective use is often limited by poor soil conditions and the intrusion of aggressive weeds. Continued reliance on slash-and-burn management is thought to promote intrusion and subsequent dominance of aggressive and poisonous bracken fern (*Pteridium arachnoideum*; Roos *et al.*, 2010), ultimately rendering the pastures untenable. Due to the competitive strength of pasture 'weeds', depletion of the soil seed bank (Aguirre *et al.*, 2011) and reduced seed deposition (Matt *et al.*, 2008), such floristically depauperate fern-shrub habitats – once established – tend to be highly stable and can severely impede natural forest regeneration (Hartig & Beck, 2003). Pastures and successional fern-shrub vegetation already represent a dominant anthropogenic land cover type in the montane regions of southern Ecuador (Göttlicher *et al.*, 2009) and are likely to expand further in the future (Thies *et al.*, 2012), reflecting the general trend throughout the Andean highlands (Wassenaar *et al.*, 2007).

The area dedicated to commercial tree plantations and artificial reforestations is increasing worldwide, thus ostensibly buffering overall deforestation rates. Such plantings, however, are frequently monocultures based on a small number of tree taxa (e.g. *Eucalyptus* spp. and *Pinus* spp.; Onyekwelu *et al.*, 2011), which are often exotic to the plantation site in question. In consequence, their ability to sustain local biodiversity and ecosystem services (e.g. pollination, biological pest control, etc.) is impaired relative to more natural forest stands (Brockerhoff *et al.*, 2013). Even the value of plantations in the sequestration of atmospheric CO₂ may be to some degree offset by the disruption of established mycorrhizal communities and the associated soil carbon flow (Chapela *et al.*, 2001).

Over the past decades, targeted reforestation based on native rather than exotic timber species has been recognized as an economic and ecologically viable strategy to reclaim degraded habitat (Weber *et al.*, 2008; Davis *et al.*, 2012; Douterlungne *et al.*, 2013). Stands of native trees can not only be expected to provide a more suitable habitat for indigenous flora and fauna (Hartley, 2002; Brockerhoff *et al.*, 2008), but also tend to show less variance in site-dependent growth performance (Piotto *et al.*, 2003). While autochthonous tree species can potentially offer financial returns similar to established timber stock (e.g. Montagnini, 2001; Griess & Knoke, 2011), a more widespread silvicultural use is currently limited by a lack of knowledge regarding ecology and management of candidate species.

Established 1997 in southern Ecuador, the Estación Científica San Francisco (ECSF; Figure 1.1) has been a center of interdisciplinary research with the aim of studying and quantifying the biotic and abiotic dynamics of montane rain- and cloud forest, as well as adjacent, human-modified habitat (summarized in Beck *et al.*, 2008a; Bendix *et al.*, 2013). Located between the provincial capitals of Loja and Zamora-Chinchipe, the station and the neighboring Reserva Biológica San Francisco (RBSF) is operated by Naturaleza y Cultura Internacional (NCI), an Ecuador-based, non-governmental organization. Bordering on the largest remaining area of montane rainforest in southern Ecuador (Parque Nacional Podocarpus), the study area harbors an astounding diversity of vascular plants (Homeier & Werner, 2008; Homeier *et al.*, 2008; Lehnert *et al.*, 2008) and has been identified as a global hotspot for Geometrid moths (Brehm *et al.*, 2005). The original cover of montane rainforest remains largely intact along the southern slopes of the Rio San Francisco Valley. The northern hillsides, on the other hand, have been heavily modified to suit human requirements and currently form a mosaic of active and abandoned cattle pastures, successional fern and shrub vegetation, exotic timber plantations and small areas of remnant ravine forest. Since 2003, silvicultural projects embedded in the research unit have tested the suitability of various native tree and shrub species for reforestation and enrichment planting in different habitats. One line of research addressed survival and growth of planted saplings along a successional gradient ranging from recently aban-

doned cattle pasture, to bracken dominated sites and finally to secondary fern-shrub vegetation (Aguirre, 2007; Günter *et al.*, 2009; Aguirre *et al.*, 2011). Other experiments tested the viability of enrichment plantings beneath an existing canopy of exotic *Pinus patula* (Aguirre *et al.*, 2006) and old growth near-natural forest (Kuptz *et al.*, 2010), respectively.

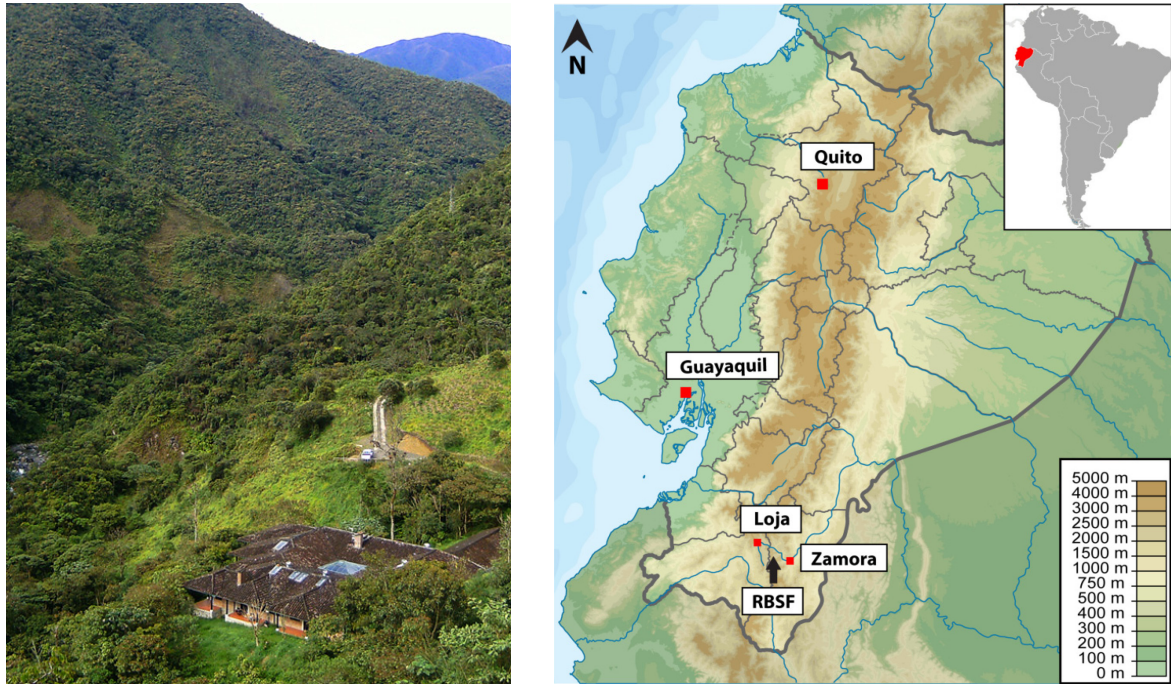


Figure 1.1 The Estación Científica San Francisco (ECSF) and the geographic location of the adjacent Reserva Biológica San Francisco (RBSF). Photograph by M.-O. Adams; Map available under Creative Commons License and modified by M.-O. Adams.

For the most part, the above studies addressed the impact of abiotic factors and plant-plant (e.g. Günter *et al.*, 2009) or plant-mycorrhizal (e.g. Haug *et al.*, 2010) interactions on sapling development. Plant-insect interactions, however, have received little attention. Insect herbivores play a dual role with regard to plantation forestry – especially if conservationist aspects are also to be taken into consideration. Economically speaking, phytophagous taxa are often perceived as potential pests. Under certain circumstances, populations may experience catastrophic outbreaks which can have a severe impact on the respective host-species (e.g. van Bael *et al.*, 2004). Even under normal conditions, insect herbivory has been associated with increased sapling mortality (Eichhorn *et al.*, 2010) and reduced growth (Marquis, 1984; Massad *et al.*, 2011; Plath *et al.*, 2011). Ecologists, on the other hand, emphasize the intrinsic value of biodiversity (Fonseca, 2009) and its effect on resilience (Naeem & Li, 1997; Yachi & Loreau, 1999) and stability (Tilman *et al.*, 2006) of the ecosystem in question, as well as the regulation of associated processes (e.g. Schowalter, 2012; Prather *et al.*, 2013). In order to accurately appraise value and viability of targeted reforestations, it is thus important to quanti-

fy not only prospective habitational value of such plantations for local flora and fauna, but also the potential impact of insect pest species on survival and growth of timber stock.

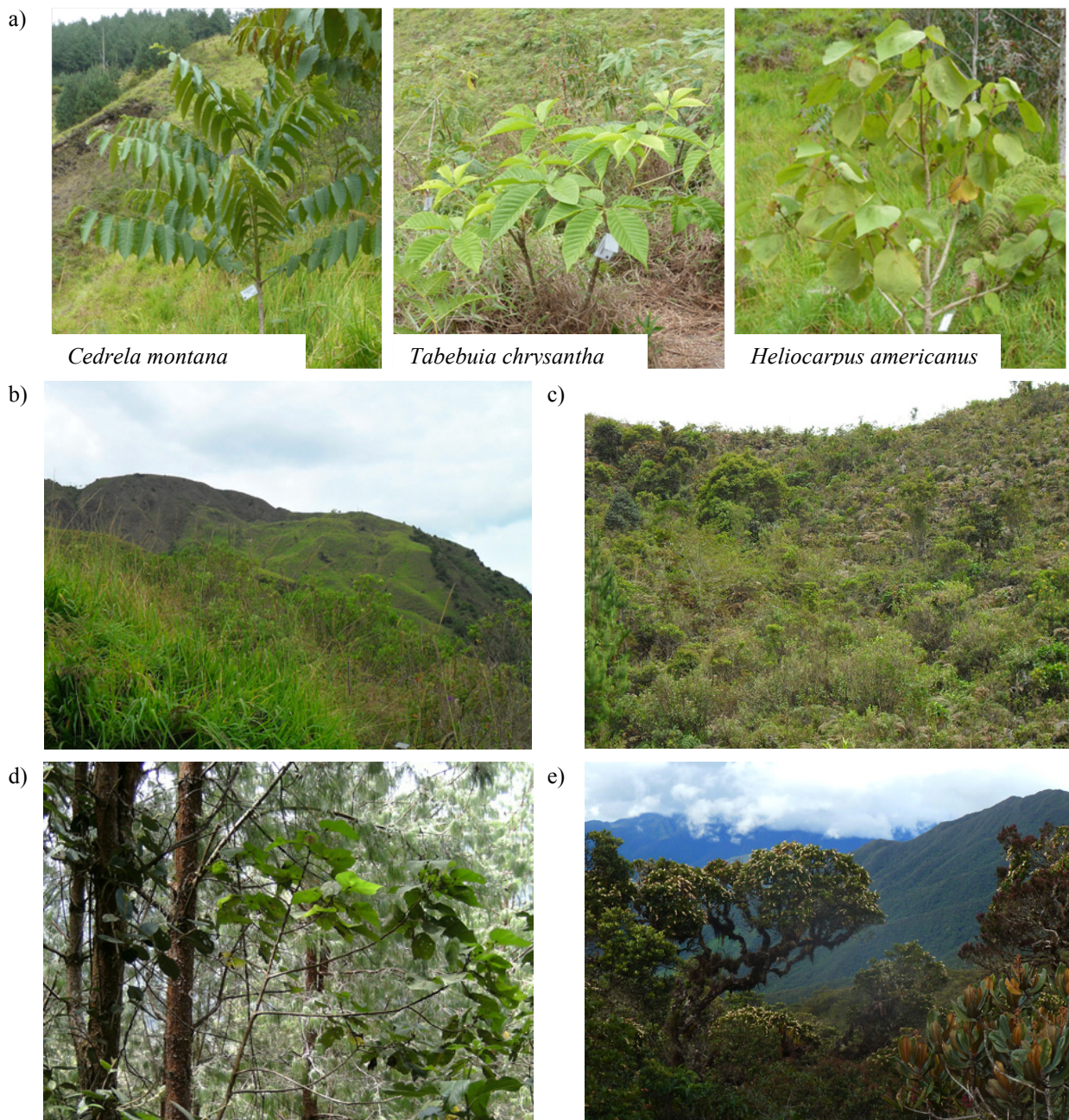


Figure 1.2 Focus tree species and major land cover types around the Estación Científica San Francisco. The images depict (a) sample treelets of the focal tree species and impressions of the vegetation surrounding experimental plantation sites, namely (b) abandoned cattle pasture, (c) secondary fern-shrub vegetation, (d) commercial timber plantation (i.e. *P. patula*), and (e) near-natural montane rainforest. All photographs: M.-O. Adams.

It is the aim of this doctoral thesis to address both aspects by examining habitat-dependent density and diversity of major phytophagous insect orders (i.e. Coleoptera, Hemiptera, and Lepidoptera), as well as the extent of insect folivory suffered by tree saplings in different settings. Surveys were conducted within pre-existing experimental plots and focused on three

tree species, selected for growth performance and silvicultural potential (Figure 1.2-a). *Cedrela montana* (Meliaceae) and *Tabebuia chrysantha* (Bignoniaceae) are characterized as deciduous, mid-successional species with high-value timber. *Heliocarpus americanus* (Malvaceae), on the other hand, is an evergreen pioneer yielding low-quality softwood. Due to its high growth-rate, however, it may prove useful in establishing initial nursery canopies for other species. Experimental reforestation plots were established among prevalent local land cover types represented by fallow pasture land, secondary fern-shrub vegetation, and a mature *P. patula* plantation. Planted saplings in these locations were then compared with conspecifics growing in adjacent, near-natural forest (Figure 1.2-b to e; Figure 1.3).

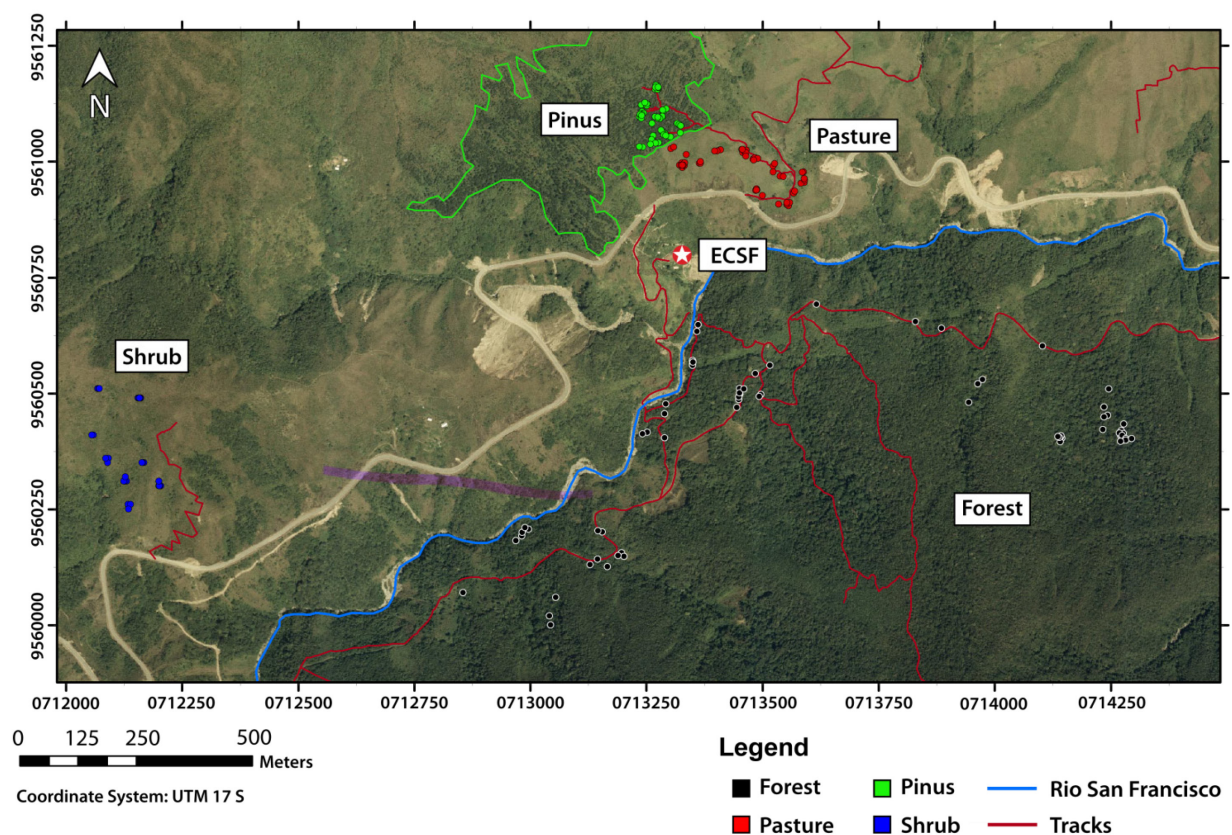


Figure 1.3 Location of sample trees and reforestation sites around the Estación Científica San Francisco (ECSF). Sample trees are indicated by circles.

The necessity to find sample trees of similar size and foliar volume imposed certain limitations to our survey design, as survival and growth rates differed markedly between experimental plantings as well as tree species. High mortality and severely stunted growth of *C. montana* saplings among secondary fern-shrub vegetation did not allow for adequate sampling and led to the exclusion of this particular tree species for the site in question. Likewise, the number and size of sample treelets from enrichment plantings beneath near-natural forest was insufficient, requiring the recruitment of matching conspecifics from natural regeneration stock. Unexpected and severe wildfires posed a further complication. The bracken dominated

sites were completely destroyed just prior to the first survey at the beginning of the dry season 2010. The secondary fern-shrub habitat suffered the same fate in 2011, curtailing further data collection. The fires vividly illustrate the inadvertent consequences of slash-and-burn management, which typically takes place at the beginning of the dry season (Figure 1.4). Due to the difficulty of the terrain, fires frequently spread beyond the intended area, and prolonged drought conditions created especially favorable condition for uncontrolled propagation in the present context. Once the fire has caught hold, effective containment is almost impossible and despite considerable efforts on the part of local fire fighters and military personnel, as well as the members of the research group the experimental plots could not be saved.

Despite the encountered problems, an effort was made to assure adequate sample size and even distribution of sample trees across the habitats.



Figure 1.4 Uncontrolled fire and its aftermath. Reforestations among bracken-dominated habitat were destroyed in 2010, secondary fern-shrub sites in 2011. Photographs: M.-O. Adams.

Specifically, the present study aimed to clarify the impact of surrounding habitat and tree species on (a) the abundance of major phytophagous and predatory arthropod orders (Chapter 2), (b) the diversity of herbivorous insects and predaceous Coleoptera (Chapter 3), and (c) the extent of foliar damage due to insect herbivores (Chapter 4). The insights gained in the present thesis may help to determine suitability and value of native tree species for targeted reforestation of degraded habitat in the Andean montane rainforest zone both from the perspective of silviculture and biodiversity conservation.

CHAPTER 2

Abundance patterns of arthropod dietary guilds across different forms of targeted reforestation in southern Ecuador

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Abstract

In the tropical Andes, abandonment of cattle pastures due to weed incursion and the persistent need to claim new land for agriculture has been a dominant driver of land cover change. This has given rise to extensive tracts of species-poor, but highly stable bracken-shrub landscape matrices. Targeted reforestation based on native timber species is increasingly seen as an ecologically and economically viable means to reclaim such habitats. Focusing on experimental tree plantations in southern Ecuador, we compared abundance and biomass patterns of dietary guilds across four arthropod orders (i.e. Araneae, Coleoptera, Hemiptera, and Lepidoptera) as a function of surrounding habitat, host tree species and climatic variation. Surveys were done on *Cedrela montana*, *Heliocarpus americanus*, and *Tabebuia chrysantha* saplings established in 2006/07 among the prevailing local land cover types (i.e. recently abandoned pasture, secondary shrub vegetation, and a commercial *Pinus patula* plantation) and compared to conspecific treelets in the understory of near-natural forest.

A small number of predominantly host-specific herbivore species was found to proliferate in reforestation sites and may potentially constitute economically relevant pests. When these dominant taxa were excluded in analysis, both abundance and biomass were generally highest in near-natural forest and decreased toward open pasture plantations (with the exception of Araneae). Secondary shrub vegetation was characterized by very low arthropod abundances, most likely due to adverse microclimatic conditions. Herbivore density on individual tree species varied significantly with habitat: In near-natural forest, herbivore abundance was greatest on *H. americanus*, but for treelets planted beneath *P. patula*, values were highest for *T. chrysantha*. For pasture sites, differences in arthropod abundance between tree species were relatively slight and varied between insect orders. A drought event in 2010/11 appears to have caused a marked decline in arthropod abundances across all orders. As climatic conditions improved in 2011/12, the respective populations showed signs of recovery, although the process seemed to be somewhat weaker or delayed in Araneae and Lepidoptera.

Keywords

Arthropod Abundance; Arthropod Biomass; Drought; Ecuadorean Andes; Feeding Guilds; Reforestation; Microclimate

Introduction

The ongoing loss and degradation of forest cover is one of the major threats to the conservation of biodiversity in tropical countries (e.g. Morris, 2010), many of which harbor hotspots of global diversity (Myers *et al.*, 2000; Fonseca, 2009; Pimm *et al.*, 2014). Furthermore, deforestation has been linked to increased erosion (e.g. Zuazo & Pleguezuelo, 2009; Ochoa-Cueva *et al.*, 2013), depletion of soil nutrients (e.g. Hamer *et al.*, 2013), and reduced carbon storage capacity (e.g. Don *et al.*, 2011). For South America, annual deforestation rates are currently highest in Ecuador, and have been steadily increasing over the past decades due to logging and a relative lack of active reforestation (FAO, 2010).

In the Andean highlands, cattle farming constitutes an important component in the livelihood of local smallholders and the need for viable pasture land remains a prevalent cause for forest loss (Wassenaar *et al.*, 2007). Typically, land cover conversion follows a recurring pattern of logging and subsequent management by periodic burning. This practice is often associated with the gradual invasion and ultimate dominance of fire-resistant, highly competitive weed species such as bracken fern (*Pteridium arachnoideum*; e.g. Roos *et al.*, 2010). Over time, increasing effort of weed control renders the pasture untenable. The resulting community is often floristically depauperate but highly stable, and this can considerably delay spontaneous succession toward the establishment of secondary forest (Hartig & Beck, 2003; Silva Matos & Belinato, 2010). Since *P. arachnoideum* is characterized by a low tolerance for shade, targeted reforestation has been suggested as a viable approach to reclaiming degraded pasture sites (Weber *et al.*, 2008; Douterlungne *et al.*, 2013). Typically, reforestation forestry in the tropics is based on a small number of exotic tree species such as *Pinus* ssp. and *Eucalyptus* ssp., chosen primarily for their fast growth, high yield and well established management practice (Onyekwelu *et al.*, 2011; Davis *et al.*, 2012 and citations therein). Such plantations may serve as nursery canopy for successional forest vegetation (e.g. Feyera *et al.*, 2002) and can potentially convey a number of other ecological benefits relative to open pasture (Hartley, 2002; Brockerhoff *et al.*, 2008; but see Felton *et al.*, 2010). However, they are unlikely to provide adequate habitat for local flora and fauna beyond purely structural aspects. In recent decades, a rising number of autochthonous timber species has been considered for reforestation and commercial cultivation (Montagnini, 2001; Davis *et al.*, 2012). Apart from prospectively greater value for the conservation of native plant and animal life, indigenous species often display a more even growth performance across varying climatic conditions (Piotto *et al.*, 2003) and can compare favorably with many exotic taxa regarding yield and financial returns (Montagnini, 2001; Griess & Knoke, 2011; Davis *et al.*, 2012). As such, targeted reforestation with local timber species may offer an ecologically and economically sustainable approach to the reclamation of abandoned pasture land. However, a comparative lack of knowledge and

experience regarding the ecology and proper management of native tree species remains one of the main obstacles for a more widespread acceptance (Stimm *et al.*, 2008).

To date, the majority of studies addressing the subject has focused on silvicultural or plant physiological aspects (e.g. Günter *et al.*, 2009), rather than on potential effects of reforestations on native fauna. Arthropods are of particular interest in this context, as they represent not only a necessary target of conservation effort (e.g. phytophagous taxa; Fonseca, 2009), and potential agents of biological pest control (e.g. spiders, or Staphylinidae, Coccinellidae, Carabidae beetles, etc.), but also potential pest species of economical importance. Generally speaking, insect herbivore abundance in plantations is a function of both bottom-up processes driven by plant quality (Huberty & Denno, 2004), diversity (e.g. Vehviläinen *et al.*, 2007; Plath *et al.*, 2012b) and functional traits (Peeters, 2002; Carmona *et al.*, 2011), as well as top-down control by vertebrate and invertebrate predators (Symondson *et al.*, 2002; Morrison & Lindell, 2012; Karp & Daily, 2014). Efficacy and population density of predatory species, in turn, may depend on the nature and physical characteristics of the habitat in question (e.g. Vehviläinen *et al.*, 2008; Giffard *et al.*, 2013). Most studies on the subject, however, were conducted in the temperate zone or at lower altitudes in the tropics.

To augment the existing body of research, the present study aims to address arthropod communities of experimental reforestations in the montane rainforest zone of southern Ecuador. Located adjacent to the largest remaining expanse of pristine forest in the region (i.e. Parque Nacional Podocarpus), the Reserva Biológica San Francisco and surrounding environs have been the focus of multi-disciplinary research over the past decade (summarized in Beck *et al.*, 2008a; Bendix *et al.*, 2013). The area is considered a hotspot of biodiversity, harboring an extraordinary richness of vascular plants (1208 spermatophyte and 257 fern species; Homeier & Werner, 2008; Lehnert *et al.*, 2008) and the highest recorded number of geometrid moth species per unit area worldwide (Brehm *et al.*, 2005). The study of arthropods in the area has hitherto been largely restricted to Lepidoptera (e.g. Brehm & Fiedler, 1999; Brehm & Fiedler, 2003; Brehm & Fiedler, 2005; Brehm *et al.*, 2005; Hilt & Fiedler, 2005; Hilt *et al.*, 2006; Bodner *et al.*, 2010a; Bodner *et al.*, 2012), and to soil microfauna (e.g. Illig *et al.*, 2010). The present work will address abundance patterns across different arthropod feeding guilds by comparing saplings planted among the prevalent local land cover types (namely direct tree planting on abandoned pasture land and among secondary shrub vegetation, as well as enrichment planting beneath a nursery canopy of exotic *Pinus patula*) to conspecifics in near-natural tropical mountain forest. As focal trees we selected three indigenous species, namely two high-value, deciduous, mid- to late-successional taxa (Meliaceae: *Cedrela montana* and Bignoniaceae: *Tabebuia chrysantha*) and one evergreen pioneer species (Malvaceae: *Heliocarpus americanus*).

Specifically, we investigated to what extent surrounding habitat, choice of tree species and

inter-annual variation in climate affect abundance and biomass of phytophagous as well as predaceous arthropods. Furthermore, we examined whether the response to these factors differs among taxonomic orders within the two feeding guilds.

Materials and Methods

Study area. The study area is located in the eastern escarpment of the Cordillera El Consuelo in the south of Ecuador between the provincial capitals of Loja and Zamora-Chinchipe and encompasses the Reserva Biológica San Francisco (3°58'18''S, 79°4'45''W, 1800-2200m a.s.l., Figure 1.1) and surrounding areas (Figure 1.3) (see Beck *et al.*, 2008b and Richter *et al.*, 2013 for further details). The natural vegetation of the region can be characterized as montane rainforest (Homeier *et al.*, 2008) and has been largely conserved along the southern slopes of the Rio San Francisco valley. The northern hillsides, on the other hand, have for the most part been converted to pasture land and currently form a mosaic of active and abandoned pastures, interspersed with areas of bracken fern, successional shrub vegetation and small pockets of remnant ravine forest. The region experiences an annual period of increased rainfall between April and July and comparatively dry weather from September to December (average annual precipitation: ~2200mm). The diurnal temperature amplitude is approximately 11.1°C, with an annual average of 15.3 (± 1.2)°C (Bendix *et al.*, 2006).

Table 2.1 Number of original sample trees by habitat and tree species

	Forest	Pinus	Pasture	Shrub	Total
<i>C. montana</i>	10	15	18	0	43
<i>H. americanus</i>	13	13	11	7	44
<i>T. chrysantha</i>	20	16	18	19	73
Total	43	44	47	26	160

Sample Trees and Study Sites. Treelets on reforestation sites were planted in 2003/4 as part of a silvicultural project (Aguirre *et al.*, 2006; Aguirre *et al.*, 2011). Of the indigenous species tested in this context, we selected *Cedrela montana* (Meliaceae), *Tabebuia chrysantha* (Bignoniaceae) and *Heliocarpus americanus* (Malvaceae) based on growth performance, silvicultural potential and adequate availability of conspecific treelets among the regeneration stock of adjacent, near-natural forest. Reforestations were established on recently abandoned pasture land (subsequently, 'Pasture'), among successional shrub vegetation ('Shrub'), and beneath the canopy of a *Pinus patula* plantation (age: 25-30 years; 'Pinus') to reflect the major anthropogenic land cover types in the region (Figure 1.2). Treelets from natural forest understory ('Forest') acted as comparison and were selected to match the planted specimens in apparent age, height and general appearance. Across all habitats, a total of 160 sample trees were selected (Table 2.1). All treelets were of intermediate height ($\bar{\varnothing}$ 2.29m \pm 0.91 SD) and

of good health as indicated by an absence of obvious discoloration or wilting of the leaves. In all cases, the entire foliage was accessible to visual search. The uneven number of sample trees across species and habitat reflects the availability of suitable saplings.

Data Collection. Two of the focal species (i.e. *T. chrysantha* and *C. montana*) are deciduous and shed their leaves between June and September (Bräuning *et al.*, 2008). For this reason, insect surveys were conducted from October to May 2010/11 and from October to April 2011/2012. As exploratory surveys indicated negligible arthropod abundance during nighttime, data collection was restricted to daytime recording. To allow for recolonization by arthropods after each sampling round, treelets were revisited roughly every six weeks, resulting in a total of five recordings per survey period. In concurrence with earlier work done in the study area (Bodner *et al.*, 2010b), collection consisted of a combination of visual search and the beating method, using a 1x1m² collection sheet. Total leaf area per treelet and survey was calculated by multiplying the respective number of leaves with the species-specific average leaf size derived from a random sample of 40 leaves per sample species. The respective sampling effort was then scaled according to estimated leaf area with three minutes of visual searching and three 'hits' by beating for every 3000cm² of foliage up to a total of 20 minutes/hits. Treelets with fewer than 15 leaves at the time of recording were not sampled.

All arthropods with the exception of Lepidoptera larvae were collected and preserved in 70% ethanol either directly upon collection or after basic feeding trials to establish the presence or absence of a trophic relationship to the host plant in question. Based on direct observation, and available literature (Dolling, 1991; Schuh & Slater, 1995; Froeschner, 1996; Lawrence *et al.*, 1999; Froeschner, 2001; Beutel & Leschen, 2011; Leschen *et al.*, 2011) specimens were assigned to the following feeding guilds: (1) Herbivores, (2) predators, and (3) other (e.g. feeding on dead organic matter or associated bacterial/fungal growth, nectar, epiphylllic growth such as lichens, algae or mosses, etc.). Caterpillars were reared in the laboratory and categorized as either herbivores or non-herbivores in accordance with observed feeding behavior and prior research (Bodner *et al.*, 2010a; F. Bodner, unpublished data). Deceased or parasitized Lepidoptera were preserved in 90% ethanol and subjected to DNA sequencing (e.g. Ahrens *et al.*, 2007; Strutzenberger *et al.*, 2011) based on the mitochondrial cytochrome-oxidase subunit I (COI) gene and using LepF/LepR primers (Hebert *et al.*, 2003; for details see Strutzenberger *et al.*, 2011). The resulting sequences were compared to available datasets (BOLD: Ratnasingham & Hebert, 2007; F. Bodner and G. Brehm, unpublished data) using neighbor-joining trees based on Kimura two-parameter distances (Kimura, 1980) in the MEGA software package (Version 6.0; Tamura *et al.*, 2013). In the context of this study, specimens with pair-wise distances of less than 3% were considered conspecific.

To approximate arthropod biomass, body length of all individuals was measured from the frontal edge of the head capsule to the tip of the abdomen (\pm 0.5mm; excluding mouthparts,

ovipositor, spinnerets etc.). For Lepidoptera larvae, an additional recording of width was taken at the broadest section of the body (excluding the head capsule). Individual dry weight was then calculated using regression coefficients given in Gruner (2003).

Total leaf area per sample tree was recorded for each successive survey. Apparent health of each tree was scored on a three-level categorical scale based on leaf coloration and general appearance at the time of survey. The spatial distribution of treelets across habitats was by necessity clumped, since the original planting design had been based on randomly distributed 10.8 x 10.8m² single and mixed species plots (Aguirre *et al.*, 2006; Aguirre *et al.*, 2011). To account for possible autocorrelation in arthropod densities between neighboring trees, we calculated the mean distance between a given treelet and its five closest neighbors based on GPS data. Tree height was measured at the beginning of the study and defined as the distance parallel to the stem from ground level to the tip of the highest branch. The degree of lateral vegetation cover was assessed using a 3.0m Robel pole, subdivided into 0.10m bands in combination with a sighting staff (David *et al.*, 2008). The percentage of cover was estimated by counting all bands that were obscured by more than 50%. Measurements were taken from the four cardinal points of the compass at a distance of 5.0m and averaged to provide a single value per sample tree. Given the often difficult terrain, correct distance was estimated by visually bringing two calibrated marks on the sighting staff into juxtaposition with a predefined 1.0m increment on the pole when the staff was held at arm's length (compare Collins & Becker, 2001). Since the secondary shrub habitat was destroyed by fire prior to measurement of lateral vegetation cover, the variable is not included as predictor when analyzing datasets that include shrub sites. Diurnal temperature and humidity profiles were recorded from March to September 2011 using automated data-loggers (EL-USB-2, Lascar Electronics). Measurements were taken at one representative location per habitat, chosen to reflect the overall vegetational and topographical characteristics of the site in question. Devices were installed at a height of 1.5m above ground and readings were taken every 30 minutes.

Statistical Analysis. Specimens were grouped by feeding guild and taxonomic order before cumulative abundance and weight were calculated per tree individual and survey period (i.e. 2010/11 and 2011/12), respectively. For the purpose of this paper, we focus on the five largest groups: herbivorous Coleoptera, Hemiptera and larval Lepidoptera (caterpillars), as well as predatory Coleoptera and Araneae. Phytophagous Hemiptera in turn were dominated by three highly abundant and host-specific taxa, namely Cicadellidae sp (on *T. chrysanthra*; 12.60% of total Hemipteran individuals), Psyllidae sp. (*C. montana*; 16.74%) and Tingidae sp. (*H. americanus*; 50.40%). To prevent masking of possible underlying patterns, analyses were carried out once for the bulk of less abundant Hemiptera and repeated separately for each of the dominant species. In the context of this paper, any statement regarding Hemiptera pertains to the aggregated non-dominant taxa.

All analyses employed a generalized linear mixed model (GLMM) framework and were executed using the R platform (R Core Team, 2013) in combination with the lme4 package (Bates *et al.*, 2014). Tree identity and the total number of sample replicates per treelet and survey period were included as random effects in all models. Analysis of arthropod abundance assumed a Poisson distribution and included an observation-level random effect to account for possible overdispersion in the data. Estimated dry weight was cubic root transformed and analyzed assuming a Gaussian distribution. In both cases, continuous explanatory variables were transformed using cubic root (i.e. height), arcsin-square root (i.e. lateral cover) or logarithm (i.e. leaf area and distance to neighboring sample trees) to establish normality, and subsequently standardized. Initial models containing all variables were simplified manually using an iterative approach based on p-values; this was continued until no further terms could be removed without generating a significant decline in fit between consecutive models as determined by analysis of variance. Explanatory value of the resulting best model is given as Nagelkerke's (pseudo-) R^2 . Conformance of models to statistical prerequisites was checked by means of visual diagnostic plots (i.e. Q-Q plot and histogram of residuals). Unfortunately, there were no suitable *C. montana* saplings available among secondary shrub vegetation and the sites were destroyed by fire in November 2011. Therefore, we split our analysis into two partitions. First, we focus on *H. americanus* and *T. chrysanthus* sample trees from all four habitats during the first recording period (2010/11). Subsequent analyses of possible inter-annual effects are restricted to 'Pasture', 'Pinus', and 'Forest' treelets, but encompass all three tree species.

Results

We collected a total of 17,832 arthropod specimens of which 276 could not be reliably classified to any feeding guild. Of the remainder, the majority (80.61%) could be assigned to one of five groups, namely phytophagous Coleoptera, Hemiptera and juvenile Lepidoptera, as well as predatory Coleoptera and Araneae (see Table 2.2 and Appendix Table A.3). Climatic conditions were notably different between the two recording periods with higher average daily temperatures, as well as lower humidity and precipitation, during the survey months (October-May) in 2010/11 compared to 2011/12 (T. Peters, unpublished data; Appendix Figure B.1). Local microclimate varied notably across habitats with a principal distinction between forested and open sites. Beneath the pine plantation and near-natural forest average midday temperatures were 2.5-5.5°C lower compared to plantings among secondary shrub vegetation or on pasture land, respectively. Conversely, corresponding humidity was 15-25% higher where canopy cover was present (Appendix Figure B.2).

Analysis of the first recording period (2010/11) indicated a strong habitat effect across all five

arthropod groups. Notably, average abundance and biomass per treelet on shrub sites was uniformly as low as or lower than corresponding values for the remaining habitats (compare Figure 2.1 and Appendix Figure C.1). Patterns in relative population density and dry weight among ‘Forest’, ‘Pinus’, and ‘Pasture’ sites were largely similar to those observed in the larger data set and will be discussed in the following section.

Table 2.2 Cumulative abundance and weight of captured arthropods by feeding guild and taxonomic order. Statistical analysis was restricted to the five most abundant groups highlighted in bold script

	Forest (384 surveys ^a)		Pinus (405 surveys ^a)		Pasture (387 surveys ^a)		Shrub^b (136 surveys ^a)	
	N	dry-weight [mg]	N	dry-weight [mg]	N	dry-weight [mg]	N	dry-weight [mg]
Phytophagous								
Coleoptera	729	1150.86	331	495.98	773	1245.31	58	70.90
Hemiptera	1208	1132.64	3050	1646.55	3193	1275.20	266	135.79
Lepidoptera	270	1218.71	184	2392.12	144	793.62	20	120.02
Other	44	641.06	50	3059.10	54	2003.30	6	479.44
Predatory								
Araneae	864	946.36	790	703.26	891	1877.07	101	78.96
Coleoptera	745	1137.99	395	550.77	118	143.51	22	21.39
Hemiptera	17	37.87	29	81.15	30	189.39	1	5.44
Other	324	243.61	310	150.44	225	61.41	66	49.06
Other	893	710.26	720	484.15	585	745.86	50	55.68

^a Total number of valid recordings (i.e. more than 15 leaves per sample tree) across survey periods and tree species.

^b Values for shrub sites are based on only six surveys, since the habitat was subsequently destroyed by fire and only include two tree species, since saplings of *C. montana* were not available. For the remaining habitats, reported values comprise all 10 sampling events and all three tree species.

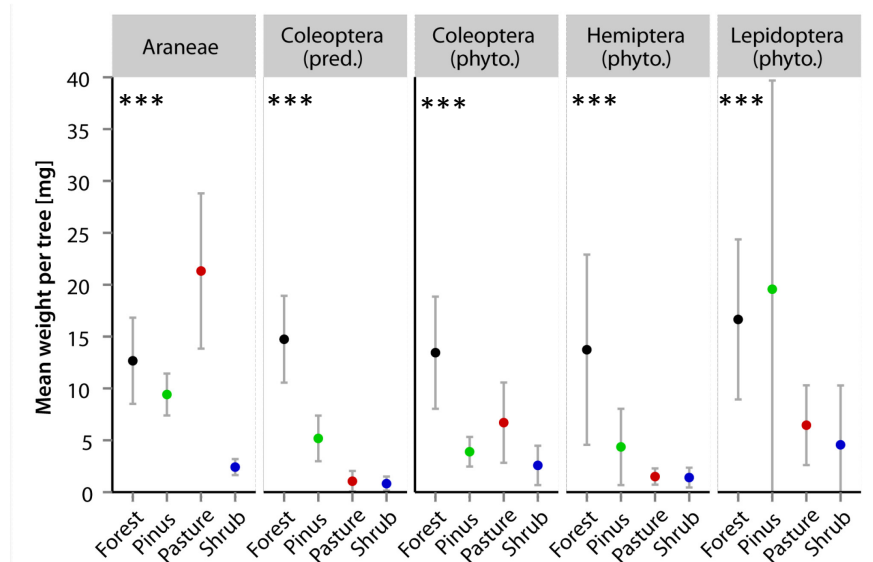


Figure 2.1 Arthropod dry weight for the first survey period (October to May 2010/11; excluding *C. montana*). Points represent means and the corresponding error bars a 95% confidence interval. * symbols denote a statistical significance of habitat for the respective insect group according to the accompanying GLMM analysis (see Appendix Table C.2).

Significance codes: $p \leq 0.001$ ‘***’; $p \leq 0.01$ ‘**’; $p \leq 0.05$ ‘*’; $p \leq 0.1$ ‘.’

When both collection periods are taken into consideration (excluding ‘Shrub’ sites), some variables emerge as strong and recurring predictors of abundance and biomass across different arthropod groups. These were habitat, tree species, recording period, leaf area and the interaction between habitat and tree species. Most other explanatory variables - including spatial proximity between neighboring treelets - had relatively weak effects or none at all (Table 2.3 and Table 2.4). Estimated leaf area had an uniformly positive effect on arthropod density and biomass, except for the dominant Cicadellidae sp. and Tingidae sp. which both showed no significant response (Table 2.3 and Table 2.4).

With regard to habitat (see Table 2.3 and Table 2.4; Figure 2.2), herbivorous Coleoptera were significantly less abundant and showed lower cumulative biomass on treelets planted beneath a cover canopy of *P. patula*. Values appeared roughly similar for forest and pasture sites, but this was primarily due to the occurrence of a ubiquitous species of Eumolpinae (Chrysomelidae) on pasture saplings. Density and biomass of phytophagous Hemiptera declined steadily along a gradient from ‘Forest’ to ‘Pasture’ treelets. A similar decline is apparent in the density of herbivorous Lepidoptera, but notably not reflected in the corresponding weights. Caterpillars beneath the *P. patula* canopy were on average larger and showed a greater variation in body mass than populations in the other habitats. This was mainly due to one fairly large species of Bombycidae which was exclusive to the ‘Pinus’ habitat and occurred between October and November shortly after the end of the wet season.

With regard to the predatory groups, Araneae did not differ greatly in number between habitats (although analysis showed slightly fewer individuals in ‘Pinus’ compared to ‘Forest’ plots), but spiders were on average significantly larger on ‘Pasture’ reforestations.

Of the dominant Hemipteran species, Cicadellidae sp. and Psyllidae sp. were characterized by significantly higher biomass in ‘Pinus’ habitat relative to the other sites, while cumulative weight of Tingidae sp. was highest among the ‘Pasture’ treelets. The overall pattern in abundance was much the same, although it did not reach significance in the case of Psyllidae sp (see Table 2.3 and Table 2.4; Appendix Figure C.3).

Host tree species (see Table 2.3 and Table 2.4; Figure 2.2) in itself was found to be a relatively weak predictor for arthropod abundance and biomass, reaching significance only in Araneae (abundance), phytophagous Hemiptera, and predatory Coleoptera. Spiders were relatively more abundant on *H. americanus*. With regard to the other two arthropod groups, both density and biomass were significantly lower on *C. montana* compared to the other tree species.

By comparison, the effect of tree species mediated by habitat (see Table 2.3 and Table 2.4; Figure 2.2) was considerably stronger, although this interaction was only significant among phytophagous taxa and notably absent for both predatory groups.

Table 2.3 GLMM analyses of arthropod abundance (excluding ‘Shrub’ habitat). Sample tree identity and total number of surveys per treelet and recording period were included as random terms. Non-significant terms were excluded in an iterative process based on p-values. Nagelkerke (Pseudo-) R^2 values refer to the simplified model shown here.

	df	Coleoptera				Lepidoptera				Hemiptera (other)			
		Chi²	p	Chi²		p	Chi²	p					
Phytophagous	Habitat	2	26.788	< 0.001	***	20.580	< 0.001	***	21.122	< 0.001	***		
	Tree sp.	2	4.828	0.089	.	0.403	0.817		41.695	< 0.001	***		
	Rec. period	1	24.215	< 0.001	***	8.917	0.003	**	13.997	< 0.001	***		
	Leaf area	1	25.677	< 0.001	***	21.395	< 0.001	***	33.066	< 0.001	***		
	Health	2	---	---		7.504	0.023	*	---	---			
	Height	1	4.220	0.040	*	---	---		---	---			
	Lat. cover	1	---	---		---	---		---	---			
	Dist. to neighbors	1	---	---		3.972	0.046	*	---	---			
	Habitat x Tree sp.	4	14.250	0.007	**	15.204	0.004	**	35.879	< 0.001	***		
	Habitat x Rec. period	2	---	---		12.100	0.002	**	20.756	< 0.001	***		
	Tree sp. x Rec. period	2	---	---		---	---		---	---			
	Habitat x Height	2	---	---		---	---		---	---			
	Habitat x Lat. cover	2	---	---		---	---		---	---			
	Habitat x	2	---	---		---	---		---	---			
	Dist. to neighbors	2	---	---		---	---		---	---			
Nagelkerke R²		0.3350			0.3474			0.4158					
Predatory			Araneae			Coleoptera							
	df	Chi²	p		df	Chi²	p						
	Habitat	2	8.396	0.015	*	129.81	< 0.001	***					
	Tree sp.	2	21.905	< 0.001	***	7.743	0.021	*					
	Rec. period	1	1.739	0.187		20.374	< 0.001	***					
	Leaf area	1	109.16	< 0.001	***	17.968	< 0.001	***					
	Health	2	---	---		10.772	0.005	**					
	Height	1	---	---		9.139	0.003	**					
	Lat. cover	1	---	---		---	---						
	Dist. to neighbors	1	4.514	0.034	*	---	---						
	Habitat x Tree sp.	4	---	---		---	---						
	Habitat x Rec. period	2	6.843	0.033	*	15.532	< 0.001	***					
	Tree sp. x Rec. period	2	9.184	0.010	*	---	---						
	Habitat x Height	2	---	---		9.741	0.008	**					
	Habitat x Lat. cover	2	---	---		---	---						
Habitat x	2	---	---		---	---							
Dist. to neighbors	2	---	---		---	---							
Nagelkerke R²		0.4013			0.5511								
Dominant Hemiptera			Cicadellidae sp.			Psyllidae sp.			Tingidae sp.				
	df	Chi²	p		df	Chi²	p		df	Chi²	p		
	Habitat	2	22.600	< 0.001	***	1.994	0.369			12.849	0.002	**	
	Rec. period	1	0.262	0.609		6.896	0.009	**		1.649	0.199		
	Leaf area	1	0.723	0.395		0.358	0.549			6.598	0.010	*	
	Health	2	---	---		---	---			---	---		
	Height	1	6.428	0.011	*	---	---			---	---		
	Lat. cover	1	---	---		---	---			---	---		
	Dist. to neighbors	1	0.172	0.678		0.005	0.943			---	---		
	Habitat x Rec. period	2	---	---		---	---			---	---		
	Habitat x Height	2	---	---		---	---			---	---		
	Habitat x Lat. cover	2	---	---		---	---			---	---		
	Habitat x	2	---	---		---	---			---	---		
	Dist. to neighbors	2	4.978	0.026	*	6.913	0.032	*		---	---		
	Nagelkerke R²		0.4892			0.2573			0.2357				

Significance codes: $p \leq 0.001$ ‘***’; $p \leq 0.01$ ‘**’; $p \leq 0.05$ ‘*’; $p \leq 0.1$ ‘.’

Table 2.4 GLMM analyses of arthropod dry weight (excluding ‘Shrub’ habitat). Sample tree identity and total number of surveys per treelet and recording period were included as random terms. Non-significant terms were excluded in an iterative process based on p-values. Nagelkerke (Pseudo-) R^2 values refer to the simplified model shown here.

	df	Coleoptera				Lepidoptera				Hemiptera (other)		
		Chi ²	p			Chi ²	p			Chi ²	p	
Phytophagous	Habitat	2	21.140	< 0.001	***	14.254	< 0.001	***		30.825	< 0.001	***
	Tree sp.	2	3.476	0.176		2.419	0.298			6.072	0.048	*
	Rec. period	1	12.659	< 0.001	***	0.912	0.340			1.981	0.159	
	Leaf area	1	23.417	< 0.001	***	4.066	0.044	*		10.839	< 0.001	***
	Health	2	8.314	0.016	*	---	---			---	---	
	Height	1	9.478	0.002	**	---	---			4.038	0.044	*
	Lat. cover	1	---	---		---	---			---	---	
	Dist. to neighbors	1	---	---		---	---			---	---	
	Habitat x Tree sp.	4	15.891	0.003	**	25.453	< 0.001	***		13.672	0.008	**
	Habitat x Rec. period	2	---	---		8.883	0.012	*		---	---	
	Tree sp. x Rec. period	2	---	---		6.823	0.033	*		---	---	
	Habitat x Height	2	---	---		---	---			---	---	
	Habitat x Lat. cover	2	---	---		---	---			---	---	
	Habitat x Dist. to neighbors	2	---	---		---	---			---	---	
	Nagelkerke R^2		0.3209			0.2025				0.2541		
Predatory	Araneae					Coleoptera						
	df	Chi ²	p			Chi ²	p					
	Habitat	2	10.613	0.005	**	158.06	< 0.001	***				
	Tree sp.	2	2.542	0.280		10.313	0.006	**				
	Rec. period	1	9.013	0.003	**	10.985	< 0.001	***				
	Leaf area	1	44.979	< 0.001	***	11.625	< 0.001	***				
	Health	2	---	---		8.046	0.005	**				
	Height	1	---	---		8.937	0.003	**				
	Lat. cover	1	---	---		---	---					
	Dist. to neighbors	1	---	---		---	---					
	Habitat x Tree sp.	4	---	---		---	---					
	Habitat x Rec. period	2	---	---		---	---					
	Tree sp. x Rec. period	2	---	---		---	---					
	Habitat x Height	2	---	---		23.064	< 0.001	***				
	Habitat x Lat. cover	2	---	---		---	---					
	Habitat x Dist. to neighbors	2	---	---		---	---					
	Nagelkerke R^2		0.2488			0.4794						
Dominant Hemiptera	Cicadellidae sp.					Psyllidae sp.				Tingidae sp.		
	df	Chi ²	p			Chi ²	p			Chi ²	p	
	Habitat	2	23.800	< 0.001	***	6.514	0.039	*		7.553	0.023	*
	Rec. period	1	0.192	0.661		9.322	0.002	**		1.425	0.233	
	Leaf area	1	0.516	0.473		0.111	0.740			13.300	< 0.001	***
	Health	2	---	---		---	---			4.588	0.032	*
	Height	1	7.392	0.007	**	0.339	0.560			---	---	
	Lat. cover	1	4.097	0.043	*	---	---			---	---	
	Dist. to neighbors	1	0.037	0.847		0.265	0.607			---	---	
	Habitat x Rec. period	2	---	---		---	---			---	---	
	Habitat x Height	2	---	---		8.550	0.014	*		---	---	
	Habitat x Lat. cover	2	---	---		---	---			---	---	
	Habitat x Dist. to neighbors	2	4.514	0.034	*	6.385	0.041	*		---	---	
	Nagelkerke R^2		0.5178	---		0.3266	---			0.3139	---	

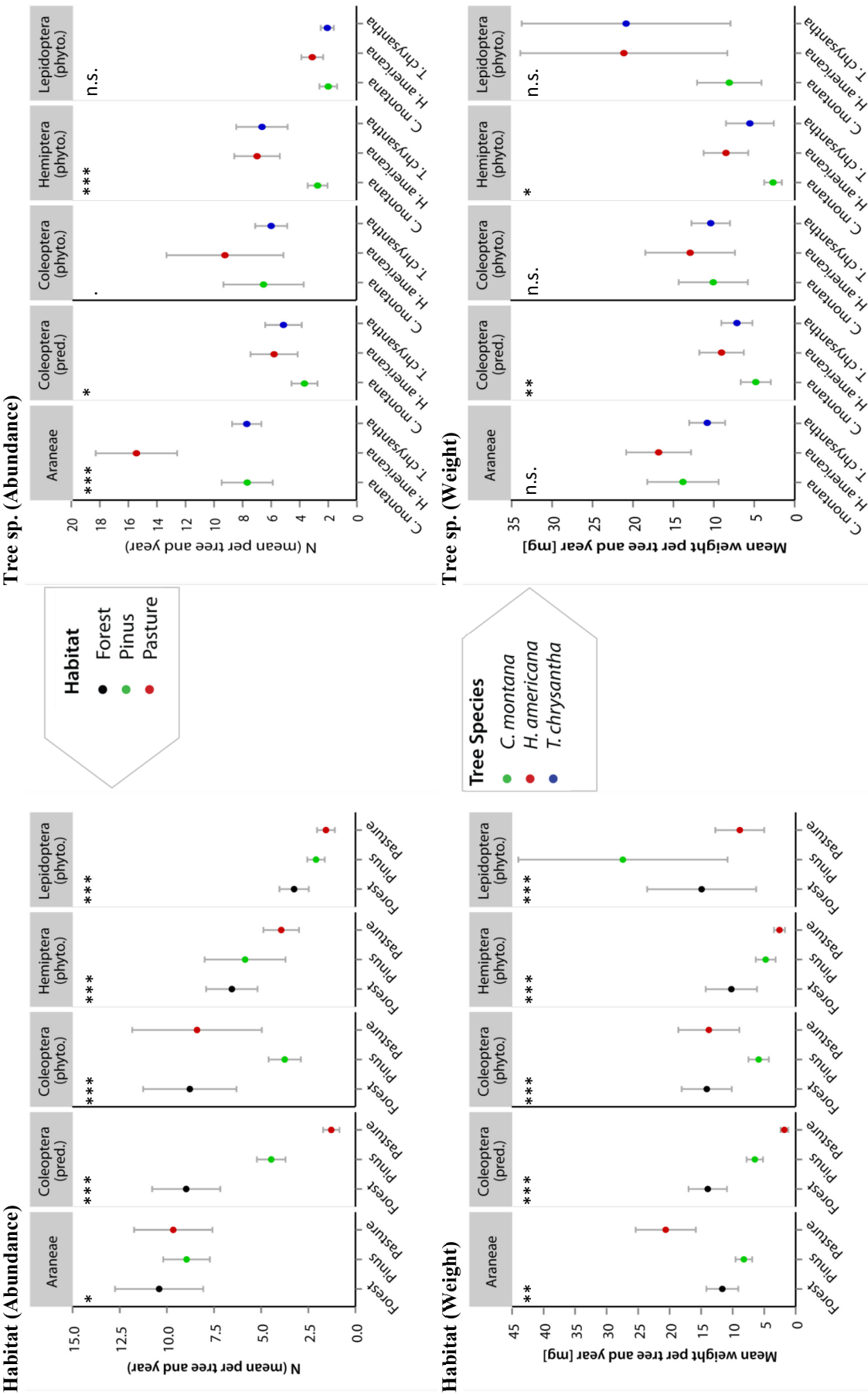


Figure 2.2 Mean arthropod abundance and dry weight as a function of habitat, tree species, recording period and interactions thereof. Whiskers correspond to a 95% confidence interval, and * symbols represent the significance level of the term based on associated GLMM analysis (Table 2.3 and Table 2.4).

-significant 'n.s.'

Significance codes: p

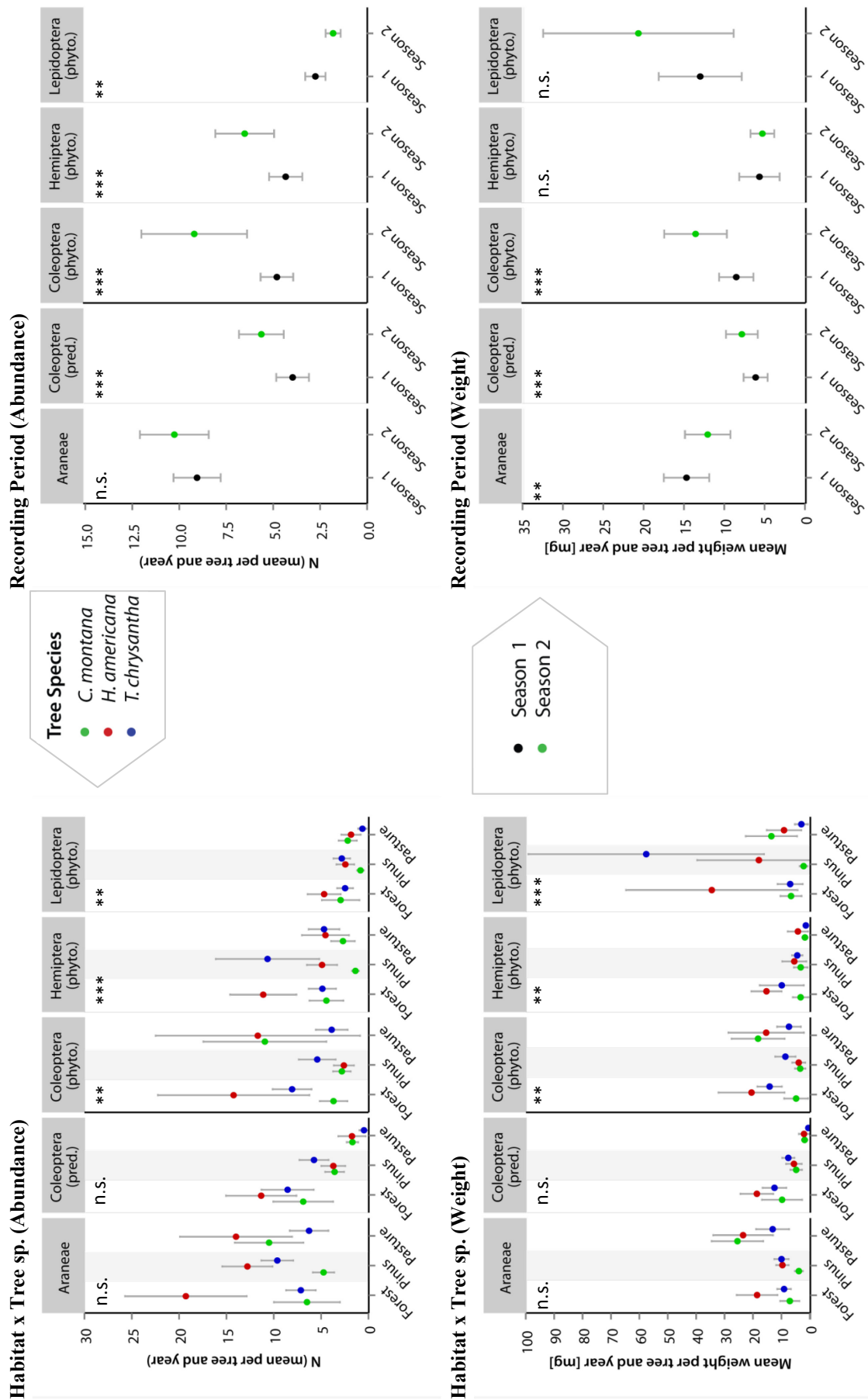


Figure 2.2 (continued)

Generally speaking, in near-natural forest all phytophagous taxa showed higher biomass and abundance on *H. americanus* relative to *C. montana* and *T. chrysantha*. Among the enrichment plantings beneath *P. patula*, on the other hand, herbivore pressure was highest on *T. chrysantha* compared to the other species. This effect was mainly one of abundance in Coleoptera and Hemiptera, while Lepidoptera differed primarily in biomass. Arthropod density on saplings in the ‘Pasture’ plantation was generally low, and differences between tree species thus relatively slight. Nonetheless, both herbivorous Coleoptera and Lepidoptera showed a trend towards lower values on *T. chrysantha* than on *C. montana* and *H. americanus*, respectively. Host differences were less distinct for phytophagous Hemiptera, but densities tended to be lower for *C. montana*.

All arthropod groups showed significant differences between the two recording periods (see Table 2.3 and Table 2.4; Figure 2.2), although this effect was generally more apparent with regard to abundance (except for Araneae) and not entirely uniform across taxonomic orders. Coleoptera as a whole showed a clear increase in both density and biomass during the second, climatically more favorable recording period. For the remaining groups, responses differed between measures of abundance and biomass. Spiders showed a small but non-significant increase in population density, but were characterized by significantly lower overall biomass during the second year. With regard to phytophagous Hemiptera, on the other hand, there was no difference in weight, but a notable increase in abundance between recording periods. Both patterns may indicate a smaller average body size during the 2011/12 collections relative to the 2010/11 surveys. Lastly, the density of herbivorous Lepidoptera was found to decline between years, although cumulative weight per treelet remained constant. The respective interaction of recording period with habitat and tree species was found to be significant in some arthropod groups, but generally this effect was attributable to slight quantitative shifts, rather than meaningful qualitative differences in response (see Appendix Figure C.2)

Among the three dominant Hemiptera species, only Psyllidae sp. showed a significant decline in both density and cumulative weight between recording periods (Appendix Figure C.3), which is related to a marked peak in abundance towards the end of the first collection period (Appendix Figure C.4). The other two taxa showed no significant interannual variation (Appendix Figure C.3), although there was a perceptible tendency towards overall higher abundance and greater variance between sample trees during the second recording period (Appendix Figure C.4).

Discussion

Over the course of two years we collected a sample of more than 10,000 herbivorous insects and almost 4,000 predatory arthropods from treelets in experimental reforestations and adjacent near-natural forest. The observed patterns in abundance and biomass were primarily

a function of surrounding habitat and tree species, but were also influenced by adverse climatic conditions (i.e. drought) during the first survey period in 2010/11. The equally prominent positive correlation between the target variables and leaf area was unsurprising, as greater resource availability for primary consumers, and by extension for their predators, would lead to expect correspondingly greater population sizes. Proximity to neighboring trees, on the other hand, had little or no impact, indicating that spatial autocorrelation did not affect tree-level abundance patterns.

The land cover types surrounding the experimental reforestations can be seen as a rough gradient of floristic and structural diversity spanning from open pasture at one extreme to near-natural forest with closed canopy at the other. The impact of plant species richness on insect herbivore communities has been extensively studied and empirical findings typically highlight two mechanisms. Among agricultural and silvicultural crops, structural and floristic homogeneity is commonly associated with greater abundance of phytophagous insects, typically due to the proliferation of a small number of specialist herbivores. In the context of such simplistic systems, crop diversification is thought to reduce susceptibility of host-plants to specialist pests by a variety of mechanisms such as associational resistance (e.g. Barbosa *et al.*, 2009), reduced visual and olfactory apparancy (e.g. Finch & Collier, 2000; Castagneyrol *et al.*, 2013), or increased abundance of natural enemies (e.g. Langellotto & Denno, 2004). On the other hand, studies have demonstrated a positive correlation between herbivore abundance and plant diversity for inherently more species-rich semi-natural or natural systems (Borges & Brown, 2001; Haddad *et al.*, 2001 for general review; Bowen *et al.*, 2007; Scherber *et al.*, 2010). In this case, greater abundance of phytophagous insects is directly related to higher overall insect species richness (compare Scherber *et al.*, 2010). Both these trends were clearly evident in the present dataset. In disturbed sites, three host specialist Hemipterans, and to a lesser degree some few individual beetle and moth species, reached high local densities, but all were rare or absent in near natural forest. Despite a general affinity to floristically depauperate habitat, however, each of these insect species showed a clear preference for a certain type of reforestation, most likely based on their individual microclimatic requirements. As such, Cicadellidae sp. (specific to *T. chrysantha*), Psyllidae sp. (on *C. montana*) and the bombycid moth *Quentalia* sp. displayed a clear preference for hosts planted beneath *P. patula*, while Tingidae sp. (on *H. americanus*) and one species of Chrysomelidae were predominantly found on more open pasture sites. Given their high abundance, the three dominant Hemipteran species may be considered a potential threat to prospective reforestations, since they affect tree fitness not only directly (e.g. Zvereva *et al.*, 2010), but may also act as possible vectors of plant diseases (e.g. Weintraub & Beanland, 2006; Hogenhout *et al.*, 2008). Conversely, once the five most abundant species are disregarded, abundance and biomass patterns for the remaining herbivore taxa showed a clear decline from natural forest towards

pastures. At least in part, this is likely the result of substantially greater plant species richness and associated biomass in forest habitat (e.g. Scherber *et al.*, 2010). In addition, microclimatic amelioration due to canopy cover and vegetation structure (e.g. Chen *et al.*, 1999; Grimbacher *et al.*, 2006) presumably played an important role as well. Similar climatic buffering effects can also account for the slightly higher population densities in ‘Pinus’ relative to ‘Pasture’ sites, although the protective value of a coniferous canopy is probably less than that of broad-leaved forest. Differences in floristic diversity are unlikely to have played a role in this regard, since both plantation sites hosted a similar number of plant species (J. Gawlik, personal communication). Given a considerably greater plant species richness among secondary shrub vegetation compared to other reforestation sites (Aguirre *et al.*, 2011), the exceedingly low overall abundance of arthropods was unexpected. Following the above line of argument, this is most likely also a function of reduced vegetative cover and resultingly harsher microclimatic conditions. While both ‘Pasture’- and ‘Shrub’-sites lacked canopy cover, former pastures still maintained a dense graminoid and herbaceous layer that was largely absent among successional shrub vegetation. Sparse ground cover may have provided insufficient shelter during periods of high temperature, and could have resulted in substantially reduced humidity at ground level, thus rendering secondary shrub habitat less hospitable to arthropods.

The two predatory arthropod groups showed somewhat diverging patterns in response to habitat. Abundance and biomass of predaceous beetles declined with decreasing vegetative/structural diversity. Notably, their response was markedly stronger than that of herbivorous beetles, indicating that predatory taxa may be more susceptible to changes in floristic diversity or ambient microclimate (compare Haddad *et al.*, 2009). With regard to Araneae, on the other hand, differences in abundance between habitats were relatively slight, although pasture sites apparently harbored somewhat larger individuals. Although the available literature on the subject is not unanimous, the absence of a decline in spider abundance between natural and disturbed/open habitat appears to be a relatively common finding (Klein *et al.*, 2002; Prieto-Benítez & Méndez, 2011 for overview). The discrepancy between the two predator orders may be related to differences in foraging strategy or prey preference, which might allow spiders to better exploit increased prey density (predominantly Hemiptera, see above) on reforestation sites.

The main effect of host plant species on arthropod abundance and biomass was relatively weak compared to the highly significant interaction effects observed between habitat and host tree species. In itself, the host plant effect was strongest among Araneae and phytophagous Hemiptera. Spiders occurred in greater number on *H. americanus* compared to the other two tree species which is likely related to differences in the plants’ architecture and phenology (e.g. Souza & Martins, 2005). *T. chrysanthus* and *C. montana* in the present study are not only deciduous, but were also characterized by comparatively simple architecture with few sec-

ondary branches. As such, they probably provided less shelter and opportunity for the affixation of nets compared to more ramous *H. americanus* treelets. The low density of phytophagous Hemiptera found on *C. montana* compared to the other host trees is probably a function of relatively aggressive phytochemical defense common to members of the Meliaceae family (Fang *et al.*, 2011) and a higher degree of host specificity often found in sap-sucking herbivores (e.g. Novotny *et al.*, 2010). Consequently, the number of species associated with *C. montana* is likely smaller compared to the other two sample trees, which might also result in lower overall abundance.

The overall weak effect of tree species on herbivore abundance is to a large part the result of opposing patterns between habitats. Notably, host preference within a given habitat tended to be similar across phytophagous insect orders (i.e. Coleoptera, Hemiptera, and Lepidoptera). The interaction was most distinct for near-natural forest and the pine plantation. For 'Forest' sites, herbivore abundance was typically highest for *H. americanus*. Ostensibly, this observation corresponds to expectations based on an underlying growth-defense trade-off (Fine *et al.*, 2006; Endara & Coley, 2011). Pioneer and early successional species such as *H. americanus* are thought to invest in high growth-rates at the expense of phytochemical means of herbivore deterrence. Late successional taxa (e.g. *C. montana* and *T. chrysantha*), on the other hand are typically slow growing, but commonly commit considerable resources to defense. As pointed out above, *C. montana* is most likely well defended (Fang *et al.*, 2011). However, a recent comparative survey of plant chemicals by Peñuelas *et al.* (2010) indicated that specimens of *H. americanus* can contain relatively high levels of phenolics, terpenes and tannins, in fact matching or exceeding those found for a congeneric of *T. chrysantha* (i.e. *Tabebuia rosea*). As carbon-based metabolites, production of these compounds is likely limited by the availability of excess carbon from photosynthesis (compare Carbon:Nutrient Balance Hypothesis; e.g. Stamp, 2003; Endara & Coley, 2011). *H. americanus* as a normally light-demanding species may have conceivably been more severely affected by relatively low light availability in the forest, thereby reducing its capacity to invest in defensive measures compared to more shade-adapted species. However, at present the question of whether or not the observed abundance pattern is related to differences in defensive capabilities is difficult to resolve without a more detailed knowledge of species-level chemical composition. The fact that greater density of chewing phytophages does not seem to coincide with higher levels of foliar damage (see Chapter 4) may suggest that other parameters play a role as well. Insect diversity in near-natural forest was relatively high with a large percentage of rare species for which there was often no detailed information on dietary habits (see Chapter 3). Consequently, there may have been a number of tourist species, which do not maintain a trophic relationship, but alight on the tree for other reasons. This possibility gains some support by the observation that noticeably higher abundance on *H. americanus* was mainly observed for the more mobile insect or-

ders (i.e. Coleoptera and Hemiptera), rather than in more sessile taxa (i.e. caterpillars). In addition to possible variations in palatability, *H. americanus* sample trees may have been structurally more complex in ways that are not sufficiently captured by measurements of height and leaf area in the present models. A higher degree of branching and resultingly greater crown volume might for example have offered better shelter than structurally more simple plants.

Among treelets planted beneath a cover canopy of *P. patula*, herbivore pressure was highest for *T. chrysantha*, although this effect was mainly a function of abundance in Coleoptera and Hemiptera, and one of biomass in Lepidoptera (i.e. occurrence of larger caterpillars). Nutrient availability within tropical pine plantations often differs from natural conditions for intrinsic (e.g. Farley & Kelly, 2004) or extrinsic (e.g. Chacón *et al.*, 2009) reasons. In the present study, planted *P. patula* stands were subject to a multiple cation deficiency (i.e. Mg^{++} , Ca^{++} , and K^{+} ; Breckle *et al.*, 2005), and indications of poor nutrient supply were more prevalent among *T. chrysantha* samplings (e.g. more frequent occurrence of chlorosis; personal observation). The species' ability to invest in anti-herbivore defense might therefore have been more severely compromised compared to the other sample trees.

In open pasture plantations, herbivore abundance was generally low and differences between tree species comparatively slight. Nonetheless, both beetle and moth caterpillar densities tended to be lowest in *T. chrysantha* and significantly higher in both *C. montana* and *H. americanus*. Hemiptera, on the other hand, were least abundant on *C. montana*. Low herbivore abundance on *T. chrysantha* may in part be connected to the activity of leaf-cutting ants (*Acromyrmex* sp.), which showed a clear preference towards this tree species on open sites (personal observation; see Chapter 3). Although not documented in leaf-cutter ants, non-consumptive encounters (Rudgers *et al.*, 2003; compare Fill *et al.*, 2012) or pheromone trails (Offenberg *et al.*, 2004) may conceivably deter other phytophagous insects from colonizing the plant. Alternatively, the recurring damage caused by leaf-cutting ants may induce treelets to invest more heavily into anti-herbivore defense (Castillo & Rossini, 2010; Kost *et al.*, 2011; see Heil, 2008 and Mithöfer & Boland, 2012 for general discussion), potentially rendering the plants less attractive to other herbivores. Ultimately, however, the underlying cause for these shifts in susceptibility between habitats are difficult to discern without more detailed knowledge about the ecology of both host tree species and herbivores.

A number of arthropod groups showed significant shifts in abundance and biomass between the two recording periods, likely related to the advent of drought during the first season and subsequent normalization of climatic conditions during the second (Appendix Figure B.1; T. Peters, unpublished data). Since data on arthropod population sizes in the investigated habitats is not available prior to 2010, the nature and dynamic of these shifts is difficult to discern. Drought events have on occasion been associated with a subsequent increase in herbivore

abundance, often due to the proliferation of a small number of species (e.g. van Bael *et al.*, 2004; Kishimoto-Yamada *et al.*, 2009). On the whole, there is little evidence that such an outbreak scenario took place in the present context. A species of Psyllidae specific to *C. montana* might be an exception in this regard, as it exhibited a conspicuous peak in population size towards the end of the drought. While individual species may on occasion profit from prolonged dry periods, the majority of arthropods appear to be negatively affected by such conditions either directly through reduced survival and reproductive success or indirectly via physiological changes in their respective host plants (e.g. Qayyum & Zalucki, 1987; Pollard *et al.*, 1997; Huberty & Denno, 2004; Kishimoto-Yamada & Itioka, 2008; Scherber *et al.*, 2013). Compared to the present surveys, a study conducted in the research area between 2007 and 2009 recorded a considerably higher abundance of Lepidopteran larvae on three shrub species (Asteraceae) in highly disturbed habitat similar to our 'Pasture' and 'Shrub' sites (Bodner *et al.*, 2012). On the whole, this would indicate that the observed patterns describe a general decline in arthropod abundance due to adverse climatic conditions, followed by a relatively swift recovery with the advent of more benign weather during the second recording period. Notably, however, taxonomic orders and dietary guilds differed in their specific responses. Phytophagous Coleoptera and Hemiptera appear to recover relatively quickly, while predatory beetles and especially spiders exhibit a less pronounced or even non-significant increase from one survey period to the next. This discrepancy may be indicative of a delay between an increase in prey availability and the corresponding response in predator population size. Among Hemiptera and spiders the observed changes in abundance relative to biomass imply a shift in community structure towards smaller, juvenile individuals, in keeping with the assumed recovery of the respective population. In contrast to the above groups, phytophagous caterpillars showed a further decline in abundance between recording periods despite improved climatic conditions. Rather than indicating a genuine downward trend, larval population size may simply take longer to recover. In the context of this study, most phytophagous Coleoptera and Hemiptera were collected as adults and an increase in respective population size would simply require immigration. Caterpillar numbers, on the other hand, are contingent on successful recolonization and mating of adult moths as well as brood development, which could account for delayed recuperation. Nonetheless, reduced nectar availability due to low precipitation or drought has been shown to negatively affect fecundity in adult Lepidoptera (e.g. Murphy *et al.*, 1983). Furthermore, low quality of water-stressed host plant can increase mortality rates of herbivorous insects (Huberty & Denno, 2004), and poor nutrition among caterpillars is not only known to reduce survival and reproductive success of the adult animal, but effects can also carry over into the next generation (e.g. Delisle & Hardy, 1997; Carisey & Bause, 2002; Boggs & Freeman, 2005). Although the time period captured by the present data set may be too short to reliably infer Lepidoptera population dynamics, the possibility of longer-lasting

drought effects can therefore not be entirely dismissed.

Conclusion

Only a small number of predominantly host-specific phytophages reached high local abundances on indigenous treelets in reforestation plots. The remaining herbivore taxa maintained relatively low densities, but showed a clear preference for structurally more complex habitats that offered at least some canopy cover. In part, this also applied to arthropod predators. In the pursuit of ecological and economical sustainability, it seems therefore advisable to establish reforestations beneath existing canopy cover or to provide such cover by the use of fast-growing, preferably autochthonous nursery trees (e.g. *H. americanus* or *Alnus acuminata*). The observed differences in herbivore density on tree species as a function of habitat warrant further investigation given the implications for tree species choice and planning of future reforestations. Differences in the response of insect orders to drought events may also need to be taken into consideration when evaluating the conservation potential of planned reforestations. Prolonged and recurring episodes of reduced humidity or precipitation may pose a serious threat for the persistence of local arthropod communities. This may be especially relevant for Lepidoptera, particularly if adverse effect should prove to propagate across generations.

CHAPTER 3

Reforestation in the Ecuadorian Andes: Can they help sustain local arthropod diversity?

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Abstract

In the Andean highlands of many South American countries, land clearance for cattle farming is a major driving force of deforestation. Targeted reforestation with native timber species has been suggested as an ecologically and economically viable approach to reclaiming degraded landscapes. In a case study conducted in the montane rainforest zone of southern Ecuador, we surveyed insect communities associated with planted treelets of *Cedrela montana*, *Heliocarpus americanus*, and *Tabebuia chrysantha*, respectively. Plantations had been established among the prevalent land cover types found in the region (i.e. pasture, secondary shrub vegetation and commercial *Pinus patula* plantations). Insect species richness and community composition was recorded for phytophagous Coleoptera, Hemiptera, and Lepidoptera, as well as for predatory beetles, and compared to that of conspecific treelets in near-natural forest.

Insect species richness on treelets in near-natural forest was relatively high with around 100 to 150 recorded species per insect group. Saplings on reforestation sites harbored only about half as many taxa, and considerably less in the case of secondary shrub habitat. Among planted treelets, more species were typically recorded when a closed canopy (i.e. pine stand) or at least intact ground cover (i.e. pasture) was present, indicating microclimatic amelioration rather than plant species richness as important determinant of insect diversity in the present context. Species composition was mainly a function of habitat among Coleoptera. Community structure of phytophagous beetles varied depending on presence or proximity of protective canopy cover, thus resulting in more or less distinct communities for forested sites (i.e. *Pinus* and forest) and open habitat (i.e. pasture), respectively. For predatory taxa, there was a relatively clear segregation into discrete near-natural forest assemblages on the one hand, and partly confluent afforestation communities on the other. In contrast, Hemiptera and Lepidoptera community composition was determined mainly by host tree species, which is likely related to the higher degree of host-specialization often reported for these orders. Overall diversity was mainly a function of tree-level alpha diversity and variation between individual trees, probably due to small-scale heterogeneity of habitat and soil conditions in the study region.

Keywords

Community composition; Ecuadorean Andes; Microclimate; Reforestation; Species diversity; Species richness

Introduction

The ongoing loss of forest habitat in the wake of anthropogenic land cover change remains one of the most pressing concerns in ecological and economical debate (Foley *et al.*, 2005; Lamb *et al.*, 2005; Morris, 2010). Annual rates of deforestation are still increasing across tropical countries (FAO, 2010), many of which harbor hotspots of global biodiversity (Myers *et al.*, 2000; Fonseca, 2009; Pimm *et al.*, 2014). While the protection of pristine forest habitats remains essential for the conservation of local biodiversity (Barlow *et al.*, 2007; Gibson *et al.*, 2011), it is important to recognize the importance and potential impact of the surrounding matrix on protected areas (Perfecto & Vandermeer, 2008; Laurance *et al.*, 2012). Active reforestation of degraded sites and even the establishment of commercial plantations based on exotic trees species was often found to benefit local biodiversity (Bowen *et al.*, 2007; Brockerhoff *et al.*, 2008; Benayas *et al.*, 2009; Paquette & Messier, 2009), although results are not unequivocal (Felton *et al.*, 2010) and effects are not uniform across taxa (Barlow *et al.*, 2007). Such planted forests can not only serve as potential surrogate habitat for a range of local plant and animal species, but also provide a low contrast matrix to facilitate dispersal between forest remnants in an increasingly fragmented landscape (Baum *et al.*, 2004).

Although tropical mountainous regions such as the Andean slopes count among the most species rich regions worldwide (Myers *et al.*, 2000; Barthlott *et al.*, 2007; Pimm *et al.*, 2014), most studies addressing the value of planted forest for local fauna were conducted at lower elevations (e.g. Pawson *et al.*, 2008; Plath *et al.*, 2012a), while knowledge about higher altitudes remains sparse. Throughout the Andean highlands, cattle-farming by smallholders constitutes one of the main driving forces of deforestation (Wassenaar *et al.*, 2007). Once cleared for grazing, pasture land is often managed by periodic burning, which is thought to promote the intrusion and eventual dominance of highly competitive bracken fern (*Pteridium arachnoideum*; Roos *et al.*, 2010). As the cost of maintenance increases, pastures are typically abandoned. The subsequent matrix of interspersed bracken and shrub vegetation is often inherently species-poor but highly stable, which in turn can greatly alter or delay natural succession towards the original forest state (Hartig & Beck, 2003; Silva Matos & Belinato, 2010). Targeted reforestation has been proposed as a means to reclaim such degraded landscapes, emphasizing the recruitment of autochthonous timber species as an alternative to exotic genera traditionally used in tropical silviculture (e.g. *Eucalyptus* ssp. and *Pinus* ssp.) (Montagnini, 2001; Weber *et al.*, 2008; Davis *et al.*, 2012). Apart from ecological considerations, native tree species show more stable growth performance across a range of environmental conditions (Piotto *et al.*, 2003) and potentially offer similar or even higher financial returns compared to exotic taxa (e.g. Griess & Knoke, 2011). At present, however, a more wide-spread recruitment

of autochthonous timber species for reforestation and commercial plantations is still impeded by the relative lack of knowledge concerning the ecology and proper management of these species (Stimm *et al.*, 2008). Nonetheless, forestry may present local small holders with an ecologically and economically sustainable alternative to the abandonment of old pasture land. Ecuador has emerged as a focal point of ecological research and conservation effort due to its extraordinary faunistic and floristic diversity (e.g. Brehm *et al.*, 2005; Barthlott *et al.*, 2007; Brehm *et al.*, 2008; Pimm *et al.*, 2014) and the threat posed by high and rising annual deforestation rates (Koopowitz *et al.*, 1994; FAO, 2010). Bordering on the largest remaining expanse of natural rainforest in southern Ecuador (Parque Nacional Podocarpus), the Reserva Biológica San Francisco has been a center of interdisciplinary research on ecological and climatic dynamics within the montane rainforest zone and adjacent anthropogenic land cover types for almost two decades (summarized in Beck *et al.*, 2008a; Bendix *et al.*, 2013). In this context, one line of study addressed the suitability of various native tree and shrub species for reforestation, and their growth performance in different habitat contexts (Aguirre *et al.*, 2006; Günter *et al.*, 2009; Aguirre *et al.*, 2011). To date, Lepidoptera communities (e.g. Brehm & Fiedler, 1999; Brehm & Fiedler, 2003; Brehm *et al.*, 2005; Hilt *et al.*, 2006; Bodner *et al.*, 2012) and soil microfauna (e.g. Illig *et al.*, 2010) have been extensively studied in the area. Insect-plant interactions for species of silvicultural interest, and the prospective conservation value of reforestations for local arthropod diversity, however, have not been examined so far. In this context, phytophagous insects constitute an important and often overlooked target of conservation effort on their own right (Fonseca, 2009). On a broader scale, maintenance and restoration of biodiversity has been linked with increased ecosystem resilience ('Insurance Hypothesis': Naeem & Li, 1997; Yachi & Loreau, 1999) and stability (Tilman *et al.*, 2006), as well as with the facilitation of important ecosystem services such as pest control (Letourneau *et al.*, 2009) or pollination (Bartomeus *et al.*, 2013). In order to accurately assess viability and ecological value of plantations, it is thus important to consider local insect diversity and community structure across taxonomic groups and functional guilds. To this end, the present study aims to characterize species richness and composition of Coleoptera, Hemiptera and Lepidoptera communities on saplings of native timber species (i.e. *Cedrela montana*, *Heliocarpus americanus*, and *Tabebuia chrysantha*) across different reforestation sites. Plantations were established among characteristic, anthropogenic land cover types found throughout the Andean highlands, namely cattle pasture, secondary fern-shrub vegetation and a *Pinus patula* plantation. Associated insect assemblages were then compared to those found among conspecific treelets in adjacent, near-natural forest.

Specifically, we wished to investigate whether and how insect species richness and community composition in reforestations is affected by surrounding habitat and host tree species, respectively, and whether patterns differed between insect orders.

Materials and Methods

Study area. Research plots were located in the Rio San Francisco Valley between the provincial capitals of Loja and Zamora (South Ecuador), encompassing the Reserva Biológica San Francisco (3°58'18''S, 79°4'45''W, 1800-2200m a.s.l., Figure 1.1) and surrounding environs (Figure 1.3) (see Beck *et al.*, 2008b and Richter *et al.*, 2013 for further details). The local climate is weakly seasonal with a relatively dry period between September and December, and a time of increased rainfall from April to July (average annual precipitation: ~2200mm). Mean annual temperature is 15.3 (± 1.2) °C with an average diurnal range of 11.1 °C (Bendix *et al.*, 2006). The southern slopes of the valley are characterized by near-natural montane rainforest (Homeier *et al.*, 2008), partly merging with the larger Parque Nacional Podocarpus. By contrast, the northern flanks of the valley are dominated by a matrix of active and fallow cattle pastures, interspersed with successional bracken/shrub vegetation and forest remnants along the more inaccessible creeks.

Sample Trees and Study Sites. Treelets have been raised from locally collected seed material and planted in the field as part of an independent silvicultural project in 2003/4 (Aguirre *et al.*, 2006; Günter *et al.*, 2009; Aguirre *et al.*, 2011). Of the autochthonous species tested in this context, we selected those with the highest potential for sustainable forestry: two high-value, mid- to late- successional timber species (Meliaceae: *Cedrela montana* and Bignoniaceae: *Tabebuia chrysantha*), as well as one fast-growing pioneer species (Malvaceae: *Heliocarpus americanus*), which may be useful in establishing a nursery canopy (Figure 1.2). We focused on plantations established on recently abandoned pastures (subsequently, 'Pasture'), among secondary shrub vegetation ('Shrub'), and enrichment plantings beneath the canopy of a 25-30 year old, commercial *Pinus patula* stand ('Pinus'), respectively. For comparison, we selected conspecific treelets of comparable age, height and architecture from the natural regeneration stock in the forest understory ('Forest') (Figure 1.2). Treelets were selected to be of good health (i.e. no excessive discoloration or wilting of the leaves) and intermediate size ($\varnothing 2.10\text{m} \pm 0.86 \text{ SD}$), assuring that all parts of the foliage could be efficiently searched. Initially, a total of 160 treelets were sampled. When it became apparent that the overall abundance of insects was unexpectedly low, additional trees were selected at the beginning of the second field period, bringing the total to 224 sample trees (Table 3.1). The unbalanced design reflects the availability of suitable treelets in the respective habitats. The original reforestation experiment had been based on randomly distributed 10.8 x 10.8m² single and mixed species plots (Aguirre *et al.*, 2006; Günter *et al.*, 2009; Aguirre *et al.*, 2011), which imposed certain constraints on the design of the present study. While an effort was made to assure that sample treelets were as evenly distributed as possible, clustering could not always be avoided. To control for any spatial autocorrelation effect arising from this caveat,

we calculated the mean distance between each tree and its five closest neighboring sample trees based on GPS coordinates and included this co-variate in some of our statistical analyses. The shrub habitat was destroyed in a fire early in the second field period, making any further sampling impossible and leading to an unbalanced number of surveys across habitats.

Table 3.1 Number of original and supplementary sample trees by habitat and tree species. Additional treelets selected at the beginning of the second year are given in parentheses. Imbalances in study design are due to differences in the availability of sample trees.

	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	Total
Forest	10 (+ 2)	13 (+ 7)	20 (+ 18)	43 (+ 27)
Pinus	15 (+ 5)	13 (+ 0)	16 (+ 8)	44 (+ 13)
Pasture	18 (+ 11)	11 (+ 1)	18 (+ 12)	47 (+ 24)
Shrub	0 (+ 0)	7 (+ 0)	19 (+ 0)	26 (+ 0)
Total	43 (+ 18)	44 (+ 8)	73 (+ 38)	160 (+ 64)

Data Collection. Sampling took place during two extended field campaigns from October to May 2010/11 and from October to April 2011/2012, respectively. The choice of time was dictated by the phenology of the deciduous species *T. chrysantha* and *C. montana*, which were largely bare between June and September (Bräuning *et al.*, 2008). Each field period was subdivided into five surveys with an average of six weeks between consecutive visits to allow for recolonization of the sample trees by insects. Following Bodner *et al.* (2010b), insects were collected by a combination of visual search and the beating method, using a 1x1m² collection sheet. Sampling effort was scaled to the size of the respective tree by counting the leaves and multiplying the number with the average leaf area of that species. Average leaf area was determined based on a randomly selected sample of 40 leaves per tree species prior to the surveys. For every 3000cm² of foliage, three minutes were spent searching and three ‘hits’ were delivered up to a total of 20 minutes and 20 hits, respectively. Tree individuals that had less than 15 leaves at the time of survey were not sampled.

All Lepidoptera larvae and the more abundant Coleoptera morphospecies were captured alive and subjected to feeding trials to determine trophic relationships to the host-plant in question. All other arthropods were preserved in 70% ethanol immediately upon collection. To facilitate identification, an effort was made to rear all Lepidoptera to the adult stage. All Coleoptera, Hemiptera and Lepidoptera were sorted into morphospecies (subsequently referred to as ‘species’) and identified to family-level or below using available taxonomic literature (Dolling, 1991; Schuh & Slater, 1995; Froeschner, 1996; Lawrence *et al.*, 1999; Froeschner, 2001; Beutel & Leschen, 2011; Leschen *et al.*, 2011). Lepidopterans were principally identified with the help of images of caterpillars and moths obtained in earlier surveys (F. Bodner and G. Brehm, unpublished data).

In some cases DNA barcodes were used to identify and distinguish species, particularly with

regard to deceased or parasitized caterpillars. Specimens were preserved in 90% ethanol and subsequently processed according to the method outlined by Ahrens *et al.* (2007) and described in detail by Strutzenberger *et al.* (2011). The methodology is based on the barcoding region (Hebert *et al.*, 2003) of the mitochondrial cytochrome-oxidase subunit I (COI) gene, which was amplified using LepF/LepR primers (Hebert *et al.*, 2003; for details see Strutzenberger *et al.*, 2011). Resulting sequences were aligned with prior datasets (BOLD: Ratnasingham & Hebert, 2007, F. Bodner and G. Brehm, unpublished data) and compared using neighbor-joining trees based on Kimura two-parameter distances (Kimura, 1980) in the MEGA software package (Version 6.0; Tamura *et al.*, 2013). For the purpose of this study, samples with a pair-wise distance of less than 3% were regarded as belonging to the same species. A total of 193 Lepidoptera samples were processed in this fashion. Where necessary, ambiguities in morphospecies affiliation among Coleoptera due to suspected color- or sexual-dimorphisms were likewise resolved by barcode comparisons using the COI sequence (42 samples).

As far as possible, all arthropods were assigned to feeding guilds. The following dietary guilds were distinguished: phytophagous (i.e. sap feeders or chewing herbivores), predatory (i.e. feeding on other arthropods), and other (e.g. feeding on dead organic matter or associated bacterial/fungal growth, nectar, epiphyllic growth of lichens, algae or mosses, etc.). If direct feeding observations were unavailable or inconclusive, morphospecies were assigned to feeding guilds based on information from prior studies in the area (Bodner, 2007; Bodner, 2011; F. Bodner, personal communication) or according to prevalent feeding habits of other species in their respective clade as listed in literature (Schuh & Slater, 1995; Lawrence *et al.*, 1999; Beutel & Leschen, 2011; Leschen *et al.*, 2011).

For each survey, apparent health of the treelets was visually assessed based on leaf color and the presence of dead tissue (scored on a three-level, categorical scale). To approximate total leaf area at the time of visit, leaves were counted and the value multiplied with the average leaf size of the tree species in question. Tree height was defined as the distance parallel to the stem from ground level to the tip of the highest branch and measured once at the beginning of the study. Mean distance between a given sapling and the five closest sample treelets was calculated based on GPS coordinates. Local microclimate was measured based on one location per habitat, chosen to be representative of the overall structural and topographical characteristics of the site in question. Automated data-loggers (EL-USB-2, Lascar Electronics) were installed at a height of 1.5m above ground. Between March and September 2011, temperature and humidity were recorded every 30 minutes.

Statistical Analysis. Specimens that could not be reliably assigned to a morphospecies were excluded from further analysis. Only the phytophagous species among Coleoptera, Hemiptera and Lepidoptera, as well as predatory beetles were sufficiently abundant to warrant

statistical analysis with regard to species richness and community composition.

For the calculation of species richness, morphospecies were aggregated by tree individual and survey for each of the above insect groups. Sample-based species accumulation curves were calculated using the combined rarefaction and extrapolation method introduced by Colwell *et al.* (2012) in the software package EstimateS (Colwell, 2013). Sparser datasets were extrapolated to approximate sample size of the largest category, respectively. Given the imbalance in design due to the low number of samples on ‘shrub’ sites, this rather conservative approach was deemed more appropriate. Due to the imbalance in experimental design caused by absence of adequate *C. montana* treelets among secondary shrub vegetation and fire damage, analyses were carried out separately for reduced datasets containing alternatively all four habitats (but excluding *C. montana*) or all three tree species (but excluding ‘Shrub’-sites). Accumulation curves were initially plotted by survey period to check for broad, interannual differences. Calculations were then repeated based on habitat and tree species, respectively, using the appropriate data subset. Non-overlap of the 95% confidence intervals was considered to imply statistically significant differences between groups. As this approach may be overly conservative, an alternative 86% confidence interval has been calculated as suggested by Payton *et al.* (2003).

To compare insect community composition, species abundance data were chord-transformed and evaluated by distance-based redundancy analysis (db-RDA; Legendre & Gallagher, 2001) in combination with permutational analysis of variance (PERMANOVA; 1000 permutations) using the vegan package (Oksanen *et al.*, 2013) in R (R Core Team, 2013). Following a recommendation of Clarke *et al.* (2006) for calculation with sparse data matrices, a dummy species with a value of ‘1’ for all samples was added to the abundance matrix prior to transformation. In addition to habitat, tree species and the interaction thereof, initial models contained plant health, cumulative leaf area, mean distance to neighboring sample trees and tree height as predictor variables. To identify the variables with the greatest explanatory power, the full model was subjected to automated forward/backward model selection based on the Akaike Information Criterion (AIC). Model-fit was calculated as adjusted R^2 and output of the best model was visualized in the form of 2-dimensional ordigrams.

Initially, species abundances were aggregated by tree individual and recording period (2010/11 vs. 2011/12) to address possible confounding effects of altered climatic conditions between the two periods. In a second set of analyses, samples were pooled further to yield a single set of values per individual treelet. To control for possible distorting effects due to the high number of rare species and of sample trees with very sparse communities, analyses were repeated with reduced datasets, excluding all singleton/doubleton species or any sample tree with a total community of less than three species, respectively. Since three highly host specific species (i.e. Cicadellidae: cica033, Psyllidae: psyl001, and Tingidae: ting001) contributed

disproportionally to overall Hemiptera abundance, their signal might conceivably mask potentially diverging patterns in the Hemiptera community as a whole. To account for this possibility, analyses were run for all Hemiptera, as well as for a subset of the less abundant taxa. The two data sets were respectively cubic- or square-root transformed to down-weight individual sample trees with high densities of a single species. Continuous explanatory variables were normalized using cubic root (i.e. height) or logarithmic transformation (i.e. leaf area and distance to neighboring sample trees), and subsequently standardized. To identify those species with the strongest contribution to the observed ordination patterns, we performed matrix correlations (Spearman rank correlation) between the full data set and a randomly generated subset of six or more species as implemented in the *bvstep* function (Clarke & Warwick, 1998) of the PRIMER software package (Clarke & Gorley, 2006). In order to reduce calculation time, all species with less than three individuals and any sample tree hosting only a single insect species were excluded. Again, a dummy species of value '1' for each sample was added to every data set prior to chord-transformation. The program was run for 2500 iterations with a target correlation of $\rho=0.90$ between the full data set and the reduced subsets. Subsequently, total occurrence of each morphospecies across all models was calculated.

α - and β -diversity components were determined by multiplicative diversity partitioning (Jost, 2007) based on the exponent of the Shannon index (Jost, 2006). The significance of partitions was determined by comparing each component with null model distributions generated from 1000 randomizations (Crist *et al.*, 2003). Calculations were done in R using the appropriate functions in the *vegan* package (Oksanen *et al.*, 2013), and carried out separately for each insect group based on reduced datasets excluding the 'Shrub' habitat. To allow better visualization, α - and β -diversity components were \log_2 -transformed (e.g. Murray *et al.*, 2012).

Table 3.2 Density, species richness and distribution of predatory beetles, as well as phytophagous Coleoptera, Hemiptera and Lepidoptera.

	Nr. of Trees ^a	Sample size	Ø Leaf area [m ²] ^b	Coleoptera (predatory)			Coleoptera (herbivore)			Lepidoptera (herbivore)			Hemiptera (herbivore) ^d		
				N	S	Ø Density [indiv./m ²] ^b	N	S	Ø Density [indiv./m ²] ^b	N	S	Ø Density [indiv./m ²] ^b	N	S	Ø Density [indiv./m ²] ^b
Forest															
<i>C. montana</i>	10 (+ 2)	100	0.49 (± 0.04)	144	30	3.27 (± 0.42)	82	44	2.14 (± 0.34)	58	26	1.39 (± 0.56)	239	29	12.08 (± 6.15)
<i>H. americanus</i>	13 (+ 7)	146	1.03 (± 0.05)	415	64	3.50 (± 0.49)	447	98	3.23 (± 0.29)	128	73	1.04 (± 0.13)	607	56	3.30 (± 0.55)
<i>T. chrysantha</i>	20 (+ 18)	267	0.55 (± 0.02)	591	54	3.88 (± 0.31)	484	94	3.63 (± 0.33)	109	64	0.84 (± 0.10)	437	46	3.70 (± 0.32)
Total	43 (+ 27)	513	0.68 (± 0.02)	1150	90	3.65 (± 0.23)	1013	167	3.22 (± 0.2)	295	126	1.01 (± 0.13)	1283	101	5.22 (± 1.23)
Pinus															
<i>C. montana</i>	15 (+ 5)	145	0.51 (± 0.02)	119	27	1.77 (± 0.21)	106	30	1.42 (± 0.19)	31	25	0.55 (± 0.11)	840	22	10.48 (± 3.29)
<i>H. americanus</i>	13 (+ 0)	128	0.99 (± 0.05)	98	26	0.83 (± 0.10)	69	26	0.52 (± 0.08)	65	37	0.58 (± 0.11)	1024	30	5.28 (± 1.29)
<i>T. chrysantha</i>	16 (+ 8)	182	0.69 (± 0.04)	198	25	1.71 (± 0.18)	189	26	1.55 (± 0.18)	111	30	1.06 (± 0.15)	1478	27	15.84 (± 1.61)
Total	44 (+ 13)	455	0.72 (± 0.02)	415	46	1.48 (± 0.10)	364	55	1.22 (± 0.10)	207	69	0.76 (± 0.08)	3342	63	11.16 (± 1.30)
Pasture															
<i>C. montana</i>	18 (+ 11)	207	1.46 (± 0.10)	70	21	0.33 (± 0.08)	436	32	1.45 (± 0.19)	93	35	0.40 (± 0.08)	581	36	2.98 (± 0.86)
<i>H. americanus</i>	11 (+ 1)	101	1.35 (± 0.13)	38	11	0.27 (± 0.07)	277	30	2.11 (± 0.57)	38	30	0.52 (± 0.13)	2558	18	24.88 (± 6.71)
<i>T. chrysantha</i>	18 (+ 12)	177	0.64 (± 0.03)	35	13	0.35 (± 0.08)	176	26	1.60 (± 0.23)	26	26	0.28 (± 0.07)	182	17	2.10 (± 0.54)
Total	47 (+ 24)	485	1.14 (± 0.05)	143	34	0.32 (± 0.05)	889	57	1.64 (± 0.17)	157	68	0.38 (± 0.05)	3321	52	7.22 (± 1.51)
Shrub ^c															
<i>H. americanus</i>	7 (+ 0)	42	0.71 (± 0.07)	8	5	0.18 (± 0.07)	12	10	0.44 (± 0.15)	8	12	0.22 (± 0.12)	199	4	5.12 (± 1.87)
<i>T. chrysantha</i>	18 (+ 6)	99	0.55 (± 0.03)	14	6	0.32 (± 0.10)	50	11	1.00 (± 0.28)	12	15	0.22 (± 0.08)	48	11	0.81 (± 0.15)
Total	25 (+ 6)	141	0.60 (± 0.03)	22	10	0.28 (± 0.07)	62	17	0.83 (± 0.21)	20	25	0.22 (± 0.06)	247	15	2.10 (± 0.59)
Grand Total	159 (+ 70)	1594	0.82 (± 0.02)	1730	115	1.72 (± 0.09)	2328	208	1.96 (± 0.09)	679	166	0.68 (± 0.05)	8193	196	7.25 (± 0.71)

N: number of individuals; S: number of species;

^a Values refer to the number of initial sample trees; trees added at the beginning of the second survey period are given in parentheses^b Values in parentheses give the standard error of the distribution^c The 'Shrub' sites were destroyed at the beginning of the second survey period. Reported values thus reflect six surveys rather than ten as in the other reforestation sites.^d The majority of Hemiptera (78.94%) belonged to three highly host-specific species, i.e. Cicadellidae sp. (*T. chrysantha*), Psyllidae sp. (*C. montana*), and Tingidae sp. (*H. americanus*)

Results

Over the course of the study, a total of 14,617 Coleoptera, Hemiptera, and Lepidoptera were collected. Of these, 877 specimens (6.0% of total; Coleoptera: 1.7%, Hemiptera: 7.6%, Lepidoptera: 11.8%) could not be reliably identified to morphospecies level and were therefore excluded from further evaluation. Furthermore, 56 Lepidoptera belonging to a single clutch were removed from the dataset. The remainder comprised mostly phytophagous taxa (76.6%) or predatory Coleoptera (11.8%), and subsequent analysis will focus on these groups. The two recording periods (2010/11 and 2011/12) differed substantially with regard to climate. On average, humidity and precipitation were substantially lower, and temperatures considerably higher during the first field campaign compared to the second (T. Peters, unpublished data; Appendix Figure B.1). Further microclimatic differences were apparent between habitats. Average midday temperatures were on average 2.5-5.5°C higher and corresponding humidity about 15-25% lower on open plantations (i.e. secondary shrub and pasture land), compared to forested sites (i.e. pine plantations and near-natural forest; Appendix Figure B.2).

Abundance was low across all insect orders (Table 3.2, Appendix Table A.1 and A.2 for details) and commonly lower during the first recording period compared to the second (see Chapter 1). The prevalence of rare species was high with 41.4% singleton species among phytophagous Coleoptera and comparable values found among the other groups (predatory Coleoptera: 40.0%, Hemiptera: 42.9%, and Lepidoptera: 50.0%). Within each clade, the majority of species belonged to a small number of families: Chrysomelidae and Curculionidae for phytophagous Coleoptera; Staphylinidae and Coccinellidae for predatory Coleoptera; Cicadellidae, Miridae, for Hemiptera; and Geometridae, Noctuidae, Erebidae and Tortricidae for Lepidoptera (Appendix Table A.1 and A.2)

The difference in sample-based species richness between survey periods did not quite reach significance, but there was a strong trend towards higher richness during the second period in all groups with the exception of Lepidoptera (Appendix Figure D.1, Appendix Table D.1). Furthermore, no qualitative shift in the relative order of habitats was observed when sample-based species richness was calculated on the basis of all three, rather than just two tree species (Appendix Figure D.2). Therefore, we present the results covering all tree species.

Across all insect groups, expected species richness for treelets in near-natural forest was approximately two to three times higher compared to that of their conspecifics on reforestation sites. Among planted treelets, enrichment plantings beneath *P. patula* typically harbored more species than those established in open habitat (i.e. pasture and secondary shrub) and in the case of Hemiptera and Lepidoptera species richness was similar to that observed for near-natural forest. Diversity of phytophagous Coleoptera was significantly lower among succes-

sional shrub vegetation compared to pasture sites. While the remaining insect groups showed no statistically significant difference between these two habitats, there was nonetheless a pervasive trend towards higher species richness on pasture land (Figure 3.1; Appendix Table D.1).

Significant differences in expected species richness as a function of host tree species were apparent in all insect groups, with the highest values typically observed for *H. americanus* (Figure 3.2; Appendix Table D.1). Accumulation curves for tree species within habitats indicated that this general effect was primarily due to clear differences between tree species in near-natural forest and to a lesser degree also in Pine forest (only Hemiptera and Lepidoptera). Saplings on pasture sites, on the other hand, showed little variation in the species richness of associated insect communities (Appendix Figure D.3).

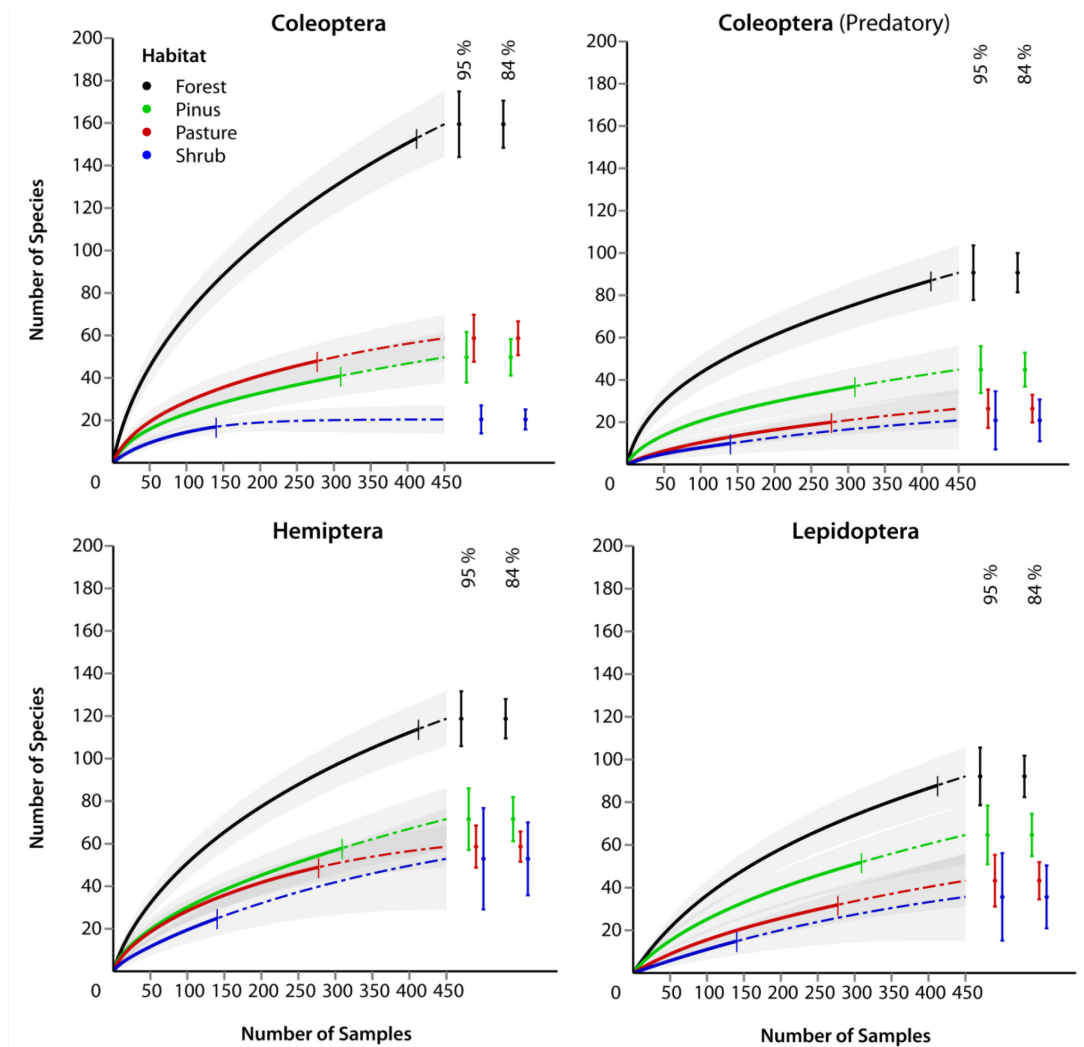


Figure 3.1 Extrapolation of sample-based species-accumulation curves for Coleoptera, Hemiptera and Lepidoptera, according to habitat (excluding *C. montana*). Solid lines: actual extent of sampling; dotted lines: extrapolation; shaded fractions: 95% confidence intervals (Ci). Left whisker plots give a conservative 95% Ci, right plots give an 84% Ci (Payton *et al.*, 2004). Non-overlap of confidence intervals indicates significant differences.

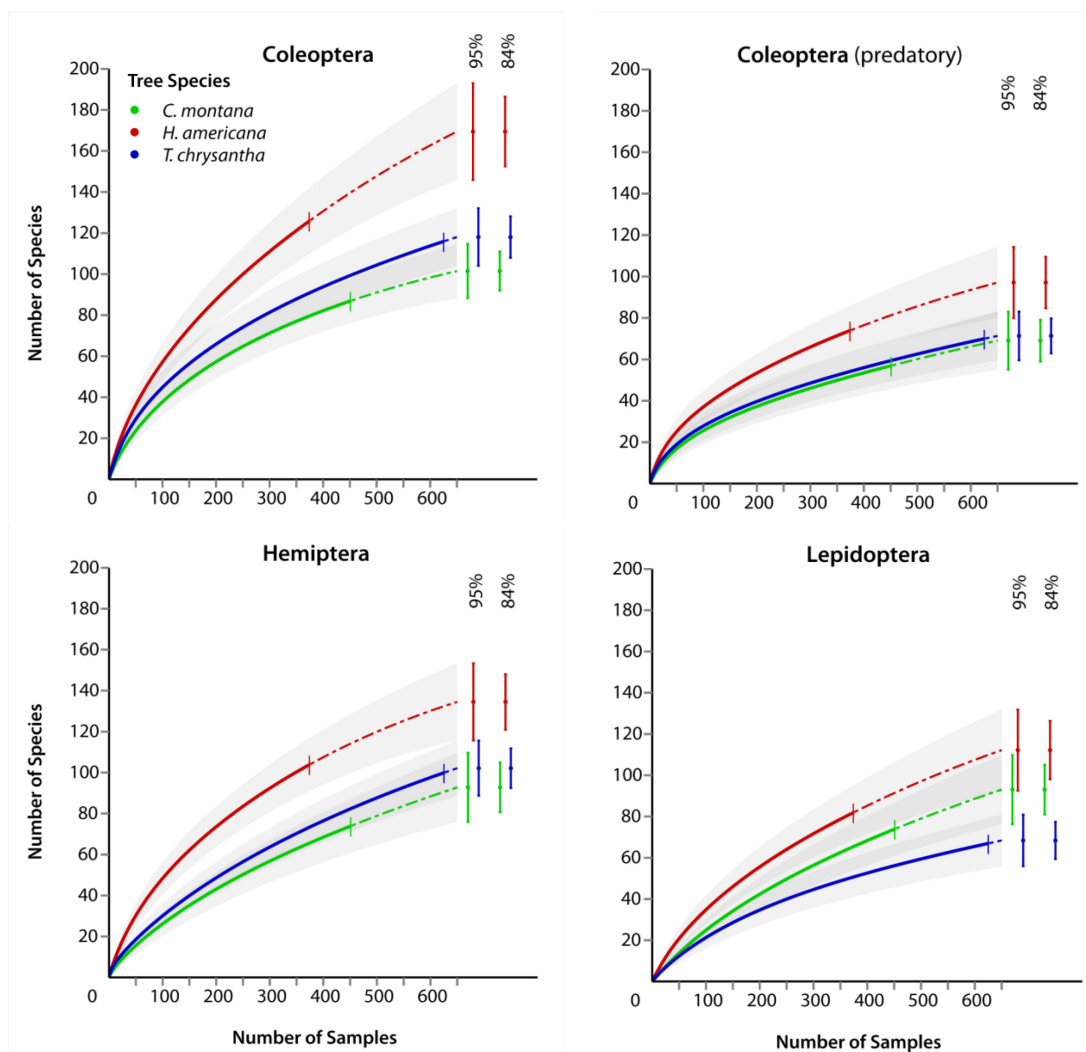


Figure 3.2 Extrapolation of sample-based species accumulation curves for Coleoptera, Hemiptera and Lepidoptera, according to host tree species (excluding 'Shrub' habitat). Solid lines: actual extent of sampling; dotted lines: extrapolation; shaded fractions: 95% confidence intervals (Ci). Left whisker plots give a conservative 95% Ci, right plots give an 84% Ci (Payton *et al.*, 2004). Non-overlap of confidence intervals indicates significant differences.

PERMANOVA evaluation of distance-based redundancy analysis (db-RDA) indicated significant main and interaction effects for recording period (Appendix Table D.2). The corresponding ordination plots, however, suggest that these effects were more a function of varying spread among the data points, rather than the result of any ecologically meaningful shift in clustering (Appendix Figure D.4 to D.6). Samples were therefore pooled across recording periods for further analyses. Despite their high prevalence, exclusion of singleton and doubleton species (Appendix Table D.3 to D.4; Appendix Figure D.7) or of treelets with extremely species-poor communities (Appendix Table D.5 to D.6; Appendix Figure D.8) likewise had no perceptible biasing effect on ordination. Further discussion will therefore be based on the complete dataset. With regard to Hemiptera, exclusion of the three highly dominant, host-specific taxa lead to a somewhat less clear-cut segregation into tree species specific communities, as might be expected. The underlying patterns, however, remained qualitatively the same

(Appendix Table D.7; Appendix Figure D.9) and subsequent analyses were therefore carried out including all Hemipteran species. Unless stated otherwise, further reference will pertain to Hemiptera as a whole. Values reported below are based on the respective best models generated by automated model selection.

Habitat, host tree species and their mutual interaction emerged as the strongest determinants of community composition among phytophagous insects as well as predatory Coleoptera, but their relative impact varied between taxonomic orders. The composition of Coleopteran communities was predominantly a function of habitat (phytophagous: $F=12.486$, $p \leq 0.001$; predatory: $F=15.901$, $p \leq 0.001$; Table 3.3), but clear differences were apparent between feeding guilds. Predatory Coleoptera formed a distinctive forest community, while the remaining habitats harbored partly convergent assemblages with a relatively clear distinction between the ‘Pinus’ community and the ‘Pasture’/‘Shrub’ sites (Figure 3.4). Among herbivorous taxa, on the other hand, ‘Pasture’ sites held a largely characteristic assemblage of species, while the ‘Pinus’ habitat yielded nested subsets of the ‘Forest’ community (Figure 3.3). In this context, a closer examination of the data suggests that the partial overlap between ‘Pasture’ and ‘Pinus’/‘Forest’ sites may be connected to the spatial proximity of certain sample trees to neighboring *P. patula* plots (10.8 x 10.8m², established as part of the original experiment, Aguirre, 2007; Aguirre *et al.*, 2011). All data points of the pasture subset with negative x-values along the principal axes relate to treelets that were within a distance of less than 10m to an adjacent pine plot. Notably, a similar effect was not observed for predacious Coleoptera (Figure 3.5). With regard to ‘Shrub’ sites, almost all sample trees that harbored a beetle population were also located in the immediate vicinity of pine plots. While a noteworthy observation in itself, it is thus not possible to discern whether the observed species composition among phytophagous Coleoptera is in fact characteristic for successional shrub habitat as such, or rather due to the presence of pine in the immediate neighborhood.

The effect of host tree species on community composition was secondary, but still significant in Coleoptera (phytophagous: $F=6.286$, $p \leq 0.001$; predatory: $F=2.692$, $p \leq 0.001$; Table 3.3). Segregation among host-specific assemblages was only discernible in the ordigrams for herbivorous taxa, however. Despite considerable convergence, there is some distinction between *H. americanus* and *T. chrysantha* communities, while the species assemblages found on *C. montana* are essentially recruited from the intersecting subset of these communities (Figure 3.3). Notably, this effect was modulated by the surrounding habitat (phytophagous: $F=3.079$, $p \leq 0.001$; predatory: $F=2.433$, $p \leq 0.001$; Table 3.3), but again, ecologically meaningful shifts in community structure as a result of the interaction were only apparent among phytophagous taxa. On ‘Forest’ and ‘Pinus’ sites, segregation between *H. americanus* and *T. chrysantha* assemblages was relatively pronounced. For treelets planted on open pasture land, on the other hand, associated insect communities were largely confluent (Figure 3.3). Furthermore, a

slight effect of tree health was apparent for phytophagous Coleoptera, but absent in predatory taxa, which in turn showed a weak effect of distance to neighboring trees. The overall explanatory value of the final models was similar for both feeding guilds with adjusted R^2 values of 0.23 (phytophagous) and 0.25 (predatory), respectively (Table 3.3).

Hemiptera community structure, on the other hand, was far more influenced by host tree species ($F = 29.977$, $p \leq 0.001$) rather than habitat ($F = 9.537$, $p \leq 0.001$; Table 3.3). Each tree species was found to support a characteristic and largely distinct assemblage of species, while differences between habitats were relatively slight (Figure 3.4). The interaction between the two predictor variables was likewise significant ($F = 3.739$, $p \leq 0.001$). *T. chrysantha* and to a lesser degree *C. montana* hosted a somewhat different species community on enrichment plantings within the pine plantation compared to pasture and natural forest sites (Appendix Figure D.3). Relatively weak effects of mean leaf area, distance to neighboring plants, and tree height were also found. Goodness of fit was somewhat higher than in Coleoptera (adj. $R^2 = 0.32$) (Table 3.3).

Lepidoptera communities were shaped to a similar extent by habitat ($F = 3.025$, $p \leq 0.001$) and tree species ($F = 4.848$, $p \leq 0.001$; Table 3.3), respectively, although the overall descriptive power of the model was weak compared to the other insect groups (adj. $R^2 = 0.10$). The habitat effect is mainly one of nestedness, with the ‘Pasture’/‘Shrub’ community forming a nested subset of the more varied ‘Pinus’/‘Forest’ assemblage. Caterpillar communities associated with *H. americanus* and *T. chrysantha* are for the most part mutually exclusive, with *C. montana* communities coinciding largely with the narrow overlap in the assemblages of the other two tree species (Figure 3.4). Although significant, the interaction effect of the two variables ($F = 1.860$, $p \leq 0.001$) was weaker than the effect of mean leaf area ($F = 2.249$, $p \leq 0.001$) and was likely related to differences in the species composition of *T. chrysantha* communities within the Pine plantation relative to those on saplings in natural forest and on pasture land, respectively (Appendix Figure D.10).

Matrix correlations via the bvstep algorithm showed that there is a small number of recurring species underlying the observed ordination patterns (Appendix Figure D.11). Species that occur in the majority of models along the iteration process are typically, but not exclusively, recruited from the more abundant taxa and usually showed a relatively clear preference for a specific habitat, tree species, or both.

Table 3.3 Summary statistics of distanced-based redundancy analyses for all four insect groups. Data was aggregated per tree individual, results are based on PERMANOVA (1000 permutations). The best model was determined by automated forward/backward model selection based on AIC. Model fit is given as adjusted R². Hemiptera results pertain to the complete datasets, including the three abundant species

Coleoptera (phytophagous)

	df	Complete model					Best Model				AIC: 1020.7970 adj. R ² : 0.2267
		Variance	F	p			Variance	F	p		
Habitat	3	23.607	12.498	0.001	***		23.607	12.486	0.001	***	
Tree sp.	2	7.923	6.292	0.001	***		7.923	6.286	0.001	***	
Health	2	2.571	2.041	0.003	**		2.573	2.041	0.002	**	
Leaf area	1	2.447	3.887	0.001	***		2.445	3.880	0.001	***	
Distance to 5 nearest neighbors	1	0.754	1.197	0.200			---	---	---		
Height	1	0.674	1.071	0.346			---	---	---		
Habitat x Tree sp.	5	9.644	3.063	0.001	***		9.702	3.079	0.001	***	
Residual	191	120.258					121.627				

Coleoptera (predatory)

	df	Complete model					Best Model				AIC: 837.4907 adj. R ² : 0.2509
		Variance	F	p			Variance	F	p		
Habitat	3	25.939	15.859	0.001	***		25.939	15.901	0.001	***	
Tree sp.	2	2.928	2.685	0.001	***		2.928	2.692	0.002	**	
Health	2	1.308	1.199	0.221			---	---	---		
Leaf area	1	2.053	3.766	0.001	***		2.061	3.791	0.001	***	
Distance to 5 nearest neighbors	1	1.211	2.221	0.012	*		1.199	2.204	0.017	*	
Height	1	0.809	1.484	0.123			0.936	1.721	0.052	.	
Habitat x Tree sp.	5	6.276	2.302	0.001	***		6.614	2.433	0.001	***	
Residual	164	89.417					90.264				

Hemiptera (phytophagous)

	df	Complete model					Best Model				AIC: 1038.1060 adj. R ² : 0.3179
		Variance	F	p			Variance	F	p		
Habitat	3	14.494	9.554	0.001	***		14.494	9.537	0.001	***	
Tree sp.	2	30.373	30.030	0.001	***		30.373	29.977	0.001	***	
Health	2	0.941	0.930	0.545			---	---	---		
Leaf area	1	1.236	2.445	0.003	**		1.247	2.461	0.005	**	
Distance to 5 nearest neighbors	1	1.138	2.251	0.004	**		1.094	2.159	0.009	**	
Height	1	1.091	2.157	0.012	*		1.154	2.278	0.005	**	
Habitat x Tree sp.	5	9.753	3.857	0.001	***		9.471	3.739	0.001	***	
Residual	202	102.155					103.349				

Lepidoptera (phytophagous)

	df	Complete model					Best Model				AIC: 887.5810 adj. R ² : 0.0959
		Variance	F	p			Variance	F	p		
Habitat	3	5.979	3.024	0.001	***		5.979	3.025	0.001	***	
Tree sp.	2	6.388	4.847	0.001	***		6.388	4.848	0.001	***	
Health	2	1.132	0.859	0.835			---	---	---		
Leaf area	1	1.455	2.208	0.001	***		1.482	2.249	0.001	***	
Distance to 5 nearest neighbors	1	0.795	1.206	0.15			---	---	---		
Height	1	0.862	1.308	0.068	.		---	---	---		
Habitat x Tree sp.	5	5.987	1.817	0.001	***		6.126	1.860	0.001	***	
Residual	167	110.052					112.674				

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'

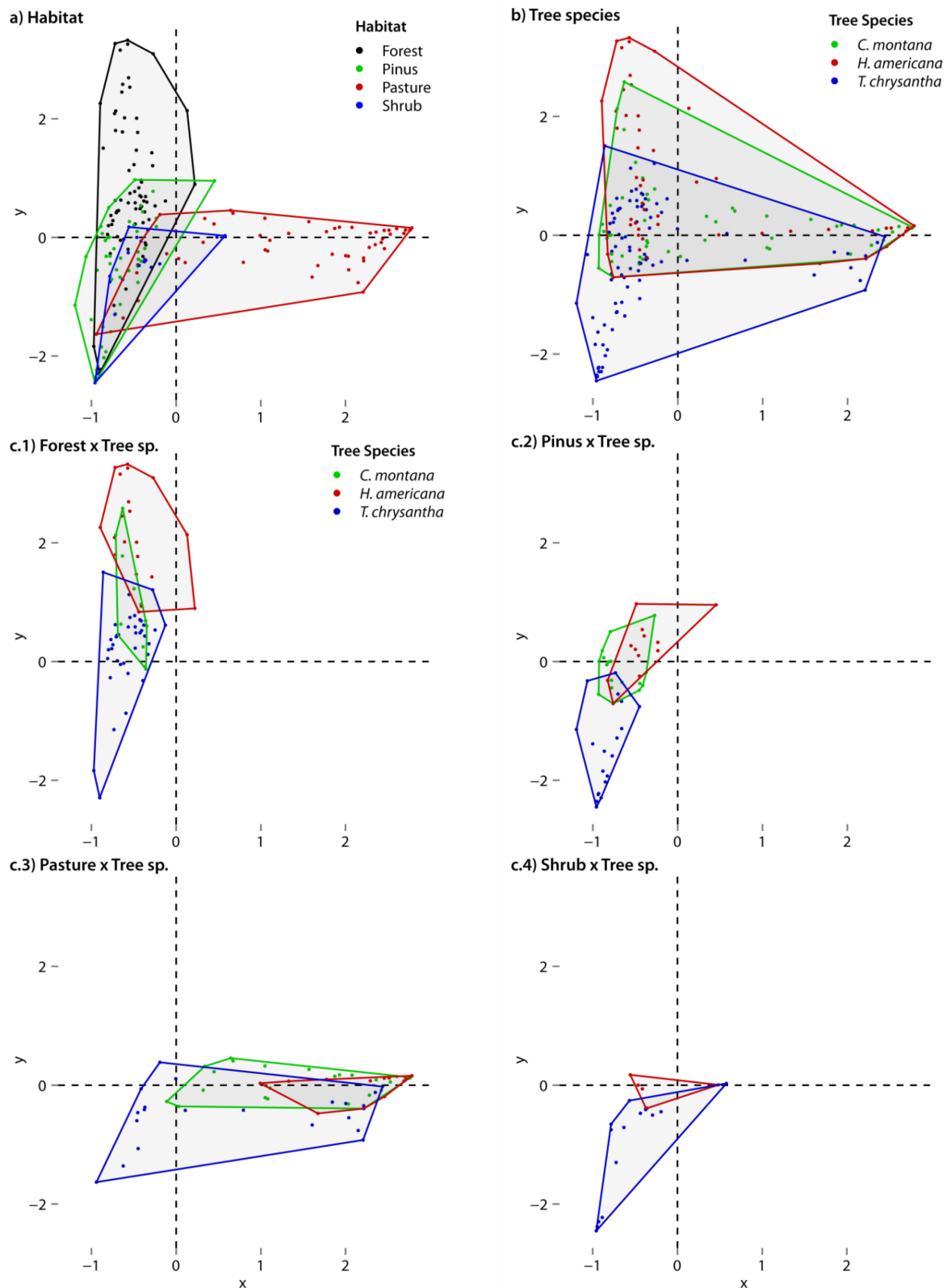


Figure 3.3 Ordination plots for phytophagous Coleoptera. Graphics correspond to the outcome of the distance-based redundancy analyses (best model) shown in Table 3.3. The upper most diagrams highlight the effect of habitat (a) and tree species (b). The four lower panels show grouping of species assemblages associated with treelets within habitat (c.1-4). Each symbol represents the fauna of one individual treelet. Polygons encompass all treelets of a given group.

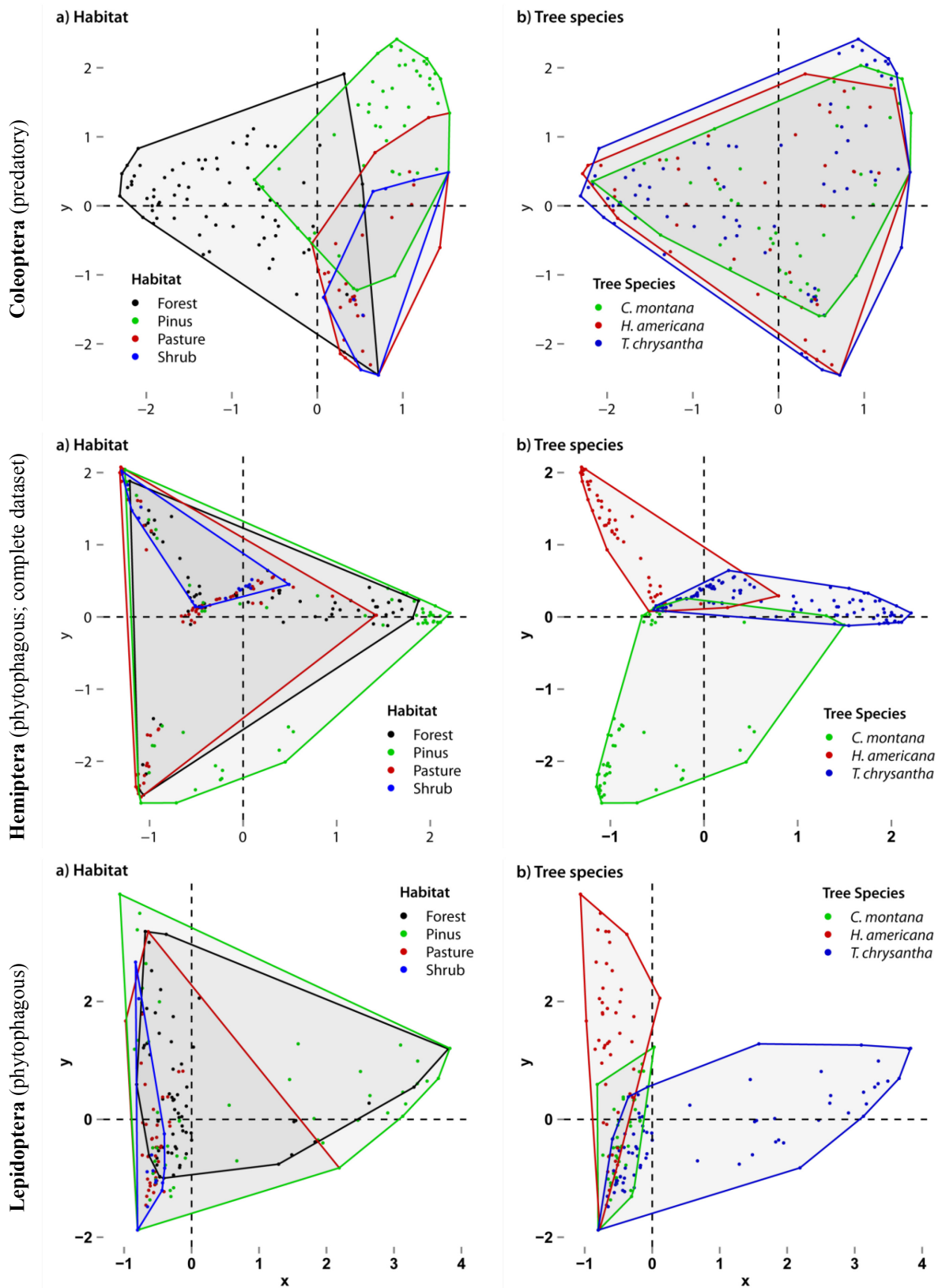


Figure 3.4 Ordination plots for predatory Coleoptera, as well as phytophagous Hemiptera and Lepidoptera by habitat and tree species. Graphics correspond to the outcome of the distance-based redundancy analyses (best model) shown in Table 3.3. Each symbol represents the fauna of one individual treelet. Polygons encompass all treelets of a given group.

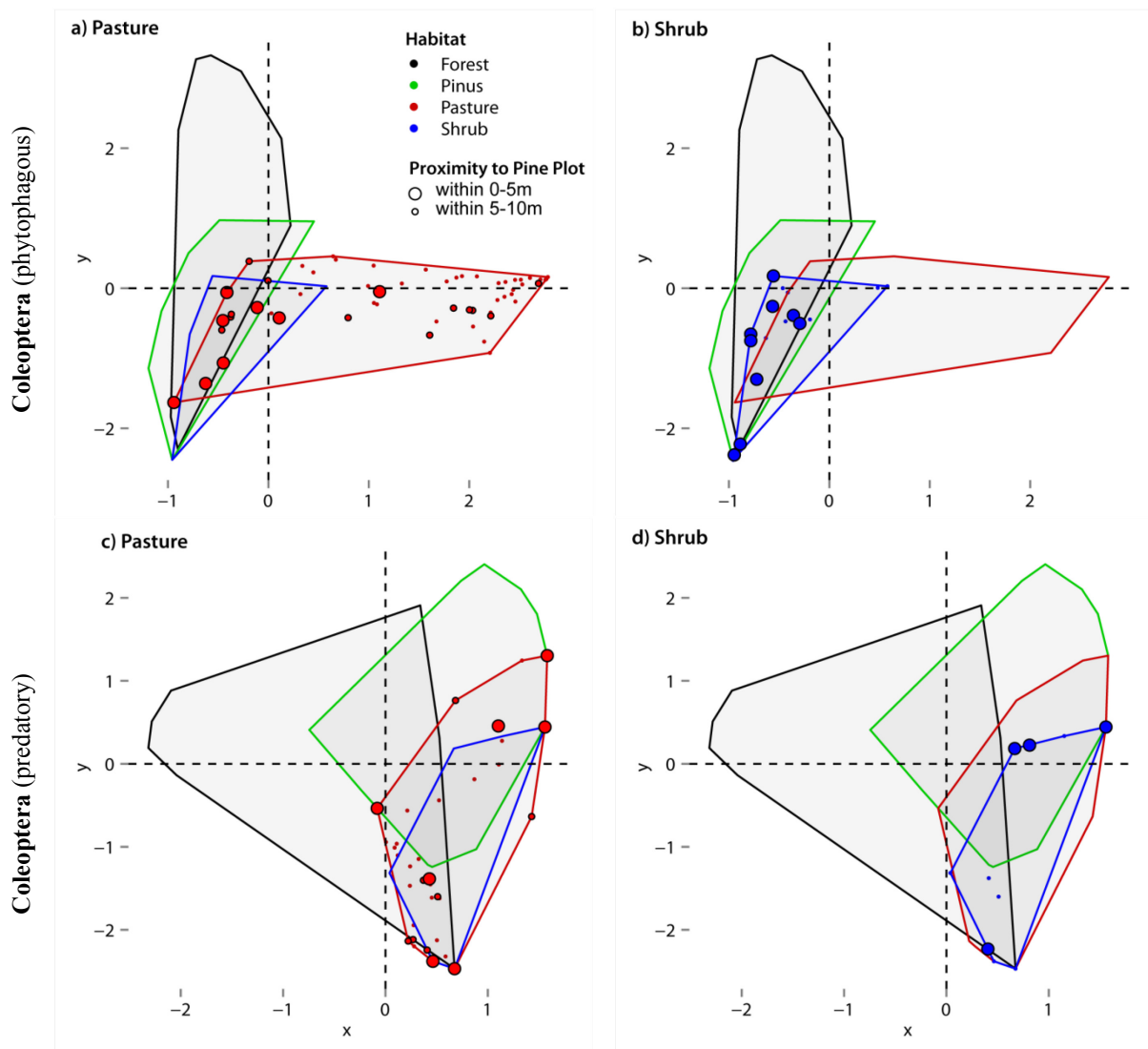


Figure 3.5 Ordination plots highlighting sample trees in proximity to *P. patula* stands. Diagrams depict phytophagous (upper panels) and predatory (lower panels) Coleoptera community composition for ‘Pasture’ (a+c) and ‘Shrub’ (b+d) habitat. Treelets within 10m to a *P. patula* plot are shown by larger symbols. Each symbol represents the fauna of one individual treelet. Polygons encompass all treelets of a given group

Multiplicative partitioning of diversity indicated that a considerable proportion of overall diversity was contained in the α component. Cumulative β -diversities accounted for an average of 66.9% of total diversity across all groups, with the most substantial turnover observed between individual sample trees (β_1). The β_1 component for Hemiptera (dominant species excluded) did not differ significantly from the null model. In all other cases, observed tree-level diversity values (α and β_1) were consistently lower than expected from the null distribution, while turnover on habitat- (β_2) and tree species level (β_3) were generally higher (except for the complete Hemiptera dataset) (Table 3.4 and Figure 3.6).

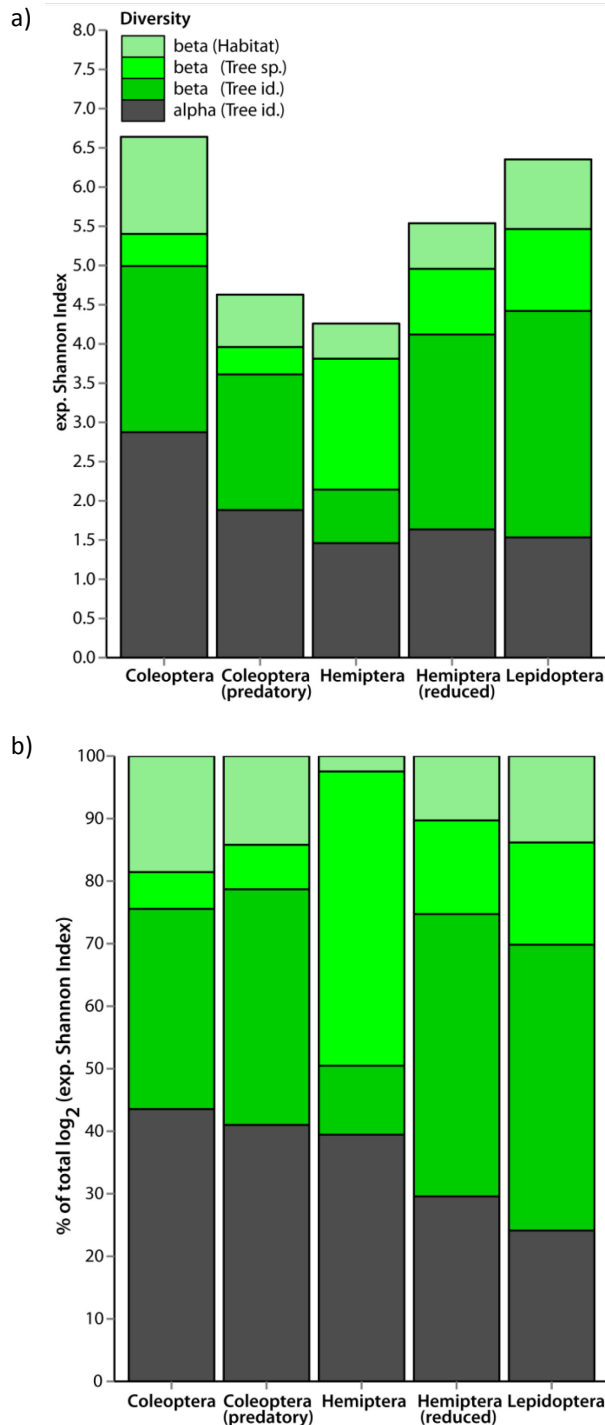


Figure 3.6 Results of multiplicative diversity partitioning for all insect groups with (a) mean α - and β -diversity values (between sites, tree species and habitats, respectively), and (b) the proportion of each diversity component expressed as a percentage of total γ -diversity. Values (exp. Shannon diversity) were transformed to an additive representation using \log_2

Table 3.4 Multiplicative partitioning of α - and β -components based on exponential Shannon diversity. Significance values were calculated based on 1000 randomizations comparing observed values to expected measures derived from the null model.

	observed	expected	p	
Coleoptera (phytophagous)				
alpha	7.334	12.896	< 0.001	***
beta 1	4.341	5.468	< 0.001	***
beta 2	1.328	1.240	< 0.001	***
beta 3	2.359	1.312	< 0.001	***
gamma	93.421			
Coleoptera (predatory)				
alpha	3.685	5.457	< 0.001	***
beta 1	3.319	3.771	< 0.001	***
beta 2	1.273	1.207	0.003	**
beta 3	1.590	1.134	< 0.001	***
gamma	22.993			
Hemiptera (total)				
alpha	2.752	3.488	0.002	**
beta 1	1.605	1.729	0.002	**
beta 2	3.180	1.069	0.002	**
beta 3	0.733	1.032	0.002	**
gamma	6.670			
Hemiptera (dom. ssp. excl.)				
alpha	3.107	4.795	0.002	**
beta 1	5.598	5.936	0.062	.
beta 2	1.786	1.498	0.002	**
beta 3	1.496	1.179	0.002	**
gamma	44.143			
Lepidoptera (phytophagous)				
alpha	2.895	3.621	0.002	**
beta 1	7.395	10.034	0.002	**
beta 2	2.064	1.693	0.002	**
beta 3	1.849	1.334	0.002	**
gamma	77.204			

Discussion

From a sample of close to 14,000 specimens we identified almost 600 phytophagous species (Coleoptera: 208 spp.; Hemiptera: 202 spp., and Lepidoptera: 169 spp.), and a further 115 species of predatory beetles. The initial field campaign from October to May 2010/11 took place during an exceptionally dry period (T. Peters, unpublished data). Such drought conditions are known to exert a negative impact on insect survival and reproductive success, affecting individuals either directly or through changes in host plant quality and phytochemistry (e.g. Qayyum & Zalucki, 1987; Pollard *et al.*, 1997; Huberty & Denno, 2004; Kishimoto-Yamada & Itioka, 2008; Scherber *et al.*, 2013). In the present study, this is reflected by changes in arthropod abundance, suggesting an initial population decline and subsequent recovery with the normalization of local climate (see Chapter 1). Since prior data on local insect communities is not available in the present context, the possible impact of drought on species richness and community composition can only be inferred but not conclusively quantified. Nonetheless, climatic condition impinge upon the interpretation of observed response patterns and will thus be addressed at appropriate points in the subsequent discussion. With regard to species richness, surrounding habitat and host tree species emerged as primary determinants. Since taxonomic orders and dietary guilds showed largely similar qualitative responses, the following section will mostly pertain to insect diversity in general, rather than differentiate between individual groups.

Species richness was highest in near natural forest with about 100 to 150 recorded species depending on insect groups (i.e. phyto. Coleoptera: 167 observed species; pred. Coleoptera: 90 spp., phyto. Hemiptera: 126 spp., and phyto. Lepidoptera: 101 spp.). These values are in rough agreement with findings of Basset & Novotny (1999) who reported between 15 and 44 caterpillar species, and 13 to 89 taxa of chewing, non-Lepidopteran herbivores (predominantly beetles) across 15 species of *Ficus* in Papua New Guinea. By comparison, we observed slightly higher values with 44 to 98 phytophagous Coleoptera species, and 30 to 57 species of phytophagous Lepidoptera larvae per sample tree species. Sap-sucking herbivores, on the other hand, were far more divers in Papua New Guinea. A second study on five species of tree saplings in French Guiana (Basset, 1999) found a total of 78 Coleopteran, and 22 Lepidopteran species with a confirmed trophic relation to the plants in question. Once more, there was a striking predominance of sap-sucking herbivores.

Among reforestations, diversity was universally lower with individual sites harboring between half and one third the number of species observed in near-natural forest. The prevalence of less complex arthropod communities in disturbed sites is a common finding (e.g. Schulze *et al.*, 2004; Hilt & Fiedler, 2005; Gormley *et al.*, 2007; Grimbacher *et al.*, 2007; Gibson *et al.*, 2011' and citations therein), although not necessarily an universal one (e.g.

Cunningham *et al.*, 2005; Hilt & Fiedler, 2006; Pawson *et al.*, 2008). High prevalence of rare species and a general lack of detailed information on habitat preference for many tropical taxa made distinction into forest specialists, generalists, and open habitat adapted species unfeasible in the present context. Nonetheless, it seems likely that lower diversity on plantation sites is partly linked to the absence of forest-specialist species (e.g. Grimbacher & Catterall, 2007). As such, the observed discrepancy between old growth forest and reforestation plots underlines the importance of maintaining existing rainforest for the conservation of local biodiversity (Barlow *et al.*, 2007; Gibson *et al.*, 2011).

Although afforestations as a whole were clearly reduced in their capacity to support local insect fauna, such sites can nonetheless provide potentially viable habitat for a considerable number of species. Habitational value, however, was largely dependent on surrounding land cover. Saplings planted beneath a pre-existing canopy (i.e. *P. patula*) typically hosted a more diverse insect community compared to their conspecifics on more open sites (i.e. pasture land and secondary shrub vegetation), particularly with regard to predatory Coleoptera and phytophagous Lepidoptera. Notably, this pattern did not coincide with the plant species richness of surrounding habitat, since floristic diversity was considerably higher among secondary shrub vegetation compared to pasture sites or the Pine plantation (Aguirre *et al.*, 2011). The latter plots in turn harbored an approximately equal number of vascular plant species (J. Gawlik, unpublished data). Generally speaking, greater floristic diversity tends to be associated with correspondingly higher insect species richness (Siemann *et al.*, 1998; Lewinsohn & Roslin, 2008; Scherber *et al.*, 2010; Castagneyrol & Jactel, 2012). The underlying causation, however, is often difficult to disentangle, and in many cases plant diversity may simply be correlate to the decisive parameter, rather than a driving force in itself (e.g. productivity: Haddad *et al.*, 2001 and Hawkins & Porter, 2003; community composition: Schaffers *et al.*, 2008; vegetation structure: Axmacher *et al.*, 2009). In the present context, structural aspects such as the capacity of canopy- or ground cover to ameliorate local microclimate (compare Chen *et al.*, 1999; Grimbacher *et al.*, 2006) seem to outweigh other possible effects of plant species richness. Consequently, as exemplified by enrichment plantings beneath *P. patula*, even the protective cover provided by exotic timber species can be of potential benefit for the conservation of local insect communities. In the absence of trees, insects appear to derive a certain benefit from the presence of dense ground cover. Our data show significantly lower diversity of phytophagous Coleoptera on treelets growing among secondary shrub vegetation compared to those planted on open pastures, and similar trends are apparent for the other groups. While former pastures retained a dense layer of grass (i.e. *Setaria sphacelata*) surrounding the planted treelets, successional shrub sites often had little or no herbaceous ground cover (personal observation). Although clearly not as effective as a closed canopy, ground vegetation may provide limited shelter during adverse climatic conditions or help maintain

ambient humidity. Its absence is therefore likely to be detrimental to the preservation of insects.

Interestingly, higher species richness in plantation forest relative to pasture sites is not an overly common finding with respect to tropical arthropods (Schulze *et al.*, 2004; Cunningham *et al.*, 2005; Felton *et al.*, 2010 for meta-analysis). The diversity pattern above may therefore have been partly the result of the unusually dry conditions during the first recording period 2010/11. Such climatic constraints could have suppressed the potential impact of other factors, such as floristic diversity, which might otherwise have been apparent. In further support of the proposed negative effects of drought on local insect communities, a comparison of our findings to similar studies seems to indicate that observed species richness as well as abundance on open habitat (e.g. pasture) were indeed lower than might have been expected. Using a methodology similar to our own, Bodner *et al.* (2012; personal communication) recorded a total of 1,250 caterpillar specimens belonging to 127 species on three species of Asteraceae growing on highly disturbed sites in the San Francisco research area. In contrast, our surveys yielded merely 157 individuals across sample treelets planted on pasture reforestations, amounting to a total of 53 species. Another study by Plath *et al.* (2012a) investigated arboreal Coleoptera communities in two-year-old, low-land timber plantations that were notably similar to the present design in species selection (i.e. *Anacardium excelsum*, *Cedrela odonata*, and *Tabebuia rosea*) and land use history (i.e. former pasture land). The researchers recorded a total of 159 phytophagous taxa. By comparison, our surveys only yielded 57 herbivorous beetle species, despite very similar taxonomic composition of this dietary guild in both studies (i.e. predominantly Chrysomelidae and Curculionidae). The discrepancy is all the more striking, since greater plantation age (Grimbacher & Catterall, 2007), less management intervention, and presumably greater palatability of *H. americanus* compared to *A. excelsum* (Dominy *et al.*, 2003) would lead to expect relatively higher, rather than lower diversity values in our study compared to the results of Plath *et al.*. The differences between the two studies may be related to altitudinal effects, but detailed information regarding the elevational distribution of phytophagous beetles in the Andes is largely lacking. Studies on other families in tropical mountain regions, however, seem to indicate a tendency towards low- to mid-elevation peaks in diversity (~ 800m: García-López *et al.*, 2012; Herzog *et al.*, 2013; ~2,500m: Yu *et al.*, 2013), rather than a general decline with altitude. In summary, although quantitative comparison of species richness between unrelated studies is often problematic due to differences in sampling protocol and other potentially confounding factors (e.g. host plant species: Summerville *et al.*, 2003; elevation: Hodkinson, 2005), there is reason to assume that the insect diversity values presented here are in part the result of adverse climatic conditions. Specifically, species richness might have been somewhat higher among open-canopy reforestations (i.e. 'Pasture' and 'Shrub') prior to the drought event, and insect communities within

near-natural forest may have been more sheltered from detrimental climatic effects. The actual gap in diversity between forest and reforestations sites under ‘normal’ conditions may thus well be smaller than indicated by our data.

Host tree species also affected insect diversity, although the impact seemed to be somewhat weaker than that of surrounding habitat. On average, saplings of *H. americanus* harbored a more diverse community of phytophagous, as well as predatory insects compared to the other sample trees. Notably, this differentiation was most pronounced for treelets growing in near natural forest and to a lesser extent also apparent on saplings planted beneath *P. patula* for some insect orders (i.e. Hemiptera and Lepidoptera). Broadly speaking, greater susceptibility of *H. americanus* to herbivores would be in keeping with the observation that fast-growing pioneer species commonly invest fewer resources in defense (growth-defence trade-off; e.g. Endara & Coley, 2011). The results of a recent comparative study on species-specific phytochemical compounds, however, seem somewhat at odds with this general framework. According to Peñuelas et al. (2010), specimens of *H. americanus* can contain concentrations of tannines, terpenes and phenolic compounds that are as high as or higher than those measured for a congeneric of *T. chrysantha* (i.e. *T. rosea*). Rather than possessing categorically weaker defenses as a pioneer tree, *H. americanus* may instead have simply been less tolerant towards shade. Since the defensive chemicals mentioned above are carbon-based, production is presumably to some extent contingent on the availability of surplus carbon from photosynthesis (compare Carbon:Nutrient Balance Hypothesis; e.g. Stamp, 2003; Endara & Coley, 2011). As a normally light-demanding species, *H. americanus* may have been disproportionately impaired by more shaded conditions beneath canopy cover, thus curtailing the allocation of resources to herbivore defense. This would allow a larger number of presumably generalist phytophagous species to exploit the tree as a host. In turn, the observed increase in predator species richness is most likely the result of a more diverse prey community (Scherber *et al.*, 2010; Castagneyrol & Jactel, 2012). Notably, however, greater diversity of chewing herbivores on *H. americanus* treelets did not coincide with higher levels of folivory (see Chapter 4), suggesting that other factors in addition to possible differences in palatability may have played a role. The discrepancy in insect diversity between *H. americanus* and the other sample species appears to be slightly more pronounced among more mobile phytophagous clades (i.e. Coleoptera and Hemiptera) as opposed to sessile herbivores (i.e. caterpillars). Furthermore, the differences were most apparent in inherently species-rich habitats (i.e. primarily near-natural forest), that also harbored a large number of rare taxa for which species-level dietary information was mostly lacking. This would suggest that the observed pattern may in part be due to a higher number of tourist species, which do not have a trophic link to the host tree in question. Their increased presence on *H. americanus* may have been due to aspects of plant architecture not explicitly recorded in the present study. A greater extent of branching or

a higher crown volume may have offered ecological niches or shelter that were absent in structurally more simple plants.

The apparent impact of drought stress on species richness may be expected to influence insect community composition as well. A study in Borneo, for example, found altered species assemblages in Chrysomelidae following an El Niño related drought (Kishimoto-Yamada & Itioka, 2008; Kishimoto-Yamada *et al.*, 2009). Notably, while most species showed a decline in population size in response to the event, some taxa increased in abundance. Similarly opposing trends were observed in Lepidoptera and have been related to changes in plant chemistry due to water stress (Gutbrodt *et al.*, 2011). Since survey data prior to the event is unfortunately not available, extent and nature of any drought related shift in community structure cannot be assessed in the present case, although there is reason to believe that it may have been relatively small. Any loss of species was likely to be biased towards already rare taxa. However, removal of such singleton/doubleton species did not alter the qualitative outcomes of db-RDA and ordination analysis in the present study, nor was there a discernible qualitative shift in species composition between the two survey periods. Proliferation of individual insect species sometimes observed after a drought (e.g. Itioka & Yamauti, 2004; van Bael *et al.*, 2004) was likewise not apparent. It therefore seems reasonable to assume that the patterns in community structure described below possess a general validity instead of simply reflecting the outcome of an extreme event.

Species composition was primarily a function of habitat and host tree species, although the relative importance of these factors differed considerable between insect orders. Generally speaking, the structure of Coleopteran communities was primarily a function of surrounding habitat, although the two dietary guilds varied in the extent of differentiation between individual sites. Hemiptera and Lepidoptera assemblages, on the other hand, were to a large degree determined by host plant identity.

Phytophagous Coleoptera formed characteristic communities depending on the presence or absence of canopy cover. For the most part, assemblages on treelets beneath *P. patula* appear to be a nested subset of those found in near natural forest, with little or no overlap between such forested sites and open pasture. This pattern is in agreement with studies documenting the importance of canopy closure for the colonization of plantations by forest species (e.g. Pawson *et al.*, 2011). Notably, the partial convergence between ‘Pasture’ and woodland communities indicated by ordination analysis was entirely due to proximity of sample treelets to small, isolated patches of *P. patula* on open pasture. This conjunction also precluded reliable assessment of beetle communities associated with secondary shrub, since almost all sample trees harboring phytophagous Coleoptera in this habitat were also located adjacent to *P. patula*. The observed small-scale effect of pine stands mirrors the findings of other studies (ants: Majer & Delabie, 1999; ants and beetles: Dunn, 2000; birds and bats: Manning *et al.*,

2006) and further highlights the importance of such isolated tree patches in the conservation of forest-associated species in otherwise unsuitable habitat. Furthermore, the fact that treelets in the vicinity of these patches were colonized by woodland taxa suggests that open habitat (i.e. 'Pasture' and 'Shrub') does not necessarily pose a dispersal barrier for phytophagous Coleoptera, provided the distance to potential source populations remains relatively short. Predatory Coleoptera notably differed from the phytophagous guild by showing a basic divergence between communities associated with natural forest and those found on reforestation sites, as well as a secondary differentiation between the *P. patula* stand and open pastures. In contrast to phytophagous taxa, communities of predaceous Coleoptera showed no overlap between the two forested sites. This discrepancy is in line with the conception that predatory species are more vulnerable to anthropogenic disturbance (e.g. Klein *et al.*, 2002; Attwood *et al.*, 2008). Consequently, while exotic timber plantations may act as surrogate habitat for a number of forest species among phytophagous beetles, they appear to be ill suited to conserve the local diversity of predatory Coleoptera.

The impact of host tree species on the structure of Coleoptera communities is weak relative to the habitat effects, and predictably weaker in predatory compared to herbivorous taxa. Reminiscent of the host-dependent species richness patterns described above, distinct host-specific communities among phytophagous beetles only emerged among saplings growing in forested sites (i.e. pine plantation and near-natural forest). On open pasture land, on the other hand, Coleoptera assemblages were largely confluent across sample trees. Presumably harsher climatic conditions on open sites may have acted as a bottleneck for colonization and persistence of beetle species, thus limiting the potential species pool to a comparatively small number of common and most likely generalist taxa. Consequently, more specialized species that are normally associated with the host plants in question and contribute to the formation of distinct communities among forested habitat seem unable to accommodate the conditions prevailing on pasture plantations.

Were a degree of segregation into host-specific communities was apparent, *T. chrysantha* and *H. americanus* showed more or less characteristic species composition. Species associated with *C. montana*, however, appeared to be common to the either or both of the other tree species as well. Consequently, *C. montana* seems to harbor relatively few specialist species and instead appears to be colonized predominantly by the more polyphagous representatives among chewing phytophages.

Compared to Coleoptera, species composition of Hemiptera and caterpillar assemblages varied little between habitats, but were instead primarily dependent on host tree species. The observed habitat effect appears to be caused primarily by differences in species composition on saplings of *T. chrysantha* beneath pine forest compared to their conspecifics in near-natural forest and on pasture sites. The *P. patula* plantation in question was subject to substantial cat-

ion deficiency (i.e. Mg^{++} , Ca^{++} , and K^{+} ; Breckle *et al.*, 2005), which is likely to affect the nutritional quality of plants, and by extension can be expected to cause shifts in the species composition of associated insect communities. In the present context, a number of *T. chrysantha* saplings showed signs of nutrient deficiency (i.e. chlorosis) which were largely absent in other sample trees, indicating that this species may be more sensitive to poor soil conditions. Although the presence of pine is apparently not necessarily the cause of nutrient depletion, Neotropical plantations are frequently established on exhausted and thus otherwise unproductive soil (Chacón *et al.*, 2009). Consequently, tree species specific deficiency effects should be taken into account if existing pine plantations are to be employed as nursery canopy for enrichment plantings.

Host tree species emerged as the principal determinant of Hemipteran and Lepidopteran species composition. This corresponds to the observation that these taxonomic orders often show a relatively high degree of host specificity, while Coleoptera as a whole are frequently more generalistic with regard to their feeding habits (Novotny *et al.*, 2002a; Novotny *et al.*, 2002b; Dyer *et al.*, 2007; Novotny *et al.*, 2010). Hemiptera segregated into three host-specific and for the most part mutually exclusive communities. The pattern found in Lepidoptera is somewhat similar to the one described above for phytophagous beetles with a fairly clear differentiation into *T. chrysantha*- and *H. americanus*-associated assemblages. Caterpillar communities on *C. montana* appear to have been recruited mostly from those taxa also shared by the other two tree species, again indicating a predominance of polyphagous generalists.

Overall biodiversity in the research area is primarily contained in tree-level α -diversity and variability of species composition between individual sample trees (β_1 -component). Turnover between host tree species (β_2) and habitat (β_3) together only accounted for 25-30% of total diversity, with a proportionally larger contribution of habitat in Coleoptera, and of tree species in Hemiptera and Lepidoptera, respectively. The predominance of tree-level α - and β -diversity is probably in part related to the low density of insects, which may have introduced an additional stochastic element to community composition. More importantly, however, it is likely to be a general characteristic of reforestation communities in the study region. Other studies in the area have shown that plant performance and diversity varies as a function of small-scale heterogeneity of soil conditions (e.g. Günter *et al.*, 2009; Homeier *et al.*, 2010). Potentially resulting changes in floristic composition, vegetation structure and host plant quality can therefore be expected to evoke similar small-scale variability among associated insect communities.

The lack of detailed information on the trophic association between many insect species and their respective host trees is a caveat of the present study, but an unavoidable consequence of the high number of rare species commonly found in tropical arthropod communities (e.g. Novotny & Basset, 2000; Coddington *et al.*, 2009). In consequence, tourist species without

direct association to the sample trees could not be reliably excluded in the present study, and may have inflated measures of species richness. While the number of such transients can be relatively high (e.g. ~20% of chewing herbivores; cited in Novotny & Basset, 2000), they do not necessarily confound biodiversity patterns (compare Truxa & Fiedler, 2012) and are therefore not expected to have affected analysis of community composition, in the present context.

Conclusion

Although the conservation value of targeted reforestations is well below that of natural forest, even young plantations can potentially provide surrogate habitat for many native forest species across a number of insect orders. The microclimatic buffer effect provided by a closed canopy appears to be a principal determinant of habitat suitability, and highlights the importance of establishing early canopy cover when planning new plantations. Although the recruitment of mature exotic timber plantations as nursery canopies is clearly a viable option, it seems advisable to use fast growing, autochthonous species like *H. americanus* whenever feasible, as such species might in themselves serve as potential host for a much broader variety of native invertebrate species. In the choice of plantation regime for prospective reforestation, mixed species stands are likely to benefit especially phytophagous Hemiptera and Lepidoptera, as many species among these clades are highly specialized with regard to their diet. Contrary to phytophagous taxa, predatory Coleoptera associated with natural forest do not seem to colonize artificial reforestations. Conservation of such species will therefore require additional measures. The observed small-scale heterogeneity of insect communities highlights the need to include environmental characteristics at a higher spatial resolution in future research to identify drivers of arthropod species composition down to the spatial scale of individual trees.

CHAPTER 4

Insect folivory as a function of tree species and surrounding habitat – A case study on targeted reforestations in the Andes of southern Ecuador

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Abstract

In the light of continuing forest cover loss in tropical regions, targeted reforestation is critical in maintaining important ecosystem services. Throughout the South-American Andes, cattle farming constitutes an important driver of land cover change, but poor soil and the intrusion of aggressive weed species limit the sustainable use of pastures. Reforestation with native tree species has been suggested as economically and ecologically viable approach to reclaiming degraded habitat, and insect herbivory constitutes an important factor in the viability and management of such plantations. Focusing on young experimental stands in the highlands of southern Ecuador, we examined progression of foliar damage as a function of tree species and habitat. Sample tree species (i.e. *Cedrela montana*, *Heliocarpus americanus*, and *Tabebuia chrysantha*) were selected based on their prospective silvicultural utility. Plantation sites were situated among the prevailing local land cover types (i.e. abandoned pasture, secondary shrub vegetation, and a *Pinus patula* plantation) and compared to adjacent near-natural forest.

Overall leaf damage caused by folivorous insects (excluding leaf-cutter ants) was relatively low, and contrary to initial expectations, average leaf loss was highest among saplings of *T. chrysantha* ($7.24\% \pm 0.38$ se of leaf area), followed by *H. americanus* ($4.78\% \pm 0.28$ se) and *C. montana* ($3.27\% \pm 0.25$ se). Despite its classification as a fast-growing pioneer, *H. americanus* appears to host effective chemical deterrents, and the observed pattern thus conformed to an underlying gradient in herbivore defense. Likewise unexpected, leaf area loss was highest among saplings in near-natural forest, followed by pine plantation, pasture, and secondary shrub sites. This corresponds to a pattern of higher abundance and species richness of phytophagous insects in forested rather than open habitat, which was presumably in part due to microclimatic buffering effects of surrounding vegetation. Generally speaking, foliar damage appeared to be highest at the onset of the dry period and gradually decline throughout the season, although there was some variation depending on species and habitat. Harvesting activity of leaf-cutting ants (*Acromyrmex* sp.) was sporadic and strongly biased towards saplings of *T. chrysantha* growing in open habitat.

Keywords

Acromyrmex sp.; Ecuadorean Andes; Habitat structure; Insect folivory; Reforestation; Microclimate

Introduction

Although the global rate of deforestation appears to be slowing down, increases in the Earth's forest cover are mostly restricted to higher latitudes and offset by net losses still taking place in the tropics (FAO, 2010). Many governments are in the process of abandoning or revising policies that actively promote the conversion of forest to agricultural land (e.g. Costa Rica: Brockett & Gottfried, 2002; Brazil: Bauch *et al.*, 2009), but market forces, population growth, and unsustainable management practices continue to foster agricultural expansion (Laurance *et al.*, 2014). In Latin America, extensive livestock farming constitutes an important driving force in this regard, as many farmers and low-income smallholders rely on cattle as part of their livelihood (Wassenaar *et al.*, 2007). In the Andean highlands, comparatively poor soil conditions and the intrusion of aggressive weeds in the wake of slash-and-burn management (e.g. *Pteridium arachnoideum*; Roos *et al.*, 2010) often render the sustained use of pastures uneconomic, thus forcing the tenants to periodically clear new land for grazing. Competition by the successional shrub/fern community (Hartig & Beck, 2003) and reduced seed deposition (Matt *et al.*, 2008) severely impede the course of natural forest regeneration on former pasture land.

While the protection of pristine forests remains essential in the conservation of biodiversity (Barlow *et al.*, 2007; Laurance *et al.*, 2012), secondary and plantation forests play an increasingly important role in maintaining vital ecosystem services (e.g. conservation: Brockerhoff *et al.*, 2008; soil protection: Zuazo & Pleguezuelo, 2009 and Hamer *et al.*, 2013; carbon sequestration: Don *et al.*, 2011), emphasizing the need for targeted reforestation of degraded landscapes. In the past, tropical forestry relied heavily on a small number of exotic genera (e.g. *Eucalyptus* spp., *Pinus* spp.; Onyekwelu *et al.*, 2011), but in recent decades the focus of interest has increasingly shifted towards the use of autochthonous timber species (Weber *et al.*, 2008; Davis *et al.*, 2012). Besides offering better prospects for the conservation of indigenous flora and fauna (Hartley, 2002; Brockerhoff *et al.*, 2008), native trees typically show less variance with regard to growth performance (Piotto *et al.*, 2003) and some species promise greater financial returns compared to exotic taxa (e.g. Montagnini, 2001; Griess & Knoke, 2011). Nonetheless, insufficient knowledge regarding ecology and management of native tree species currently limits their silvicultural use (Stimm *et al.*, 2008).

The successful establishment of a plantation is not only contingent on species-specific requirements regarding climate and soil conditions (Onyekwelu *et al.*, 2011), but also on herbivore pressure at the prospective site. A number of studies have demonstrated that the extent of leaf damage may have a substantial impact on plant growth (Marquis, 1984; Massad *et al.*, 2011; Plath *et al.*, 2011) and mortality (Eichhorn *et al.*, 2010). In this context, fitness is not only impaired by direct or indirect reduction of photosynthetic capacity (Zangerl *et al.*, 2002),

but also due to an increased risk of viral or fungal infections through wounded plant tissues (García-Guzmán & Dirzo, 2001). The degree to which saplings are susceptible to herbivores is - among other factors - a function of tree species and surrounding environment. Herbivory is typically highest in young leaves (Coley & Barone, 1996), and tree species tend to fall along an escape/defense continuum regarding their strategic response to minimize this window of vulnerability. Pioneer species are thought to be characterized by rapid growth and leaf development, but typically suffer considerable leaf damage due to otherwise weak defenses. Late successional species, on the other hand, tend to invest heavily into phytochemical and physical deterrents to reduce herbivory at the expense of lower growth rates (Kursar & Coley, 2003). With regard to surrounding habitat, folivory is to a large part mediated by vegetational and structural diversity, but findings remain somewhat equivocal as to the directionality of this effect. In the context of forestry, a reduction of leaf damage with increasing plant diversity at the stand level seems to be a relatively common finding (Jactel & Brockerhoff, 2007). It is, however, highly contingent on the nature of tree species involved (Barbosa *et al.*, 2009), the structural characteristics of surrounding vegetation (Giffard *et al.*, 2012; Castagneyrol *et al.*, 2013; Giffard *et al.*, 2013), as well as the identity and degree of host-specialization of the principal herbivores. Depending on the underlying dynamics, beneficial effects of stand diversification can be restricted to individual tree species, but absent in others (Plath *et al.*, 2011), or overall foliar damage may even increase with plant species richness (Schuldt *et al.*, 2010; Plath *et al.*, 2012b).

In the present study, we focus on experimental reforestations in the montane rainforest zone of southern Ecuador, established as part of an interdisciplinary research group (summarized in: Beck *et al.*, 2008a; Bendix *et al.*, 2013). Focal species were chosen among indigenous tree taxa based on timber value (*Cedrela montana* and *Tabebuia chrysantha*) or prospective growth performance (*Heliocarpus americanus*). Specifically, we assessed foliar damage in 6- to 7-year old saplings planted among the dominant anthropogenic habitat types (i.e. pasture land, secondary shrub vegetation, and exotic timber plantations), as well as in conspecific treelets growing in the understory of near-natural forest. Sample sites thus spanned a rough gradient of structural complexity and plant species richness, from near-natural forest to recently abandoned pasture land.

Specifically, we tested the following hypotheses: (1) Saplings of the pioneer *H. americanus* experience a higher level of leaf damage compared to two later successional species, since the latter tend to invest more resources into herbivore defence, and (2) Folivory decreases along a gradient of structural complexity/plant species richness from pasture reforestations to near-natural forest due to potentially more effective biocontrol in increasingly diverse habitat. Furthermore, we addressed the extent of interannual variation in herbivory and potential patterns in the level of leaf damage throughout the season.

Materials and Methods

Study area. The study was conducted in and around the Reserva Biológica San Francisco (RBSF, 3°58'18''S, 79°4'45''W, 1800-2200m a.s.l.; Figure 1.1), located in Zamora-Chinchipe province, southern Ecuador (see Beck *et al.*, 2008b and Richter *et al.*, 2013 for general details). The original vegetation of the San Francisco Valley (i.e. montane rainforest; Homeier *et al.*, 2008) is largely conserved along the southern slopes, where the RBSF borders on the Parque Nacional Podocarpus. The opposing hillsides have been converted to agricultural use (mainly cattle farming) and currently form a patchwork of active pastures, successional shrub habitat, exotic timber plantations and small pockets of remnant ravine forest. The region is characterized by a wet season between April and July and moderately dry conditions from September to December (average annual precipitation: ~2200mm). Temperatures show a daily amplitude of approximately 11.1°C with an annual mean of 15.3 (\pm 1.2 SD)°C (Bendix *et al.*, 2006).

Sample Trees and Study Sites. Experimental reforestations were established in the years 2003 and 2004 among the prevalent land cover types of the region (Aguirre *et al.*, 2006; Aguirre *et al.*, 2011), namely an exotic timber plantation (i.e. 25-30 year old *Pinus patula* stand, subsequently referred to as 'Pinus'), recently abandoned pasture still dominated by exotic grass (i.e. *Setaria sphacelata* or *Melinis minutiflora*; 'Pasture'), and mid-successional vegetation characterized largely by shrubs and bracken fern thickets ('Shrub'). From among the autochthonous tree species tested in this experimental reforestations, we selected two deciduous, high value, mid-successional timber species (Meliaceae: *Cedrela montana* and Bignoniaceae: *Tabebuia chrysantha*), as well as a fast-growing, light-demanding ever-green pioneer/early-successional species (Malvaceae: *Heliocarpus americanus*). Reforestation treelets were compared to conspecific saplings from the natural regeneration pool in near-natural forest ('Forest'), chosen to match the planted specimens in apparent age, height and foliage volume. A total of 160 sample treelets were selected across the four habitats (Table 2.1). Saplings were of good apparent health (i.e. no conspicuous discoloration or necrosis), and on average 2.29m (\pm 0.91 SD) in height, assuring that all foliage could be reached for data collection. The somewhat unbalanced distribution of sample trees among species and habitat results from restrictions posed by the availability of suitable saplings.

Data collection. Since the two deciduous species among the sample trees do not bare leaves between June and September (Bräuning *et al.*, 2008), surveys were conducted in six-week intervals between October 2010 and May 2011. One further recording was done in October 2011 to allow for an interannual comparison, resulting in a total of six surveys per individual treelet.

For each survey we randomly selected ten leaves per sapling. Since destructive sampling

might have interfered with ongoing silvicultural studies, leaves were recorded in situ using a digital camera (Panasonic Lumix DMC-TZ10). Leaves were spread out beneath a clear acrylic cover and photographed without flash against a white background including a black 1x1 cm² reference scale. During digital post-processing, overly bright reflections and shadows that obscured actual herbivore damage were corrected manually with the tools available in Adobe Photoshop CS4 before assessing remnant leaf area using ImageJ (Version 1.48; Rasband, 2014). In case of peripheral damage, the original area of the leaf in question was approximated by manually completing its contour. Based on these values, folivory was calculated as the percentage of leaf area lost to herbivore activity. Depending on the presence and nature of damage, leaves were assigned to one of three categories: completely undamaged leaves (“*no damage*”), leaves that showed the characteristic, semi-circular incisions of leaf-cutting ants (“*ant damage*”), and leaves with varying, non-descript feeding patterns (“*general damage*”). Where both kinds of damage were present, each leaf was classified according to the more prevalent type.

In addition to folivory, we recorded the total number of leaves per tree and survey, and approximated total available leaf area by multiplying that number with the average leaf size of the tree species in question. Average leaf area was calculated prior to data collection on the basis of 40 randomly selected leaves per species. Although an effort was made to ensure an even distribution of sample trees within habitats, a degree of spatial clustering could not be totally avoided due to the original design of reforestations (i.e. randomly distributed plots; Aguirre *et al.*, 2006; Aguirre *et al.*, 2011). The resulting possibility of spatial autocorrelation within our data was taken into account by calculating the mean distance between a given sample tree and its five closest neighbors based on GPS coordinates and including this variable in subsequent analysis. Furthermore, the extent of lateral cover by surrounding vegetation was quantified for each sample tree using a 3.0m Robel pole (0.1m bands; David *et al.*, 2008). Measurements were taken from the cardinal points of the compass at a distance of 5.0m using a sighting staff. Given the often rough terrain, a heuristic method of optical range finding was employed, which consisted of bringing two observer-specific marks on the sighting staff into conjunction with a 1m increment on the target pole when the staff was held at arm’s length (Collins & Becker, 2001). Lateral vegetation cover was calculated as the percentage of bands obscured to more than 50% by interjacent vegetation and averaged across all four measurements to yield a single value per tree. ‘Shrub’ reforestations were destroyed in a fire prior to vegetation cover measurements and data is thus not available for these sites. Lastly, tree height was assessed once at the beginning of the study and measured parallel to the stem from ground level to the tip of the highest branch.

Ambient temperature and humidity were recorded 1.5m above ground at one location per habitat. Respective recording sites were chosen to be representative of the surrounding topogra-

phy and vegetation structure. Readings were taken throughout the day at 30min. intervals from March to September 2011 using an automated data-logger (EL-USB-2, Lascar Electronics).

Statistical analysis. Intermittent, atypical flushing events - particularly among *T. chrysantha* saplings - may have lead to a reduction in apparent herbivory between consecutive surveys, and thus affect the interpretation of our leaf damage data. For this reason, we quantified the percentage of trees per species and survey that showed a transition from a state of defoliation to new leaf growth during the six week period between successive recordings. The first and sixth survey (Nov./Dec. 2010 and Oct./Nov. 2011; i.e. the beginning of the dry period) were not taken into account, since both deciduous species typically exhibit flushing around this time.

Given the imbalance in the study design imposed by the lack of suitable *C. montana* treelets among secondary shrub vegetation, analysis of folivory in the strict sense (i.e. not caused by leaf-cutting ants) was conducted twice, each time with a reduced data set: For the comparison between all four habitats, *C. montana* was excluded prior to statistical evaluation; conversely, to compare all three tree species, analyses were done without ‘Shrub’ samples. In all cases, leaf damage was aggregated per sample tree and survey. To address the possibility of interannual variation in herbivore damage, data was compared between the first survey (Nov. /Dec. 2010) and the sixth survey (Oct. /Nov. 2011), both at the onset of the dry season. All other analyses encompassed all six surveys.

Statistical evaluation was done using the R platform (R Core Team, 2013) and based on a generalized linear mixed model (GLMM) framework as implemented in the lme4 package (Bates *et al.*, 2014). Sample tree identity was included as random term in all models. The percent leaf damage was arcsin–square-root transformed and subsequently standardized to achieve Gaussian distribution. Continuous predictor variables were variously transformed using cubic-root (i.e. height), arcsin–square-root (i.e. lateral cover) or logarithm (i.e. leaf area and distance to neighboring sample trees) to meet normality assumptions and then standardized. Full models were manually simplified in an iterative process based on p-values to identify the most parsimonious solution. Goodness of fit of the best model was expressed as Nagelkerke’s (pseudo-) R^2 .

Ant-related damage was aggregated by sample tree and survey and expressed as percentage relative to the corresponding total surface area of sampled leaves. Due to the clear bias of leaf-cutting ants towards saplings of *T. chrysantha* on pasture- and shrub sites, subsequent analysis was restricted to these data points. Habitat-specific distributions were compared by a two sample Cramér-von Mises test using functions from the R packages CDFt (Vrac & Michelangeli, 2014) and CvM2SL2Test (Xiao, 2012), respectively.

Results

Over the course of the study, we sampled a total of 8,490 leaves across three tree species and four habitats. Leaf area loss due to harvesting activity of leaf-cutting ants was clearly biased towards saplings of *T. chrysantha* growing on more open habitat. Among secondary shrub habitat 57.9% of sample trees exhibited signs of foraging activity at least once during the course of the study, with 23.6% of respective leaf samples showing ant-related damage. By comparison, only 7 out of 18 saplings (38.9%) and 4.5% of sample leaves showed signs of harvesting activity on pasture sites (Figure 4.1). On average, leaf area loss due to leaf-cutting ants per tree and survey was significantly lower for *T. chrysantha* saplings on pasture sites (Pasture: $2.1\% \pm 11.2$ SD; Shrub: $10.1\% \pm 17.6$ SD; $T=3.928$, $p < 0.001$). In both habitats, damage to individual treelets could nonetheless be extensive with losses of up to 90.2% of leaf area in pasture reforestations and 77.1% for sample trees among secondary shrub vegetation. Instances of defoliation and new flush during the course of the study were likewise most prevalent among *T. chrysantha* treelets planted in ‘Pasture’ and ‘Shrub’ reforestations. With regard to other habitats and plant species, the phenomenon was rare and restricted to single plant individuals (Table 4.1).

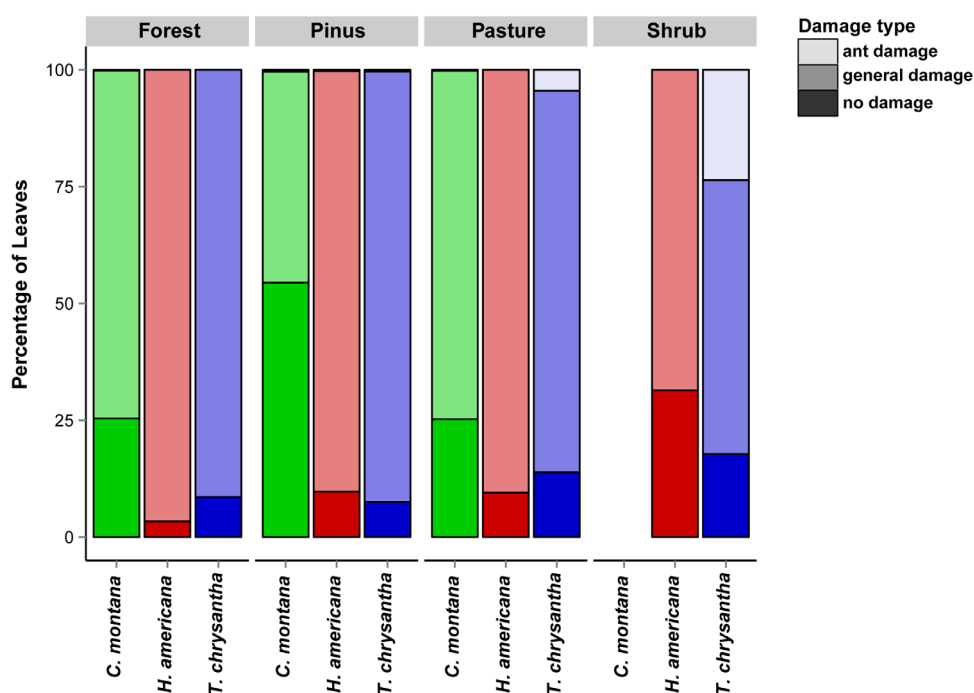


Figure 4.1 Relative abundance of leaf damage type across tree species and habitat. Respective values are based the number of individual sample leaves. Shading corresponds to the three major damage types (i.e. no herbivore damage, general damage caused by true insect herbivores, and damage by leaf-cutter ants).

Table 4.1 Overview of the number of trees per survey that exhibited atypical flushing after being leafless in the previous recording. The numerals before and after the slash denote the number of trees exhibiting fresh leaves, and the total number of foliage-bearing trees, respectively. The corresponding percentage value is given in parentheses. The first and sixth survey are not taken into account since both deciduous species (i.e. *C. montana* and *T. chrysantha*) had undergone recent flushing associated with the beginning of the dry season.

Habitat	Tree sp.	N	Survey									
			1	2	3	4	5	6				
Forest	<i>C. montana</i>	10	---	0/10 (0.0%)	0/9 (0.0%)	0/8 (0.0%)	0/7 (0.0%)	---				
	<i>H. americanus</i>	13	---	0/13 (0.0%)	0/13 (0.0%)	0/13 (0.0%)	0/12 (0.0%)	---				
	<i>T. chrysantha</i>	20	---	3/20 (15.0%)	0/20 (0.0%)	0/16 (0.0%)	0/14 (0.0%)	---				
Pinus	<i>C. montana</i>	15	---	0/15 (0.0%)	0/15 (0.0%)	0/14 (0.0%)	1/12 (8.3%)	---				
	<i>H. americanus</i>	13	---	1/13 (7.7%)	0/13 (0.0%)	0/13 (0.0%)	0/13 (0.0%)	---				
	<i>T. chrysantha</i>	16	---	0/16 (0.0%)	0/16 (0.0%)	0/14 (0.0%)	0/13 (0.0%)	---				
Pasture	<i>C. montana</i>	18	---	0/18 (0.0%)	0/18 (0.0%)	0/18 (0.0%)	0/14 (0.0%)	---				
	<i>H. americanus</i>	11	---	0/11 (0.0%)	0/10 (0.0%)	0/10 (0.0%)	1/11 (9.1%)	---				
	<i>T. chrysantha</i>	18	---	1/15 (6.7%)	3/15 (20.0%)	1/8 (12.5%)	9/15 (60.0%)	---				
Shrub	<i>H. americanus</i>	7	---	0/7 (0.0%)	0/7 (0.0%)	0/7 (0.0%)	0/7 (0.0%)	---				
	<i>T. chrysantha</i>	19	---	0/14 (0.0%)	4/17 (23.5%)	1/17 (5.9%)	2/16 (12.5%)	---				

With regard to folivory in the strict sense, inter-annual differences were found to be non-significant or very weak, manifesting only in a slightly significant interaction between habitat and year when all three tree species were taken into consideration (Table 4.2). For this reason data was pooled for subsequent analysis and calculations were done across all six surveys. The average level of leaf damage due to herbivore activity was relatively low throughout the study. Nonetheless, analyses indicated several strong predictors of folivore damage, namely surrounding habitat, sample tree species, date of survey, and various interactions thereof. Leaf area loss was highest in near natural forest and significantly lower for reforestations established in more open habitat such as pastures and secondary shrub vegetation. Treelets planted beneath a cover of *P. patula* showed values intermediate between forest and pasture sites (Table 4.3-a; Figure 4.2-a). Sample tree species was likewise found to have a highly significant effect on herbivory, with the highest mean damage observed for *T. chrysantha* saplings ($7.24\% \pm 0.38$ se of leaf area), followed by *H. americanus* ($4.78\% \pm 0.28$ se) and *C. montana* ($3.27\% \pm 0.25$ se), respectively (Table 4.3-b; Figure 4.2-b). With regard to survey date, we registered a significant increase in average leaf area loss in February 2011 relative to an otherwise fairly even baseline (Table 4.3-b; Figure 4.2-c). This peak may, however, represent an oversimplification as it arises from the overlap of underlying, but quite distinct habitat- and species-specific patterns (see below).

The effect of tree species as a function of habitat was found to be highly significant. Relative to ‘Forest’ and ‘Pasture’ sites, reforestations beneath *P. patula* were characterized by higher proportional leaf damage in *T. chrysantha*, but lower values in both *C. montana* and *H. americanus*. As a result, the relative differences between species regarding the level of damage were more pronounced among treelets in ‘Pinus’ habitat (Table 4.3-b; Figure 4.2-d). The pattern of leaf damage across survey events as a function of tree species or habitat, respective-

ly, are best interpreted in light of the underlying and likewise significant three-way interaction (Table 4.3-b), which will therefore be addressed first.

Table 4.2 Results for GLMM analyses of interannual differences in proportional leaf area damage at the onset of the dry season with sample tree identity included as random term. Leaves damaged by leaf-cutter ants were excluded. Calculations are based on reduced datasets a) across all four habitats but excluding *C. montana* and b) across all three tree species but excluding ‘Shrub’ habitat. Values given below refer to the most parsimonious model derived from manual simplification based on p-values. Corresponding goodness of fit is expressed as Nagelkerke’s (pseudo-) R^2 .

	a)				b)			
	df	Chi ²	p		df	Chi ²	p	
Habitat	3	10.888	0.012	*	2	1.849	0.397	
Tree sp.	1	0.001	0.971		2	16.688	< 0.001	***
year	1	1.059	0.304		1	0.000	0.997	
Leaf area	1	0.286	0.593		1	0.021	0.884	
Height	1	---	---		1	0.153	0.696	
Lat. Cover ^a	1	---	---		1	---	---	
Dist. to neighbors	1	---	---		1	0.004	0.948	
Habitat x Tree sp.	3	---	---		4	26.396	< 0.001	***
Habitat x year	3	---	---		2	6.394	0.041	*
Tree sp. x year	1	---	---		2	---	---	
Habitat x Height	3	---	---		2	7.051	0.029	*
Habitat x Lat. cover ^a	2	---	---		2	---	---	
Habitat x Dist. to neighbors	3	---	---		2	12.304	0.002	**
Habitat x Tree sp. x year	3	---	---		4	---	---	
Nagelkerke R^2		0.0775				0.2782		

Significance codes: $p \leq 0.001$ ‘***’; $p \leq 0.01$ ‘**’; $p \leq 0.05$ ‘*’; $p \leq 0.1$ ‘.’

Table 4.3 Results for GLMM analyses of proportional leaf area damage across all surveys with sample tree identity as random term. Leaves damaged by leaf-cutter ants were excluded. Calculations are based on reduced datasets a) across all four habitats but excluding *C. montana* and b) across all three tree species but excluding ‘Shrub’ habitat. Values given below refer to the most parsimonious model derived from manual simplification based on p-values. Corresponding goodness of fit is expressed as Nagelkerke’s (pseudo-) R^2 .

	a)				b)			
	df	Chi ²	p		df	Chi ²	p	
Habitat	3	24.657	< 0.001	***	2	16.006	< 0.000	***
Tree sp.	1	7.151	0.007	**	2	43.550	< 0.001	***
Survey nr.	5	31.876	< 0.000	***	5	31.050	< 0.001	***
Leaf area	1	0.902	0.342		1	0.456	0.499	
Height	1	0.085	0.771		1	1.008	0.315	
Lat. Cover ^a	1	---	---		1	4.070	0.044	*
Dist. to neighbors	1	---	---		1	---	---	
Habitat x Tree sp.	3	6.008	0.111		4	29.978	< 0.001	***
Habitat x Survey nr.	15	28.121	0.021	*	10	19.472	0.035	*
Tree sp. x Survey nr.	5	59.937	< 0.000	***	10	81.727	< 0.001	***
Habitat x Height	3	9.372	0.025	*	2	9.340	0.009	**
Habitat x Lat. cover ¹	2	---	---		2	---	---	
Habitat x Dist. to neighbors	3	---	---		2	---	---	
Habitat x Tree sp. x Survey nr.	15	33.232	0.004	**	20	49.073	< 0.001	***
Nagelkerke’s R^2		0.2611				0.3101		

Significance codes: $p \leq 0.001$ ‘***’; $p \leq 0.01$ ‘**’; $p \leq 0.05$ ‘*’; $p \leq 0.1$ ‘.’

^a The ‘Shrub’ habitat was destroyed by fire before lateral vegetation cover could be assessed. Consequently the variable had to be excluded from models containing ‘Shrub’ data.

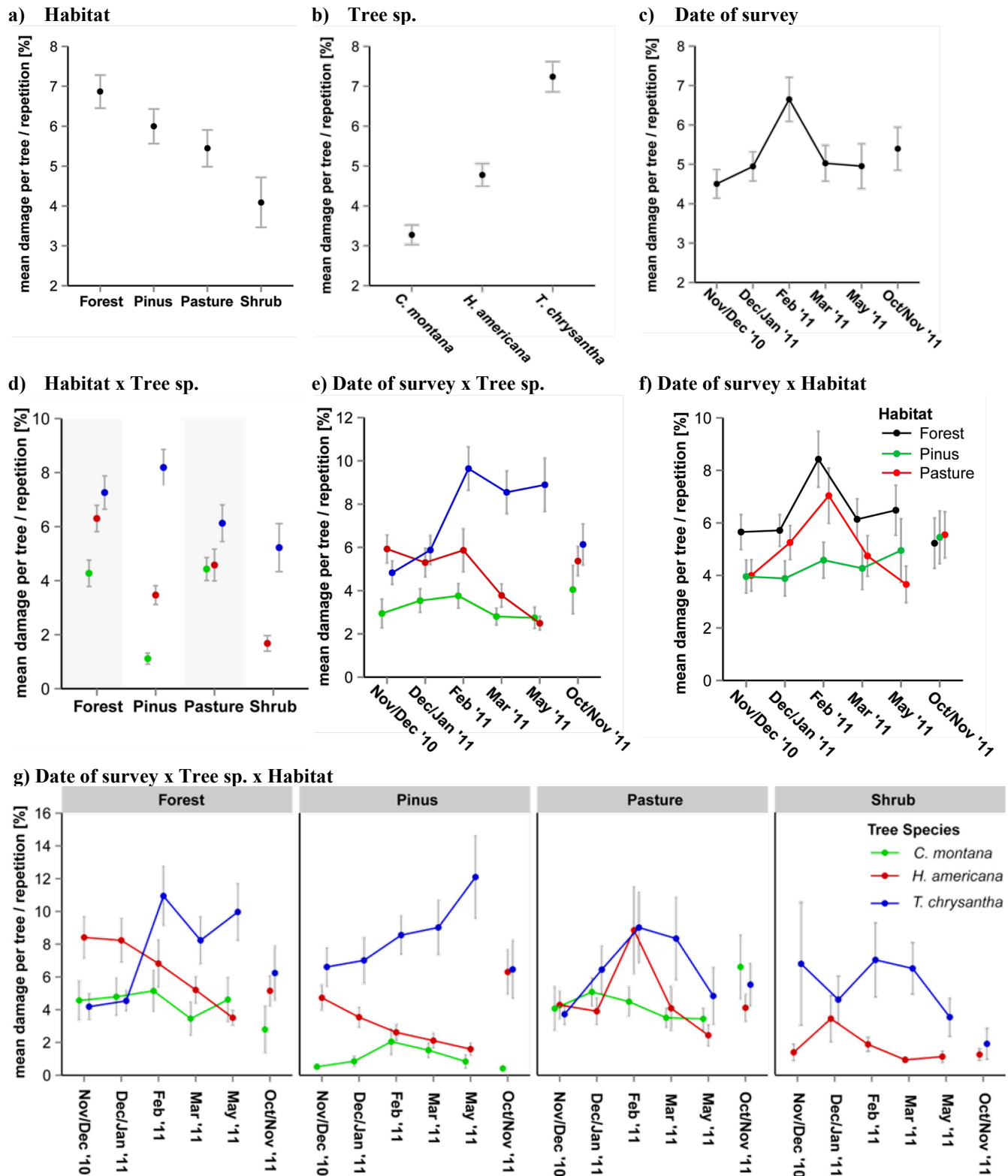


Figure 4.2 Percentile leaf damage as a function of habitat, tree species, date of survey and various interaction terms thereof. Due to the imbalance in the dataset, analyses had to be based on different data subsets. In diagram (a) mean damage was calculated for *H. americanus* and *T. chrysantha* only, excluding *C. montana*. For diagrams (b), (c), (e), and (f), 'Shrub' reforestations were excluded prior to aggregation. Graphics (d) and (g) are based on the complete dataset to facilitate comparison. Points represent mean proportional leaf damage and whiskers the corresponding standard error of the mean. The first five recordings span the duration of the initial dry season and are therefore connected by lines. The sixth survey marks the beginning of the next dry period.

Throughout the dry season, *C. montana* maintained a fairly consistent level of herbivory across all habitats (Figure 4.2-g), a characteristic which is also apparent in the two-way interaction between the date of survey and tree species (Figure 4.2-e). *H. americanus* and *T. chrysantha*, on the other hand, seem to exhibit divergent patterns between treelets under canopy cover and those that were planted in more open habitat. *H. americanus* saplings on forested sites displayed a steady decline in leaf damage during the course of the season. Treelets on pasture land and to a lesser degree on secondary shrub habitat, on the other hand, showed a conspicuous peak in herbivory around January/February, followed by a subsequent decline (Figure 4.2-g). The gradual decrease in damage over time was perhaps the most salient feature in this regard, and as such also noticeable in the corresponding two-way interaction (Figure 4.2-e). With regard to *T. chrysantha*, leaf damage accumulated steadily in saplings beneath *P. patula* and asymptotically in near-natural forest. By comparison, treelets growing in more open habitat exhibit a more or less distinct peak in the development of herbivory with a maximum around January/February (Figure 4.2-g). Due to the confounding effect of atypical leaf flush among saplings growing on the latter sites, the more or less asymptotic rise in leaf area apparent in the ‘date of survey x tree species’ interaction (Figure 4.2-e) may be considered more characteristic for *T. chrysantha*, despite the superficial difference in response patterns across habitats. Likewise, the apparent similarity in the development of herbivory over time between near-natural forest and pasture sites (Figure 4.2-f) appears to result from different species-specific trends across the respective habitats. With regard to ‘Forest’ sites, the conspicuous peak in February was mainly caused by *T. chrysantha*, but in pasture reforestations it was due jointly to *H. americanus* and *T. chrysantha*.

Other environmental predictor variables, including total leaf area, spatial proximity to neighboring sample trees, and their respective interaction terms had no or only comparatively weak effects on herbivore damage (Table 4.3-b).

Microclimatic conditions varied markedly between habitats. On average, noon-time temperatures were 3-5°C higher on reforestations without canopy cover (Pasture: 22.0°C ±4.0 SD; Shrub: 20.9°C ±4.1 SD), compared to forested sites (Pinus: 17.6°C ±2.3 SD; Forest: 16.5°C ±1.9 SD; Figure 4.3). Furthermore, open habitat was characterized by a steeper rise in temperature during the morning hours. Humidity showed a complementary pattern with considerably lower midday values for ‘Pasture’ and ‘Shrub’ sites (68.8% ±15.2 SD and 69.9% ±17.4 SD, respectively), relative to the *P. patula* plantation (85.2% ±11.3 SD) and near-natural forest (93.49% ± 8.45 SD; Figure 4.3).

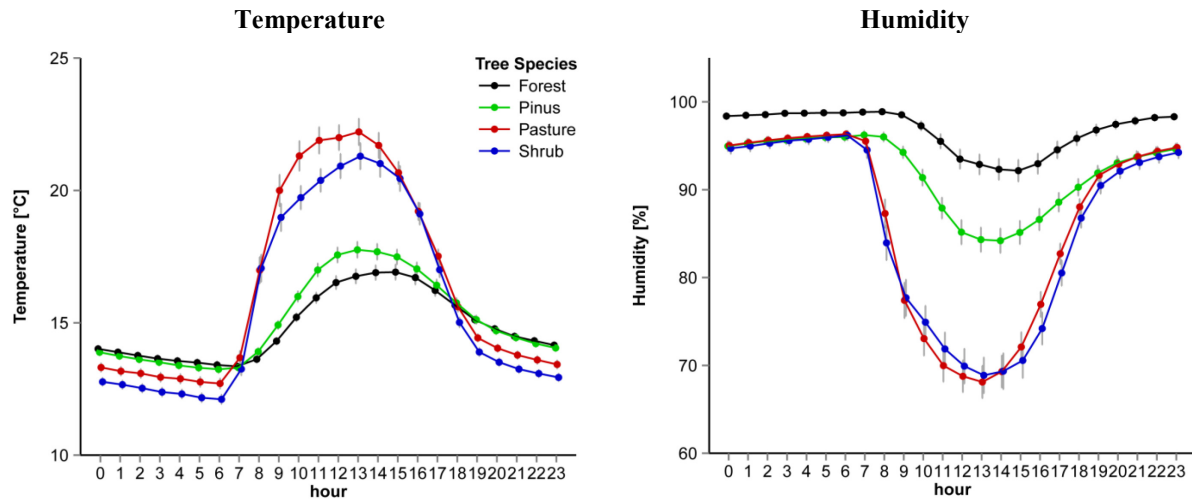


Figure 4.3 Diurnal patterns of mean temperature and humidity as a function of habitat. Measurements were recorded at intervals of 30 minutes from March to September, 2011. Points represent hourly means and whiskers the corresponding standard error of the mean.

Discussion

Based on a sample of almost 8,500 leaves, we determined the level of insect folivory for three autochthonous tree species across different reforestation sites in the tropical Andes and compared them to baseline conditions in adjacent, near-natural forest. With regard to foliar damage, we distinguished between insect folivory in the strict sense (i.e. primarily Coleoptera and Lepidoptera) and the foraging activity of leaf-cutting ants, which constitute key herbivores in Neotropical ecosystems and are often considered major pest in silvicultural plantations (Hölldobler & Wilson, 2010; Montoya-Lerma *et al.*, 2012). In the research area at elevations of about 2000m a.s.l., however, only a single species of *Acromyrmex* was encountered and it was mainly confined to anthropogenically disturbed, non-forest environments. In the following, both types of feeding damage will be addressed individually.

With regard to true insect folivory, we observed an average leaf area loss of 3-7% depending on tree species, which is considerably lower than the values typically cited for tropical rainforest (i.e. 11.1% for shade-tolerant understory species and 48.0% for gap specialists in lowlands; Coley & Barone, 1996). According to a recent meta-analysis, however, herbivory is not necessarily higher in the tropics compared to temperate systems (Moles *et al.*, 2011), and relatively low levels of damage may therefore not be unusual. Indeed, a number of studies on tropical trees have found leaf damage values in the same range as those reported here (e.g. Ribeiro *et al.*, 1994; Massad *et al.*, 2011; Paul *et al.*, 2012). In the present context, altitude is likely to be a contributing factor as well, since herbivory is known to decline with elevation (Metcalf *et al.*, 2014). On the whole, folivory was found to be primarily a function of tree species, surrounding habitat, date of survey and the respective two- and three-way interactions of these factors.

The extent of host-specific folivore damage in the present study corresponded to the levels observed for congeneric species at other tropical plantation sites (e.g. *Tabebuia ochracea*: Ribeiro *et al.*, 1994; *T. rosea*: Plath *et al.*, 2011), and was frequently lower in comparison (e.g. *Tabebuia aurea* and *T. ochracea*: Ribeiro & Brown, 2006; *Cedrela odorata*: Dawson *et al.*, 2009; *Heliocarpus pallidus*: Cuevas-Reyes *et al.*, 2011). Consequently, in the present context, leaf area loss due to insect herbivory does not seem to constitute a major limiting factor in the establishment of reforestation plots. Nonetheless, susceptibility to leaf damage varied significantly between individual sample species. Contrary to initial expectations based on the differentiation between growth-oriented pioneer species and defense-oriented, slow-growing successional taxa (Endara & Coley, 2011), folivory was highest in *T. chrysantha* followed by *H. americanus* and *C. montana*. As is common with members of the Meliaceae family (Fang *et al.*, 2011), *C. montana* most likely employs potent secondary metabolites to deter herbivores, thus explaining the low levels of damage. Somewhat incongruent with the basic growth-defense framework, *H. americanus* has been shown to contain fairly high levels of phenolics, terpenes and tannines. Notably, the concentrations were higher than respective values measured in a conspecific of *T. chrysantha* (i.e. *Tabebuia rosea*; Peñuelas *et al.*, 2010). Consequently, the observed pattern in leaf damage is likely related to an underlying gradient in toxicity, rather than to the classic conception of poorly defended pioneer species. A further difference in defensive syndromes between tree species may also have contributed to the observed results. Unlike *C. montana*, *T. chrysantha* and possibly *H. americanus* appear to possess extra-floral nectaries (personal observation) and therefore rely on ant mutualism as part of their defensive strategy. Such mutualistic ant-plant relations are generally beneficial (Chamberlain & Holland, 2009), but the degree of protection is contingent on the presence of suitable ant species (e.g. Mody & Linsenmair, 2004; Riedel *et al.*, 2013). Abundance and species richness of ants typically decline with altitude (Brühl *et al.*, 1999; Longino & Colwell, 2011), and ant-based defensive strategies may therefore become increasingly ineffective with elevation.

Foraging activity of leaf-cutting *Acromyrmex* ants was limited almost exclusively to saplings of *T. chrysantha* on open habitat, where they could occasionally cause severe damage. Although polyphagous, leaf-cutter ants are highly selective in their choice of host, and tend to avoid plants containing high concentrations of secondary metabolites that might negatively affect the growth of their fungal cultivar (Farji-Brener, 2001; Kost *et al.*, 2011; Estrada *et al.*, 2013). Consequently, observed host-plant preference in *Acromyrmex* sp. corresponds to the gradient of toxicity proposed above and may have been reinforced by a predisposition of leaf-cutting ants towards drought-stressed foliage (Vasconcelos & Cherrett, 1996; Ribeiro Neto *et al.*, 2012). Successional species like *T. chrysantha* are physiologically adapted to shaded environments and may therefore experience water-stress in open habitat sooner than light-seeking

pioneers.

Likewise contrary to our initial assumption, leaf damage was highest in near-natural forest as opposed to reforestation sites. Though unexpected, this finding is in line with observations of higher abundance (see Chapter 2) and diversity (see Chapter 3) of phytophagous insects in forest habitat. Similar results have been reported from studies on temperate-zone grassland systems which demonstrated an increase in diversity and abundance of phytophagous insects with greater plant species richness (Scherber *et al.*, 2010; Borer *et al.*, 2012), accompanied by a concurrent increase in herbivory (Gossner *et al.*, 2014; Loranger *et al.*, 2014). With regard to silvicultural settings, the often cited inverse correlation between stand diversification and herbivory on which our initial prediction was based, seems to be more typical for inherently species-poor plantation systems (Jactel & Brockerhoff, 2007 and citations therein). More natural forest stands, on the other hand, often seem to show increased levels of folivory with greater tree species richness (e.g. Schuldt *et al.*, 2010). Increased baseline levels of foliar damage in more diverse habitat relative to disturbed sites may thus be the rule rather the exception, at least in the absence of pronounced pest outbreaks.

Interestingly, this broad pattern did not hold among managed reforestations in our study. While floristic diversity was considerably higher in successional shrub habitat compared to the other reforestation sites (Aguirre *et al.*, 2011; J. Gwalik, personal communication), associated sample trees experienced significantly lower folivory than their conspecifics on pasture land or beneath *P. patula*, respectively. Again this pattern corresponds to observations regarding arthropod density and diversity (see Chapters 1 and 2). Especially predatory taxa were rare on secondary shrub sites, thus indicating general microclimatic effects on arthropod abundance as the primary determinant of observed folivory, rather than variations in the strength of top down control by predation. Ameliorating effects of surrounding vegetation on local microclimate are most pronounced beneath canopy cover (e.g. Chen *et al.*, 1999; Grimbacher *et al.*, 2006), and may to a lesser extent be provided by dense grass cover (mainly *Setaria sphacelata*) on open pasture land. Secondary shrub sites, on the other hand, typically lacked any insulating gramineous or herbaceous ground layer between sample treelets (personal observation), thus creating a potentially more taxing environment for arthropods with regard to microclimate. In this context, lower herbivore pressure may be caused in part by insects actively avoiding adverse temperature or humidity conditions, but could also be related to reduced attractivity of potential host plants. Studies have shown that water stress in plants often exerts negative effects on associated herbivores (Huberty & Denno, 2004). Along a similar vein, increased insolation has been linked to a decrease in leaf damage due to alterations in host-plant phytochemistry and physiology (Dudt & Shure, 1994; Henriksson *et al.*, 2003; Guerra *et al.*, 2010). Conversely, shaded conditions may lead to possible shifts in the nutritional content of host plants or slower metabolical rates in consumers, thus resulting in

higher *per capita* consumption rates as has been demonstrated in some phytophagous caterpillars (Muth *et al.*, 2008). Although leaf area loss is lower on open reforestation sites, any benefits resulting from reduced herbivore pressure may potentially be offset by negative effects on survival and growth of treelets due to increased exposure. Especially shade-adapted mid- to late-successional timber species such as *C. montana* and *T. chrysantha* show reduced performance at a canopy openness above 30% (Kuptz *et al.*, 2010).

Appreciable leaf damage due to the harvesting activity of *Acromyrmex* ants was only observed in open habitat without canopy cover. Due to the narrow thermal optima of their symbiotic fungi, the geographic distribution of leaf-cutting ants is typically restricted to altitudes below 2,000m a.s.l. (Brener & Ruggiero, 1994; Montoya-Lerma *et al.*, 2012 and citations therein), indicating that our research area was located close to the upper elevational distribution limit of the species. Ambient temperatures on secondary shrub and pasture sites increased more rapidly in the morning and reached higher day-time averages, apparently allowing successful colonization and subsequent persistence of leaf-cutting ants in open habitat, but effectively excluding them from forested sites (compare Jaffe & Vilela, 1989). A tendency towards greater activity and presumably abundance of *Acromyrmex* ants on successional shrub sites is likely connected to the lack of insulating ground cover, which can be expected to coincide with a higher maximum surface and soil temperatures. Consequently, establishment of a nursery canopy or to a lesser degree retention of dense ground cover (e.g. pasture land) seem currently sufficient for an effective control of leaf-cutting ants in highland reforestations. As average temperatures are predicted to rise in the course of climate change (Peters *et al.*, 2013), however, *Acromyrmex* ants and other species are likely to become a more serious problem in the region.

Notably, the effect of habitat on folivory levels differed as a function of tree species. Interspecific differences in leaf area loss were considerably more pronounced beneath *P. patula*, with saplings of *T. chrysantha* showing increased foliar damage compared to their conspecifics at other sites, while members of the other two tree species showed the opposite pattern. Pine plantations in the Andean highlands are often established on poor soil and can be subject to severe nutrient deficiencies (Breckle *et al.*, 2005; Chacón *et al.*, 2009). It seems likely that the observed discrepancy in herbivore susceptibility is in some way related to species-specific differences in the physiological and metabolic responses of treelets to local soil cation concentrations and effective cation exchange capacity. Without more detailed data on soil and phytochemistry, however, the underlying causes cannot be resolved at this point. Alternatively, biotic or abiotic conditions beneath *P. patula* may favor certain phytophagous taxa that feed preferentially on *T. chrysantha*. Two fairly abundant species of leaf beetles (Chrysomelidae: Galerucinae spp.) and two species of Lepidoptera (Gelechiidae sp. and Bombycidae: Bombycinae sp.) may be of interest in this regard, since the taxa showed nota-

bly higher densities on pine sites and fed almost exclusively on *T. chrysantha* (see Appendix Figure D.11).

The development of leaf damage over time depended on tree species and habitat in a complex three-way interaction. Specifically the two deciduous taxa seem to incur a substantial percentage of overall folivory at the beginning of the dry season, coinciding with the flush of fresh foliage. Generally speaking, such increased vulnerability of young leaves is a common finding in tropical systems (Coley & Barone, 1996), but further progression of damage throughout the season differed notably between tree species. *C. montana* suffered little further folivory after initial leaf area loss. *T. chrysantha*, on the other hand, seemed to accumulate damage, although there is indication that herbivore pressure diminished towards the end of the dry period. In this regard, the asymptotical progression of leaf damage observed on forested sites appears to be more typical for *T. chrysantha* as a whole. On open habitat, this pattern seems to have been disrupted by the occasional defoliation of individual trees by leaf-cutting ants and the subsequent development of new foliage. Saplings of *H. americanus* on open sites (i.e. pasture and secondary shrub) showed a conspicuous peak in herbivory during the first half of the dry period, but this does not seem to coincide with any marked increase in the abundance of individual Coleoptera or Lepidoptera species or of the respective insect orders as a whole (see Appendix Table E.1). There is thus a possibility, that some important herbivores of *H. americanus* may have been missed in the present study. Otherwise, folivory in *H. americanus* seems to follow broadly similar lines as *T. chrysantha* above, although the observed pattern appears to differ on first sight. As an evergreen species, foliage is exchanged by continuously renewing individual leaves, and folivory damage is thus not necessarily accumulated over time when averaged across the entire tree. Consequently, the diminution of leaf damage over the course of the dry season corresponds to the asymptotical progression observed for *T. chrysantha*, both indicating a decrease in herbivore pressure over time. The decline in the abundance of phytophagous insects is reflected in our data and more or less uniform across habitat and tree species, although the effect seems to be more pronounced among Coleoptera compared to Lepidoptera larvae (Appendix Figure E.1). The pattern is presumably related to unusual and prolonged dry weather conditions in the study region at the time of survey (Appendix Figure B.1)

Conclusion

Given the relatively low levels of leaf damage observed in the study area, insect herbivory does not appear to be a severely limiting factor in the establishment of targeted re-forestations with native tree species in the Andean highlands. Leaf-cutting ants of the genus *Acromyrmex* are a notable exception in this context, since they can not only cause extensive

damage, but may also selectively target high-value timber species (i.e. *T. chrysantha*). While their activity is fairly limited at present, the rise in average temperatures predicted by climate change models implies a far greater pest potential in the future. Nursery canopies of exotic or preferentially native tree species may offer a cost effective way to control leaf-cutting ants. The autochthonous pioneer *H. americanus* is a promising candidate in this regard, due to its high growth rate and comparatively low apparent attractiveness to leaf-cutter ants and other potential herbivores. The progression of folivory throughout the dry season may carry potential implications for the targeted application of pest control measures, should they become necessary.

CHAPTER 5

Synopsis

Despite considerable complications due to the unforeseen destruction of experimental plots by wildfires and unexpected climatic irregularities, the present thesis yielded important insights into ecological processes influencing targeted reforestations and associated arthropod assemblages. Specifically, the study addressed abundance patterns of arthropod feeding guilds (Chapter 2), insect species richness and community composition (Chapter 3), and the extent of folivory (Chapter 4) as a function of tree species and surrounding land cover. Furthermore, unusually warm and dry conditions during the first survey period (October 2010 to May 2011) allowed preliminary insights into the effect of drought on arthropod populations in a tropical montane forest zone which is usually characterized by per-humid climate conditions. In the following, the core findings will be briefly recapitulated and set in relation to each other in order to develop recommendations for the future planning and management of targeted reforestations.

Overall arthropod abundance was relatively low, although individual host-specific herbivores (predominantly Hemiptera) were occasionally observed in high numbers with a clear preference for treelets on reforestation sites. When these dominant taxa were excluded, the remainder of phytophagous insects showed remarkably similar patterns across taxonomic orders (i.e. Coleoptera, Hemiptera, and Lepidoptera). Most likely due to significantly greater floristic diversity, herbivorous taxa were generally more abundant on saplings in near-natural forest compared to reforestations (compare Scherber *et al.*, 2010). Among plantation sites, the capacity of surrounding vegetation to mediate local microclimate (e.g. Chen *et al.*, 1999) seemed to outweigh plant species richness as primary determinant of herbivore density. In the presence of a closed canopy (i.e. pine plantation) phytophagous insects were more abundant than on open sites. Where trees were absent, dense herbaceous or graminaceous vegetation (i.e. pasture sites) may have acted as a minor climatic buffer. As such, the exceedingly low herbivore density observed among treelets on secondary shrub sites despite relatively high plant species richness is likely related to the sparsity of both canopy and ground cover. Based on the present data, however, it is unclear whether this effect is primarily host-plant mediated (i.e. food quality; Huberty & Denno, 2004) or based on species-specific climatic preferences among insects. The effect of habitat on potential agents of biological control differed between taxonomic orders. By and large, predaceous Coleoptera showed a response similar to that of phytophagous taxa, although they appeared to be more sensitive regarding differences in surrounding habitat (Haddad *et al.*, 2009). Local spider density, on the other hand, was for the most part unaffected by habitat (compare Prieto-Benítez & Méndez, 2011). Significant main effects of host tree species were restricted to lower abundance of Hemiptera

on *Cedrela montana* and higher density of spiders on *Heliocarpus americanus*. The apparent aversion of Hemiptera against *C. montana* may be related to a higher percentage of host specialists among sap-sucking herbivores (Novotny *et al.*, 2010) in combination with the presumably more potent phytochemical defense commonly found among members of the Meliaceae family (Fang *et al.*, 2011). Higher abundance of Araneae on *H. americanus* was most likely related to its greater structural complexity (e.g. branching, higher crown volume, non-deciduous habitus) relative to the other sample tree species (Souza & Martins, 2005). Beyond these two effects, host tree preference of phytophagous insects was largely dependent on surrounding habitat. In near-natural forest, *H. americanus* – a pioneer species – was found to harbor more herbivores relative to the two late-successional taxa (*C. montana* and *Tabebuia chrysantha*). Although this observation would correspond to a theoretical trade-off between growth rate and herbivore defense (Endara & Coley, 2011), a comparative study of secondary plant metabolites has shown that the foliage of *H. americanus* can contain relatively high levels of terpenes, tannines, and phenolic compounds. Notably, the recorded concentrations were in fact higher than those found for a congeneric of *T. chrysantha* (*T. rosea*; Peñuelas *et al.*, 2010). Rather than following the proposed dichotomy between fast-growing pioneers and well-defended successional species, the observed pattern may instead be due to a reduced capacity of the normally light-demanding *H. americanus* to synthesize the mentioned carbon-based metabolites under more shaded conditions (Stamp, 2003). Additionally, greater overall insect diversity on forest sites would suggest a higher number of tourist species, which may have preferentially alighted on *H. americanus* for structural (e.g. branching, crown volume), rather than trophic reasons. A discrepancy in the patterns of herbivore abundance and associated folivory damage (Chapter 4) seems to support this assumption. In the enrichment plantings beneath *P. patula*, on the other hand, density of phytophagous insects was highest on *T. chrysantha* saplings, suggesting that this tree species may cope less well with the often poor soil conditions found among Neotropical *Pinus* spp. plantations (Breckle *et al.*, 2005; Chacón *et al.*, 2009), thus rendering it more vulnerable to herbivore attack. Due to the overall sparsity of insects on pasture-sites, differentiation between tree species was more obscure, although there was a tendency towards lower abundance of Coleoptera and Lepidoptera on *T. chrysantha* saplings.

Although the lack of prior data precludes conclusive interpretation, there is strong circumstantial evidence that a drought event during the first recording period (2010/11) has contributed to a significant decline in population size across almost all insect orders (compare Scherber *et al.*, 2013). With the normalization of climatic conditions, populations showed clear signs of recovery, although the process seemed to be impeded in Araneae and even more so in Lepidoptera. With regard to spiders, this is most likely due to the delayed response of predator populations to fluctuations in prey availability. Re-colonization of isolated reforestation sites

by Lepidopteran populations may take longer, since it requires active immigration of mated females rather than passive, air-borne drift as in many spiders. There is however, a possibility that negative effects may propagate across generations, thus leading to a protracted recovery period. Based on the present dataset, this point cannot be conclusively settled.

Patterns of insect species diversity in many ways mirrored those found for insect abundance. As proposed above, overall species richness of phytophagous and predatory taxa was indeed considerably greater in the structurally and floristically more complex environment of near-natural forest (i.e. phyto. Coleoptera: 167 observed species; pred. Coleoptera: 90 spp., phyto. Hemiptera: 126 spp., and phyto. Lepidoptera: 101 spp.). By comparison, reforestation sites established in habitat with lower vegetational diversity harbored only about half as many species or less (compare Scherber *et al.*, 2010). Among plantation sites, saplings planted beneath closed canopy (i.e. *P. patula*) commonly supported a more diverse insect community than those growing in open habitat, again highlighting the importance of microclimatic amelioration by surrounding vegetation. Species richness was higher on *H. americanus* compared to saplings of *C. montana* or *T. chrysantha*, but for the reasons given in the previous section this is presumably not necessarily due to inherently weaker herbivore defense in pioneers as opposed to successional species. Notably, the differentiation was most striking in near-natural forest habitat and mostly absent among reforestation sites.

As with abundance, the lack of prior survey data makes it difficult to appraise the effect of drought on species richness. Nonetheless, a trend toward overall higher species numbers with improving climatic conditions and a tentative comparison of the present findings with related studies (e.g. Bodner *et al.*, 2012; Plath *et al.*, 2012a) suggest a negative impact of drought on local insect diversity (Scherber *et al.*, 2013). Based on the present findings, it is not possible to discern whether the observed reduction in species richness was a result of true local extinction events, or rather due to already rare species falling beneath the detection threshold following a general decline in arthropod abundance (see Chapter 2).

Community composition varied between habitat and host tree species, although the respective importance of these variables as predictors depended on taxonomic order and dietary guild. Habitat emerged as the primary determinant of Coleoptera assemblages. Phytophagous taxa showed a characteristic community composition on pasture sites and a degree of convergence between communities in shaded habitats (i.e. near-natural forest and pine plantation), underlining the importance of canopy cover for forest species (e.g. Pawson *et al.*, 2011). Reminiscent of the findings regarding species richness, host tree-specific communities were only observed in forested sites, suggesting the prevalence of a less differentiated generalist species pool in open habitat. A closer inspection of individual sample treelets indicated that even the presence of small tree patches on otherwise open habitat is sufficient to support species otherwise found in forested areas. This underlines the value of remnant natural vegetation in dis-

turbed habitat (compare Majer & Delabie, 1999; Dunn, 2000). Predacious Coleoptera, on the other hand, formed clearly delineated forest communities with little or no overlap to those found in reforestation sites. In contrast, species composition of phytophagous Hemiptera and Lepidoptera was largely dependent on host tree species, indicating a higher degree of host plant specialization among these taxa compared to Coleoptera (Dyer *et al.*, 2007; Novotny *et al.*, 2010). In this regard, Hemiptera formed characteristic and for the most part mutually exclusive communities for each of the sample tree species. Phytophagous Coleoptera and Lepidoptera, on the other hand, were characterized by more or less distinct assemblages on *H. americanus* and *T. chrysantha*, but communities associated with *C. montana* seemed to be recruited from presumably more generalist species also shared with the other two tree taxa. Habitat effects among Hemiptera and Lepidoptera were weak by comparison and appeared to be mediated by differences in the communities associated with *T. chrysantha* beneath *P. patula* compared to conspecifics at other sites. The underlying cause may have been low host quality due to poor soil conditions (Breckle *et al.*, 2005).

Tree-level α -diversity and turnover between individual sample trees were identified as the largest contributors to overall diversity. In part, this may be a result of low overall insect abundance during the field surveys and the correspondingly greater impact of stochasticity on community composition. In addition, the high spatial heterogeneity of soil conditions within the study area (Günter *et al.*, 2009) may have caused variation in nutrient content of foliage and in susceptibility of treelets to herbivores, resulting in plant-mediated effects on associated insects at the level of individual treelets. This idea could not be further tested as it was not possible to harvest foliage for chemical analysis.

Due to the amount of post-processing workload involved, analysis of leaf damage had to be largely restricted to the first recording period. On the whole, saplings showed relatively low levels of folivory with about 3 to 7% leaf area loss per tree and survey depending on tree species. Once again, surrounding habitat and host species emerged as important predictor variables, as did date of survey. With respect to habitat, the relative extent of leaf damage corresponds closely to the patterns of abundance and species richness, with the highest levels observed in near-natural forest and progressively lower values for pinus, pasture and shrub sites, respectively. Unexpectedly, folivory was highest in *T. chrysantha* followed by *H. americanus* and *C. montana*. Limited leaf damage in *C. montana* was to be expected given the low abundance and diversity of associated herbivore communities, thus further supporting the existence of an effective phytochemical defense. As mentioned before, *H. americanus* seems to possess effective chemical deterrents to ward off herbivores (Peñuelas *et al.*, 2010), and therefore the observed pattern in leaf damage probably corresponds to underlying gradient in the strength of phytochemical defense. In addition, both *T. chrysantha* and *H. americanus* seem to rely on extra-floral nectaries (ENF) and ant mutualism as part of their defensive strategy

(personal observation), which may be ineffective at higher altitudes due to a lack of suitable ant species on tropical mountains (Brühl *et al.*, 1999; Longino & Colwell, 2011). Progression of leaf damage over time differed between tree species. While all species suffered a relatively high percentage of overall leaf damage at the beginning of the dry period, *C. montana* experienced little subsequent folivory. Saplings of *H. americanus* and *T. chrysantha*, on the other hand suffered further damage, although herbivore pressure notably declined over time.

Although leaf-cutting ants are typically rare at higher elevations (Brener & Ruggiero, 1994; Montoya-Lerma *et al.*, 2012 and citations therein), members of the genus *Acromyrmex* were shown to have considerable impact on reforestation sites. Notably, their activity was restricted to *T. chrysantha* saplings on open habitat and ant-related leaf damage was greater for treelets planted among secondary shrub vegetation (\bar{O} 10.1% \pm 17.6 SD of leaf area per tree and survey; max: 77.1%) than on open pastures (\bar{O} 2.1% \pm 11.2 SD; max: 90.2%). The observed pattern is likely due to thermal restrictions acting on the distribution of leaf-cutting ants, resulting in a preference for habitats with higher ground level temperatures in the montane zone.

On the basis of the findings presented in this thesis, it is possible to formulate a number of basic conclusions and recommendations for the planning and management of future reforestations in tropical mountain forest zones.

The extent of leaf damage in the present study was as low as, or even lower than comparable levels reported from other tropical plantation sites (e.g. Ribeiro *et al.*, 1994; Coley & Barone, 1996; Massad *et al.*, 2011; Paul *et al.*, 2012). Insect folivory can therefore not be regarded as a limiting factor in the establishment of new reforestations. With the possible exception of three Hemipteran species, none of the encountered insect taxa were abundant enough to qualify their categorization as potential pest species. By and large, plantation sites with autochthonous tree species in the tropical Andes appear to require little insect pest management, at least at this early stage of development.

Although leaf-cutting ants can have a substantial impact on vulnerable tree species (e.g. *T. chrysantha*) under certain conditions (Montoya-Lerma *et al.*, 2012), they currently seem to pose a relatively minor threat to silvicultural measures in the Andean highlands. In the present context, *Acromyrmex* sp. was clearly near the altitudinal limit of its distribution and factors such as increased canopy cover or even establishment of a continuous herbaceous/graminaceous layer may prove effective measures of control. As local temperatures are predicted to rise in the course of climate change (Peters *et al.*, 2013), however, leaf-cutting ants can be expected to become a more serious problem in the future. In this event, the prevalence of anthropogenic land cover throughout the Andean highlands (i.e. pastures and secondary shrub vegetation; Wassenaar *et al.*, 2007; Thies *et al.*, 2012) is likely to accelerate their rate of expansion, since ant queens on their nuptial flight seem to prefer open and thus warmer habitats for the establishment of new colonies (compare Jaffe & Vilela, 1989). Given

the widely polyphagous diet of leaf-cutting ants, subsequent colony growth is unlikely to be hindered by the common lack of floristic diversity on such sites. As colonies mature, ant foraging activities may then spread to nutritionally more attractive environments such as remaining areas of forest or agricultural crops, if these are available.

The present results once more outline the importance of retaining old-growth rain forest for the conservation of local arthropod diversity (e.g. Barlow *et al.*, 2007). Nonetheless, even young targeted reforestations were shown to potentially support a relatively high number of insect species. In this context, the buffering effect of surrounding vegetation on microclimate rather than plant species richness at the reforestation sites emerged as a primary determinant of habitat value. For the reclamation of fallow pastures, it therefore seems advisable to begin active reforestation soon after abandonment instead of allowing successional development towards bracken-shrub communities. Such an approach would seem to serve the dual purpose of promoting insect diversity (e.g. Bockerhoff *et al.*, 2008) and containing bracken infestation (Douterlungne *et al.*, 2013). Relatively high overall species diversity and partial convergence of phytophagous beetle communities between natural forest and pine plantations indicate that even exotic timber species can be of some potential ecological benefit in reforestations. As such, existing plantations can serve as nursery canopy (Feyera *et al.*, 2002) and form a viable basis for further re-naturalization projects. Nonetheless, it is preferable to recruit fast-growing native tree taxa to establish initial canopy cover in order to offer a more compatible habitat for local plant and animal life (compare Hartley, 2002; Bockerhoff *et al.*, 2008). *H. americanus* may be a suitable candidate in this respect, given the relatively high number of associated insect species observed in the present study. Another promising species is *Alnus acuminata* (Kwapil, 2013), which may also help improve soil quality and benefit accompanying species in mixed stands due to its association with nitrogen-fixating bacteria (Richards *et al.*, 2010; Schwintzer & Tjepkema, 2012). From a conservationist viewpoint, at least partial retention of a relatively dense grass or herbaceous layer during the establishment phase of reforestations may to some extent help to buffer climatic extremes and thus increase habitat value for insect species. While such practice may have a negative impact on the survival of planted treelets due to light and most likely nutrient competition, such adverse effects are not necessarily observed for all timber species (Aguirre, 2007). Instead, a reduction in the activity of leaf-cutting ants due to ground vegetation may prove beneficial for young treelets.

Although the provisioning of shade and structural complexity was shown to promote insect diversity and abundance, there were distinct differences between taxonomic orders and feeding guilds. With regard to phytophagous Coleoptera, canopy cover and even small forested patches were sufficient to maintain a number of forest species, while host tree species was of secondary importance. Conversely, none of the examined reforestation sites seemed to offer alternative habitat for predacious beetles normally associated with natural forest. The seem-

ingly higher percentage of forest specialists within the local community of predatory Coleoptera suggests the need of more targeted conservation measures for these taxa, especially by retaining old-growth forest. Among phytophagous Hemiptera and Lepidoptera, on the other hand, species composition was highly host-specific but differed little between habitats. This implies that anthropogenic land cover does not necessarily pose a barrier to migration and colonization by forest species among these orders, provided that suitable host plants are available and prospective source populations in intact or remnant forest are not too far away (Brehm & Fiedler, 1999; Ricketts *et al.*, 2001). To maximize the potential conservation value of targeted afforestations for a broad spectrum of taxonomic orders, it is therefore advisable to establish polycultures of suitable native tree species. In addition, studies have shown that increased stand diversity is often associated with lower overall herbivory (Jactel & Brockerhoff, 2007).

In closing, there remain a number of aspects that warrant further research. Given the prediction of increased frequency and severity of drought events (IPCC, 2013), it is important to gain a better understanding of the long-term effect such events have on insect communities and population dynamics in the Andean highlands. The present study indicates that predatory species are slower to recover, which may have important implications for the top-down control of herbivore populations. Likewise, Lepidoptera show possible signs of prolonged negative effects following the drought, suggesting that this insect order may be more vulnerable than others. Furthermore, it would be instructive to compare the conservation value of different mature commercial plantations for arthropods. By contrasting plantations of native *Alnus acuminata* with corresponding *Pinus* or *Eucalyptus* stands, it may be possible to disentangle the impact of purely structural aspects (i.e. canopy cover, shading, etc.) from the effects of tree species (i.e. native vs. exotic taxa). Lastly, investigating the value of targeted reforestations for arthropods as a function of surrounding habitat on a broader spatial scale poses a promising venue for future research. In the present context, plantation sites were located in relative proximity to old-growth forest, which is likely to have favored immigration and colonization by forest species. With increasing distance, the nature of intervening landscape matrix is likely to become more important, which in turn may influence the community composition of arthropods in reforestations.

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References

- Aguirre, N. (2007) *Silvicultural contributions to the reforestation with native species in the tropical mountain rainforest region of South Ecuador*. Doctoral thesis. Technische Universität München, Germany.
<http://mediatum.ub.tum.de/doc/623642/document.pdf>
- Aguirre, N., Günter, S. & Stimm, B. (2006) Enrichment of *Pinus patula* plantations with native species in southern Ecuador. *Lyonia*, **10**, 17-29
- Aguirre, N., Palomeque, X., Weber, M., Stimm, B. & Günter, S. (2011) Reforestation and natural succession as tools for restoration on abandoned pastures in the Andes of south Ecuador. In: Günter, S., Weber, M., Stimm, B. & Mosandl, R. (Eds.). *Silviculture in the Tropics* (pp. 513-524). Springer Berlin Heidelberg.
- Ahrens, D., Monaghan, M.T. & Vogler, A.P. (2007) DNA-based taxonomy for associating adults and larvae in multi-species assemblages of chafers (Coleoptera: Scarabaeidae). *Molecular Phylogenetics and Evolution*, **44**, 436-449
- Attwood, S.J., Maron, M., House, A.P.N. & Zammit, C. (2008) Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecology and Biogeography*, **17**, 585-599
- Axmacher, J.C., Brehm, G., Hemp, A., Tünte, H., Lyaruu, H.V.M., Müller-Hohenstein, K. & Fiedler, K. (2009) Determinants of diversity in Afrotropical herbivorous insects (Lepidoptera: Geometridae): plant diversity, vegetation structure or abiotic factors? *Journal of Biogeography*, **36**, 337-349
- Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. (2009) Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 1-20
- Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C. & Peres, C.A. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences*, **104**, 18555-18560
- Barthlott, W., Hostert, A., Kier, G., Küper, W., Kreft, H., Mutke, J., Rafiqpoor, M.D. & Sommer, H. (2007) Geographic patterns of vascular plant diversity at continental to global scales. *Erdkunde*, **61**, 305-315
- Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N. & Winfree, R. (2013) Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters*, **16**, 1331-1338
- Basset, Y. (1999) Diversity and abundance of insect herbivores foraging on seedlings in a rainforest in Guyana. *Ecological Entomology*, **24**, 245-259
- Basset, Y. & Novotny, V. (1999) Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biological Journal of the Linnean Society*, **67**, 477-499
- Bates, D., Maechler, M. & Bolker, B. (2014). *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7.
<http://CRAN.R-project.org/package=lme4>
- Bauch, S., Sills, E., Rodriguez, L.C.E., McGinley, K. & Cubbage, F. (2009) Forest policy reform in Brazil. *Journal of Forestry*, **107**, 132-138
- Baum, K.A., Haynes, K.J., Dilleuth, F.P. & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671-2676
- Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (2008a) *Gradients in a Tropical Mountain Ecosystem of Ecuador*. Springer Berlin Heidelberg.
- Beck, E., Makeschin, F., Haubrich, F., Richter, M., Bendix, J. & Valerezo, C. (2008b) The ecosystem (Reserva Biológica San Francisco). In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 1-13). Springer Berlin Heidelberg.
- Benayas, J.M.R., Newton, A.C., Diaz, A. & Bullock, J.M. (2009) Enhancement of biodiversity and

- ecosystem services by ecological restoration: A meta-analysis. *Science*, **325**, 1121-1124
- Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S. & Wilcke, W. (2013) *Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of south Ecuador*. Springer, Berlin, Heidelberg.
- Bendix, J., Homeier, J., Cueva Ortiz, E., Emck, P., Breckle, S.W., Richter, M. & Beck, E. (2006) Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *International Journal of Biometeorology*, **50**, 370-384
- Beutel, R.G. & Leschen, R. (2011) *Handbook of Zoology, Part 38, Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. De Gruyter, Berlin, Boston.
- Bodner, F. (2007) *Early stages and feeding ecology of loopers (Lepidoptera: Geometridae) in a south Ecuadorian montane rainforest*. Diploma thesis. University of Vienna, Austria
<http://othes.univie.ac.at/885/>
- Bodner, F. (2011) *Caterpillar communities on shrubs in the montane forest zone of southern Ecuador*. Doctoral thesis. University of Vienna, Austria
<http://othes.univie.ac.at/15967/>
- Bodner, F., Brehm, G., Homeier, J., Strutzenberger, P. & Fiedler, K. (2010a) Caterpillars and host plant records for 59 species of Geometridae (Lepidoptera) from a montane rainforest in southern Ecuador. *Journal of Insect Science*, **10**
- Bodner, F., Mahal, S. & Fiedler, K. (2010b) 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
- Bodner, F., Strutzenberger, P., Brehm, G. & Fiedler, K. (2012) Species richness and host specificity among caterpillar ensembles on shrubs in the Andes of southern Ecuador. *Neotropical Entomology*, **41**, 375-385
- Boggs, C.L. & Freeman, K.D. (2005) Larval food limitation in butterflies: Effects on adult resource allocation and fitness. *Oecologia*, **144**, 353-361
- Borer, E.T., Seabloom, E.W. & Tilman, D. (2012) Plant diversity controls arthropod biomass and temporal stability. *Ecology Letters*, **15**, 1457-1464
- Borges, P.A.V. & Brown, V.K. (2001) Phytophagous insects and web-building spiders in relation to pasture vegetation complexity. *Ecography*, **24**, 68-82
- Bowen, M.E., McAlpine, C.A., House, A.P.N. & Smith, G.C. (2007) Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. *Biological Conservation*, **140**, 273-296
- Bräuning, A., Homeier, J., Cueva, E., Beck, E. & Günter, S. (2008) Growth dynamics of trees in tropical mountain ecosystems. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 291-302). Springer Berlin Heidelberg.
- Breckle, S.-W., Breckle, U., Homeier, J. & Scheffer, A. (2005) Mineral deficiencies in a pine plantation in southern Ecuador. *Ecotropica*, **11**, 79-85
- Brehm, G. & Fiedler, K. (1999) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14
- Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography*, **30**, 431-440
- Brehm, G. & Fiedler, K. (2005) Diversity and community structure of geometrid moths of disturbed habitat in a montane area in the Ecuadorian Andes. *Journal of Research on the Lepidoptera*, **38**, 1-14
- Brehm, G., Homeier, J., Fiedler, K., Kottke, I., Illig, J., Noeske, N.M., Werner, F.A. & Breckle, S.W. (2008) Mountain rain forests in southern Ecuador as a hotspot of biodiversity - Limited knowledge and diverging patterns. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 15-23). Springer Berlin Heidelberg.
- Brehm, G., Pitkin, L.M., Hilt, N. & Fiedler, K. (2005) Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, **32**, 1621-1627
- Brockerhoff, E.G., Jactel, H., Parrotta, J.A. & Ferraz, S.F.B. (2013) Role of eucalypt and other planted

- forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *Forest Ecology and Management*, **301**, 43-50
- Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P. & Sayer, J. (2008) Plantation forests and biodiversity: Oxymoron or opportunity? *Biodiversity and Conservation*, **17**, 925-951
- Brockett, C.D. & Gottfried, R.R. (2002) State policies and the preservation of forest cover: Lessons from contrasting public-policy regimes in Costa Rica. *Latin American Research Review*, **37**
- Brühl, C.A., Mohamed, M. & Linsenmair, K.E. (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, **15**, 265-277
- Carisey, N. & Bauce, É. (2002) Does nutrition-related stress carry over to spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) progeny? *Bulletin of Entomological Research*, **92**, 101-108
- Carmona, D., Lajeunesse, M.J. & Johnson, M.T.J. (2011) Plant traits that predict resistance to herbivores. *Functional Ecology*, **25**, 358-367
- Castagneyrol, B., Giffard, B., Péré, C. & Jactel, H. (2013) Plant apparency, an overlooked driver of associational resistance to insect herbivory. *Journal of Ecology*, **101**, 418-429
- Castagneyrol, B. & Jactel, H. (2012) Unraveling plant-animal diversity relationships: A meta-regression analysis. *Ecology*, **93**, 2115-2124
- Castillo, L. & Rossini, C. (2010) Bignoniaceae metabolites as semiochemicals. *Molecules*, **15**, 7090-7105
- Chacón, G., Gagnon, D. & Paré, D. (2009) Comparison of soil properties of native forests, *Pinus patula* plantations and adjacent pastures in the Andean highlands of southern Ecuador: Land use history or recent vegetation effects? *Soil Use and Management*, **25**, 427-433
- Chamberlain, S.A. & Holland, J.N. (2009) Quantitative synthesis of context dependency in ant-plant protection mutualisms. *Ecology*, **90**, 2384-2392
- Chapela, I.H., Osher, L.J., Horton, T.R. & Henn, M.R. (2001) Ectomycorrhizal fungi introduced with exotic pine plantations induce soil carbon depletion. *Soil Biology and Biochemistry*, **33**, 1733-1740
- Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosfokske, K.D., Mroz, G.D., Brookshire, B.L. & Franklin, J.F. (1999) Microclimate in forest ecosystem and landscape ecology. *BioScience*, **49**, 288-297
- Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth
- Clarke, K.R., Somerfield, P.J. & Chapman, M.G. (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, **330**, 55-80
- Clarke, K.R. & Warwick, R.M. (1998) Quantifying structural redundancy in ecological communities. *Oecologia*, **113**, 278-289
- Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M. & Hormiga, G. (2009) Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*, **78**, 573-584
- Coe, M.T., Marthews, T.R., Costa, M.H., Galbraith, D.R., Greenglass, N.L., Imbuzeiro, H.M.A., Levine, N.M., Malhi, Y., Moorcroft, P.R., Muza, M.N., Powell, T.L., Saleska, S.R., Solorzano, L.A. & Wang, J. (2013) Deforestation and climate feedbacks threaten the ecological integrity of south-southeastern Amazonia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **368**
- Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305-335
- Collins, W.B. & Becker, E.F. (2001) Estimation of horizontal cover. *Journal of Range Management*, **54**, 67-70
- Colwell, R.K. (2013) *EstimateS: Statistical estimation of species richness and shared species from samples*, Version 9.1.0
<http://viceroy.eeb.uconn.edu/estimates/>
- Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L. & Longino, J.T. (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, **5**, 3-21
- Crist, T.O., Veech, J.A., Gering, J.C. & Summerville, K.S. (2003) Partitioning species diversity across

- landscapes and regions: A hierarchical analysis of α , β , and γ diversity. *The American Naturalist*, **162**, 734-743
- Cuevas-Reyes, P., Oyama, K., González-Rodríguez, A., Fernandes, G.W. & Mendoza-Cuenca, L. (2011) Contrasting herbivory patterns and leaf fluctuating asymmetry in *Heliocarpus pallidus* between different habitat types within a Mexican tropical dry forest. *Journal of Tropical Ecology*, **27**, 383-391
- Cunningham, S.A., Floyd, R.B. & Weir, T.A. (2005) Do Eucalyptus plantations host an insect community similar to remnant eucalyptus forest? *Austral Ecology*, **30**, 103-117
- David, T.P., Abbott, L.B. & Herrick, J.E. (2008) Cover pole design for easy transport, assembly, and field use. *The Journal of Wildlife Management*, **72**, 564-567
- Davis, A.S., Jacobs, D.F. & Dumroese, R.K. (2012) Challenging a paradigm: Toward integrating indigenous species into tropical plantation forestry. In: Stanturf, J., Lamb, D. & Madsen, P. (Eds.). *Forest landscape restoration: Integrating natural and social sciences* (pp. 293-308). Springer, Dordrecht, Netherlands.
- Dawson, W., Burslem, D.F.R.P. & Hulme, P.E. (2009) Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions*, **15**, 141-147
- Delisle, J. & Hardy, M. (1997) Male larval nutrition influences the reproductive success of both sexes of the Spruce Budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Functional Ecology*, **11**, 451-463
- Dolling, W.R. (1991) *The Hemiptera*. Oxford University Press.
- Dominy, N.J., Lucas, P.W. & Wright, S.J. (2003) Mechanics and chemistry of rain forest leaves: Canopy and understorey compared. *Journal of Experimental Botany*, **54**, 2007-2014
- Don, A., Schumacher, J. & Freibauer, A. (2011) Impact of tropical land-use change on soil organic carbon stocks - A meta-analysis. *Global Change Biology*, **17**, 1658-1670
- Douterlungne, D., Thomas, E. & Levy-Tacher, S.I. (2013) Fast-growing pioneer tree stands as a rapid and effective strategy for bracken elimination in the Neotropics. *Journal of Applied Ecology*, **50**, 1257-1265
- Dudt, J.F. & Shure, D.J. (1994) The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology*, **75**, 86-98
- Dunn, R.R. (2000) Isolated trees as foci of diversity in active and fallow fields. *Biological Conservation*, **95**, 317-321
- Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morais, H.C., Diniz, I.R., Kursar, T.A. & Coley, P.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696-699
- Eichhorn, M.P., Nilus, R., Compton, S.G., Hartley, S.E. & Burslem, D.F.R.P. (2010) Herbivory of tropical rain forest tree seedlings correlates with future mortality. *Ecology*, **91**, 1092-1101
- Endara, M.-J. & Coley, P.D. (2011) The resource availability hypothesis revisited: A meta-analysis. *Functional Ecology*, **25**, 389-398
- Estrada, C., Weislo, W.T. & Van Bael, S.A. (2013) Symbiotic fungi alter plant chemistry that discourages leaf-cutting ants. *New Phytologist*, **198**, 241-251
- Fang, X., Di, Y.T. & Hao, X.J. (2011) The advances in the limonoid chemistry of the Meliaceae family. *Current Organic Chemistry*, **15**, 1363-1391
- FAO (2010) *Global forest resources assessment 2010: Main report*. Food and Agriculture Organization of the United Nations, Rome.
- Farji-Brener, A.G. & Ruggiero, A. (1994) Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical range sizes. *Journal of Biogeography*, **21**, 391-399
- Farji-Brener, A.G. (2001) Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos*, **92**, 169-177
- Farley, K.A. & Kelly, E.F. (2004) Effects of afforestation of a Páramo grassland on soil nutrient status. *Forest Ecology and Management*, **195**, 281-290
- Felton, A., Knight, E., Wood, J., Zammit, C. & Lindenmayer, D. (2010) A meta-analysis of fauna and flora species richness and abundance in plantations and pasture lands. *Biological Conservation*, **143**, 545-554
- Feyera, S., Beck, E. & Lüttge, U. (2002) Exotic trees as nurse-trees for the regeneration of natural

- tropical forests. *Trees*, **16**, 245-249
- Fill, A., Long, E.Y. & Finke, D.L. (2012) Non-consumptive effects of a natural enemy on a non-prey herbivore population. *Ecological Entomology*, **37**, 43-50
- Finch, S. & Collier, R.H. (2000) Host-plant selection by insects – A theory based on ‘appropriate/inappropriate landings’ by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata*, **96**, 91-102
- Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Schultz, J.C. & Coley, P.D. (2006) The growth-defense trade-off and habitat specialization by plants in Amazonian Forest. *Ecology*, **87**, S150-S162
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570-574
- Fonseca, C.R. (2009) The silent mass extinction of insect herbivores in biodiversity hotspots. *Conservation Biology*, **23**, 1507-1515
- Froeschner, R.C. (1996) Lace bug genera of the world, I: Introduction, subfamily Cantacaderinae (Heteroptera: Tingidae). *Smithsonian Contributions to Zoology*, **574**, 1-43
- Froeschner, R.C. (2001) Lace bug genera of the world, II: Subfamily Tinginae: Tribes Litadeini and Ypsotingini (Heteroptera: Tingidae). *Smithsonian Contributions to Zoology*, **611**, 1-26
- García-Guzmán, G. & Dirzo, R. (2001) Patterns of leaf-pathogen infection in the understory of a Mexican rain forest: Incidence, spatiotemporal variation, and mechanisms of infection. *American Journal of Botany*, **88**, 634-645
- García-López, A., Micó, E. & Galante, E. (2012) From lowlands to highlands: Searching for elevational patterns of species richness and distribution of scarab beetles in Costa Rica. *Diversity and Distributions*, **18**, 543-553
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378-381
- Giffard, B., Barbaro, L.U.C., Jactel, H. & Corcket, E. (2013) Plant neighbours mediate bird predation effects on arthropod abundance and herbivory. *Ecological Entomology*, **38**, 448-455
- Giffard, B., Jactel, H., Corcket, E. & Barbaro, L. (2012) Influence of surrounding vegetation on insect herbivory: A matter of spatial scale and herbivore specialisation. *Basic and Applied Ecology*, **13**, 458-465
- Gormley, L.H.L., Furley, P.A. & Watt, A.D. (2007) Distribution of ground-dwelling beetles in fragmented tropical habitats. *Journal of Insect Conservation*, **11**, 131-139
- Gossner, M.M., Weisser, W.W. & Meyer, S.T. (2014) Invertebrate herbivory decreases along a gradient of increasing land-use intensity in German grasslands. *Basic and Applied Ecology*
- Göttlicher, D., Obregón, A., Homeier, J., Rollenbeck, R., Nauss, T. & Bendix, J. (2009) Land-cover classification in the Andes of southern Ecuador using Landsat ETM+ data as a basis for SVAT modelling. *International Journal of Remote Sensing*, **30**, 1867-1886
- Griess, V. & Knoke, T. (2011) Can native tree species plantations in Panama compete with teak plantations? An economic estimation. *New Forests*, **41**, 13-39
- Grimbacher, P., Catterall, C., Kanowski, J. & Proctor, H. (2007) Responses of ground-active beetle assemblages to different styles of reforestation on cleared rainforest land. *Biodiversity and Conservation*, **16**, 2167-2184
- Grimbacher, P.S. & Catterall, C.P. (2007) How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? *Biological Conservation*, **135**, 107-118
- Grimbacher, P.S., Catterall, C.P. & Kitching, R.L. (2006) Beetle species' responses suggest that microclimate mediates fragmentation effects in tropical Australian rainforest. *Austral Ecology*, **31**, 458-470
- Gruner, D.S. (2003) Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. *Pacific Science*, **57**, 325-336
- Guerra, P., Becerra, J. & Gianoli, E. (2010) Explaining differential herbivory in sun and shade: The case of *Aristotelia chilensis* saplings. *Arthropod-Plant Interactions*, **4**, 229-235
- Günter, S., Gonzalez, P., Álvarez, G., Aguirre, N., Palomeque, X., Haubrich, F. & Weber, M. (2009)

- Determinants for successful reforestation of abandoned pastures in the Andes: Soil conditions and vegetation cover. *Forest Ecology and Management*, **258**, 81-91
- Gutbrodt, B., Mody, K. & Dorn, S. (2011) Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. *Oikos*, **120**, 1732-1740
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H. & Tilman, D. (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, **12**, 1029-1039
- Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, J.M.H. (2001) Contrasting effects of plant richness and composition on insect communities: A field experiment. *The American Naturalist*, **158**, 17-35
- Hamer, U., Potthast, K., Burneo, J. & Makeshin, F. (2013) Nutrient stocks and phosphorus fractions in mountain soils of southern Ecuador after conversion of forest to pasture. *Biogeochemistry*, **112**, 495-510
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O. & Townshend, J.R.G. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850-853
- Hartig, K. & Beck, E. (2003) The bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) dilemma in the Andes of southern Ecuador. *Ecotropica*, **9**, 3-13
- Hartley, M.J. (2002) Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management*, **155**, 81-95
- Haug, I., Wubet, T., Aguirre, N., Weber, M., Günter, S. & Kottke, I. (2010) Species-rich but distinct arbuscular mycorrhizal communities in reforestation plots on degraded pastures and in neighboring pristine tropical mountain rain forest. *Tropical Ecology*, **51**, 125
- Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity? The case of california butterflies. *The American Naturalist*, **161**, 40-49
- Hebert, P.D.N., Cywinska, A., Ball, S.L. & deWaard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 313-321
- Heil, M. (2008) Indirect defence via tritrophic interactions. *New Phytologist*, **178**, 41-61
- Henriksson, J., Haukioja, E., Ossipov, V., Ossipova, S., Sillanpää, S., Kapari, L. & Pihlaja, K. (2003) Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of water, primary and secondary compounds. *Oikos*, **103**, 3-16
- Herzog, S.K., Hamel-Leigue, A.C., Larsen, T.H., Mann, D.J., Soria-Auza, R.W., Gill, B.D., Edmonds, W.D. & Spector, S. (2013) Elevational distribution and conservation biogeography of phanaeine dung beetles (Coleoptera: Scarabaeinae) in Bolivia. *PLoS ONE*, **8**, e64963
- Hilt, N., Brehm, G. & Fiedler, K. (2006) Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes. *Journal of Tropical Ecology*, **22**, 155-166
- Hilt, N. & Fiedler, K. (2005) Diversity and composition of Arctiidae moth ensembles along a successional gradient in the Ecuadorian Andes. *Diversity and Distributions*, **11**, 387-398
- Hilt, N. & Fiedler, K. (2006) Arctiid moth ensembles along a successional gradient in the Ecuadorian montane rain forest zone: how different are subfamilies and tribes? *Journal of Biogeography*, **33**, 108-120
- Hodkinson, I.D. (2005) Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews*, **80**, 489-513
- Hogenhout, S.A., Ammar, E.-D., Whitfield, A.E. & Redinbaugh, M.G. (2008) Insect vector interactions with persistently transmitted viruses. *Annual Review of Phytopathology*, **46**, 327-359
- Hölldobler, B. & Wilson, E.O. (2010) *The leafcutter ants: civilization by instinct*. WW Norton & Company.
- Homeier, J., Breckle, S.-W., Günter, S., Rollenbeck, R.T. & Leuschner, C. (2010) Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica*, **42**, 140-148
- Homeier, J. & Werner, F.A. (2008) Spermatophyta. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S-Ecuador). In: Liede-Schumann, S. & Breckle, S.-W. (Eds.). *Provisional*

- checklists of Flora and Fauna of the San Francisco valley and its surroundings (Estación Científica San Francisco), Southern Ecuador* (pp. 15-58). Ecological Monographs, Vol. 4.
- Homeier, J., Werner, F.A., Gradstein, S.R., Breckle, S.W. & Richter, M. (2008) Potential vegetation and floristic composition of Andean forests in south Ecuador, with a focus on the RBSF. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 87-100). Springer Berlin Heidelberg.
- Huberty, A.F. & Denno, R.F. (2004) Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology*, **85**, 1383-1398
- Illig, J., Norton, R., Scheu, S. & Maraun, M. (2010) Density and community structure of soil- and bark-dwelling microarthropods along an altitudinal gradient in a tropical montane rainforest. *Experimental and Applied Acarology*, **52**, 49-62
- IPCC (2013) Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M. (Eds.). Cambridge University Press, United Kingdom and New York, NY, USA.
- Itioka, T. & Yamauti, M. (2004) Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest. *Journal of Tropical Ecology*, **20**, 479-482
- Jactel, H. & Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters*, **10**, 835-848
- Jaffe, K. & Vilela, E. (1989) On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. *Biotropica*, **21**, 234-236
- Jost, L. (2006) Entropy and diversity. *Oikos*, **113**, 363-375
- Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, **88**, 2427-2439
- Karp, D.S. & Daily, G.C. (2014) Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology*, **95**, 1065-1074
- Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, **16**, 111-120
- Kishimoto-Yamada, K. & Itioka, T. (2008) Consequences of a severe drought associated with an El Niño-Southern Oscillation on a light-attracted leaf-beetle (Coleoptera, Chrysomelidae) assemblage in Borneo. *Journal of Tropical Ecology*, **24**, 229-233
- Kishimoto-Yamada, K., Itioka, T., Sakai, S., Momose, K., Nagamitsu, T., Kalias, H., Meleng, P., Chong, L., Hamid Karim, A.A., Yamane, S., Kato, M., Reid, C.A.M., Nakashizuka, T. & Inoue, T. (2009) Population fluctuations of light-attracted chrysomelid beetles in relation to supra-annual environmental changes in a Bornean rainforest. *Bulletin of Entomological Research*, **99**, 217-227
- Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2002) Predator-prey ratios on cocoa along a land-use gradient in Indonesia. *Biodiversity and Conservation*, **11**, 683-693
- Koopowitz, H., Thornhill, A.D. & Andersen, M. (1994) A general stochastic model for the prediction of biodiversity losses based on habitat conversion. *Conservation Biology*, **8**, 425-438
- Kost, C., Tremmel, M. & Wirth, R. (2011) Do leaf cutting ants cut undetected? Testing the effect of ant-induced plant defences on foraging decisions in *Atta colombica*. *PLoS ONE*, **6**, e22340 doi: 10.1371/journal.pone.0022340
- Kuptz, D., Grams, T.E. & Günter, S. (2010) Light acclimation of four native tree species in felling gaps within a tropical mountain rainforest. *Trees*, **24**, 117-127
- Kursar, T.A. & Coley, P.D. (2003) Convergence in defense syndromes of young leaves in tropical rainforests. *Biochemical Systematics and Ecology*, **31**, 929-949
- Kwapil, K. (2013) Herbivore communities on *Alnus acuminata* in relation to different reforestation methods - a case study in the cloud forest zone of Ecuador. Diploma thesis. University of Vienna, Austria
- Lamb, D., Erskine, P.D. & Parrotta, J.A. (2005) Restoration of degraded tropical forest landscapes. *Science*, **310**, 1628-1632
- Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, **139**, 1-10

- Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benitez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G, J., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Bruhl, C.A., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazare Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H.-b., Klop, E., Knott, C., Kone, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rodel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K.E., Sukumar, R., Surbeck, M., Tobler, M., Tscharnkte, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Vereza, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L., Yonzon, P. & Zamzani, F. (2012) Averting biodiversity collapse in tropical forest protected areas. *Nature*, **489**, 290-294
- Laurance, W.F., Sayer, J. & Cassman, K.G. (2014) Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, **29**, 107-116
- Lawrence, J.F., Hastings, A.M., Dallwitz, M.J., Paine, T.A. & Zurcher, E.J. (1999) *Beetles of the world: A key and information system for families and subfamilies*. CSIRO Publishing, Melbourne
- Legendre, P. & Gallagher, E. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271-280
- Lehnert, M., Kessler, M., Salazar, L.I., Navarrete, H. & Gradstein, S.R. (2008) Pteridophytes. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, Ecuador). In: Liende-Schumann, S. & Breckle, S.-W. (Eds.). *Provisional checklists of Flora and Fauna of the San Francisco valley and its surroundings (Estación Científica San Francisco), Southern Ecuador* (pp. 59-68). Ecological Monographs, Vol. 4.
- Leschen, R.A.B., Beutel, R.G. & Lawrence, J.F. (2011) *Handbook of Zoology, Part 39, Volume 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)*. De Gruyter, Berlin, Boston.
- Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009) Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 573-592
- Lewinsohn, T.M. & Roslin, T. (2008) Four ways towards tropical herbivore megadiversity. *Ecology Letters*, **11**, 398-416
- Longino, J.T. & Colwell, R.K. (2011) Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere*, **2**, art29

- Loranger, H., Weisser, W.W., Ebeling, A., Eggers, T., Luca, E., Loranger, J., Roscher, C. & Meyer, S.T. (2014) Invertebrate herbivory increases along an experimental gradient of grassland plant diversity. *Oecologia*, **174**, 183-193
- Majer, J.D. & Delabie, J.H.C. (1999) Impact of tree isolation on arboreal and ground ant communities in cleared pasture in the Atlantic rain forest region of Bahia, Brazil. *Insectes Sociaux*, **46**, 281-290
- Manning, A.D., Fischer, J. & Lindenmayer, D.B. (2006) Scattered trees are keystone structures - Implications for conservation. *Biological Conservation*, **132**, 311-321
- Marquis, R.J. (1984) Leaf herbivores decrease fitness of a tropical plant. *Science*, **226**, 537-539
- Massad, T.J., Chambers, J.Q., Rolim, S.G., Jesus, R.M. & Dyer, L.A. (2011) Restoration of pasture to forest in Brazil's Mata Atlântica: The roles of herbivory, seedling defenses, and plot design in reforestation. *Restoration Ecology*, **19**, 257-267
- Matt, F., Almeida, K., Arguero, A. & Reudenbach, C. (2008) Seed dispersal by birds, bats and wind. *Gradients in a Tropical Mountain Ecosystem of Ecuador*. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 157-165). Springer Berlin Heidelberg.
- Metcalfe, D.B., Asner, G.P., Martin, R.E., Silva Espejo, J.E., Huasco, W.H., Farfán Amézquita, F.F., Carranza-Jimenez, L., Galiano Cabrera, D.F., Baca, L.D., Sinca, F., Huaraca Quispe, L.P., Taype, I.A., Mora, L.E., Dávila, A.R., Solórzano, M.M., Puma Vilca, B.L., Laupa Román, J.M., Guerra Bustios, P.C., Revilla, N.S., Tupayachi, R., Girardin, C.A.J., Doughty, C.E. & Malhi, Y. (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, **17**, 324-332
- Mithöfer, A. & Boland, W. (2012) Plant defense against herbivores: Chemical aspects. *Annual Review of Plant Biology*, **63**, 431-450
- Mody, K. & Linsenmair, K.E. (2004) Plant-attracted ants affect arthropod community structure but not necessarily herbivory. *Ecological Entomology*, **29**, 217-225
- Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R. & Foley, W.J. (2011) Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*, **25**, 380-388
- Montagnini, F. (2001) Strategies for the recovery of degraded ecosystems: Experiences from Latin America. *Interciencia - Caracas*, **26**, 498-503
- Montoya-Lerma, J., Giraldo-Echeverri, C., Armbrrecht, I., Farji-Brener, A. & Calle, Z. (2012) Leaf-cutting ants revisited: Towards rational management and control. *International Journal of Pest Management*, **58**, 225-247
- Morris, R.J. (2010) Anthropogenic impacts on tropical forest biodiversity: A network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3709-3718
- Morrison, E.B. & Lindell, C.A. (2012) Birds and bats reduce insect biomass and leaf damage in tropical forest restoration sites. *Ecological Applications*, **22**, 1526-1534
- Murphy, D.D., Launer, A.E. & Ehrlich, P.R. (1983) The Role of adult feeding in egg production and population dynamics of the Checkerspot Butterfly *Euphydryas editha*. *Oecologia*, **56**, 257-263
- Murray, T.E., Fitzpatrick, Ú., Byrne, A., Fealy, R., Brown, M.J.F. & Paxton, R.J. (2012) Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology*, **49**, 998-1008
- Muth, N.Z., Kluger, E.C., Levy, J.H., Edwards, M.J. & Niesenbaum, R.A. (2008) Increased per capita herbivory in the shade: Necessity, feedback, or luxury consumption. *Ecoscience*, **15**, 182-188
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858
- Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature*, **390**, 507-509
- Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: Pondering the mystery of singletons. *Oikos*, **89**, 564-572
- Novotny, V., Basset, Y., Miller, S.E., Drozd, P. & Cizek, L. (2002a) Host specialization of leaf-chewing insects in a New Guinea rainforest. *Journal of Animal Ecology*, **71**, 400-412
- Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P. (2002b) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841-844
- Novotny, V., Miller, S.E., Baje, L., Balagawi, S., Basset, Y., Cizek, L., Craft, K.J., Dem, F., Drew, R.A.I., Hulcr, J., Leps, J., Lewis, O.T., Pokon, R., Stewart, A.J.A., Allan Samuelson, G. &

- Weiblen, G.D. (2010) Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. *Journal of Animal Ecology*, **79**, 1193-1203
- Ochoa-Cueva, P., Fries, A., Montesinos, P., Rodríguez-Díaz, J.A. & Boll, J. (2013) Spatial estimation of soil erosion risk by land-cover change in the Andes of southern Ecuador. *Land Degradation & Development*, online first
- Offenberg, J., Nielsen, M.G., MacIntosh, D.J., Havanon, S. & Aksornkoae, S. (2004) Evidence that insect herbivores are deterred by ant pheromones. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, S433-S435
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-7.
<http://CRAN.R-project.org/package=vegan>
- Onyekwelu, J.C., Stimm, B. & Evans, J. (2011) Review plantation forestry. In: Günter, S., Weber, M., Stimm, B. & Mosandl, R. (Eds.). *Silviculture in the Tropics* (pp. 399-454). Springer Berlin Heidelberg
- Paquette, A. & Messier, C. (2009) The role of plantations in managing the world's forests in the Anthropocene. *Frontiers in Ecology and the Environment*, **8**, 27-34
- Paul, G., Montagnini, F., Berlyn, G., Craven, D., Breugel, M. & Hall, J. (2012) Foliar herbivory and leaf traits of five native tree species in a young plantation of Central Panama. *New Forests*, **43**, 69-87
- Pawson, S., Brockerhoff, E., Meenken, E. & Didham, R. (2008) Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. *Biodiversity and Conservation*, **17**, 1127-1148
- Pawson, S.M., Brockerhoff, E.G., Watt, M.S. & Didham, R.K. (2011) Maximising biodiversity in plantation forests: Insights from long-term changes in clearfell-sensitive beetles in a *Pinus radiata* plantation. *Biological Conservation*, **144**, 2842-2850
- Payton, M.E., Greenstone, M.H. & Schenker, N. (2003) Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? *Journal of Insect Science*, **3**
- Peeters, P.J. (2002) Correlations between leaf structural traits and the densities of herbivorous insect guilds. *Biological Journal of the Linnean Society*, **77**, 43-65
- Peñuelas, J., Sardans, J., Llusia, J., Owen, S.M., Silva, J. & Niinemets, Ü. (2010) Higher allocation to low cost chemical defenses in invasive species of Hawaii. *Journal of Chemical Ecology*, **36**, 1255-1270
- Perfecto, I. & Vandermeer, J. (2008) Biodiversity conservation in tropical agroecosystems. *Annals of the New York Academy of Sciences*, **1134**, 173-200
- Peters, T., Drobnik, T., Meyer, H., Rankl, M., Richter, M., Rollenbeck, R., Thies, B. & Bendix, J. (2013) Environmental changes affecting the Andes of Ecuador. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S. & Wilcke, W. (Eds.). *Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador* (pp. 19-29). Springer Berlin Heidelberg
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**
- Piotto, D., Montagnini, F., Ugalde, L. & Kanninen, M. (2003) Performance of forest plantations in small and medium-sized farms in the Atlantic lowlands of Costa Rica. *Forest Ecology and Management*, **175**, 195-204
- Plath, M., Dorn, S., Barrios, H. & Mody, K. (2012a) Diversity and composition of arboreal beetle assemblages in tropical pasture afforestations: Effects of planting schemes and tree species identity. *Biodiversity and Conservation*, **21**, 3423-3444
- Plath, M., Dorn, S., Riedel, J., Barrios, H. & Mody, K. (2012b) Associational resistance and associational susceptibility: Specialist herbivores show contrasting responses to tree stand diversification. *Oecologia*, **169**, 477-487
- Plath, M., Mody, K., Potvin, C. & Dorn, S. (2011) Establishment of native tropical timber trees in monoculture and mixed-species plantations: Small-scale effects on tree performance and insect herbivory. *Forest Ecology and Management*, **261**, 741-750

- Pollard, E., Greatorex-Davies, J.N. & Thomas, J.A. (1997) Drought reduces breeding success of the butterfly *Aglais urticae*. *Ecological Entomology*, **22**, 315-318
- Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P., Del Toro, I., Ho, C.-K., Kominoski, J., Newbold, T.A.S., Parsons, S. & Joern, A. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews*, **88**, 327-348
- Prieto-Benítez, S. & Méndez, M. (2011) Effects of land management on the abundance and richness of spiders (Araneae): A meta-analysis. *Biological Conservation*, **144**, 683-691
- Qayyum, A. & Zalucki, M.P. (1987) Effects of high temperature on survival of eggs of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae). *Australian Journal of Entomology*, **26**, 295-298
- R Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Rasband, W.S. (2014) *ImageJ*. U. S. National Institutes of Health, Bethesda, Maryland, USA
<http://imagej.nih.gov/ij/>
- Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). *Molecular Ecology Notes*, **7**, 355-364
- Ribeiro Neto, J.D., Pinho, B.X., Meyer, S.T., Wirth, R. & Leal, I.R. (2012) Drought stress drives intraspecific choice of food plants by *Atta* leaf-cutting ants. *Entomologia Experimentalis et Applicata*, **144**, 209-215
- Ribeiro, S.P. & Brown, V.K. (2006) Prevalence of monodominant vigorous tree populations in the tropics: herbivory pressure on *Tabebuia* species in very different habitats. *Journal of Ecology*, **94**, 932-941
- Ribeiro, S.P., Pimenta, H.R. & Fernandes, G.W. (1994) Herbivory by chewing and sucking insects on *Tabebuia ochracea*. *Biotropica*, **26**, 302-307
- Richards, A.E., Forrester, D.I., Bauhus, J. & Scherer-Lorenzen, M. (2010) The influence of mixed tree plantations on the nutrition of individual species: A review. *Tree Physiology*, **30**, 1192-1208
- Richter, M., Beck, E., Rollenbeck, R. & Bendix, J. (2013) The study area. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S. & Wilcke, W. (Eds.). *Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador* (pp. 3-17). Springer Berlin Heidelberg.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: Biodiversity in native and agricultural habitats. *Conservation Biology*, **15**, 378-388
- Riedel, J., Dorn, S., Brand, G., Barrios, H. & Mody, K. (2013) Effects of ants on arthropod assemblages of a native timber tree in a tropical reforestation plantation. *Journal of Applied Entomology*, **137**, 418-428
- Roos, K., Rollenbeck, R., Peters, T., Bendix, J. & Beck, E. (2010) Growth of tropical bracken (*Pteridium arachnoideum*): Response to weather variations and burning. *Invasive Plant Science and Management*, **3**, 402-411
- Rudgers, J., Hodgen, J. & White, J.W., III (2003) Behavioral mechanisms underlie an ant-plant mutualism. *Oecologia*, **135**, 51-59
- Schaffers, A.P., Raemakers, I.P., Sýkora, K.V. & ter Braak, C.J.F. (2008) Arthropod assemblages are best predicted by plant species composition. *Ecology*, **89**, 782-794
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Beszler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.-M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M. & Tschardtke, T. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553-556
- Scherber, C., Gladbach, D.J., Stevnbak, K., Karsten, R.J., Schmidt, I.K., Michelsen, A., Albert, K.R., Larsen, K.S., Mikkelsen, T.N., Beier, C. & Christensen, S. (2013) Multi-factor climate change effects on insect herbivore performance. *Ecology and Evolution*, **3**, 1449-1460
- Schowalter, T.D. (2012) Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry*, **31**, 518-536

- Schuh, R.T. & Slater, J.A. (1995) *True bugs of the world: Classification and natural history*. Comstock, Ithaca, New York
- Schuldt, A., Baruffol, M., Böhnke, M., Bruelheide, H., Härdtle, W., Lang, A.C., Nadrowski, K., Von Oheimb, G., Voigt, W., Zhou, H. & Assmann, T. (2010) Tree diversity promotes insect herbivory in subtropical forests of south-east China. *Journal of Ecology*, **98**, 917-926
- Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tschardt, T. (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications*, **14**, 1321-1333
- Schwintzer, C.R. & Tjepkema, J.D. (2012) *The biology of Frankia and actinorhizal plants*. Elsevier.
- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, **152**, 738-750
- Silva Matos, D.M. & Belinato, T.A. (2010) Interference of *Pteridium arachnoideum* (Kaulf.) Maxon. (Dennstaedtiaceae) on the establishment of rainforest trees. *Brazilian Journal of Biology*, **70**, 311-316
- Souza, A.L.T.d. & Martins, R.P. (2005) Foliage density of branches and distribution of plant-dwelling spiders. *Biotropica*, **37**, 416-420
- Stamp, N. (2003) Out of the quagmire of plant defense hypotheses. *The Quarterly Review of Biology*, **78**, 23-55
- Stimm, B., Beck, E., Günter, S., Aguirre, N., Cueva, E., Mosandl, R. & Weber, M. (2008) Reforestation of abandoned pastures: Seed ecology of native species and production of indigenous plant material. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 417-429). Springer Berlin Heidelberg.
- Strutzenberger, P., Brehm, G. & Fiedler, K. (2011) DNA barcoding-based species delimitation increases species count of Eois (Geometridae) moths in a well-studied tropical mountain forest by up to 50%. *Insect Science*, **18**, 349-362
- Summerville, K.S., Crist, T.O., Kahn, J.K. & Gering, J.C. (2003) Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. *Ecological Entomology*, **28**, 747-757
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, **47**, 561-594
- Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution*, **30**, 2725-2729
- Thies, B., Meyer, H., Nauss, T. & Bendix, J. (2012) Projecting land-use and land-cover changes in a tropical mountain forest of Southern Ecuador. *Journal of Land Use Science*, **9**, 1-33
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629-632
- Truxa, C. & Fiedler, K. (2012) Down in the flood? How moth communities are shaped in temperate floodplain forests. *Insect Conservation and Diversity*, **5**, 389-397
- van Bael, S.A., Aiello, A., Valderrama, A., Medianero, E., Samaniego, M. & Wright, S.J. (2004) General herbivore outbreak following an El Niño-related drought in a lowland Panamanian forest. *Journal of Tropical Ecology*, **20**, 625-633
- Vasconcelos, H.L. & Cherrett, J.M. (1996) The effect of wilting on the selection of leaves by the leaf-cutting ant *Atta laevigata*. *Entomologia Experimentalis et Applicata*, **78**, 215-220
- Vehviläinen, H., Koricheva, J. & Ruohomäki, K. (2007) Tree species diversity influences herbivore abundance and damage: Meta-analysis of long-term forest experiments. *Oecologia*, **152**, 287-298
- Vehviläinen, H., Koricheva, J. & Ruohomäki, K. (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. *Oikos*, **117**, 935-943
- Vrac, M. & Michelangeli, P.-A. (2014) *CDFt*. R package version 1.0.1. <http://CRAN.R-project.org/package=CDFt>
- Wassenaar, T., Gerber, P., Verburg, P.H., Rosales, M., Ibrahim, M. & Steinfeld, H. (2007) Projecting land use changes in the Neotropics: The geography of pasture expansion into forest. *Global Environmental Change*, **17**, 86-104
- Weber, M., Günter, S., Aguirre, N., Stimm, B. & Mosandl, R. (2008) Reforestation of abandoned

- pastures: Silvicultural means to accelerate forest recovery and biodiversity. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (Eds.). *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 431-441). Springer Berlin Heidelberg.
- Weintraub, P.G. & Beanland, L. (2006) Insect vectors of phytoplasmas. *Annual Review of Entomology*, **51**, 91-111
- Xiao, Y. (2012) *CvM2SL2Test*. R package version 2.0-1
<http://CRAN.R-project.org/package=CvM2SL2Test>.
- Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences*, **96**, 1463-1468
- Yu, X.-D., Lü, L., Luo, T.-H. & Zhou, H.-Z. (2013) Elevational gradient in species richness pattern of epigaeic beetles and underlying mechanisms at east slope of Balang Mountain in southwestern China. *PLoS ONE*, **8**, e69177
- Zangerl, A.R., Hamilton, J.G., Miller, T.J., Crofts, A.R., Oxborough, K., Berenbaum, M.R. & de Lucia, E.H. (2002) Impact of folivory on photosynthesis is greater than the sum of its holes. *Proceedings of the National Academy of Sciences*, **99**, 1088-1091
- Zuazo, V.H.D. & Pleguezuelo, C.R.R. (2009) Soil-erosion and runoff prevention by plant covers: A review. In: Lichtfouse, E., Navarrete, M., Debaeke, P., Véronique, S. & Alberola, C. (Eds.). *Sustainable Agriculture* (pp. 785-811). Springer Netherlands.
- Zvereva, E., Lanta, V. & Kozlov, M. (2010) Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: A meta-analysis of experimental studies. *Oecologia*, **163**, 949-960

Appendix

Appendix A

Appendix Table A.1 Overview of Coleopteran, Hemipteran and Lepidopteran families arranged by tree species (*i.e.* *Cedrela montana*, *Heliocarpus americanus*, and *Tabebuia chrysantha*). Specimens were collected during a 2-year survey period 2010-2012. Families are sorted according to dietary guild.

	<i>C. montana</i>					<i>H. americanus</i>					<i>T. chrysantha</i>				
	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}
Coleoptera															
Phytophagous															
Cerambycidae	4	2	1	---	1	11	6	2	1	2	3	3	---	1	---
Chrysomelidae	476	57	6	8	7	547	76	11	14	18	644	93	16	17	30
Curculionidae	124	37	9	11	15	200	65	23	19	34	187	40	7	10	10
Elateridae	19	9	2	3	2	44	14	3	6	5	63	17	2	7	5
Erotylidae	---	---	---	---	---	---	---	---	---	---	4	3	2	1	3
Scarabaeidae	1	1	---	1	---	3	3	1	2	1	1	1	1	---	1
Predatory															
Cantharidae	35	7	1	1	1	122	17	4	5	7	274	11	---	4	2
Carabidae	3	1	---	---	---	19	6	2	2	3	3	2	---	1	---
Cleridae	3	2	---	---	---	13	3	1	---	1	8	3	1	1	2
Coccinellidae	99	26	5	6	5	74	22	2	7	2	113	26	3	6	4
Histeridae	1	1	1	---	1	2	2	2	---	2	---	---	---	---	---
Lampyridae	2	2	---	---	---	12	4	1	---	1	3	3	2	---	2
Phengodidae	1	1	1	---	1	---	---	---	---	---	1	1	1	---	1
Scirtidae	6	2	---	---	---	2	1	---	---	---	1	1	---	---	---
Scydmaenidae	1	1	---	---	---	2	1	---	---	---	7	1	---	---	---
Staphylinidae	182	35	2	11	4	313	50	7	15	9	432	50	10	14	13
Detritivorous															
Anobiidae	---	---	---	---	---	---	---	---	---	---	1	1	1	---	1
Erotylidae	---	---	---	---	---	6	2	---	---	2	1	1	1	---	1
Hydrophilidae	---	---	---	---	---	7	2	1	---	2	---	---	---	---	---
Leiodidae	---	---	---	---	---	---	---	---	---	---	1	1	1	---	1
Monotomidae	1	1	1	---	1	---	---	---	---	---	1	1	1	---	1
Nitidulidae	7	4	---	1	---	13	7	1	3	2	29	10	4	2	4
Tenebrionidae	6	4	1	2	1	15	9	4	3	4	14	6	1	3	2
Zopheridae	4	4	2	2	2	2	2	2	---	2	4	4	2	2	2
Other															
Aderidae	10	8	1	5	1	1	1	---	1	---	8	7	---	4	---
Anobiidae	1	1	1	---	1	---	---	---	---	---	3	3	1	2	3
Anthribidae	6	4	---	2	---	14	5	1	2	1	1	1	1	---	1
Artematopodidae	---	---	---	---	---	6	4	2	2	3	3	3	2	1	2
Biphyllidae	---	---	---	---	---	---	---	---	---	---	1	1	1	---	1

Appendix Table A.1 (continued)

	<i>C. montana</i>					<i>H. americanus</i>					<i>T. chrysantha</i>				
	N	S	S _{ingleton}	S _{rare}	S _{unique}	N	S	S _{ingleton}	S _{rare}	S _{unique}	N	S	S _{ingleton}	S _{rare}	S _{unique}
Coleoptera (cont.)															
Other (cont.)															
Corylophidae	7	3	1	1	1	8	6			5	19	3		2	
Curculionidae	21	1				6	1				9	1			
Erotylidae	4	4	4		4						4	4	4		4
Lampyridae	1	1	1		1	1	1	1			1	1	1		1
Latridiidae	1	1	1		1	2	2				7	1			
Linnichidae											2	1		1	1
Lycidae	7	6	2	3	2	5	5	1	2	1	9	7		5	2
Melyridae	1	1	1	1		5	3	1	2	3	2	1		1	
Mordellidae	8	4	1	1	1	19	6	1	3	1	32	4		2	
Oedemeridae	1	1				2	2	1		1	5	1			
Ptiliidae						1	1	1		1	1	1	1		1
Ptilodactylidae	11	5		1		4	4		1		16	8		4	2
Silvanidae	2	2	2		2										
Staphylinidae						1	1		1		1	1		1	
Tenebrionidae	6	4				5	2				9	3			
Throscidae	1	1	1		1										
Trogossitidae											1	1	1		1
Hemiptera															
Phytophagous															
Acanthosomatidae	1	1	1		1										
Achilidae	5	4	1	2	3	6	1				13	6	1	3	4
Aphididae	7	4	1		1	12	5	1		1	17	6			
Aphrophoridae	1	1	1		1	16	6	2	3	4	3	2		1	
Berytidae	5	1									3	3	1		1
Calophyidae											2	1		1	1
Cicadellidae	125	27	3	9	5	104	46	9	18	17	1905	44	10	11	13
Cixiidae	1	1		1							2	2	1	1	1
Clastopteridae						1	1		1		2	2		2	
Coreidae						7	4		1		2	3	2		2
Delphacidae	5	5	2	1	2	19	6	1	2	1	14	4	1		1
Derbidae	18	7	2	1	3	6	5	1	2	3	9	5	2		2
Dictyopharidae						1	1	1		1					
Flatidae	2	2		2	2										

Appendix Table A.1 (continued)

	<i>C. montana</i>					<i>H. americanus</i>					<i>T. chrysanthra</i>				
	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}
Hemiptera (cont.)															
Phytophagous (cont.)															
Lygaeidae	3	2	---	1	---	55	14	1	4	5	18	13	1	10	7
Membracidae	6	6	4	2	4	38	11	2	5	9	4	4	4	---	4
Miridae	50	14	3	4	3	143	37	6	9	13	46	20	5	6	7
Nogodinidae	---	---	---	---	---	1	1	1	---	1	3	2	1	1	2
Pentatomidae	1	1	---	1	---	1	1	---	1	---	3	2	---	2	1
Psyllidae	1432	5	2	5	5	2	2	1	1	1	4	2	1	1	1
Rophalidae	---	---	---	---	---	---	---	---	---	---	1	1	1	---	1
Tingidae	---	---	---	---	---	3970	6	1	1	1	7	3	---	1	1
Triozidae	6	5	1	2	3	2	2	---	1	---	127	8	---	1	3
Predatory															
Anthocoridae	---	---	---	---	---	1	1	1	---	1	1	1	1	---	1
Ceratocombidae	---	---	---	---	---	---	---	---	---	---	2	2	2	---	2
Enicocephalidae	---	---	---	---	---	2	2	2	---	2	3	1	---	1	1
Geocoridae	3	1	---	---	---	3	2	---	---	---	1	1	---	---	---
Lasiophilidae	---	---	---	---	---	1	1	1	---	1	---	---	---	---	---
Lytocoridae	---	---	---	---	---	1	1	---	1	---	1	1	---	1	---
Plokiophilidae	---	---	---	---	---	1	1	1	---	1	---	---	---	---	---
Reduviidae	9	3	---	1	1	35	8	4	1	4	7	6	2	1	2
Other															
Aradidae	1	1	1	---	1	1	1	1	---	1	---	---	---	---	---
Lepidoptera															
Phytophagous															
Bombycidae	---	---	---	---	---	1	1	---	---	---	25	3	2	---	2
Bucculatricidae	2	2	2	---	2	17	2	---	---	2	1	1	1	---	1
Choreutidae	19	1	---	---	1	---	---	---	---	---	---	---	---	---	---
Elachistidae	30	7	1	3	6	2	2	1	1	1	---	---	---	---	---
Erebidae	5	5	3	1	3	43	19	5	8	14	5	5	3	2	3
Gelechiidae	1	1	1	---	1	22	5	---	2	3	72	5	1	1	4
Geometridae	70	41	10	9	13	77	43	10	10	14	110	56	12	12	17
Hesperiidae	1	1	1	---	1	24	4	---	---	4	---	---	---	---	---
Lasiocampidae	---	---	---	---	---	1	1	1	---	1	---	---	---	---	---
Lycanidae	3	2	---	1	1	6	2	---	---	---	---	---	---	---	---
Noctuidae	10	10	2	4	2	19	13	5	6	7	15	12	5	2	5

Appendix Table A.1 (continued)

		<i>C. montana</i>					<i>H. americanus</i>					<i>T. chrysantha</i>				
		N	S	S _{Singleton}	S _{Rare}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}
Lepidoptera (cont.)																
Phytophagous (cont.)																
1	Nolidae	2	1	---	1	1	4	1	---	1	1	2	1	---	1	1
	Notodontidae	---	---	---	---	---	1	1	1	---	1					
1	Nymphalidae	---	---	---	---	---	---	---	---	---	---	1	1	1	---	1
2	Psychidae	3	1	---	1	---	---	---	---	---	---	5	3	1	2	2
---	Saturniidae	---	---	---	---	---	1	1	1	---	1	---	---	---	---	---
---	Sematuridae	---	---	---	---	---	1	1	1	---	1	---	---	---	---	---
---	Sphingidae	---	---	---	---	---	1	1	1	---	1	---	---	---	---	---
---	Thyrididae	2	1	---	1	1	---	---	---	---	---	---	---	---	---	---
6	Tortricidae	34	14	4	3	6	18	10	3	1	3	23	14	2	4	6
Detritivorous																
	Erebidae	8	8	2	6	2	11	10	5	5	5	11	9	2	7	2
	Geometridae	1	1	---	1	---	2	2	---	2	---	10	6	2	4	3
	Noctuidae	2	2	1	1	1	4	3	2	1	2	7	7	4	3	7

Appendix Table A.2 Overview of Coleopteran, Hemipteran and Lepidopteran families arranged by habitat type (i.e. natural forest, *Pinus patula* plantation, pasture land and secondary shrub vegetation). Samples were collected during a 2-year survey period 2010-2012. Families are sorted according to dietary guild.

Coleoptera	Forest						Pinus						Pasture						Shrub											
	N			S			N			S			N			S			N			S			N			S		
	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}	N	S	S _{unique}			
Phytophagous	Cerambycidae	6	5	1	2	3	6	3	1	1	6	3	1	6	3	1	6	3	1	6	3	1	6	3	1	6	3	1		
	Chrysomelidae	660	119	26	29	63	291	51	4	4	9	671	42	3	4	14	45	14	2	2	2	2	2	2	2	2	2			
	Curculionidae	276	85	32	26	59	64	23	3	8	7	158	29	3	6	14	13	5	1	1	1	1	1	1	1	1	1			
	Elateridae	67	23	5	9	15	5	5		2		51	11	2	5	4	3	1												
	Erotylidae	4	3	2	1	3																								
	Scarabaeidae	1	1	1		1						3	3	1	2	1	1	1												
	Predatory	Cantharidae	349	18	4	6	6	35	10	1	1	1	39	4		2	1	8	3	1										
		Carabidae	20	6	2	2	3	5	3		1																			
		Cleridae	14	6	2	1	3	10	2																					
Coccinellidae		145	24	2	4	4	79	25	1	9	1	58	21	6	5	7	4	4	1	1	1	1	1	1	1	1				
Histeridae		2	2	2		2	1	1	1		1	2	2																	
Lampyridae		10	4	3		3	5	3																						
Phengodidae		1	1	1		1	1	1	1		1																			
Scirtidae		4	3									5	1																	
Scydmaenidae		9	2									1	1																	
Detritivorous	Staphylinidae	596	82	13	27	43	283	33	4	9	4	38	16	2	4	2	10	4												
	Anobiidae	1	1	1		1																								
	Erotylidae	6	2	1		1						1	1																	
	Hydrophilidae	7	2	1		2																								
	Leiodidae	1	1	1		1																								
	Monotomidae						1	1	1	1	1	1	1	1	1	1	1	1												
	Nitidulidae	28	13	3	3	11	19	6	2	2	2	1	1		1		1	1												
	Tenebrionidae	21	10	4	3	5	13	8	1	5	5	1	1	1	1	1														
	Zopheridae	4	4	1	3	3	4	4	3	1	3	2	2	2	2															
Other	Aderidae	7	7		6	4	7	5		3	2	5	4	1	1	1														
	Anobiidae	1	1		1		2	2	1	1	1	1	1	1	1	1														
	Anthribidae	1	1	1		1	18	7	1	4	5	1	1				1	1												
	Artematopodidae	2	2	2		2						6	4	2	2	3	1	1												
	Biphylidae	1	1	1		1																								

Appendix Table A.2 (continued)

	Forest					Pinus					Pasture					Shrub				
	N	S	S _{singleton}	S _{rare}	S _{unique}	N	S	S _{singleton}	S _{rare}	S _{unique}	N	S	S _{singleton}	S _{rare}	S _{unique}	N	S	S _{singleton}	S _{rare}	S _{unique}
Coleoptera (cont.)																				
Other (cont.)																				
Corylophidae	4	4	1	3	1	28	6	---	3	3	2	2	---	2	2	---	---	---	---	---
Cureulionidae	36	3	---	---	3	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Erotylidae	5	5	5	---	5	3	3	3	---	3	---	---	---	---	---	---	---	---	---	---
Lampyridae	1	1	1	---	1	1	1	1	---	1	1	1	1	---	1	---	---	---	---	---
Latridiidae	1	1	---	---	---	8	2	---	---	---	1	1	1	---	1	---	---	---	---	---
Limnichidae	2	1	---	1	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Lycidae	7	7	2	4	2	11	8	1	4	1	1	1	---	1	---	2	2	---	1	---
Melyridae	7	4	1	3	3	---	---	---	---	---	1	1	---	1	---	---	---	---	---	---
Mordellidae	11	5	1	1	1	45	6	1	2	1	2	2	---	2	---	1	1	---	1	---
Oedemeridae	---	---	---	---	---	7	3	---	---	3	1	1	1	---	1	---	---	---	---	---
Ptilidae	---	---	---	---	---	1	1	1	---	1	1	1	1	---	1	---	---	---	---	---
Ptilodactylidae	18	10	---	5	4	1	1	---	1	---	11	5	---	---	---	1	1	---	---	---
Silvanidae	2	2	2	---	2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Staphylinidae	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Tenebrionidae	2	1	---	---	---	11	5	---	---	---	2	2	---	2	2	---	---	---	---	---
Throscidae	---	---	---	---	---	1	1	1	1	1	---	---	---	---	---	---	---	---	---	---
Trogossitidae	1	1	1	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Hemiptera																				
Phytophagous																				
Acanthosomatidae	---	---	---	---	---	---	---	---	---	---	1	1	1	1	---	1	---	---	---	---
Achilidae	18	6	---	4	3	1	1	1	---	1	4	3	1	1	---	1	1	---	---	---
Aphididae	2	2	---	---	---	20	6	1	---	1	14	7	1	---	3	---	---	---	---	---
Aphrophoridae	15	6	3	1	5	---	---	---	---	---	2	2	---	2	---	3	1	---	1	---
Berytidae	---	---	---	---	---	1	1	---	---	---	7	3	1	---	1	---	---	---	---	---
Calophyidae	2	1	---	1	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Cicadellidae	374	49	11	18	26	1577	31	4	8	4	143	30	6	9	9	40	7	1	3	1
Cixiidae	1	1	1	---	1	---	---	---	---	---	2	2	---	2	2	---	---	---	---	---
Clastopteridae	---	---	---	---	---	---	---	---	---	---	2	2	---	2	---	1	1	---	1	---
Coreidae	2	2	1	---	1	1	1	1	---	1	5	2	---	1	---	2	2	---	---	---
Delphacidae	30	11	3	3	9	7	3	---	---	---	---	---	---	---	---	1	1	1	---	1
Derbidae	11	8	3	1	5	4	1	---	1	1	18	8	2	1	5	---	---	---	---	---
Dictyopharidae	1	1	1	---	1	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Flatidae	1	1	---	1	---	---	---	---	---	---	1	1	---	1	---	---	---	---	---	---

Appendix Table A.2 (continued)

	Forest						Pinus						Pasture						Shrub					
	N			S			N			S			N			S			N			S		
	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	S _{Unique}	N	S	S _{Singleton}	S _{Rare}	S _{Unique}	S _{Unique}
Hemiptera (cont.)																								
Phytophagous (cont.)																								
Lygaeidae	32	16	1	9	10	1	24	5	1	2	1	13	4	7	4	2	2	2	7	4	1	2	1	1
Membracidae	29	11	7	2	9	1	6	3	1	1	1	13	7	2	4	4	4	4	14	5	1	1	1	1
Miridae	116	33	7	10	20	3	41	22	3	8	7	68	11	3	3	3	3	3	14	5	1	1	1	1
Nogodinidae	4	3	2	1	3	1	5	4	1	4	4	1	1	1	1	1	1	1	1	1	1	1	1	1
Pentatomidae																								
Psyllidae	193	3	1	2	2	1	756	2	1	1	1	488	3	2	2	2	2	2	1	1	1	1	1	1
Rophalidae							1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tingidae	386	4	1	2	2	1	922	2	1	1	1	2495	2	1	1	1	1	1	174	1	1	1	1	1
Triozidae	65	4	1	1	1	1	21	5	1	2	1	47	4	1	1	1	1	1	2	2	1	1	1	1
Predatory																								
Anthocoridae	2	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ceratocombidae	2	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Enicocephalidae	5	3	2	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Geocoridae							6	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lasiophilidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lytocoridae	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Plokiophilidae							1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Reduviidae	6	5	3	1	3	1	17	6	2	1	2	27	5	1	1	1	1	1	2	1	1	1	1	1
Other																								
Aradidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidoptera																								
Phytophagous																								
Bombycidae	3	3	2	1	2	1	23	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Bucculatricidae	17	4	3	1	3	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1
Choreutidae	19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Elachistidae	4	3	1	1	2	1	2	2	1	1	1	26	4	2	3	3	3	3	1	1	1	1	1	1
Erebidae	36	21	9	9	16	1	13	4	1	2	1	4	4	2	2	2	2	2	1	1	1	1	1	1
Gelechiidae	30	4	1	1	1	1	58	4	1	2	2	7	3	1	1	1	1	1	1	1	1	1	1	1
Geometridae	129	60	14	15	33	1	72	45	10	12	20	45	25	3	4	6	6	6	11	10	5	5	5	5
Hesperiidae	5	1	1	1	1	1	10	1	1	1	1	5	2	1	1	1	1	1	5	1	1	1	1	1
Lasiocampidae												1	1	1	1	1	1	1	1	1	1	1	1	1
Lycaenidae							2	1	1	1	1	7	3	1	1	1	1	1	1	1	1	1	1	1
Noctuidae	23	17	7	6	13	1	11	9	4	1	4	8	7	1	4	3	3	3	2	2	1	1	1	1

Appendix Table A.2 (continued)

	Forest						Pinus						Pasture						Shrub											
	N	S	S _{singleton}	S _{rare}	S _{unique}		N	S	S _{singleton}	S _{rare}	S _{unique}		N	S	S _{singleton}	S _{rare}	S _{unique}		N	S	S _{singleton}	S _{rare}	S _{unique}		N	S	S _{singleton}	S _{rare}	S _{unique}	
Hemiptera (cont.)																														
Phytophagous (cont.)																														
Nolidae	4	1		1	1		2	1		1	1		2	1			1	1												
Notodontidae							1	1																						
Nymphalidae														1	1		1													
Psychidae	3	1		1	1								5	3		1	2	3												
Saturniidae	1	1	1		1																									
Sematuridae	1	1	1		1																									
Sphingidae							1	1		1																				
Thyrididae	2	1		1	1																									
Tortricidae	18	12	2	5	7		13	9	2	2	2		42	15		4	1	7		2	2		1							1
Bombycidae	3	3	2		2		23	1																						
Bucculatricidae	17	4	3		3								3	1																
Choreutidae	19	1			1																									
Detritivorous																														
Erebidae	19	18	8	10	15		8	6		6			2	2		1	1	1		1	1									1
Geometridae	12	8	2	6	5		1	1		1																				
Noctuidae	7	6	4	2	4		5	5	3	2	3									1	1									1

N: number of individuals,
S: number of species,
S_{rare}: number of rare species (represented with less than five specimens),
S_{unique}: unique species occurring exclusively on one of the four habitats
S_{singleton}: number of singletons (encountered only once in the dataset)

Appendix A

Appendix Table A.3 Overview of all collected arthropods classified to family-level and aggregated by habitat and tree species. Specimens were collected during 10 successive surveys across a two-year period. All specimens were assigned to feeding guilds based on literature or personal observation. With the exception of Lepidoptera, dietary information pertains to adult individuals. Less common feeding habits are given in parentheses:

d: detritivorous, h: herbivorous, m: mycophagous, n: nectar/pollen, o: omnivorous, p: predaceous, s: surface-feeder (algae/lichen), x: does not feed, Indet.: indeterminate; * parasitoid hymenoptera

Order	Family	Diet	Forest			Pasture			Pinus			Shrub ^b	
			<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>H. americanus</i>	<i>T. chrysantha</i>
Acari													
---	^a	Indet.	41	20	48	1	---	1	22	18	55	3	3
Araneae													
---	^a	p	140	590	436	505	321	298	161	334	372	40	61
Archaeognatha													
---	^a	s	3	2	1	---	---	---	---	---	1	---	---
Blattodea													
---	^a	o	3	8	17	147	38	52	5	9	6	2	6
Coleoptera													
	Aderidae	Indet.	2	1	4	3	---	2	5	---	2	---	---
	Anobiidae	d, m	---	---	2	1	---	---	---	---	2	---	---
	Anthribidae	s	---	---	1	1	---	---	5	13	---	1	---
	Artematopodidae	s	---	2	---	---	4	2	---	---	---	---	1
	Biphylidae	m	---	---	1	---	---	---	---	---	---	---	---
	Cantharidae	p	19	87	243	---	20	19	16	10	9	5	3
	Carabidae	p	3	17	---	---	---	---	---	2	3	---	---
	Cerambycidae	h	---	4	2	4	2	---	---	5	1	---	---
	Chrysomelidae	h	48	287	326	347	209	115	81	44	166	9	37
	Cleridae	p	1	5	8	---	---	---	2	8	---	---	---
	Coccinellidae	p	20	47	78	45	5	8	34	20	25	2	2
	Corylophidae	m	1	2	1	---	1	1	6	5	17	---	---
	Curculionidae	h	46	135	132	75	49	34	24	19	21	3	11
	Elaterridae	h	9	27	31	9	16	26	1	1	3	---	4
	Endomychidae	m	1	---	---	---	---	---	---	---	---	---	---
	Erotylidae	d, h, m	2	5	8	---	1	---	2	---	1	---	---
	Eucnemidae	n	2	---	---	---	---	---	---	---	---	---	---
	Histeridae	p	---	2	---	---	---	---	1	---	---	---	---
	Hydrophilidae	d	---	7	---	---	---	---	---	---	---	---	---
	Lampyridae	p, (x)	1	8	2	1	1	1	1	4	1	---	---
	Latridiidae	m	---	1	---	1	---	---	---	1	7	---	---
	Leiodidae	d	---	---	1	---	---	---	---	---	---	---	---
	Limnichidae	s	---	---	2	---	---	---	---	---	---	---	---
	Lycidae	n	2	3	2	1	---	---	4	1	6	1	1
	Melyridae	n	1	4	2	---	1	---	---	---	---	---	---
	Monotomidae	d	---	---	---	1	---	---	---	---	1	---	---
	Mordellidae	n	1	6	4	---	1	1	7	12	26	---	1
	Nitidulidae	d	2	11	15	---	1	---	5	---	14	1	---
	Oedemeridae	n	---	---	---	---	1	---	1	1	5	---	---
	Phengodidae	p	1	---	---	---	---	---	---	---	1	---	---
	Ptilidae	m	---	---	---	---	---	1	---	1	---	---	---
	Ptilodactylidae	s	5	2	11	6	2	3	---	---	1	---	1
	Scarabaeidae	h	---	1	---	5	1	1	---	---	---	1	---
	Scirtidae	p	1	2	1	5	---	---	---	---	---	---	---
	Scydmaenidae	p	---	2	7	1	---	---	---	---	---	---	---

Appendix Table A.3 (continued)

Order	Family	Diet	Forest			Pasture			Pinus			Shrub ^b	
			<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>H. americanus</i>	<i>T. chrysantha</i>
Coleoptera (continued)													
	Silvanidae	m	2	---	---	---	---	---	---	---	---	---	---
	Staphylinidae	p	99	245	252	18	13	9	65	55	163	1	9
	Tenebrionidae	d, (n)	4	8	11	4	4	---	4	8	12	---	---
	Throscidae	m	---	---	---	---	---	---	1	---	---	---	---
	Trogossitidae	m	---	---	1	---	---	---	---	---	---	---	---
	Zopheridae	d	2	1	1	2	---	---	---	1	3	---	---
	unidentified	Indet.	5	9	24	4	2	3	4	5	10	---	2
Collembola													
	--- ^a	s	27	22	57	6	---	9	1	3	11	---	1
Dermaptera													
	Anisolabididae	o	---	1	---	---	---	---	1	2	---	---	---
	Chelisochidae	o	---	1	---	---	---	---	---	---	---	---	---
	Forficulidae	o	3	---	---	---	---	---	---	---	---	---	---
	Spongiphoridae	o	---	1	---	---	---	---	---	---	---	---	---
	unidentified	o	4	5	4	---	---	---	---	---	---	---	---
Diptera													
	--- ^a	Indet.	33	65	64	35	43	44	35	21	15	1	1
Embioptera													
	--- ^a	s	---	---	---	---	---	1	---	---	---	---	---
Ephemeroptera													
	--- ^a	x	2	1	---	1	---	---	---	1	---	---	---
Hemiptera													
	Acanthosomatidae	h	---	---	---	1	---	---	---	---	---	---	---
	Achilidae	h	1	6	11	4	---	---	---	---	1	---	1
	Anthocoridae	P	---	1	1	---	---	---	---	---	---	---	---
	Aphididae	h	---	1	1	6	4	10	4	10	8	---	---
	Aphrophoridae	h	1	12	2	---	1	1	---	---	---	3	---
	Aradidae	m	---	1	---	---	---	---	1	---	---	---	---
	Berytidae	h	---	---	---	5	---	2	---	---	1	---	---
	Calophyidae	h	---	---	2	---	---	---	---	---	---	---	---
	Ceratocombidae	p	---	---	2	---	---	---	---	---	---	---	---
	Cercopidae	h	---	1	---	---	1	---	---	---	---	---	1
	Cicadellidae	h	29	52	293	29	12	102	67	39	1471	1	39
	Cixiidae	h	---	1	1	1	---	1	---	---	---	---	---
	Clastopteridae	h	---	---	---	---	1	1	---	---	---	---	1
	Coreidae	h	---	1	1	---	5	---	---	---	1	1	1
	Cydnidae	h	---	---	1	---	---	---	---	---	---	---	---
	Delphacidae	h	6	17	11	4	4	2	2	4	3	---	1
	Derbidae	h	5	1	5	9	5	5	4	---	---	---	---
	Dictyopharidae	h	---	1	---	---	---	---	---	---	---	---	---
	Enicocephalidae	p	---	2	3	---	---	---	---	---	---	---	---
	Flatidae	h	1	---	---	1	---	---	---	---	---	---	---
	Fulgoridae	h	1	---	---	---	---	---	---	---	---	---	---
	Geocoridae	p	---	---	---	---	1	---	3	2	1	---	---
	Lasiochilidae	p	---	1	---	---	---	---	---	---	---	---	---
	Lyctocoridae	p	---	1	1	---	---	---	---	---	---	---	---
	Lygaeidae	h	2	16	14	1	11	1	---	22	2	6	1
	Membracidae	h	1	25	4	4	9	---	1	5	---	---	---
	Miridae	h	3	90	23	34	21	13	14	20	9	13	1
	Nogodinidae	h	---	1	3	---	---	---	---	---	---	---	---

Appendix Table A.3 (continued)

Order	Family	Diet	Forest			Pasture			Pinus			Shrub ^b	
			<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>H. americanus</i>	<i>T. chrysantha</i>
Hemiptera (continued)													
	Pentatomidae	h	---	---	---	---	---	---	1	1	3	---	---
	Plokiophilidae	p	---	---	---	---	---	---	---	1	---	---	---
	Psyllidae	h	189	1	3	487	1	---	756	---	1	---	1
	Reduviidae	p	2	7	2	5	179	2	5	12	6	---	1
	Rophalidae	h	---	---	---	---	---	---	---	---	1	---	---
	Tingidae	h	---	384	2	---	2490	5	---	922	---	174	---
	Triozidae	h	3	---	62	1	1	45	2	---	19	1	1
	unidentified	Indet.	39	116	32	67	45	19	26	58	113	6	27
Hymenoptera													
	Agaonidae *	n	---	---	---	---	---	---	---	---	1	---	---
	Apidae *	n	---	1	---	---	---	---	---	---	---	---	---
	Bethylidae *	n	2	3	2	5	2	2	3	2	7	---	---
	Braconidae *	n	17	22	38	17	8	10	54	24	39	1	2
	Ceraphronidae *	n	1	3	6	---	---	2	9	1	4	---	---
	Cynipidae	n	---	---	---	1	---	---	---	---	---	---	---
	Diapriidae *	n	17	16	28	2	1	2	8	8	5	---	---
	Dryinidae *	n	---	5	2	2	---	---	2	1	1	---	1
	Embolemidae *	n	---	---	---	---	---	---	1	---	---	---	---
	Encyrtidae *	n	---	1	1	5	3	9	2	2	2	---	---
	Eucharitidae *	n	1	7	10	---	---	---	---	---	---	---	---
	Eucoilidae *	n	4	4	2	5	3	---	4	1	1	---	---
	Eulophidae	n.	3	8	14	7	4	17	6	7	12	---	---
	Eupelmidae *	n	---	1	2	3	---	---	1	1	1	---	1
	Eurytomidae	n	1	---	---	---	1	---	---	---	1	---	---
	Figitidae *	n	---	---	---	---	---	5	---	---	---	---	---
	Formicidae	o, (p)	21	314	67	88	94	107	116	102	86	19	42
	Ichneumonidae *	n	4	7	8	7	3	4	5	2	3	1	1
	Mellinidae	n	---	1	---	1	---	---	---	---	---	---	---
	Mutillidae	p	---	2	---	---	---	---	---	---	---	---	---
	Mymaridae *	n	1	1	---	3	---	1	---	1	1	---	---
	Pemphredonidae	n	---	1	---	---	---	1	1	---	2	---	---
	Pergidae	n	---	1	---	---	---	---	---	---	---	---	---
	Perilampidae *	n	---	---	---	---	1	---	---	5	1	---	---
	Philanthidae *	n	---	1	---	---	1	1	---	---	---	---	---
	Platygastridae	n	4	---	6	---	---	1	2	2	1	---	---
	Pompilidae *	n	---	---	---	---	1	---	---	---	---	---	---
	Proctotrupidae *	n	---	1	2	---	---	1	---	---	---	---	---
	Pteromalidae	n	2	---	---	1	1	---	2	1	---	---	---
	Scelionidae *	n	2	1	4	1	---	4	2	1	---	---	---
	Sierolomorphida*	p	---	---	---	---	---	---	---	---	2	---	---
	Signiphoridae *	n	---	---	---	---	---	1	---	---	---	---	---
	Tanaostigmatidae	n	---	1	---	---	---	---	---	---	---	---	---
	Tenthredinidae	n	---	20	---	---	---	---	1	---	---	---	---
	Tiphidae	Indet.	---	---	---	---	---	---	1	---	---	---	---
	Torymidae	n	---	1	1	---	3	---	---	---	---	---	---
	Vespidae	p	---	---	1	---	2	1	---	3	2	---	1
	unidentified	Indet.	---	---	---	2	2	1	---	---	---	---	---
Isopoda													
	--- ^a	d	23	25	38	---	---	---	---	---	---	---	---

Appendix Table A.3 (continued)

Order	Family	Diet	Forest			Pasture			Pinus			Shrub ^b		
			<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	
Lepidoptera ^c														
	Bombycidae	h	---	1	2	---	---	---	---	---	23	---	---	
	Bucculatricidae	h	3	14	1	---	3	---	---	---	---	---	---	
	Choreutidae	h	19	---	---	---	---	---	---	---	---	---	---	
	Elachistidae	h	3	1	---	25	1	---	2	---	---	---	---	
	Erebidae	d , h	10	36	13	3	3	1	2	16	3	1	---	
	Gelechiidae	h	1	8	21	---	5	2	---	9	49	---	---	
	Geometridae	(d), h	22	54	70	29	5	11	22	20	35	2	10	
	Hesperiidae	h	---	5	---	1	4	---	---	10	---	5	---	
	Lasiocampidae	h	---	---	---	---	1	---	---	---	---	---	---	
	Lycanidae	h	---	---	---	3	4	---	---	2	---	---	---	
	Noctuidae	(d), h	3	14	17	5	4	1	4	7	6	1	2	
	Nolidae	h	---	4	---	2	---	---	---	---	2	---	---	
	Notodontidae	h	---	---	---	---	---	---	---	1	---	---	---	
	Nymphalidae	h	---	---	---	---	---	1	---	---	---	---	---	
	Psychidae	h	---	---	3	3	---	2	---	---	---	---	---	
	Saturniidae	h	---	1	---	---	49	---	---	---	---	---	---	
	Sematuridae	h	---	1	---	---	---	---	---	---	---	---	---	
	Sphingidae	h	---	---	---	---	---	---	---	1	---	---	---	
	Thyrididae	h	2	---	---	---	---	---	---	---	---	---	---	
	Tortricidae	h	7	8	8	23	11	9	5	2	6	---	2	
	unidentified	Indet.	3	9	37	10	5	2	1	4	6	---	1	
Mantodea														
	Mantidae	p	---	---	---	---	1	---	---	---	1	---	---	
Myriapoda														
	---	d, o, p	17	14	59	12	1	8	4	4	6	---	---	
Neuroptera														
	Chrysopidae	p	4	4	4	1	---	---	---	---	---	---	---	
	Hemeroibiidae	p	1	2	1	---	1	4	3	---	6	---	2	
	Neurorthidae	p	2	---	1	1	---	---	1	---	---	---	---	
	unidentified	p	3	5	6	3	1	9	2	1	6	---	---	
Opiliones														
	---	p	1	---	1	---	---	---	---	---	---	---	---	
Orthoptera														
	Acrididae	h	---	2	1	1	---	15	---	---	---	---	---	
	Eumasticidae	h	---	---	2	---	---	---	---	---	---	---	---	
	Gryllidae	o	4	---	8	2	1	2	---	---	1	---	---	
	Tettigoniidae	o	7	5	13	26	15	5	11	5	11	2	3	
	unidentified	o	1	4	2	2	1	---	---	1	4	---	1	
Phasmatodea														
	Phasmatidae	h	3	1	1	---	---	---	1	3	27	---	---	
Pseudoscorpiones														
	Cheliferidae	p	---	1	---	---	---	---	---	---	---	---	---	
Psocoptera														
	Caeciliusidae	s	1	5	18	4	---	4	1	1	4	---	1	
	Ectopsocidae	s	---	---	---	---	---	1	---	---	---	---	---	
	Lachesillidae	s	---	---	---	---	---	1	2	1	3	---	---	
	Lepidopsocidae	s	---	---	1	---	---	---	---	1	---	---	---	
	Peripsocidae	s	1	---	1	---	---	---	---	---	---	---	---	
	Pseudocaeciliidae	s	---	1	2	---	---	---	---	---	---	---	---	
	Psocidae	s	---	1	3	1	1	1	---	2	---	1	---	

Appendix Table A.3 (continued)

Order	Family	Diet	Forest			Pasture			Pinus			Shrub ^b	
			<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysantha</i>	<i>H. americanus</i>	<i>T. chrysantha</i>
Psocoptera (continued)													
	Stenopsocidae	s	---	---	1	---	---	---	---	1	12	---	2
	unidentified	s	13	2	10	5	---	5	1	4	12	---	2
Thysanoptera													
	Phlaeothripidae	Indet.	1	2	3	5	4	1	12	6	4	---	1
	unidentified	Indet.	---	---	---	1	---	---	---	---	---	---	---
Trichoptera													
	Philopotamidae	n	---	---	1	---	---	---	---	---	---	---	---
	unidentified	n	---	1	---	---	---	---	---	---	---	---	---

^a No identification at family level was attempted.

^b The numbers reflect aggregation across only six surveys, since the shrub sites were destroyed in a wildfire 2011

^c Assignment to dietary guild is based on direct feeding observations from individual species and therefore not necessarily representative for the family as a whole.

Appendix Table A.4 Overview of all species with observed or probable trophic relationship to at least one of the sample host plants. Chewing phytophages (i.e. Coleoptera, Hymenoptera, and Lepidoptera) were subjected to feeding trials by presenting them with leaves from the tree they were originally found on. Hemiptera were considered feeding on a given plant if more than 90% of collected individuals were observed on only one tree species. Trophic relationship is indicated by symbols: (+) Tree was accepted as host, (–) Tree was rejected as host (note that this may also have been caused by disease or parasitism), (~) apparent feeding traces, but uncertain trophic relation due to the premature death of the specimen in question, (NA) Insect was never found on the respective plant and consequently no feeding trials were conducted. For each insect species, the number of individuals is given.

Order	Family	Subfamily	Tribe	Species	Morphospecies	n	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysanthra</i>
Coleoptera									
	Chrysomelidae								
		Chrysomelinae	Indet.	Indet.	chry126	17	–	+	–
		Cryptocephalinae	Cryptocephalini	Indet.	chry139	2	~	NA	–
		Eumolpinae	Indet.	Indet.	chry045	23	–	+	–
		Eumolpinae	Indet.	Indet.	chry056	23	–	+	+
		Galerucinae	Alticini	Indet.	chry007	22	–	–	+
		Galerucinae	Alticini	Indet.	chry008	43	–	–	+
		Galerucinae	Alticini	Indet.	chry009	121	–	–	+
		Galerucinae	Alticini	Indet.	chry023	73	–	+	–
		Galerucinae	Alticini	Indet.	chry035	27	+	–	–
		Galerucinae	Alticini	Indet.	chry082	14	–	–	+
		Galerucinae	Alticini	Indet.	chry117	9	–	–	+
		Galerucinae	Alticini	Indet.	chry128	3	–	–	~
		Galerucinae	Alticini	Indet.	chry129	7	NA	–	+
		Galerucinae	Alticini	Indet.	chry144	3	NA	–	~
		Galerucinae	Indet.	Indet.	chry149	4	+	–	–
		Hispinae	Indet.	Indet.	chry025	22	–	~	–
		Hispinae	Dorynotini	<i>Dorynota</i> sp.	chry014	6	NA	–	+
	Curculionidae								
		Indet.	Indet.	Indet.	curcu004	57	+	+	+
		Indet.	Indet.	Indet.	curcu016	23	+	+	+
		Indet.	Indet.	Indet.	curcu032	7	–	+	–
		Indet.	Indet.	Indet.	curcu048	16	+	+	+
Hemiptera									
	Cicadellidae								
		Indet.	Indet.	Indet.	Cica002	34	–	–	+
		Indet.	Indet.	Indet.	Cica018	17	~	+	–
		Indet.	Indet.	Indet.	Cica029	36	+	~	~
		Indet.	Indet.	Indet.	Cica031	137	–	–	+
		Indet.	Indet.	Indet.	Cica032	305	–	–	+
		Indet.	Indet.	Indet.	Cica033	1445	–	–	+
	Lygaidae								
		Indet.	Indet.	Indet.	Lygae007	35	–	+	~
		Indet.	Indet.	Indet.	Lygae010	13	–	+	–
	Membracidae								
		Indet.	Indet.	Indet.	Memb005	18	–	+	–
		Indet.	Indet.	Indet.	Memb013	12	–	+	–
	Miridae								
		Indet.	Indet.	Indet.	Miri008	53	~	+	~
		Indet.	Indet.	Indet.	Miri015	51	+	+	+

Appendix Table A.4 (continued)

Order	Family	Subfamily	Tribe	Species	Morphospecies	n	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysanthra</i>
Miridae (continued)									
		Indet.	Indet.	Indet.	Miri023	19	–	+	–
Psyllidae									
		Spondyliaspidinae	Indet.	Indet.	Psyl001	1430	+	–	–
Tingidae									
		Tinginae	Tingini	---	Ting001	3969	–	+	–
Triozidae									
		Indet.	Indet.	Indet.	Trio001	121	–	–	+
Hymenoptera									
Tenthredinidae									
		Indet.	Indet.	Indet.	tenth001	20	NA	+	NA
Lepidoptera									
Bombycidae									
		Apatelodinae	---	<i>Olceclostera</i> sp.	bomb002	1	NA	NA	+
		Apatelodinae	---	<i>Colobata</i> sp.	bomb003	1	NA	NA	+
		Bombycinae	---	<i>Quentalia tolima</i>	bomb001	24	NA	+	+
Bucculatricidae									
		Indet.	Indet.	Indet.	bucc001	13	NA	+	NA
		Indet.	Indet.	Indet.	bucc002	1	NA	NA	+
		Indet.	Indet.	Indet.	bucc003	1	+	NA	NA
		Indet.	Indet.	Indet.	bucc004	1	+	NA	NA
Choreutoidea									
		Indet.	Indet.	Indet.	chor001	20	+	NA	NA
Elachistidae									
		Stenomatinae	---	<i>Antaeotricha</i> sp.	elach001	23	+	NA	NA
		Indet.	Indet.	Indet.	elach002	2	–	+	NA
Erebidae									
		Arctiinae	---	<i>Pelochyta apud lystra</i>	ereb018	1	NA	NA	+
		Arctiinae	Arctiini	<i>Halysidota atra rindgei</i>	ereb005	2	NA	+	NA
		Arctiinae	Arctiini	<i>Bertholdia</i> sp.	ereb022	1	+	NA	NA
		Arctiinae	Lithosiini	<i>Nodozana fifina</i>	ereb026	1	+	NA	NA
		Arctiinae	Phaegopterini	<i>Phaegoptera decrepidoides</i>	ereb006	1	NA	+	NA
		Arctiinae	Phaegopterini	<i>Elysius hades</i>	ereb008	3	+	+	+
		Arctiinae	Phaegopterini	<i>Phaegoptera</i> sp.	ereb010	1	NA	+	NA
		Arctiinae	Phaegopterini	<i>Melese nebulosa</i>	ereb013	3	NA	+	+
		Arctiinae	Phaegopterini	<i>Amastus coccinator</i>	ereb025	1	NA	+	NA
		Arctiinae	Phaegopterini	Indet.	ereb031	1	NA	+	NA
		Hermiinae	Indet.	Indet.	ereb002	2	NA	NA	+
		Hypeninae	---	<i>Hypena adraca</i>	ereb011	3	NA	+	NA
		Hypeninae	---	<i>Hypena</i> sp.	ereb020	4	NA	+	NA
		Hypeninae	---	<i>Hypena</i> sp.	ereb001	17	–	+	NA
		Hypeninae	---	<i>Hypena</i> sp.	ereb032	1	NA	NA	+
		Hypeninae	Indet.	Indet.	ereb027	8	NA	+	NA
Gelechiidae									
		Indet.	Indet.	Indet.	gele001	70	NA	NA	+
		Indet.	Indet.	Indet.	gele002	1	+	NA	NA
		Indet.	Indet.	Indet.	gele003	3	NA	+	–

Appendix Table A.4 (continued)

Order	Family	Subfamily	Tribe	Species	Morphospecies	n	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysanthra</i>
Gelechiidae (continued)									
		Indet.	Indet.	Indet.	gele004	18	NA	+	NA
		Indet.	Indet.	Indet.	gele005	1	NA	NA	+
Geometridae									
	Ennominae	Azelinini	<i>Pero</i> sp.	geo032	1	NA	NA	+	
	Ennominae	Boarmiini	<i>Physocleora celosoides</i>	geo007	10	+	–	–	
	Ennominae	Boarmiini	<i>Iridopsis</i> sp.	geo055	1	+	NA	NA	
	Ennominae	Boarmiini	<i>Physocleora accessilinea</i>	geo068	5	NA	+	NA	
	Ennominae	Boarmiini	<i>Pherotesia</i> sp.	geo069	1	+	NA	NA	
	Ennominae	Boarmiini	<i>Physocleora curvifera</i>	geo072	3	NA	NA	+	
	Ennominae	Boarmiini	<i>Melanolophia recucta meridiana</i>	geo002	22	+	+	+	
	Ennominae	Boarmiini	<i>Glena juga</i>	geo003	4	NA	+	+	
	Ennominae	Boarmiini	<i>Iridopsis subnigrata</i>	geo008	4	NA	NA	+	
	Ennominae	Boarmiini	<i>Physocleora</i> sp.	geo021	1	NA	+	NA	
	Ennominae	Boarmiini	<i>Iridopsis scolancala</i>	geo029	12	~	+	+	
	Ennominae	Caberini	<i>Oenoptila</i> sp.	geo052	1	+	NA	NA	
	Ennominae	Cratoptera Group	<i>Mychonia violacea</i>	geo001	6	+	+	NA	
	Ennominae	Cratoptera Group	<i>Apiciopsis</i> sp.	geo006	8	+	+	+	
	Ennominae	Cratoptera Group	<i>Cirsodes acuminata</i>	geo010	10	+	+	+	
	Ennominae	Cratoptera Group	<i>Melinodes detersaria</i>	geo060	2	NA	+	~	
	Ennominae	Cratoptera Group	<i>Cirsodes meridaria</i>	geo067	1	NA	NA	+	
	Ennominae	Nacophorini	<i>Charca daphnea</i>	geo009	1	NA	NA	+	
	Ennominae	Nacophorini	<i>Ischnopteris brehmi</i>	geo012	6	+	+	+	
	Ennominae	Nacophorini	<i>Ischnopteris</i> sp.	geo025	3	+	NA	+	
	Ennominae	Nacophorini	<i>Rucana bisecta</i>	geo028	3	NA	–	+	
	Ennominae	Nacophorini	<i>Cargolia arana</i>	geo030	7	+	–	+	
	Ennominae	Nacophorini	<i>Nephodia astyochides</i>	geo018	6	–	NA	+	
	Ennominae	Nacophorini	<i>Bonatea viridilinea</i>	geo016	5	+	+	+	
	Ennominae	Nacophorini	<i>Bonatea duciata</i>	geo033	2	+	+	NA	
	Ennominae	Ourapterygini	<i>Isochromodes</i> sp.	geo020	1	NA	NA	+	
	Ennominae	Ourapterygini	<i>Isochromodes</i> sp.	geo034	18	+	–	+	
	Ennominae	Ourapterygini	<i>Isochromodes</i> sp.	geo039	4	+	~	+	
	Ennominae	Ourapterygini	<i>Isochromodes</i> sp.	geo040	1	NA	NA	+	
	Ennominae	Ourapterygini	<i>Isochromodes polvoreata</i>	geo045	2	+	NA	NA	
	Ennominae	Ourapterygini	<i>Bassania amethystata</i>	geo049	4	NA	+	+	
	Ennominae	Ourapterygini	<i>Sabulodes bolivaria</i>	geo004	6	+	+	–	
	Ennominae	Ourapterygini	<i>Isochromodes pecticornata</i>	geo005	3	NA	NA	+	
	Ennominae	Ourapterygini	<i>Oxydia distichata</i>	geo011	5	+	NA	+	
	Ennominae	Ourapterygini	<i>Oxydia optima</i>	geo014	3	+	+	NA	

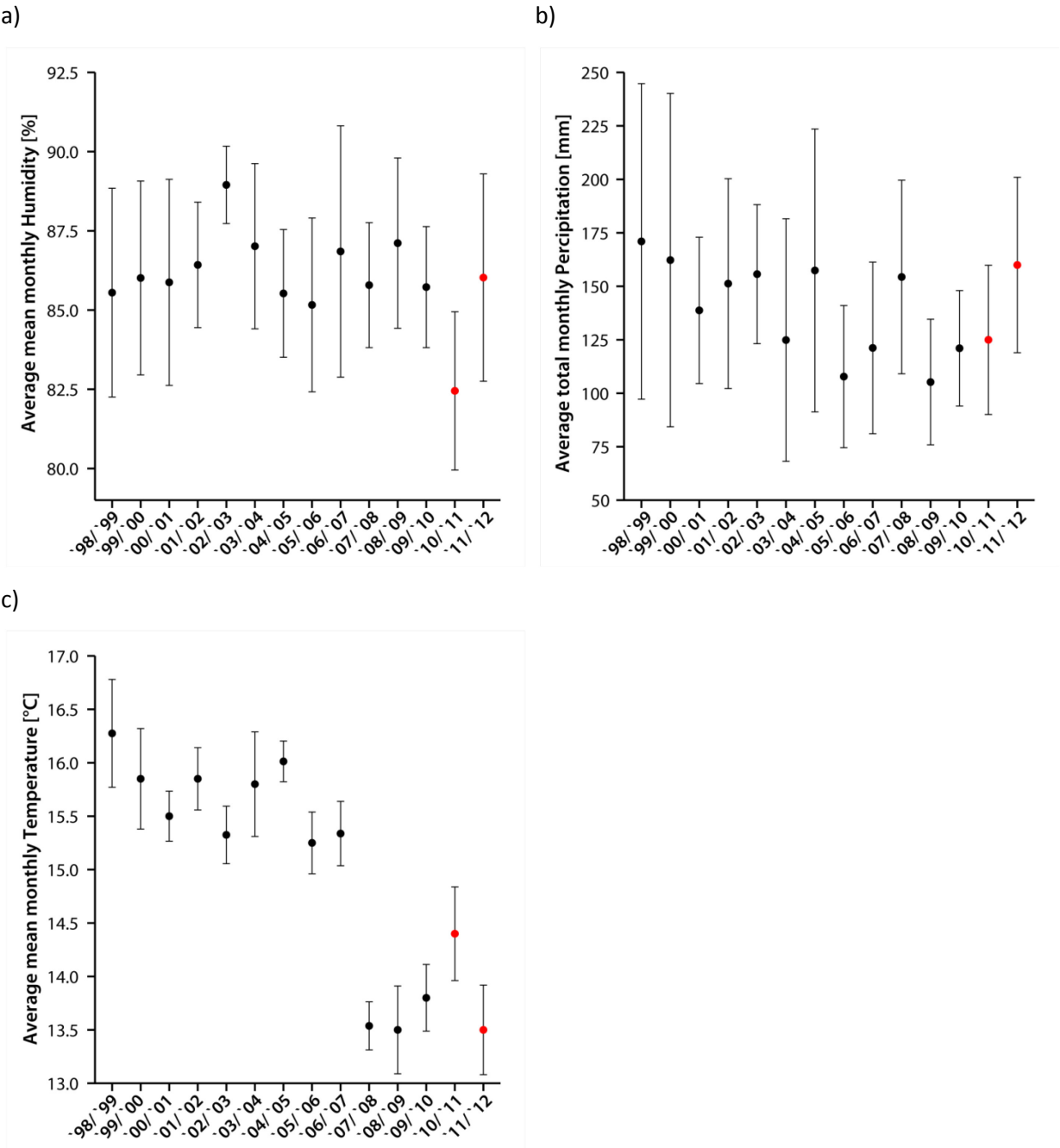
Appendix Table A.4 (continued)

Order	Family	Subfamily	Tribe	Species	Morphospecies	n	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysanthra</i>
Geometridae (continued)									
		Ennominae	Ourapterygini	<i>Oxydia trychiata</i>	geo026	6	+	+	NA
		Ennominae	Ourapterygini	<i>Isochromodes extimaria</i>	geo027	9	–	~	~
		Ennominae	Ourapterygini	<i>Oxydia</i> sp.	geo058	1	+	NA	NA
		Ennominae	Ourapterygini	<i>Hygrochroma nondina</i>	geo064	1	NA	NA	+
		Ennominae	Ourapterygini	<i>Phyla versatile</i>	geo066	1	NA	+	NA
		Ennominae	Ourapterygini	<i>Mesedra confinis</i>	geo073	7	+	NA	+
		Ennominae	Ourapterygini	<i>Certima planaria</i>	geo017	8	+	NA	+
		Ennominae	Ourapterygini	<i>Herbita dognini</i>	geo062	2	NA	+	NA
		Ennominae	Ourapterygini	<i>Phyllodaonta angulosa</i>	geo065	1	+	NA	NA
		Ennominae	Ourapterygini	Indet.	geo024	2	NA	NA	+
		Ennominae	Ourapterygini	Indet.	geo035	1	NA	~	NA
		Geometrinae	Nemoriini	<i>Nemoria imitans</i>	geo015	7	NA	+	NA
		Larentiinae	---	<i>Eupithecia</i> sp.	geo046	3	+	NA	NA
		Larentiinae	---	<i>Eupithecia duena</i>	geo051	1	~	NA	NA
		Larentiinae	---	<i>Eupithecia</i> sp.	geo075	4	–	–	~
		Sterrhinae	---	<i>Scopula</i> sp.	geo019	1	NA	NA	+
Hesperiidae									
		Pyrginae	Carcharodini	<i>Noctuana haematospila</i>	hesp001	23	NA	+	NA
Lycaenidae									
		Theclinae	Eumaeini	<i>Micandra comae</i>	lycae001	2	+	NA	NA
		Theclinae	Eumaeini	Indet.	lycae002	7	–	+	NA
Noctuidae									
		Hadeninae	Hadenini	<i>Heterochroma beryllus</i>	noct001	3	+	+	NA
		Hadeninae	Hadenini	<i>Hampsonodes</i> sp.	noct002	10	–	+	+
		Hadeninae	Hadenini	<i>Hampsonodes</i> sp.	noct019	3	–	–	+
		Hadeninae	Orthosiini	<i>Lacinipolia</i> sp.	noct020	1	NA	+	NA
		Noctuinae	Elaphriini	<i>Bryolymnia bicon</i>	noct022	1	NA	NA	+
		Noctuinae	Eriophygini	<i>Eriophyga rhadata</i>	noct023	1	+	NA	NA
		Noctuinae	Eriopygini	Indet.	noct012	5	+	NA	+
		Noctuinae	Eriopygini	<i>Eriopyga</i> sp.	noct013	3	NA	+	NA
		Ophiderinae	Indet.	Indet.	noct027	1	NA	NA	+
		Pantheinae	---	<i>Lichnoptera moestra</i>	noct006	3	+	+	NA
		Pantheinae	---	<i>Lichnoptera gulo</i>	noct007	1	+	+	NA
		Xyleninae	---	<i>Calymniodes pyrostroma</i>	noct009	2	+	NA	+
		Indet.	Indet.	Indet.	noct014	1	NA	+	NA
		Indet.	Indet.	Indet.	noct015	2	+	NA	+
		Indet.	Indet.	Indet.	noct017	2	NA	+	NA
		Indet.	Indet.	Indet.	noct025	1	NA	NA	+
Nolidae									
		Nolinae	---	<i>Megalona</i> sp.	noli003	4	NA	+	NA
Psychidae									
		Indet.	Indet.	Indet.	psych001	5	+	NA	–
Saturiidae									
		Hemileucinae	---	<i>Pseudodirphia</i> sp.	satu001	20	NA	+	NA

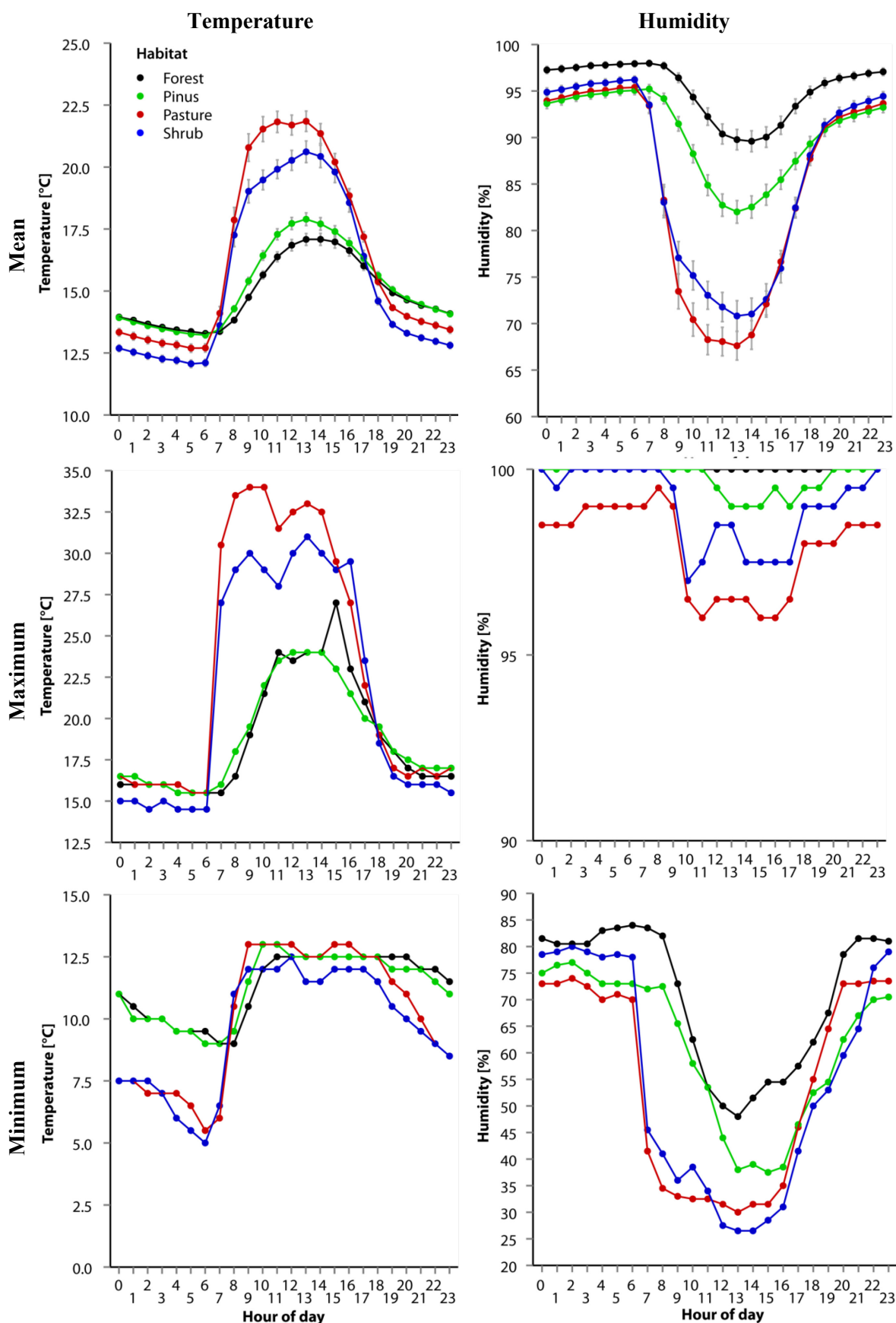
Appendix Table A.4 (continued)

Order	Family	Subfamily	Tribe	Species	Morphospecies	n	<i>C. montana</i>	<i>H. americanus</i>	<i>T. chrysanthra</i>
	Sematuridae								
		Sematurinae	---	<i>Homidiana</i> sp.	sema001	1	NA	+	NA
	Sphingidae								
		Indet.	Indet.	Indet.	sphing001	1	NA	+	NA
	Thyrididae								
		Thyridinae	---	<i>Dysodia</i> sp.	thyr001	2	+	NA	NA
	Tortricidae								
		Tortricinae	---	<i>Cuproxena neonereidana</i>	tort007	2	+	NA	NA
		Tortricinae	Indet.	Indet.	tort008	1	NA	+	NA
		Indet.	Indet.	Indet.	tort001	11	+	+	NA
		Indet.	Indet.	Indet.	tort003	16	+	+	+
		Indet.	Indet.	Indet.	tort005	2	+	+	NA
		Indet.	Indet.	Indet.	tort006	13	+	+	+
		Indet.	Indet.	Indet.	tort011	4	+	+	NA
		Indet.	Indet.	Indet.	tort012	1	+	NA	NA
		Indet.	Indet.	Indet.	tort013	4	NA	+	+
		Indet.	Indet.	Indet.	tort014	3	NA	NA	+
		Indet.	Indet.	Indet.	tort015	1	+	NA	NA
		Indet.	Indet.	Indet.	tort016	1	NA	+	NA
		Indet.	Indet.	Indet.	tort017	2	+	NA	NA
		Indet.	Indet.	Indet.	tort018	2	NA	NA	+
		Indet.	Indet.	Indet.	tort019	1	NA	NA	+
		Indet.	Indet.	Indet.	tort020	1	NA	NA	+

Appendix B

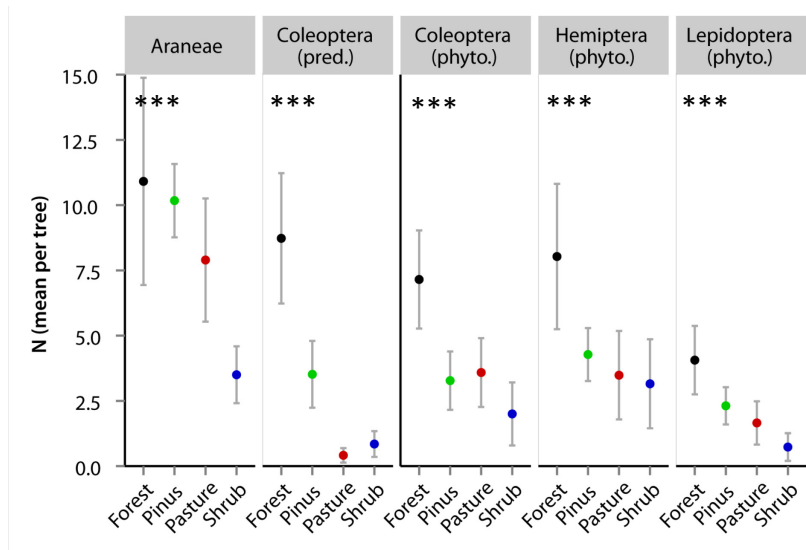


Appendix Figure B.1 Mean temperature, humidity and precipitation between October and May during the past 14 years (T. Peters, unpublished data). Whiskers represent a 95% confidence interval. The conspicuous downward shift in temperature in 2007 is due to a change in measuring hardware at the time. Values before and after that date are in themselves consistent. The two recording periods of the present study are highlighted in red.



Appendix Figure B.2 Diurnal patterns of hourly means for temperature and humidity as a function of habitat. Measurements were recorded 1.5m above ground at intervals of 30 minutes from March to September, 2011. Graphs display mean (\pm standard error of the mean), maximum and minimum values, respectively.

Appendix C



Appendix Figure C.1 Arthropod abundance per habitat for the 1st survey period (October to May 2010/11; excluding *C. montana*). Points represent means and the corresponding error bars a 95% confidence interval. * symbols denote a statistical significance of habitat for the respective insect group according to the accompanying GLMM analysis (see Appendix Table C.1).

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'

Appendix Table C.1 GLMM analyses of arthropod abundance for the 1st survey period (October to May 2010/11; excluding *C. montana*). Sample tree identity and total number of surveys were included as random terms. Non-significant terms were excluded based on p-values. Nagelkerke's (Pseudo-) R^2 refers to the simplified model shown here.

	df	Coleoptera				Lepidoptera				Hemiptera (<i>Dom. excl.</i>)			
		Chi²	p			Chi²	p			Chi²	p		
Habitat	3	37.094	< 0.001	***		29.887	< 0.001	***		24.032	< 0.001	***	
Tree sp.	1	0.792	0.374			3.116	0.078	.		3.752	0.053	.	
Leaf area	1	11.126	< 0.001	***		4.045	0.044	*		17.767	< 0.001	***	
Health	2	13.620	0.001	**		---	---			---	---		
Tree height	1	---	---			---	---			---	---		
Distance to neighbors	1	---	---			---	---			---	---		
Habitat x Tree sp.	3	16.265	0.001	**		---	---			11.345	0.010	*	
Habitat x Tree height	3	---	---			---	---			---	---		
Habitat x	3	---	---			---	---			---	---		
Distance to neighbors	3	---	---			---	---			---	---		
Nagelkerke R²		0.4463				0.2989				0.3157			

	df	Araneae				Coleoptera							
		Chi²	p			Chi²	p						
Habitat	3	22.903	< 0.001	***		87.685	< 0.001	***					
Tree sp.	1	5.265	0.022	*		1.759	0.185						
Leaf area	1	16.919	< 0.001	***		1.328	0.249						
Health	2	8.087	0.018	*		---	---						
Tree height	1	3.870	0.049	*		4.610	0.032	*					
Distance to neighbors	1	---	---			---	---						
Habitat x Tree sp.	3	12.369	0.006	**		7.826	0.050	*					
Habitat x Tree height	3	---	---			---	---						
Habitat x	3	---	---			---	---						
Distance to neighbors	3	---	---			---	---						
Nagelkerke R²		0.5044				0.5781							

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'

Appendix Table C.2 GLMM analyses of arthropod dry weight for the 1st survey period (October to May 2010/11; excluding *C. montana*). Sample tree identity and total number of surveys were included as random terms. Non-significant terms were excluded based on p-values. Nagelkerke's (Pseudo-) R² refers to the simplified model shown here.

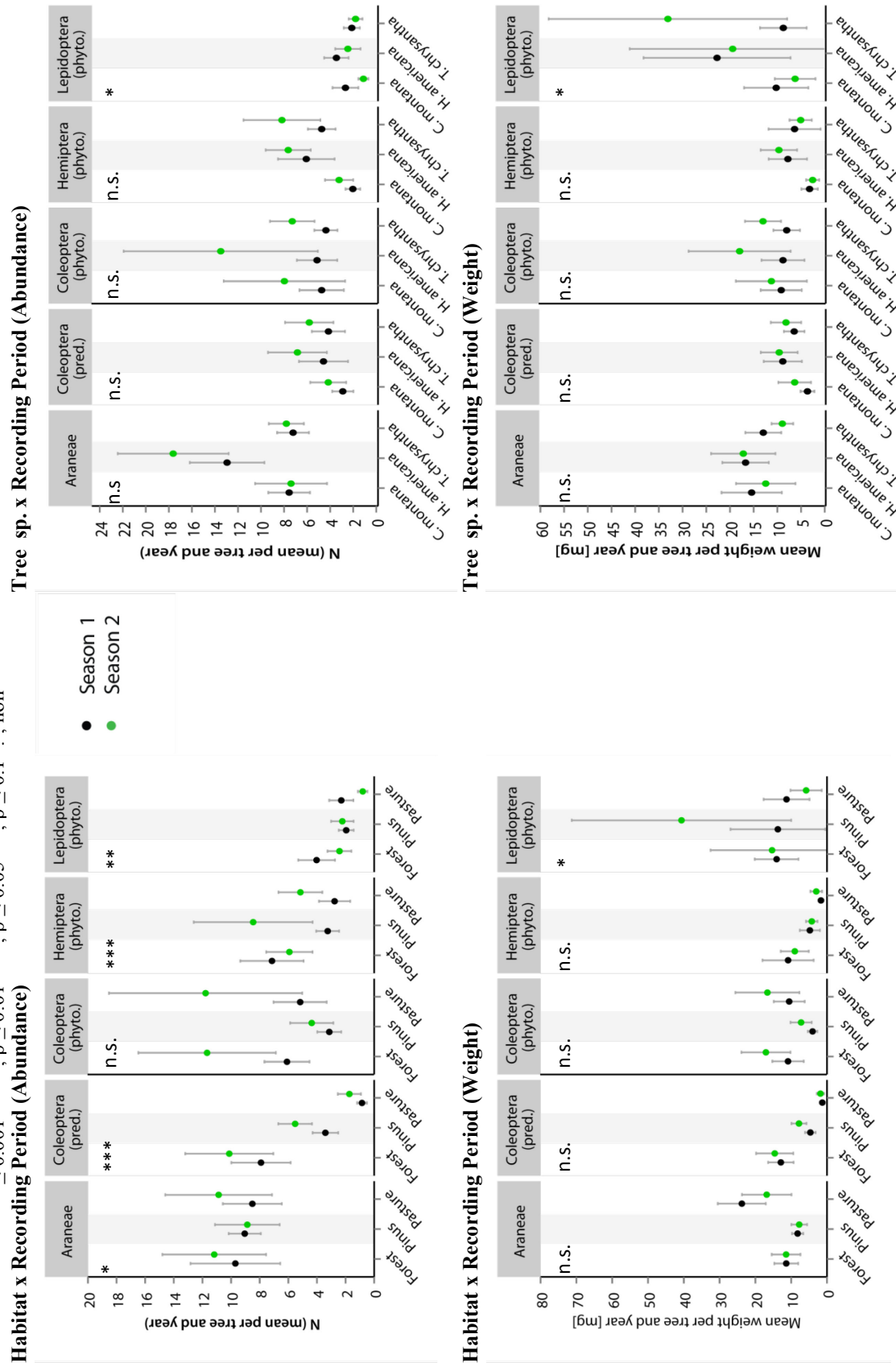
	df	Coleoptera				Lepidoptera			Hemiptera (<i>Dom. excl.</i>)		
		Chi ²	p			Chi ²	p		Chi ²	p	
Habitat	3	33.694	< 0.001	***		20.621	< 0.001	***	40.524	< 0.001	***
Tree sp.	1	2.422	0.120			7.500	0.006	**	0.000	0.990	
Leaf area	1	10.640	0.001	**		2.775	0.096	.	9.416	0.002	**
Health	2	15.887	< 0.001	***		---	---		---	---	
Tree height	1	---	---			---	---		---	---	
Distance to neighbors	1	---	---			0.051	0.822		---	---	
Habitat x Tree sp.	3	---	---			---	---		---	---	
Habitat x Tree height	3	---	---			---	---		---	---	
Habitat x	3	---	---			17.097	< 0.001	***	---	---	
Distance to neighbors	3	---	---			---	---		---	---	
Nagelkerke		0.3902				0.3442			0.3130		

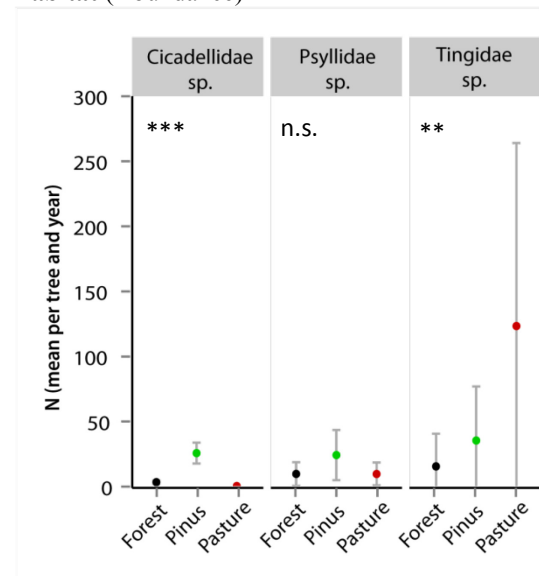
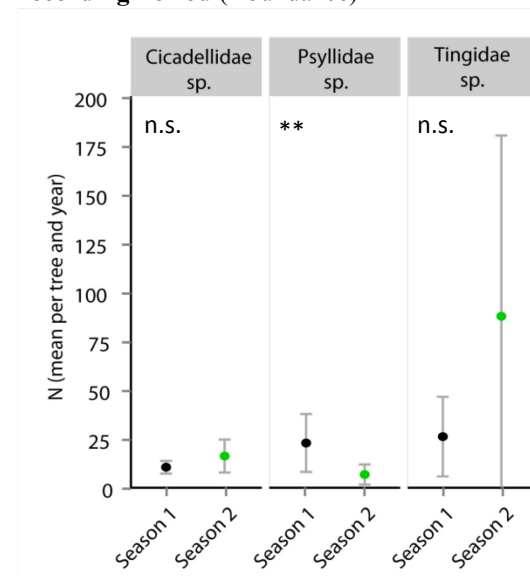
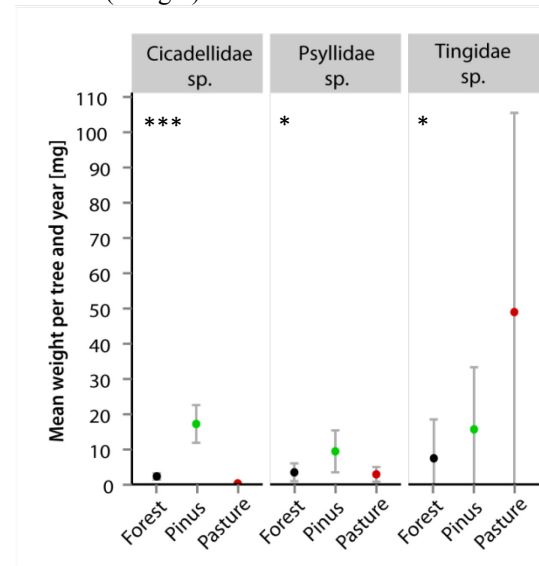
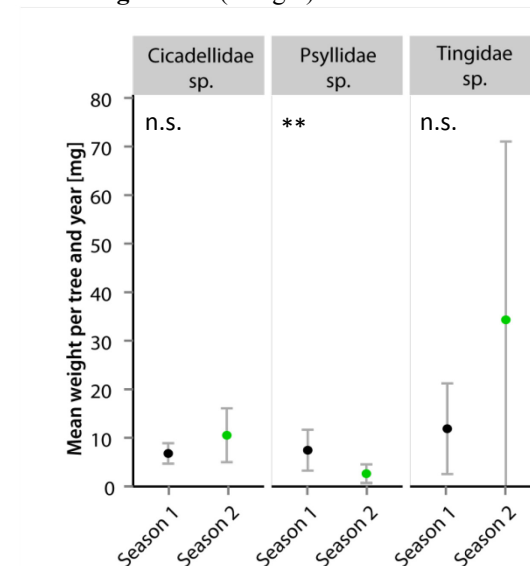
	df	Araneae				Coleoptera		
		Chi ²	p			Chi ²	p	
Habitat	3	53.645	0.000	***		81.901	0.000	***
Tree sp.	1	2.543	0.111			0.021	0.885	
Leaf area	1	11.795	0.001	***		2.824	0.093	.
Health	2	7.333	0.026	*		---	---	
Tree height	1	---	---			4.140	0.042	*
Distance to neighbors	1	---	---			0.160	0.689	
Habitat x Tree sp.	3	---	---			---	---	
Habitat x Tree height	3	---	---			---	---	
Habitat x	3	---	---			8.423	0.038	*
Distance to neighbors	3	---	---			---	---	
Nagelkerke		0.4914				0.5642		

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.

Appendix Figure C.2 Mean arthropod abundance and weight as a function of the interaction between habitat and recording period. Whiskers correspond to a 95% confidence interval, and * symbols represent the significance level of the interaction term based on GLMM analysis (Table 2.3 and Table 2.4).

Significance codes: $p \leq 0.001$ '***', $p \leq 0.01$ '**', $p \leq 0.05$ '*', $p \leq 0.1$ '.'; non-significant 'n.s.'

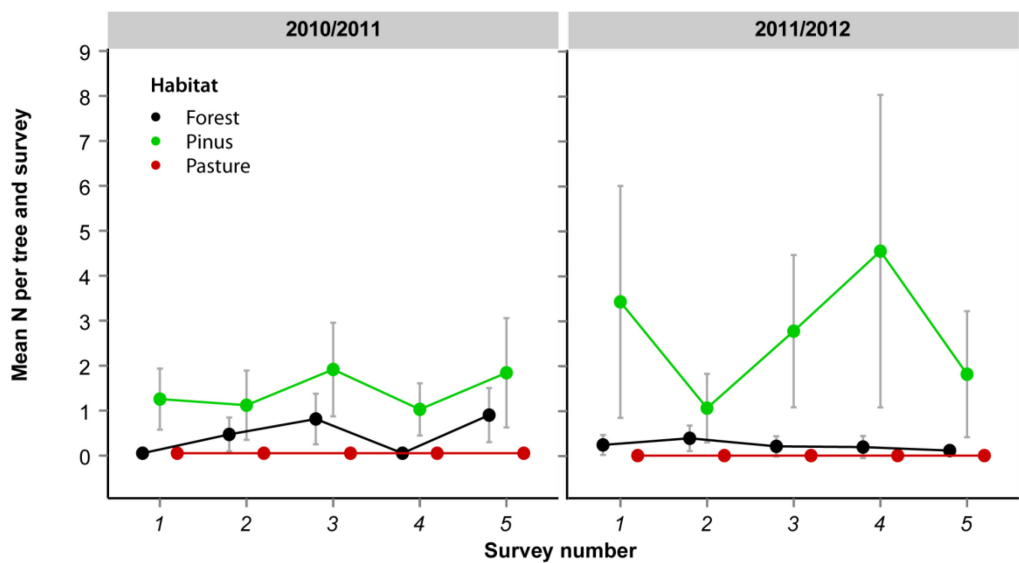


Habitat (Abundance)**Recording Period (Abundance)****Habitat (Weight)****Recording Period (Weight)**

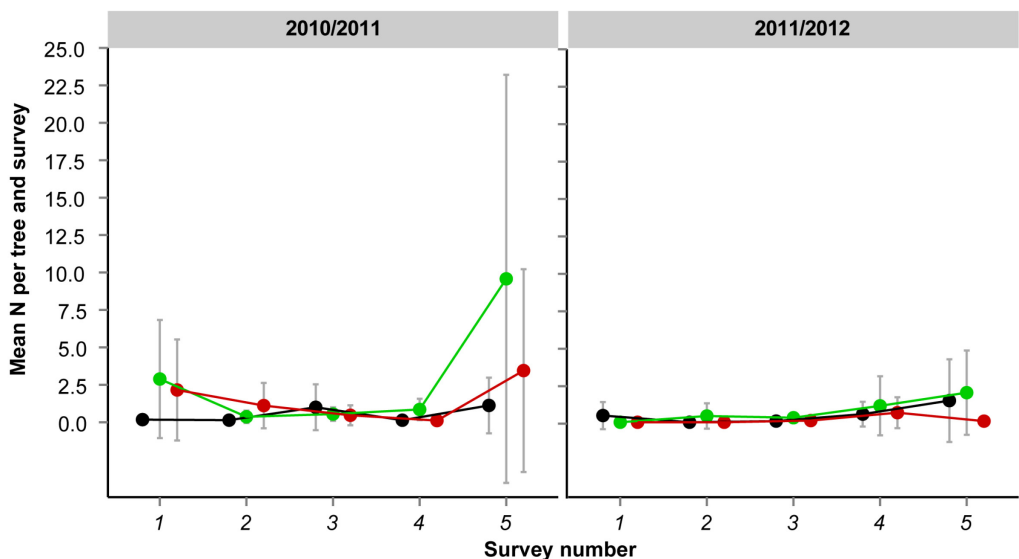
Appendix Figure C.3 Mean abundance and dry weight of the three dominant Hemipteran species as a function of habitat and recording period, respectively. Whiskers correspond to a 95% confidence interval, and * symbols represent the significance level of the term based on associated GLMM analysis (see Table 2.3 and Table 2.4).

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'; non-significant 'n.s.'

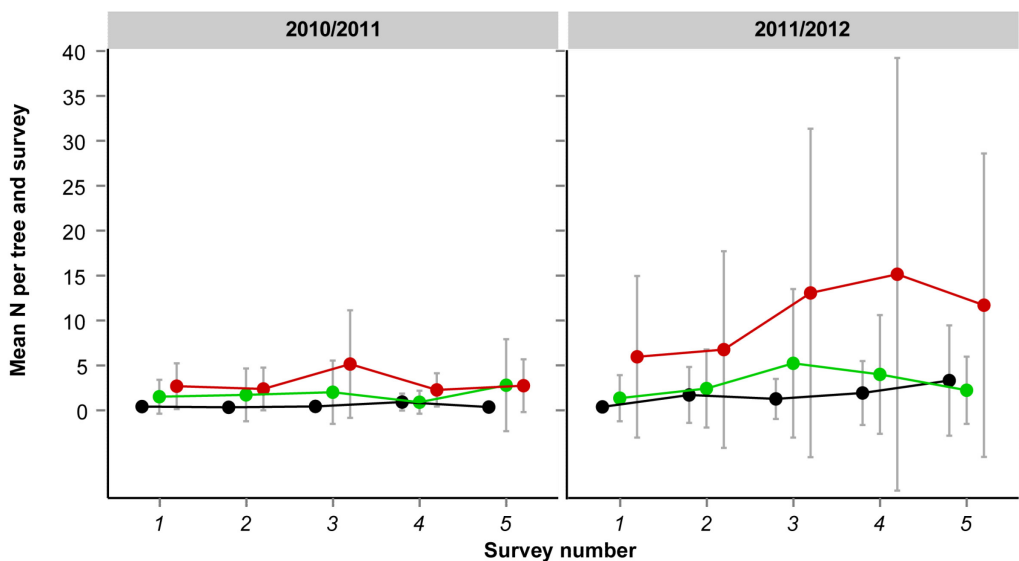
Cicadellidae sp.
(host-specific to *T. chrysantha*)



Psyllidae sp.
(host-specific to *C. montana*)



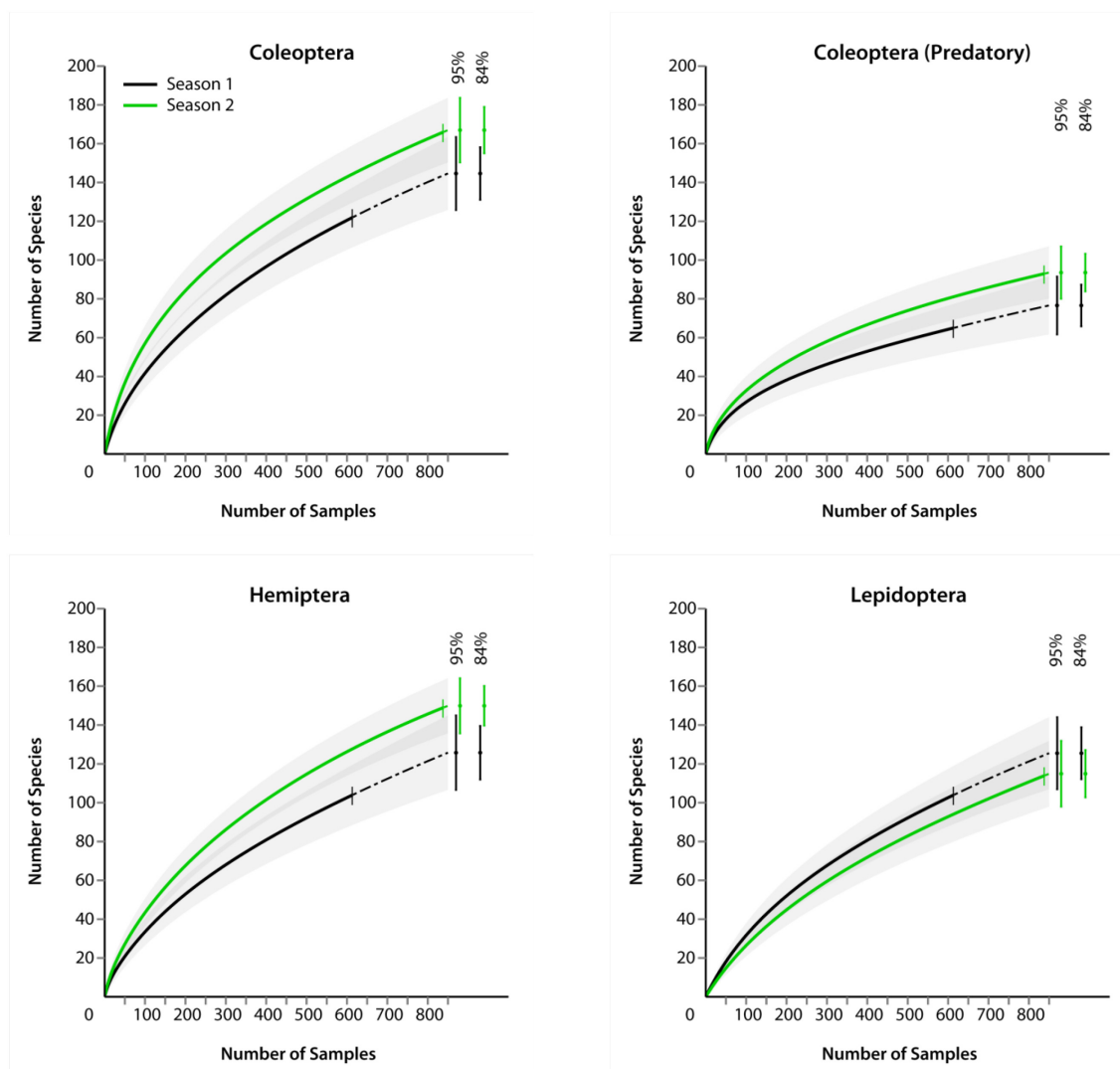
Tingidae sp.
(host-specific to *H. americanus*)



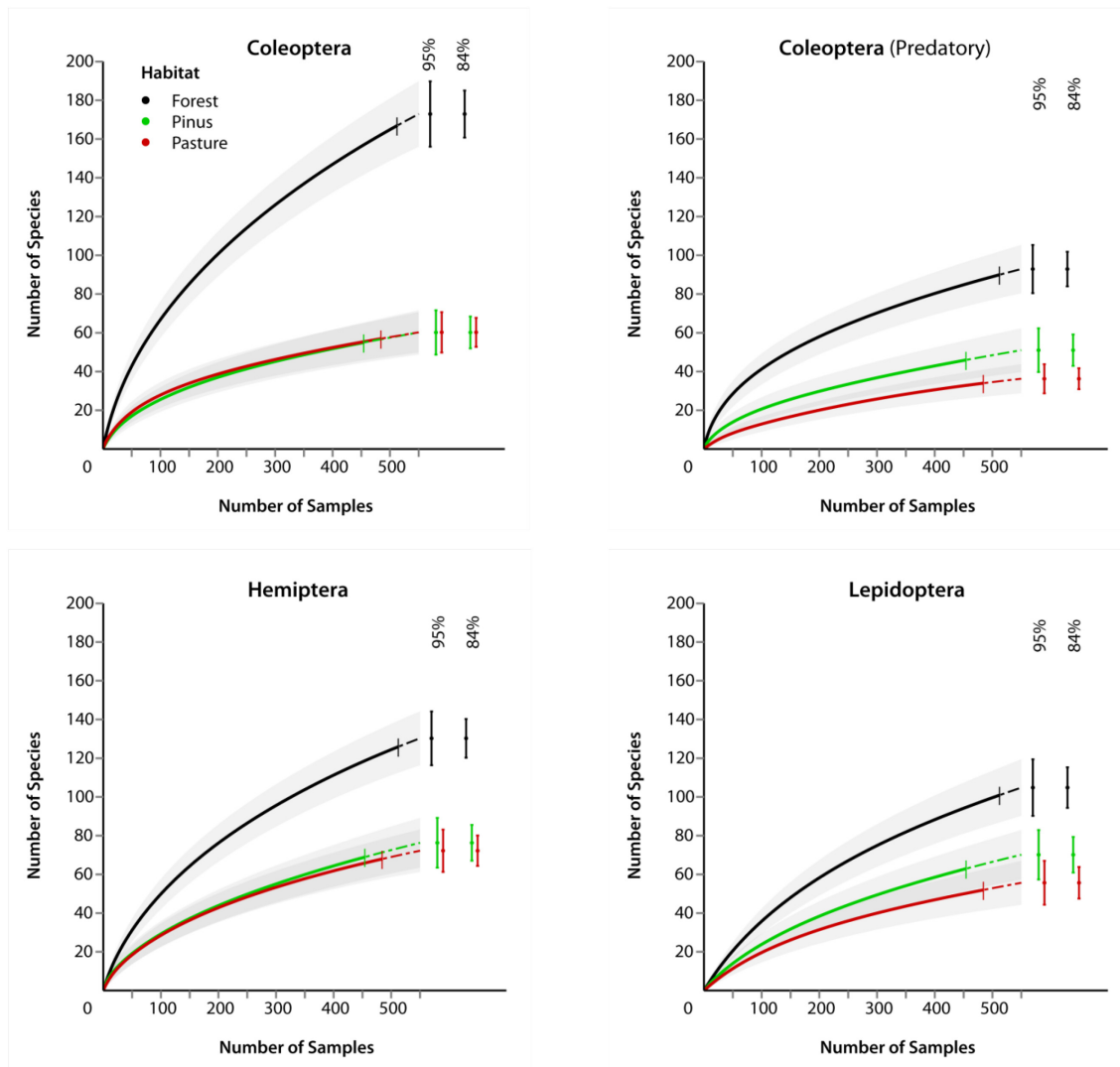
Appendix Figure C.4 Mean abundances for the dominant Hemiptera species per sample tree by habitat, year and survey. Points represent means and the corresponding error bars a 95% confidence interval.

Appendix D

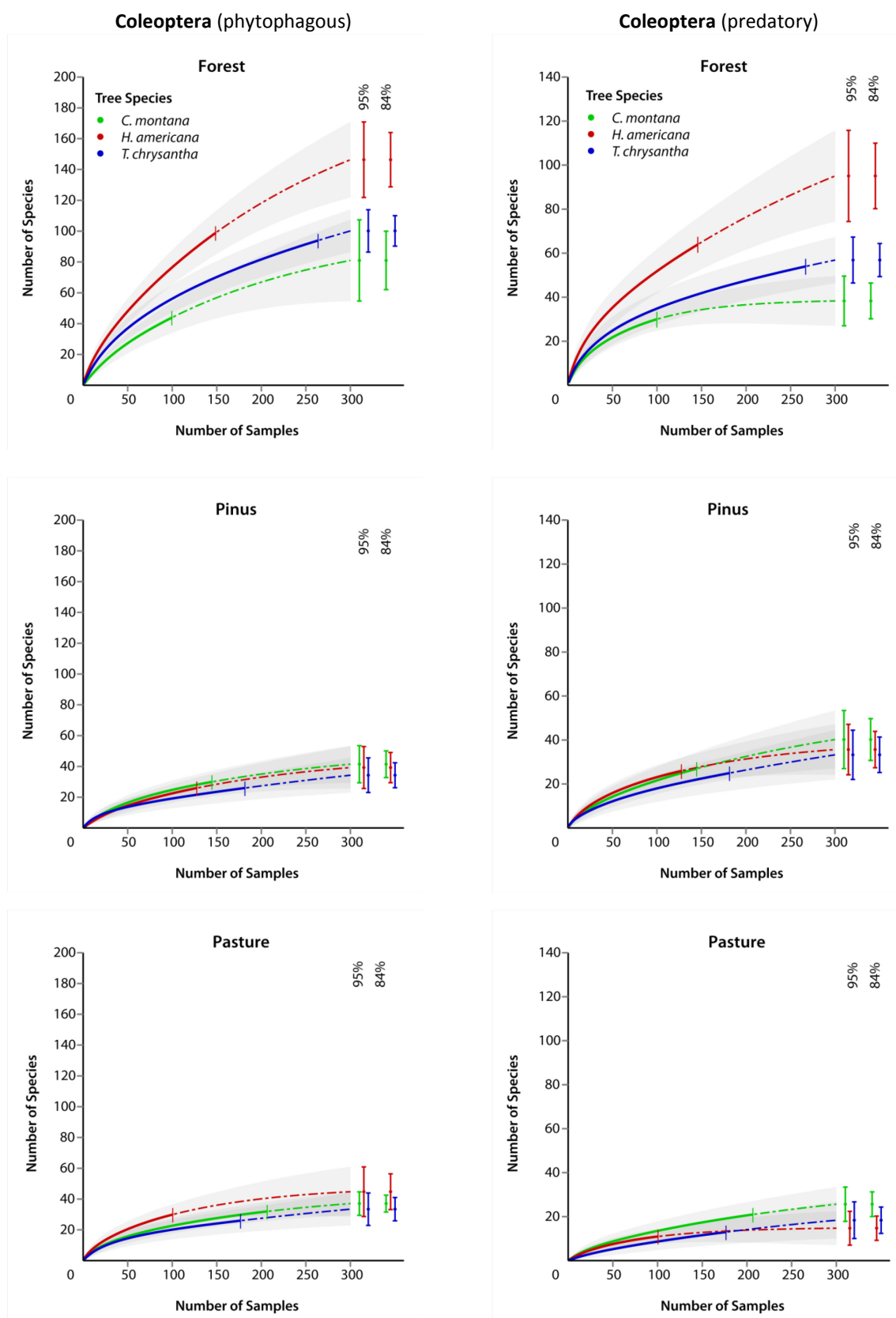
Species accumulation curves (supplementary)



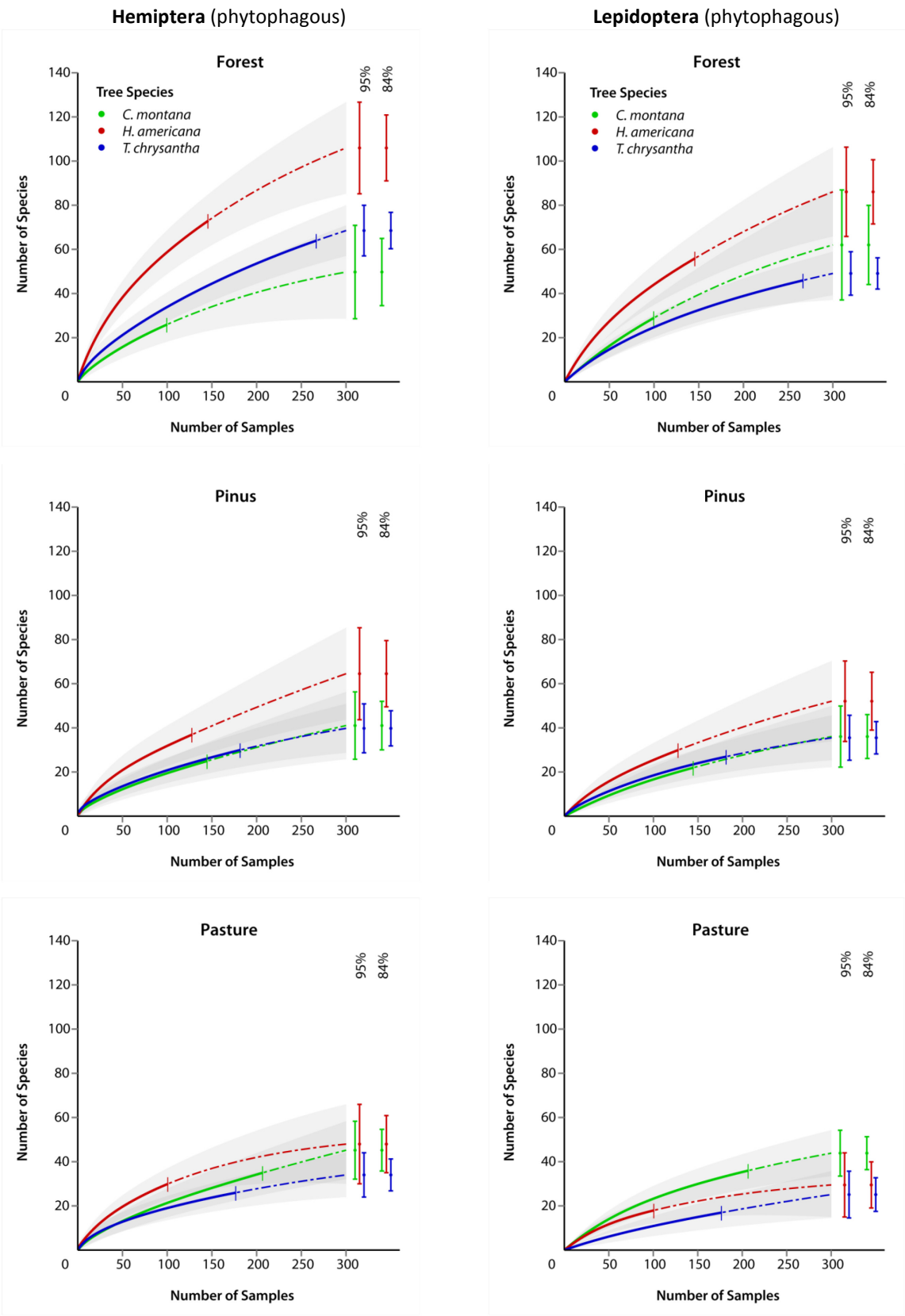
Appendix Figure D.1 Extrapolation of sample-based species accumulation curves by recording period for phytophagous Coleoptera, Hemiptera and Lepidoptera, as well as for predatory Coleoptera. Calculations were based on a reduced dataset, including all three host tree species, but excluding treelets from the shrub habitat. Solid lines: actual extent of sampling; dotted lines: extrapolation; shaded fractions: 95% confidence intervals (Ci). Left whisker plots give a conservative 95% Ci, right plots give an 84% Ci (Payton *et al.*, 2003). Non-overlap of confidence intervals implies significant differences.



Appendix Figure D.2 Extrapolation of sample-based species accumulation curves by habitat based on all three sample tree species (excluding ‘Shrub’ sites) for phytophagous Coleoptera, Hemiptera and Lepidoptera, as well as for predatory Coleoptera. Solid lines: actual extent of sampling; dotted lines: extrapolation; shaded fractions: 95% confidence intervals (Ci). Left whisker plots give a conservative 95% Ci, right plots give an 84% Ci (Payton *et al.*, 2003). Non-overlap of confidence intervals implies significant differences.



Appendix Figure D.3 Extrapolation of sample-based species accumulation curves by habitat and tree species based on all three sample tree species (excluding ‘Shrub’ sites). Solid lines: actual extent of sampling; dotted lines: extrapolation; shaded fractions: 95% confidence intervals (Ci). Left whisker plots give a conservative 95% Ci, right plots give an 84% Ci (Payton *et al.*, 2003). Non-overlap of confidence intervals implies significant differences.



Appendix Figure D.3 (continued)

Appendix Table D.1 Rarefied and extrapolated species richness by habitat, tree species and survey period based on sample-based species accumulation curves 95% confidence intervals are given in brackets. Species accumulation as a function of habitat was calculated initially on the basis of only *H. americanus* and *T. chrysanthus* to allow accurate comparison between all four habitats ('*C. montana* excluded'). Calculations were then repeated on the basis of all three tree species, but excluding 'Shrub' habitat. Species richness across tree species and recording periods was likewise calculated excluding shrub habitat.

The given values correspond to the curves given in Figure 3.1, Figure 3.2, Appendix Figure D.1, and Appendix Figure D.2

		Rarefied			
		Coleoptera (phytophag.)	Coleoptera (predatory)	Hemiptera (phytophag.)	Lepidoptera (phytophag.)
<i>C. montana</i> excluded	Forest ^a	85.4 (± 10.2)	51.5 (± 8.9)	63.0 (± 8.5)	46.4 (± 7.9)
	Pinus ^a	27.5 (± 7.0)	13.1 (± 4.5)	36.9 (± 7.9)	31.8 (± 7.1)
	Pasture ^a	34.4 (± 6.5)	24.7 (± 6.5)	34.6 (± 5.7)	20.1 (± 5.6)
	Shrub ^a	17.0 (± 3.3)	10.0 (± 5.1)	25.0 (± 8.1)	15.0 (± 6.5)
Shrub habitat excluded	Forest ^b	157.1 (± 15.4)	85.2 (± 11.4)	118.8 (± 12.7)	94.7 (± 13.2)
	Pinus ^b	55.0 (± 10.3)	32.9 (± 6.7)	69.0 (± 11.5)	63.0 (± 11.3)
	Pasture ^b	55.4 (± 9.5)	46.0 (± 10.1)	65.9 (± 9.9)	50.2 (± 10.2)
	Shrub ^b	---	---	---	---
	<i>C. montana</i> ^c	79.6 (± 9.8)	51.7 (± 10.2)	65.7 (± 11.6)	65.5 (± 11.5)
	<i>H. americanus</i> ^c	126.0 (± 16.0)	74.0 (± 11.8)	104.0 (± 12.8)	82 (± 13.2)
	<i>T. chrysanthus</i> ^c	90.9 (± 11.4)	54.2 (± 9.4)	73.4 (± 10.2)	50.7 (± 9.7)
	Period 1 ^d	122.0 (± 15.4)	65.0 (± 12.3)	104.0 (± 15.5)	104.0 (± 15.0)
	Period 2 ^d	144.3 (± 14.7)	81.1 (± 11.9)	127.8 (± 12.4)	94.1 (± 14.1)
		Extrapolated			
		Coleoptera (phytophag.)	Coleoptera (predatory)	Hemiptera (phytophag.)	Lepidoptera (phytophag.)
<i>C. montana</i> excluded	Forest ^a	159.5 (± 15.4)	118.7 (± 12.9)	92.1 (± 13.5)	90.7 (± 12.9)
	Pinus ^a	49.7 (± 11.9)	71.6 (± 14.4)	64.7 (± 13.7)	44.8 (± 11.1)
	Pasture ^a	58.7 (± 11.1)	58.6 (± 9.9)	43.2 (± 12.1)	26.4 (± 9.1)
	Shrub ^a	20.4 (± 6.6)	52.9 (± 23.8)	35.7 (± 20.4)	20.9 (± 13.7)
Shrub habitat excluded	Forest ^b	164.9 (± 16.1)	124.5 (± 13.2)	99.6 (± 13.8)	89.0 (± 11.9)
	Pinus ^b	57.5 (± 10.8)	72.6 (± 12.1)	66.5 (± 12.0)	48.4 (± 10.6)
	Pasture ^b	57.8 (± 9.9)	69.0 (± 10.4)	52.9 (± 10.7)	34.6 (± 7.1)
	Shrub ^b	---	---	---	---
	<i>C. montana</i> ^c	101.5 (± 13.2)	92.8 (± 16.9)	93.0 (± 16.7)	69.1 (± 14.0)
	<i>H. americanus</i> ^c	169.4 (± 23.6)	134.5 (± 18.8)	112.2 (± 19.7)	97.1 (± 17.2)
	<i>T. chrysanthus</i> ^c	118.0 (± 14.0)	102.2 (± 13.4)	68.4 (± 12.5)	71.3 (± 11.7)
	Period 1 ^d	144.6 (± 18.8)	125.8 (± 19.2)	125.5 (± 18.6)	76.6 (± 14.9)
	Period 2 ^d	167.0 (± 16.6)	149.9 (± 14.2)	114.9 (± 16.9)	93.5 (± 13.4)

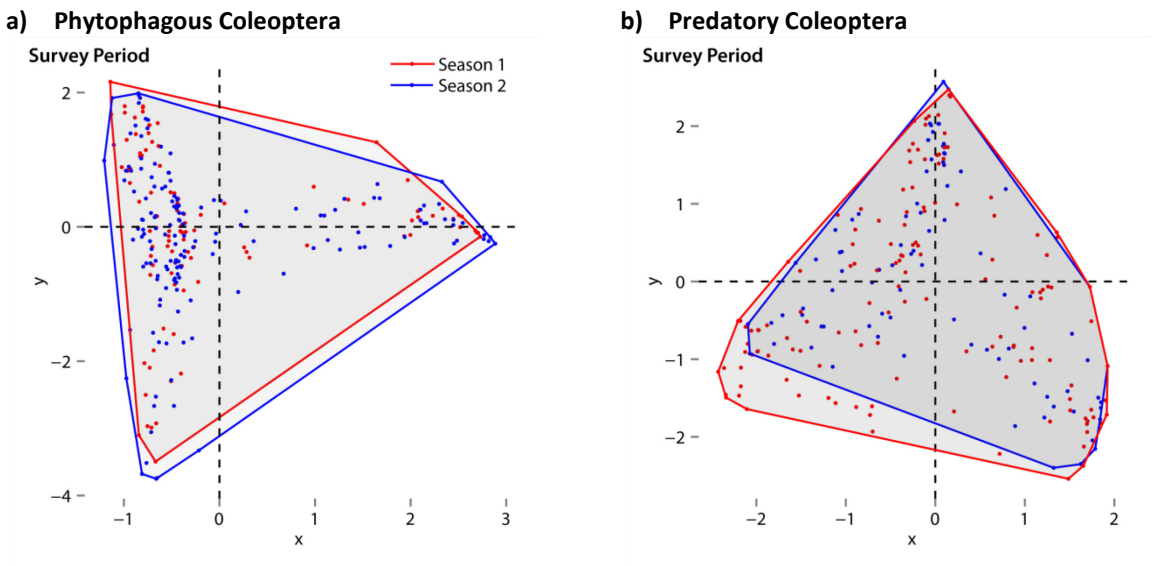
^a Rarefied: 141 samples; Extrapolated: 450 samples

^b Rarefied: 455 samples; Extrapolated: 500 samples

^c Rarefied: 375 samples; Extrapolated: 650 samples

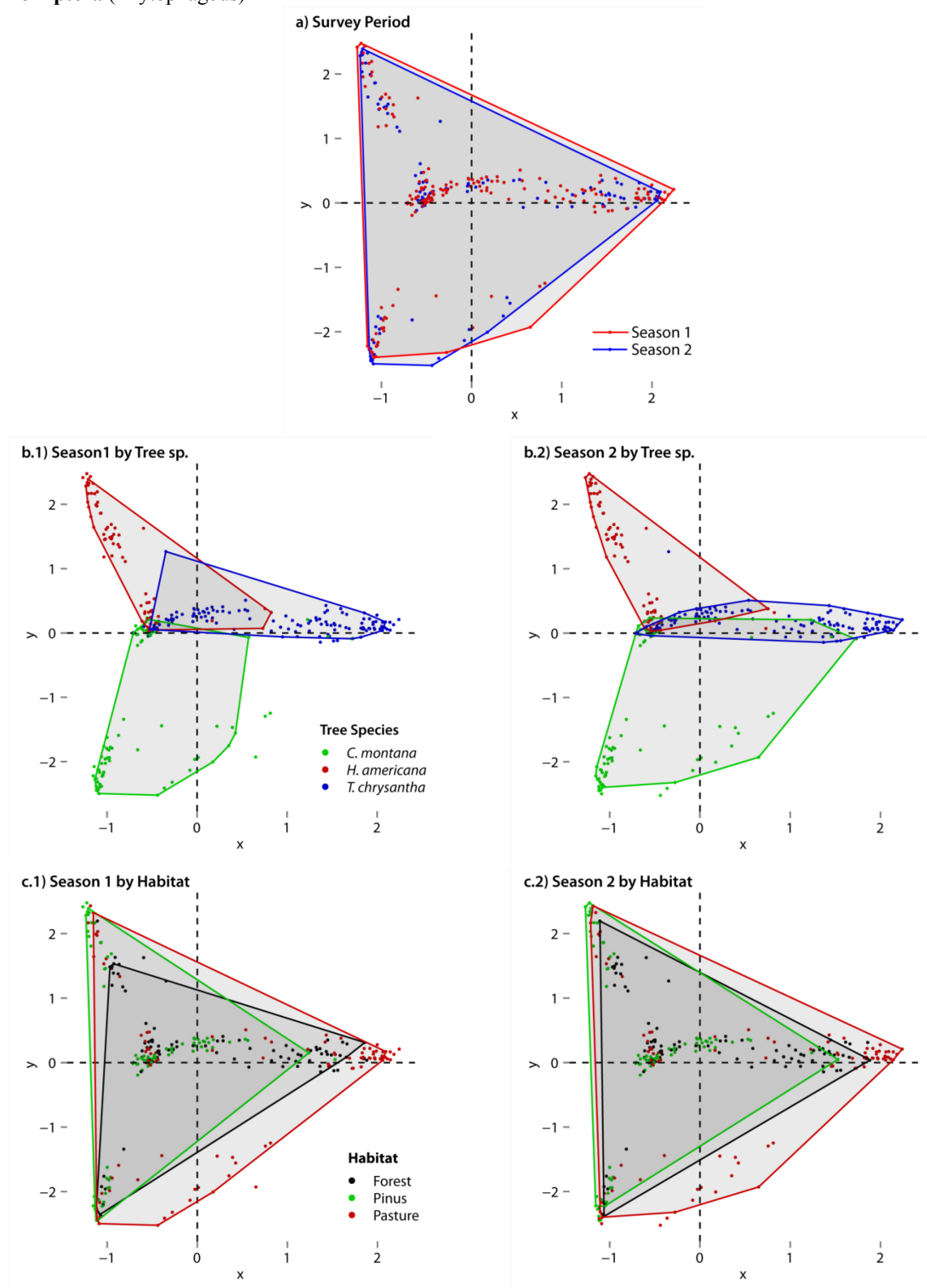
^d Rarefied: 614 samples; Extrapolated: 850 samples

Community composition (supplementary)

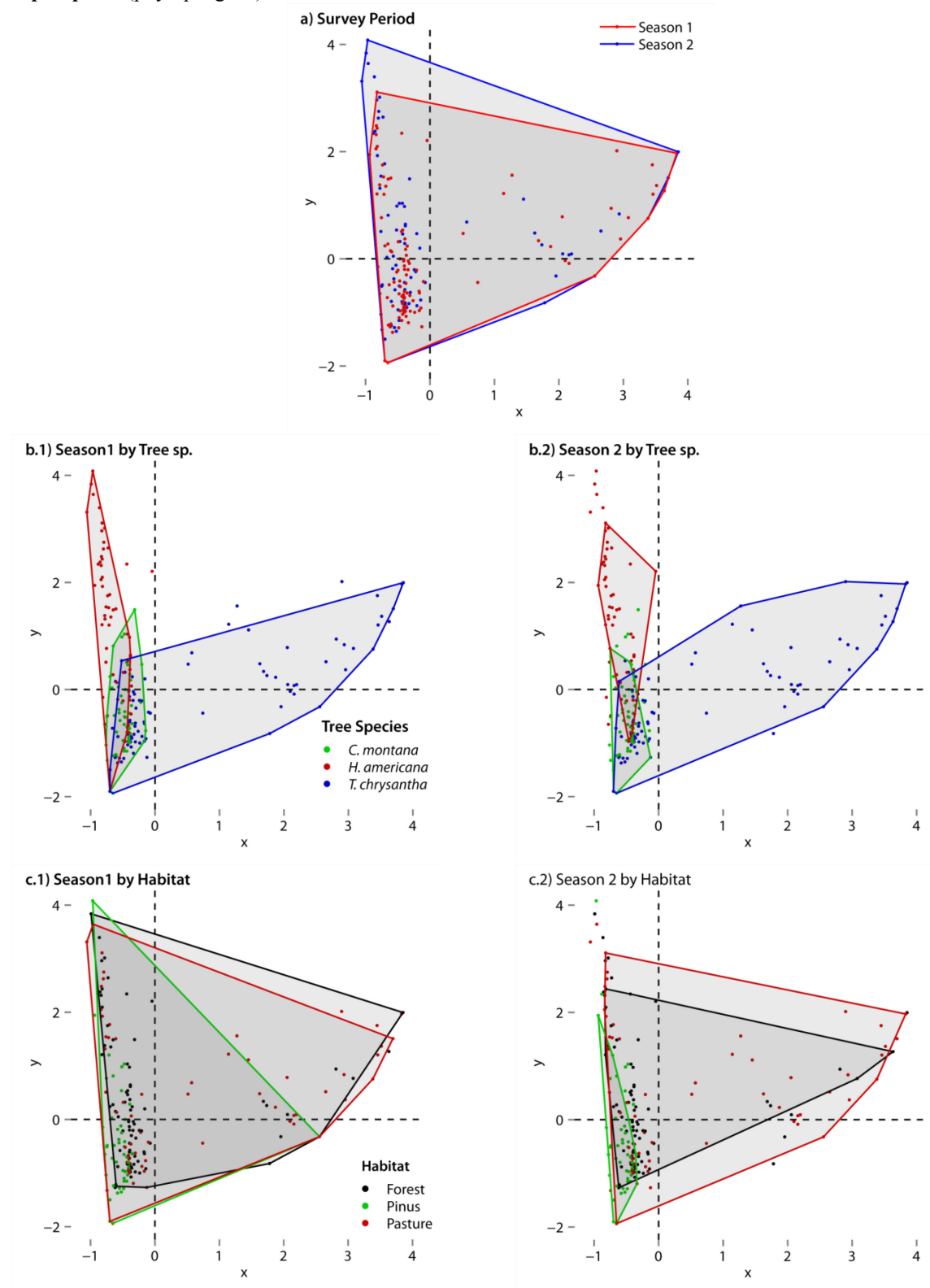


Appendix Figure D.4 Ordination plots for (a) phytophagous and (b) predatory Coleoptera by recording period. Graphs pertain to the best model distance-based redundancy analyses shown in Appendix Table D.2. Each symbol represents the fauna of one treelet.

Hemiptera (Phytophagous)



Appendix Figure D.5 Ordination plots for Hemiptera (complete dataset) as a function of recording period and its interaction with habitat and tree species. Graphs correspond to the outcome of the distance-based redundancy analyses shown in Appendix Table D.2. Each symbol represents the fauna of one treelet.

Lepidoptera (phytophagous)

Appendix Figure D.6 Ordination plots for Lepidoptera as a function of recording period and its interaction with habitat and tree species. Graphs correspond to the outcome of the distance-based redundancy analyses shown in Appendix Table D.2. Each symbol represents the fauna of one treelet.

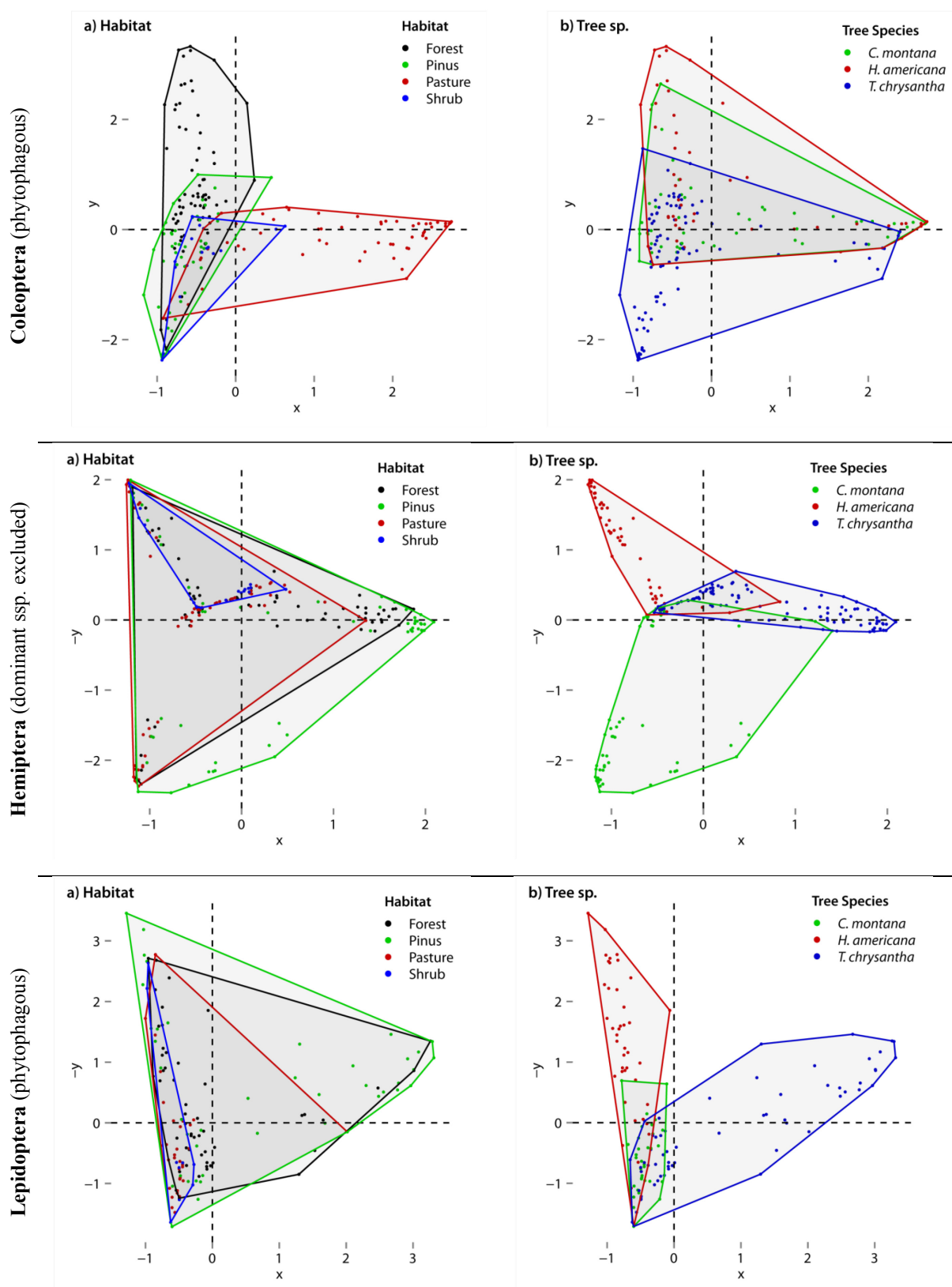
Appendix Table D.2 Distanced-based redundancy analysis including survey period as predictor variable. Data was aggregated per tree and survey period. Results are based on PERMANOVA (1000 permutations). The best model was determined by automated forward/backward model selection based on AIC. Model fit is given as adjusted R^2 .

Coleoptera (phytophagous)	Complete model					Best Model			AIC:
	df	Variance	F	p		Variance	F	p	1504.076
	Habitat	2	27.164	21.597	0.002 ***	27.164	21.577	0.001 ***	adj. R ² : 0.2043
	Tree sp.	2	9.649	7.671	0.002 ***	9.649	7.664	0.001 ***	
	Survey period	1	1.205	1.916	0.006 ***	1.205	1.914	0.007 **	
	Health	2	2.687	2.136	0.002 ***	2.687	2.134	0.001 ***	
	Leaf area	1	2.876	4.574	0.002	2.876	4.569	0.001 ***	
	Distance to 5 nearest neighbors	1	0.942	1.498	0.052	---	---	---	
	Height	1	0.931	1.480	0.056 ***	0.965	1.533	0.054 .	
	Habitat x								
	Survey period	2	1.496	1.190	0.170	---	---	---	
	Tree sp. x								
	Survey period	2	1.308	1.040	0.366	---	---	---	
	Habitat x Tree sp.	4	9.716	3.863	0.002	9.857	3.915	0.001 ***	
Habitat x Tree sp. x Survey period	4	2.254	0.896	0.758	---	---	---		
Residual	264	166.023			171.848				
Coleoptera (predatory)	Complete model					Best Model			AIC:
	df	Variance	F	P		Variance	F	p	1267.737
	Habitat	2	26.466	23.508	0.002 **	26.466	23.455	0.001 ***	adj. R ² : 0.2486
	Tree sp.	2	3.584	3.183	0.002 **	3.584	3.176	0.001 ***	
	Survey period	1	1.615	2.870	0.002 **	1.615	2.863	0.002 **	
	Health	2	1.183	1.051	0.350	---	---	---	
	Leaf area	1	2.276	4.044	0.002 **	2.211	3.919	0.001 ***	
	Distance to 5 nearest neighbors	1	1.26	2.238	0.012 *	1.337	2.370	0.004 **	
	Height	1	0.929	1.650	0.050 *	---	---	---	
	Habitat x								
	Survey period	2	2.149	1.909	0.004 **	2.152	1.907	0.007 **	
	Tree sp. x								
	Survey period	2	1.485	1.319	0.106	---	---	---	
	Habitat x Tree sp.	4	6.967	3.094	0.002 **	7.243	3.210	0.001 ***	
Habitat x Tree sp. x Survey period	4	2.067	0.918	0.608	---	---	---		
Residual	230	129.47			134.842				
Hemiptera (phytophagous)	Complete model					Best Model			AIC:
	df	Variance	F	p		Variance	F	p	1561.596
	Habitat	2	12.612	12.703	0.002 **	12.612	12.700	0.001 ***	adj. R ² : 0.2906
	Tree sp.	2	35.681	35.939	0.002 **	35.681	35.920	0.001 ***	
	Survey period	1	2.383	4.800	0.002 **	2.383	4.798	0.001 ***	
	Health	2	1.333	1.343	0.076 .	---	---	---	
	Leaf area	1	0.947	1.908	0.034 *	0.928	1.868	0.020 *	
	Distance to 5 nearest neighbors	1	0.875	1.763	0.024 *	---	---	---	
	Height	1	1.482	2.985	0.002 **	1.597	3.217	0.001 ***	
	Habitat x								
	Survey period	2	1.905	1.918	0.004 **	1.975	1.988	0.003 **	
	Tree sp. x								
	Survey period	2	2.815	2.836	0.002 **	2.984	3.005	0.001 ***	
	Habitat x Tree sp.	4	10.541	5.309	0.002 **	10.794	5.433	0.001 ***	
Habitat x Tree sp. x Survey period	4	2.659	1.339	0.056 .	2.726	1.372	0.026 *		
Residual	284	140.984			142.537				

Appendix Table D.2 (continued)

	df	Complete model					Best Model					AIC: 1188.716 adj. R ² : 0.0925
		Variance	F	p			Variance	F	p			
Lepidoptera (phytophagous)	Habitat	2	5.049	4.147	0.002	**	5.049	4.129	0.001	***		
	Tree sp.	2	6.879	5.651	0.002	**	6.879	5.625	0.001	***		
	Survey period	1	1.101	1.808	0.006	**	1.101	1.8	0.007	**		
	Health	2	1.449	1.191	0.104		1.449	1.185	0.095	.		
	Leaf area	1	1.222	2.008	0.002	**	1.222	1.999	0.002	**		
	Distance to 5 nearest neighbors	1	0.749	1.23	0.136		---	---	---			
	Height	1	0.748	1.229	0.142		---	---	---			
	Habitat x	2	1.801	1.48	0.008	**	1.805	1.476	0.004	**		
	Survey period	2	1.794	1.474	0.006	**	1.78	1.456	0.006	**		
	Tree sp. x	2	1.794	1.474	0.006	**	1.78	1.456	0.006	**		
	Survey period	2	1.794	1.474	0.006	**	1.78	1.456	0.006	**		
	Habitat x Tree sp.	4	5.092	2.092	0.002	**	5.151	2.106	0.001	***		
	Habitat x Tree sp. x Survey period	4	2.81	1.154	0.096	.	---	---	---			
	Residual	213	129.645				133.902					

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'



Appendix Figure D.7 Ordination plots with all singleton and doubleton insect species excluded. Graphs correspond to the outcome of the distance-based redundancy analyses shown in Appendix Table D.4. Only the main effects of habitat and tree species are shown for each group. Each symbol represents the fauna of an individual treelet.

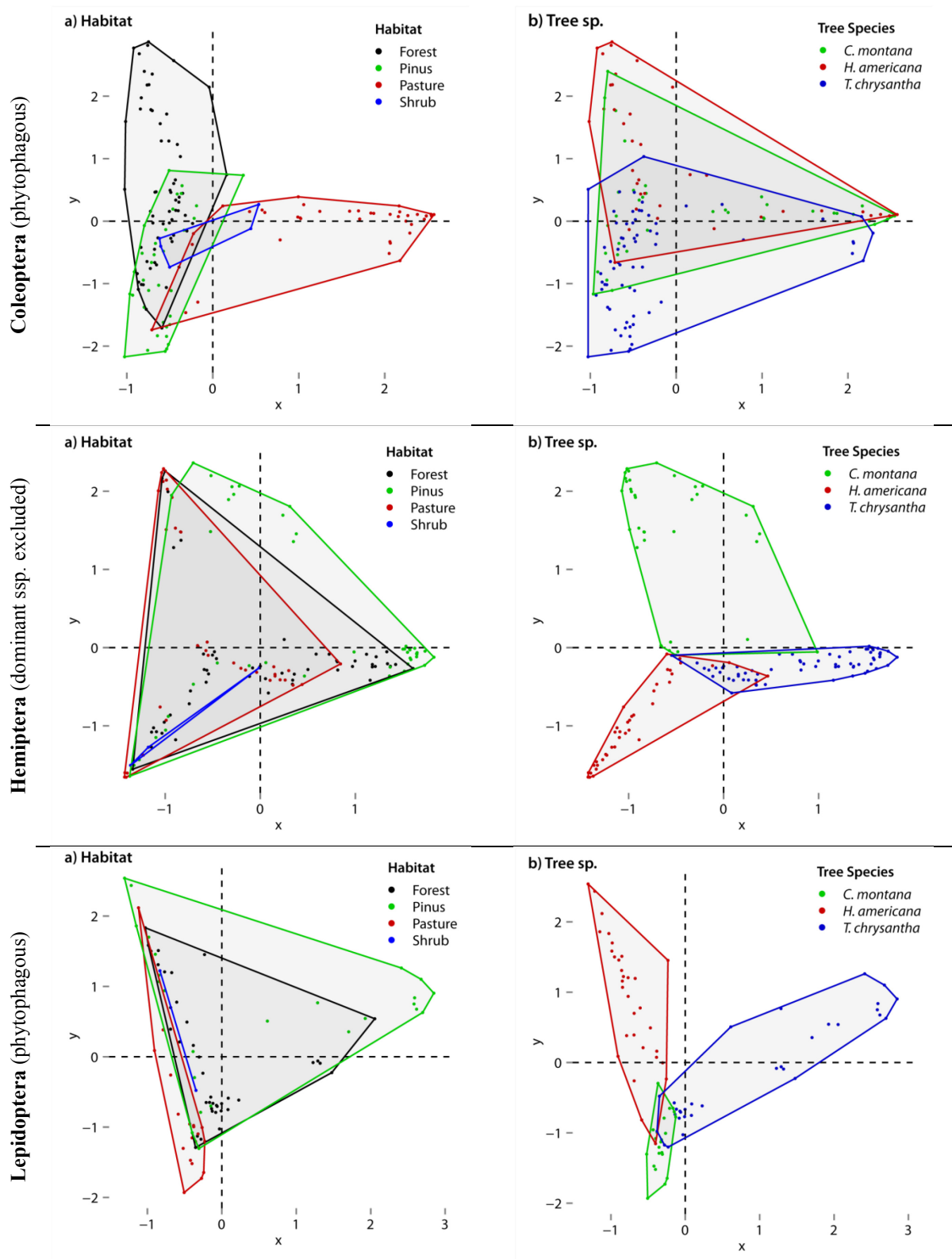
Appendix Table D.3 Number of sample trees when all single- and doubleton insect species are excluded. Treelets per habitat and species are given for phytophagous Coleoptera, phytophagous Hemiptera (dominant ssp. excluded), and phytophagous Lepidoptera (original species numbers: Coleoptera 208; Hemiptera 196; Lepidoptera 166).

		Total nr. of trees	Nr. or trees for phyt. Coleoptera	Nr. or trees for 'rare'. Hemiptera	Nr. or trees for phyt. Lepidoptera
Remaining Herbivore sp.		---	87	77	59
Forest	<i>C. montana</i>	12	12	11	11
	<i>H. americanus</i>	20	20	20	19
	<i>T. chrysantha</i>	38	38	37	29
	Total	70	70	68	59
Pasture	<i>C. montana</i>	28	25	26	22
	<i>H. americanus</i>	12	12	12	10
	<i>T. chrysantha</i>	30	26	30	13
	Total	70	63	68	45
Pinus	<i>C. montana</i>	20	19	20	12
	<i>H. americanus</i>	13	12	13	12
	<i>T. chrysantha</i>	24	23	24	24
	Total	57	54	57	48
Shrub	<i>H. americanus</i>	7	5	7	3
	<i>T. chrysantha</i>	19	14	14	6
	Total	26	19	21	9
Grand Total		223	206	214	161

Appendix Table D.4 Distanced-based redundancy analysis with singleton and doubleton species excluded. Data was aggregated per treelet. PERMANOVA (1000 permutations). The best model was determined by automated forward/backward model selection based on AIC. Model fit is given as adjusted R².

		Complete model					Best Model			AIC:
		df	Variance	F	p		Variance	F	p	
Coleoptera (phytophagous)	Habitat	3	23.800	12.845	0.001 ***		23.800	12.839	0.001 ***	1010.8720
	Tree sp.	2	8.196	6.635	0.001 ***		8.196	6.632	0.001 ***	adj. R ² : 0.2349
	Health	2	2.602	2.106	0.001 ***		2.604	2.107	0.001 ***	
	Leaf area	1	2.506	4.058	0.001 ***		2.505	4.053	0.001 ***	
	Distance to 5 nearest neighbors	1	0.750	1.214	0.242		---	---	---	
	Height	1	0.609	0.986	0.455		---	---	---	
	Habitat x Tree sp.	5	9.744	3.155	0.001 ***		9.810	3.175	0.001 ***	
	Residual	190	117.347				118.639			
Hemiptera (phytophagous)	Habitat	3	14.952	10.606	0.001 ***		14.952	10.582	0.001 ***	999.7224
	Tree sp.	2	32.388	34.459	0.001 ***		32.388	34.382	0.001 ***	adj. R ² : 0.3499
	Health	2	0.863	0.918	0.557		---	---	---	
	Leaf area	1	1.093	2.326	0.010 **		1.103	2.341	0.01 **	
	Distance to 5 nearest neighbors	1	1.085	2.308	0.011 *		1.092	2.317	0.013 *	
	Height	1	1.092	2.324	0.012 *		1.11	2.357	0.009 **	
	Habitat x Tree sp.	5	9.804	4.172	0.001 ***		9.481	4.026	0.001 ***	
	Residual	198	93.052				94.202			
Lepidoptera (phytophagous)	Habitat	3	6.498	3.550	0.001 ***		6.498	3.5543	0.001 ***	748.9064
	Tree sp.	2	7.092	5.812	0.001 ***		7.092	5.8185	0.001 ***	adj. R ² : 0.1267
	Health	2	0.885	0.726	0.949		---	---	---	
	Leaf area	1	1.099	1.801	0.011 *		---	---	---	
	Distance to 5 nearest neighbors	1	0.789	1.292	0.142		---	---	---	
	Height	1	0.817	1.339	0.092		1.116	1.8317	0.012 *	
	Habitat x Tree sp.	5	6.002	1.968	0.001 ***		6.139	2.0146	0.001 ***	
	Residual	145	88.472				90.809			

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.



Appendix Figure D.8 Ordination plots based on treelets with a community of three or more species. Graphs correspond to the outcome of the distance-based redundancy analyses shown in Appendix Table D.6. Only the main effects of habitat and tree species are shown for each group. Each symbol represents the fauna of an individual treelet.

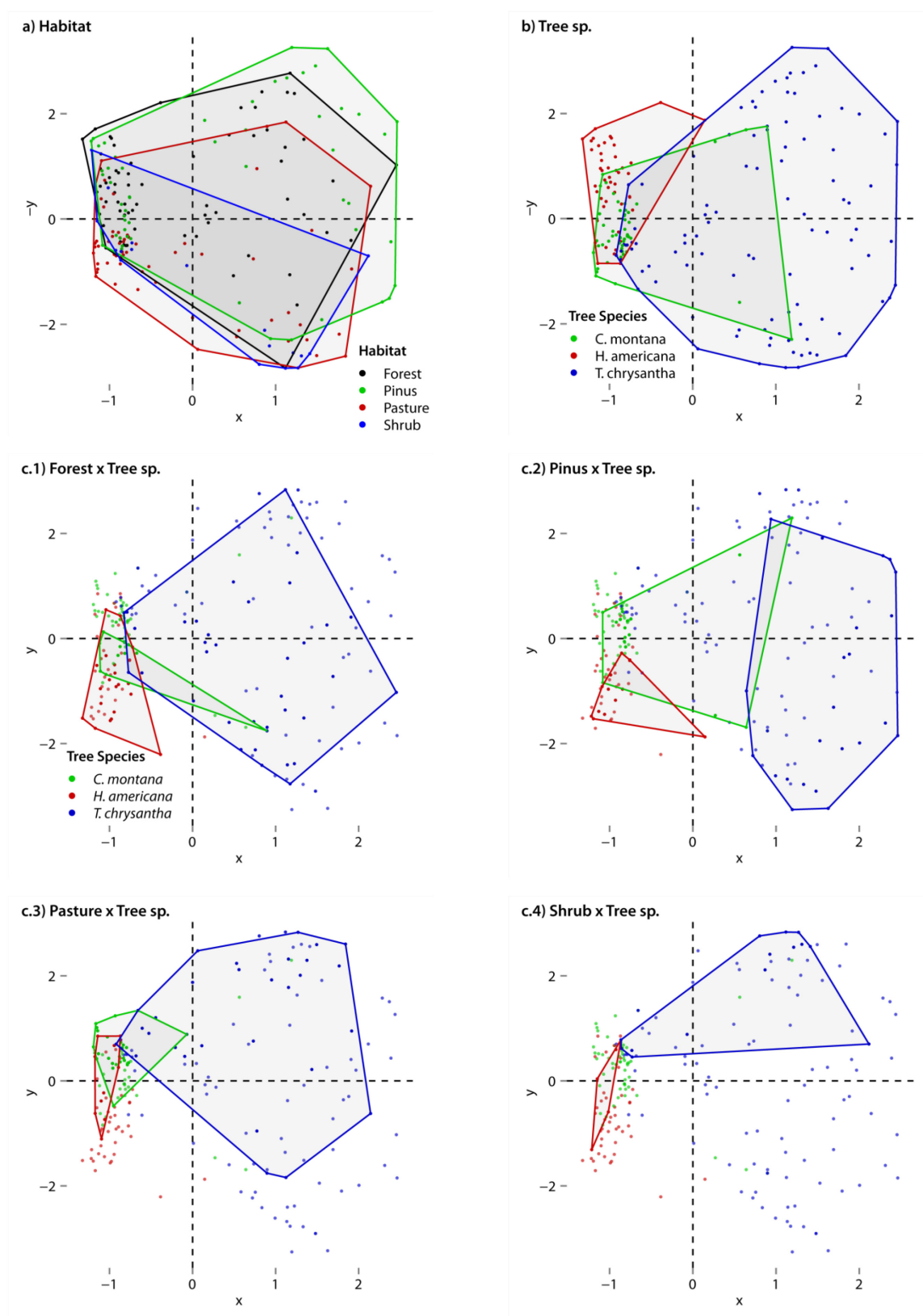
Appendix Table D.5 Number of sample trees hosting three or more species. Treelets per habitat and species are given for phytophagous Coleoptera, phytophagous Hemiptera (dominant ssp. excluded), and phytophagous Lepidoptera (original species numbers: Coleoptera 208; Hemiptera 196; Lepidoptera 166).

		Total nr. of trees	Nr. or trees for phyt. Coleoptera	Nr. or trees for 'rare'. Hemiptera	Nr. or trees for phyt. Lepidoptera
Remaining Herbivore sp.		---	206	187	141
Forest	<i>C. montana</i>	10	8	5	11
	<i>H. americanus</i>	19	17	16	19
	<i>T. chrysantha</i>	35	28	19	29
	Total	64	53	40	59
Pasture	<i>C. montana</i>	17	15	12	22
	<i>H. americanus</i>	9	8	6	10
	<i>T. chrysantha</i>	14	15	2	13
	Total	40	38	20	45
Pinus	<i>C. montana</i>	11	13	5	12
	<i>H. americanus</i>	9	12	9	12
	<i>T. chrysantha</i>	15	21	11	24
	Total	35	46	25	48
Shrub	<i>H. americanus</i>	1	2	1	3
	<i>T. chrysantha</i>	4	1	1	6
	Total	5	3	2	9
Grand Total		223	144	140	87

Appendix Table D.6 Distanced-based redundancy analysis based on treelets with a community of three or more species. Data was aggregated per treelet. PERMANOVA (1000 permutations). The best model was determined by automated forward/backward model selection based on AIC. Model fit is given as adjusted R^2 .

		Complete model					Best Model				AIC:	adj. R^2 :
		df	Variance	F	p		Variance	F	p			
Coleoptera (phytophagous)	Habitat	3	18.681	9.489	0.001	***	18.681	9.464	0.001	***	666.7507	
	Tree sp.	2	7.14	5.440	0.001	***	7.14	5.426	0.001	***		0.2297
	Health	2	2.356	1.795	0.003	**	2.356	1.791	0.002	**		
	Leaf area	1	0.732	1.116	0.322		---	---	---			
	Distance to 5 nearest neighbors	1	0.871	1.327	0.116		---	---	---			
	Height	1	0.687	1.046	0.388		---	---	---			
	Habitat x Tree sp.	5	7.687	2.343	0.001	***	7.783	2.366	0.001	***		
	Residual	128	84.002				86.196					
Hemiptera (phytophagous)	Habitat	3	9.295	6.222	0.001	***	9.295	6.186	0.001	***	606.3857	
	Tree sp.	2	25.135	25.237	0.001	***	25.135	25.091	0.001	***		0.3439
	Health	2	0.938	0.942	0.487		---	---	---			
	Leaf area	1	0.714	1.434	0.098	.	0.718	1.434	0.115			
	Distance to 5 nearest neighbors	1	0.794	1.594	0.081	.	---	---	---			
	Height	1	0.895	1.798	0.039	*	0.872	1.742	0.05	*		
	Habitat x Tree sp.	5	6.601	2.651	0.001	***	6.490	2.592	0.001	***		
	Residual	124	61.749				63.611					
Lepidoptera (phytophagous)	Habitat	3	4.856	2.298	0.001	***	4.856	2.302	0.001	***	367.9979	
	Tree sp.	2	5.226	3.71	0.001	***	5.226	3.715	0.001	***		0.1241
	Health	2	1.294	0.919	0.712		---	---	---			
	Leaf area	1	1.074	1.525	0.017	*	1.054	1.498	0.026	*		
	Distance to 5 nearest neighbors	1	0.837	1.189	0.161		---	---	---			
	Height	1	0.708	1.005	0.434		---	---	---			
	Habitat x Tree sp.	5	5.059	1.437	0.001	***	5.173	1.471	0.001	***		
	Residual	71	50.003				52.750					

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'

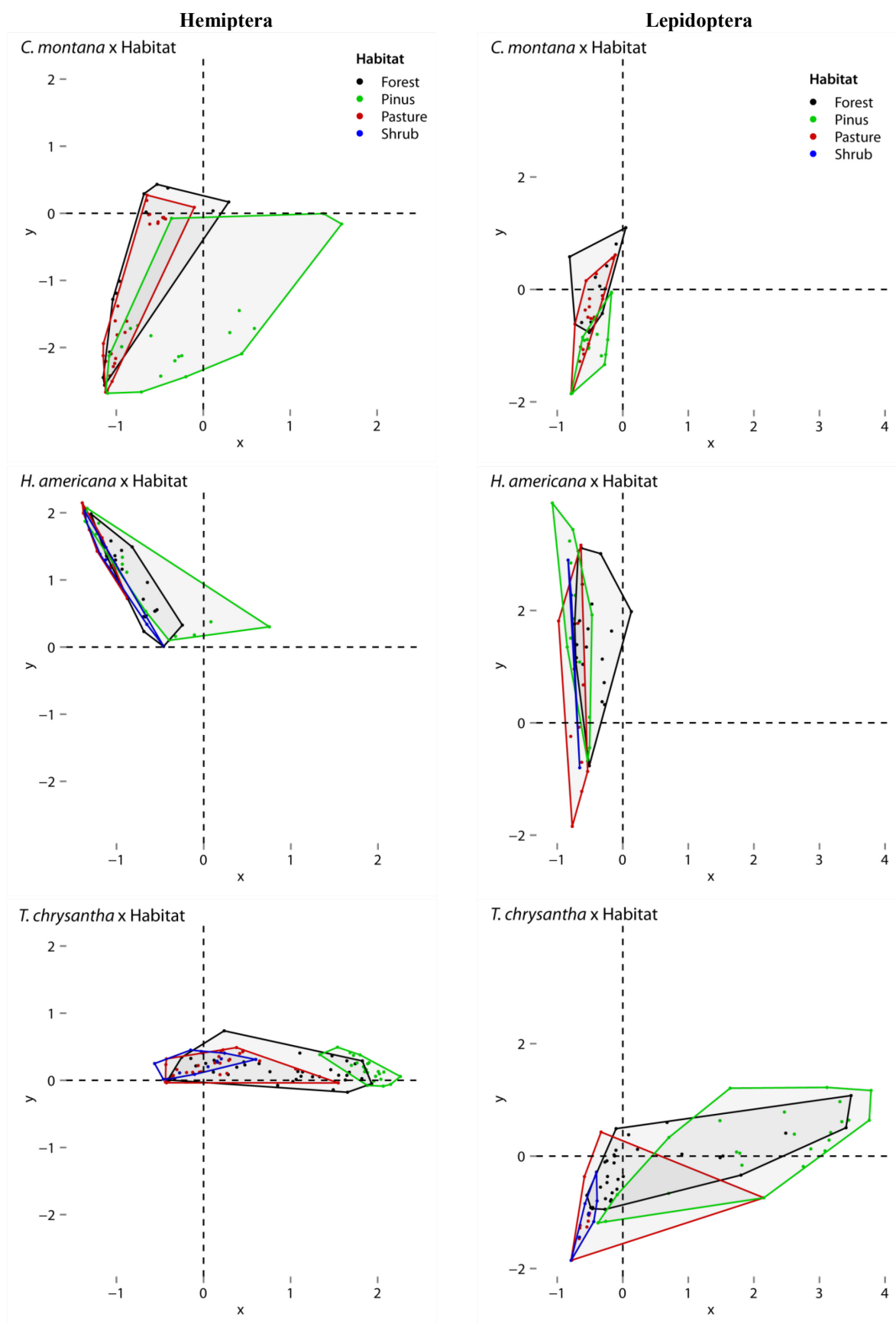


Appendix Figure D.9 Ordination plots for Hemiptera (dominant species excluded). Graphs correspond to the outcome of the distance-based redundancy analyses shown in Appendix Table D.7. The upper most diagrams highlight the effect of habitat (a) and tree species (b). The lower panels illustrate the interaction between habitat and tree species (c.1 to 4). Each symbol represents the fauna of one treelet.

Appendix Table D.7 Distanced-based redundancy analysis for less abundant Hemiptera. The three dominant taxa (i.e. Cicadellidae sp., Psyllidae sp., and Tingidae sp.) were excluded prior to calculation. Data were cubic root transformed and results are based on PERMANOVA (1000 permutations). The best model was determined by automated forward/backward model selection based on AIC. Model fit is given as adjusted R².

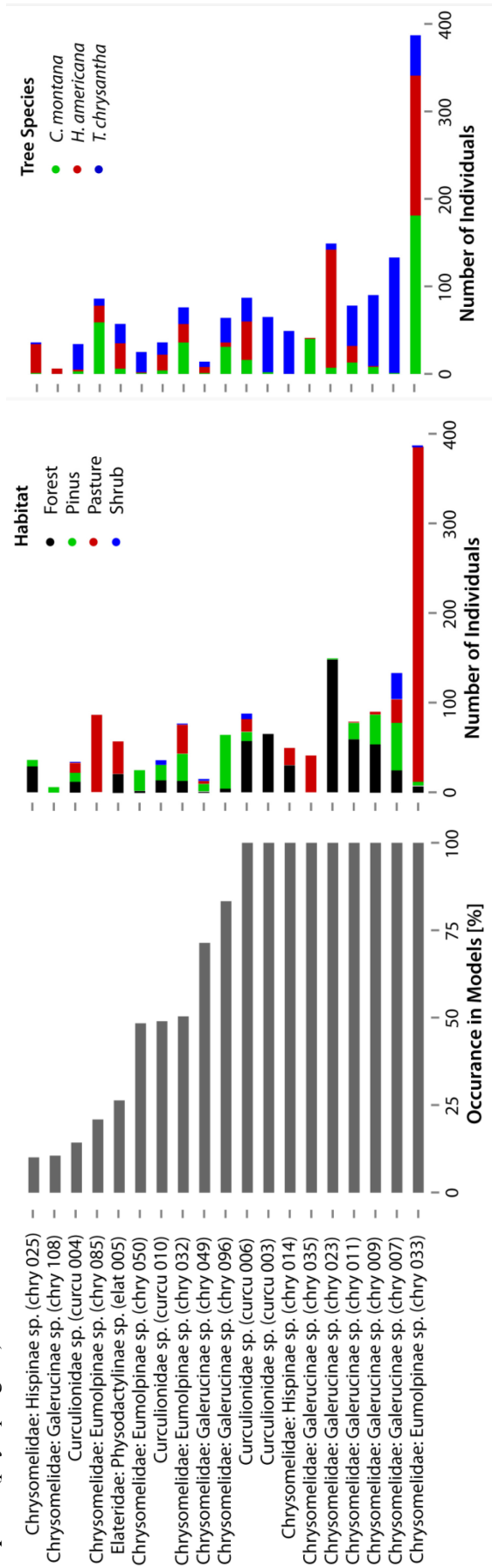
	Complete model					Best Model				AIC: 1034.7530 adj. R ² : 0.1638
	df	Variance	F	p		Variance	F	p		
Habitat	3	8.568	4.731	0.001	***	8.568	4.722	0.001	***	
Tree sp.	2	13.789	11.421	0.001	***	13.789	11.398	0.001	***	
Health	2	1.228	1.017	0.399		---	---	---		
Leaf area	1	1.601	2.653	0.001	***	1.615	2.670	0.001	***	
Distance to 5 nearest neighbors	1	1.585	2.625	0.001	***	1.530	2.530	0.001	***	
Height	1	0.544	0.902	0.575		---	---	---		
Habitat x Tree sp.	5	6.879	2.279	0.001	***	6.635	2.194	0.001	***	
Residual	195	117.713				119.769				

Significance codes: $p \leq 0.001$ '***'; $p \leq 0.01$ '**'; $p \leq 0.05$ '*'; $p \leq 0.1$ '.'

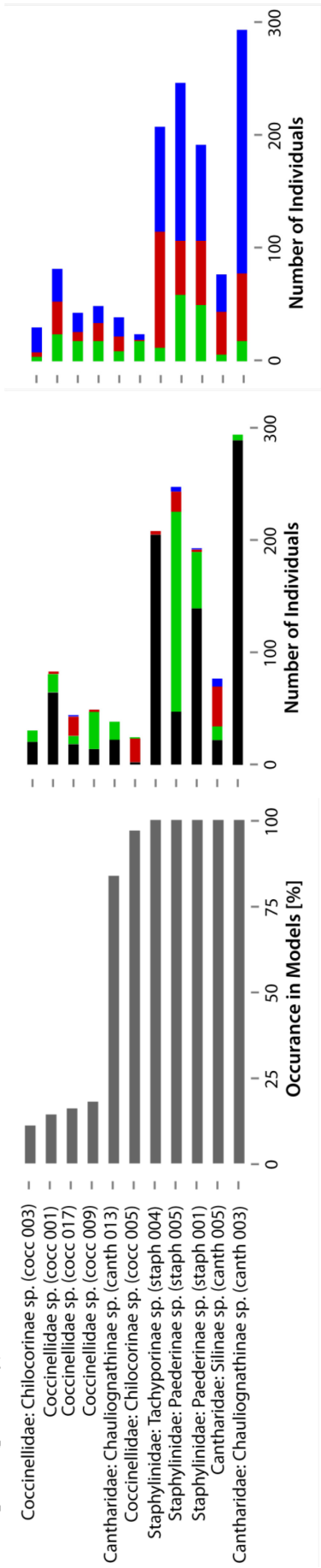


Appendix Figure D.10 Ordination plots for Hemiptera and Lepidoptera as a function of the interaction between habitat and tree species. Graphs correspond to the outcome of the distance-based redundancy analyses shown in Table 3.3. Each symbol represents the fauna of one treelet.

Coleoptera (phytophagous)

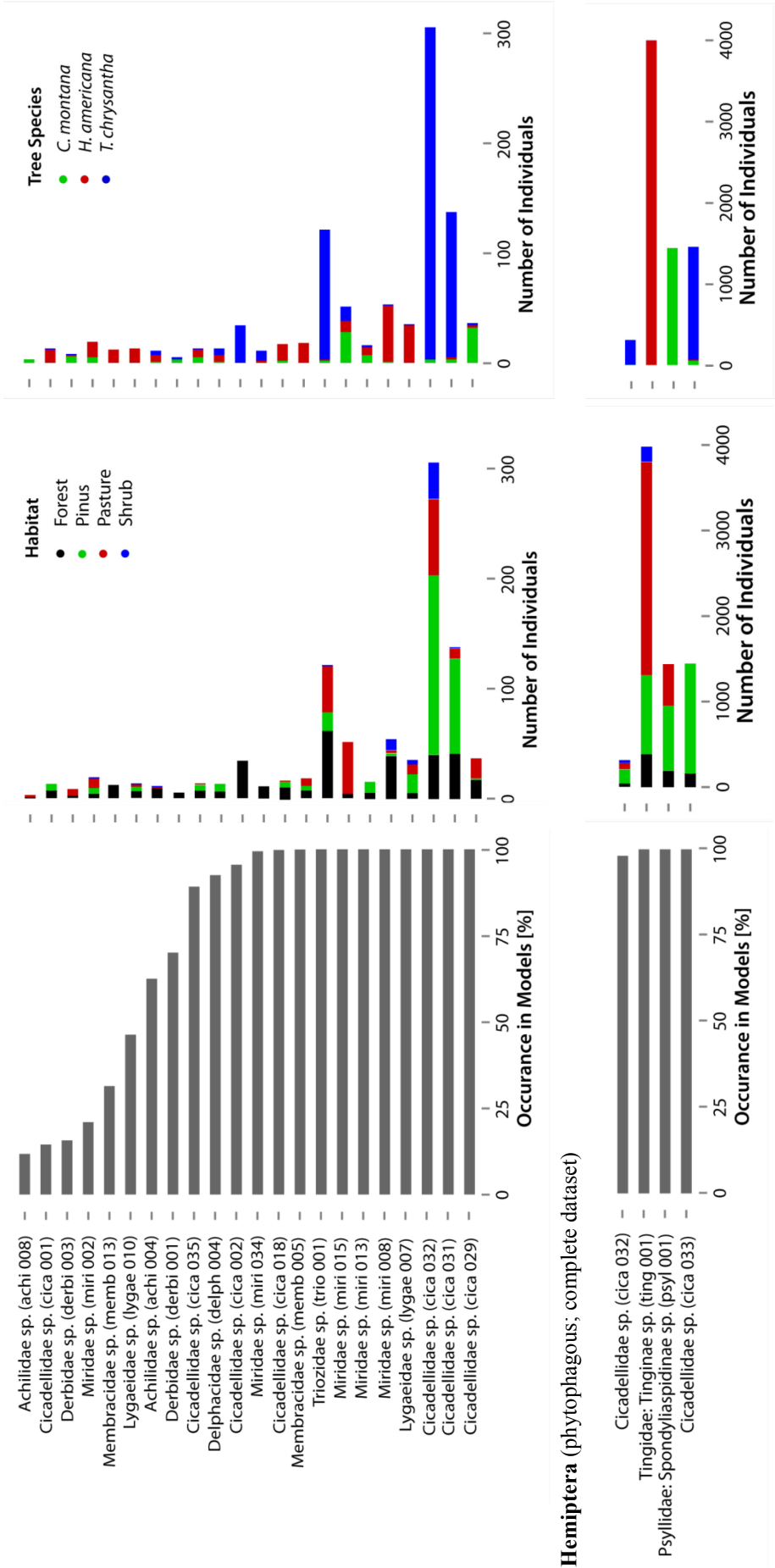


Coleoptera (predatory)

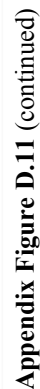


Appendix Figure D.11 The principal species underlying the patterns observed in distance-based redundancy analysis. Selection is based on matrix correlation between the complete data and randomly selected subsets of species as implemented in the bvstep function (2500 iterations; Spearman's $\rho = 0.9$). The first column shows the percentage of subsets that include a given species. The second and third columns display the abundance of the species in question, subdivided by habitat and tree species, respectively. Only species that occurred in more than 10% of subsets are presented here.

Hemiptera (phytophagous; Cicadellidae: Cica033,Psyllidae: Psyl001, and Tingidae: Ting001 excluded)



Appendix Figure D.11 (continued)



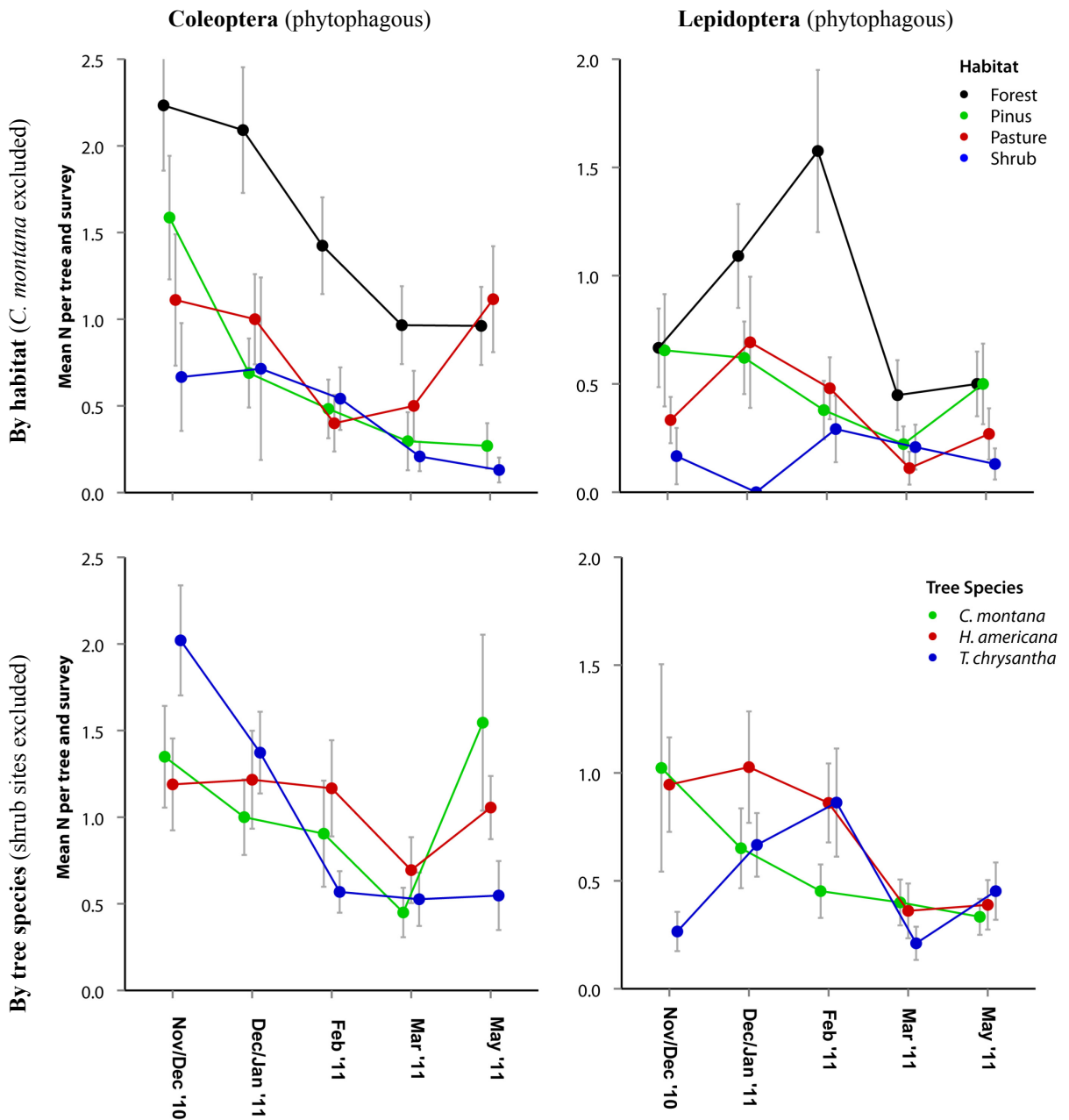
Appendix E

Appendix Table E.1 Abundance of chewing herbivores on *H. americanus* during the first five surveys. Morphospecies that were represented with more than 15 individuals in the dataset are listed individually, all others are aggregated on family level.

Family	Subfamily	Morphosp.	Forest					Pinus					Pasture					Shrub				
			1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Coleoptera Total			73	77	53	29	30	60	31	22	15	10	68	50	34	19	72	16	15	13	5	3
Cerambycidae Total			---	1	2	---	1	---	---	---	---	---	---	4	---	---	2	---	---	---	---	---
Chrysomelidae Total			49	52	34	19	19	51	23	20	8	9	56	39	26	18	66	13	12	6	3	1
Eumolpinae	Chry032		---	1	---	1	1	10	4	2	---	1	2	3	8	2	3	---	1	---	---	---
Eumolpinae	Chry033		---	1	---	---	---	---	---	---	---	2	14	15	4	16	57	---	---	---	---	---
Galerucinae	Chry007		2	3	---	1	1	22	2	2	2	---	8	3	---	---	---	11	10	3	---	1
Galerucinae	Chry009		1	6	---	1	1	1	5	1	---	---	---	---	---	---	---	---	---	---	---	---
Galerucinae	Chry023		6	12	7	4	3	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Galerucinae	Chry035		---	---	---	---	---	---	---	---	---	---	17	4	5	---	2	---	---	---	---	---
Galerucinae	Chry096		---	1	---	---	---	5	4	5	5	3	---	---	---	---	---	---	---	---	---	---
Hispininae	Chry014		9	3	2	1	---	---	---	---	---	---	9	8	2	---	---	---	---	---	---	---
Curculionidae Total			20	22	14	7	6	7	8	2	7	1	10	4	3	1	1	1	1	7	2	2
indet.	Curcu006		2	6	1	4	---	---	1	---	---	---	3	1	---	---	---	1	1	4	---	---
indet.	Curcu010		3	2	1	---	---	3	6	---	3	---	---	---	---	---	---	---	---	3	2	---
Elateridae Total			4	2	3	3	4	2	---	---	---	---	1	3	5	---	3	1	2	---	---	---
Physodactylinae	Elat005		---	1	3	1	---	---	---	---	---	---	---	3	5	---	3	---	---	---	---	---
Scarabaeidae Total			---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Lepidoptera Total			42	38	37	16	17	22	23	15	11	15	29	36	20	10	12	4	0	7	5	3
Bombycidae Total			3	4	2	---	---	2	---	---	---	---	---	---	2	---	---	---	---	---	---	---
Bucculatricidae Total			19	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Choreutidae Total			19	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
indet.	Chor001		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
Elachistidae Total			1	---	---	---	---	1	---	---	---	---	12	10	---	---	---	---	---	---	---	---
Stenomatinae	Elach001		---	---	---	---	---	1	---	---	---	---	12	9	---	---	---	---	---	---	---	---
Erebidae Total			3	4	7	2	7	---	1	1	---	1	---	---	1	1	---	---	---	---	---	---
Gelechiidae Total			2	8	8	1	1	4	10	2	1	7	1	5	1	---	---	---	---	---	---	---
indet.	Gele001		---	4	7	1	1	1	6	---	1	7	1	---	---	---	---	---	---	---	---	---
indet.	Gele004		2	3	1	---	---	3	4	1	---	---	---	5	---	---	---	---	---	---	---	---
Geometridae Total			11	14	11	6	5	8	10	6	7	4	1	6	6	4	8	3	---	2	3	3
Hesperiidae Total			---	1	1	---	---	4	1	1	1	---	1	1	1	---	---	---	5	---	---	---
Pyrginae	Hesp001		---	1	1	---	---	4	1	1	1	---	1	1	1	---	---	---	---	5	---	---
Lycanidae Total			---	---	---	---	---	---	---	2	---	---	1	2	2	---	---	---	---	---	---	---
Noctuidae Total			1	1	3	1	2	1	---	1	1	1	---	---	1	1	1	---	---	---	2	---

Appendix Table E.1 (continued)

[illegible]



Appendix Figure E.1 Mean abundance of chewing herbivores per survey depending on habitat and tree species. Since there were no suitable *C. montana* sample trees on shrub-sites, graphs were generated based on reduced subsets, either excluding *C. montana* saplings or secondary shrub habitat, respectively. Whiskers represent the corresponding standard error of the mean.

Curriculum Vitae

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