School of Doctoral Studies in Biological Sciences

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# Ecological factors affecting the structure, diversity, and specialisation of caterpillar communities in forest ecosystems

Ph.D. Thesis

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## Annotation

The aim of the thesis was to explore how caterpillar assemblages are spatially, functionally, and taxonomically structured in temperate and tropical forest ecosystems. Firstly, we investigated to what extent caterpillar assemblages are vertically structured in a temperate forest in eastern North America. By using a comprehensive dataset of temperate forest sites across three continents, we further examined if distance metrics derived from plant phylogeny can be used to predict structural changes in caterpillar assemblages among co-occurring plants. We further studied if folivorous caterpillars associated with bamboo in an Ecuadorian montane rainforest can be considered as 'classical' herbivores (sensu stricto). In the last chapter, we introduce and compare plot-based sampling approaches to study interaction networks in forest ecosystems and provide comprehensive guidelines for replication in future studies.

## Declaration [in Czech]

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Carlo L. Seifert

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## List of papers, manuscripts, and statement of personal contribution

The thesis is based on the following papers and manuscripts:

**Chapter I** **Seifert CL,** Lamarre GPA, Volf M, Jorge LR, Miller SE, Wagner DL, Anderson-Teixeira KJ & Novotný V (2020) Vertical stratification of a temperate forest caterpillar community in eastern North America. *Oecologia*, 192, 501-514.

*Personal contribution:*

*Field work; Conceptualisation; Data analysis; Coordination of DNA sequencing efforts, Species identifications; Literature survey; Preparation of figures; Leading role in writing the manuscript.*

**Chapter II** **Seifert CL**, Volf M, Jorge LR, Abe T, Carscallen G, Drozd P, […] & Novotný V (Manuscript) Plant phylogeny structures arboreal caterpillar assemblages in temperate deciduous forests of three continents.

*Personal contribution:*

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**Chapter III** **Seifert CL**, Lehner L, Bodner F & Fiedler K (2016) Caterpillar assemblages on *Chusquea* bamboos in southern Ecuador: abundance, guild structure, and the influence of host plant quality. *Ecological Entomology*, 41, 698-706.

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**Chapter IV** Volf M, Klimeš P, Lamarre G, Redmond CM, **Seifert CL**, Abe T, […] & Novotný V (2019) Quantitative assessment of arthropod-plant interactions in forest canopies: a plot-based approach. *PLoS ONE*, 14, 1-20. https://doi.org/10.1371/journal.pone.0222119

*Personal contribution:*

*Co-leader of field work; Sampling of insect and plant material; Methodology, Data processing; Contribution in writing the manuscript.*

## Co-author agreement

**Vojtěch Novotný**, the supervisor of this Ph.D. thesis and senior author of chapters I, II & IV, fully acknowledges the major contribution of Carlo L. Seifert to these manucripts.

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prof. RNDr. Vojtěch Novotný, CSc.

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RNDr. Martin Volf, PhD

## Table of Contents

# ~ GENERAL INTRODUCTION ~

One of the most challenging tasks in current ecological research is to understand how local insect communities and their interaction networks are spatially and functionally structured. This may enable deeper insights into the underlying processes and determinants that shape patterns of species richness and specialisation as well as trophic interactions among sites, regions, and ecological gradients. Especially at a time of widely-reported decline in insect species and biomass around the globe (Bell et al. 2020, Montgomery et al. 2020, Wagner 2020), a fundamental knowledge about the mechanisms structuring insect communities can help to establish measures for effective and prosperous conservation management.

More than half of all insect species are associated with plants (Pierce 1995; and references therein) and represent a substantial fraction of global species diversity (e.g., Ødegaard et al. 2000, Wiens et al. 2015). Furthermore, phytophagous insects play an important role in ecosystem functioning as primary consumers (Metcalfe et al. 2014, McArt et al. 2013, Kristensen et al. 2019), prey for higher trophic levels (Kalka & Kalko 2005, Visser et al. 2006, Singer et al. 2017), as well as interaction partners in a variety of mutualistic relationships (Fiedler 2001, Janson et al. 2008, Hahn & Brühl 2016).

Among phytophagous insects, the order Lepidoptera is considered as one of the largest single radiations (Menken et al. 2010, Mitter et al. 2017), covering more than 157,000 validly described species (van Nieukerken et al. 2011). The total richness, however, is expected to be much higher with estimations ranging between 255,000 and 500,000 species worldwide (Kristensen et al. 2007). Furthermore, members of this speciose order can be found in nearly every region and habitat (Kristensen et al. 2007, Solis 2008). The close association with plants as a food source, high species richness, and ecological diversity as well as their widespread occurrence in most terrestrial ecosystems, makes the order Lepidoptera an ideal model organism group with which to investigate plant-herbivore interaction networks and assemblage characteristics in local and regional communities.

A large proportion of Lepidoptera species, if not the majority, is associated with forests, which cover approximately 30% of the world's terrestrial area (Pan et al. 2013). Plant traits, resource availability, resource specialisation, and vertical niche partitioning are considered important drivers of this outstanding diversity (Lewinsohn et al. 2005, Novotny & Basset 2005, Lewinsohn & Roslin 2008, Ashton et al. 2016). In this thesis, I study how caterpillar assemblages are spatially, functionally, and taxonomically structured in temperate and tropical forest ecosystems and discuss potential ecological and evolutionary factors driving these patterns.

## VERTICAL CHANGES IN FOREST CATERPILLAR ASSEMBLAGES – A HUGE KNOWLEDGE GAP

Forests represent complex three-dimensional ecosystems with changing biotic and abiotic conditions along the vertical axis, such as temperature, humidity, plant species composition, and foliage biomass (Ulyshen 2011, Nakamura et al. 2017). These vertical gradients further shape the structure and composition of arthropod communities (Basset et al. 2003, Floren & Schmidl 2008), and thus might play a key role in explaining the high diversity found in forest ecosystems due to spatial niche partitioning (Wardhaugh 2014, Nice et al. 2019).

Studies on the vertical stratification of caterpillars allow for deeper insights into how assemblages are spatially structured in local forest communities. This could yield information on the importance of different strata as development habitat for larval stages and in maintaining local species diversity. Additionally, the results might provide a baseline helping us to understand foraging and stratification patterns observed for their associated predators and parasitoids (Pearson 1971, Murakami 2002, Stireman et al. 2012, Di Giovanni et al. 2015).

Despite several studies investigating the stratification patterns of Lepidoptera assemblages in tropical (e.g., De Vries 1988, Brehm 2007, Ribeiro et al. 2016) and temperate forest ecosystems (e.g., Hacker & Müller 2008, Hirao et al. 2009, De Smedt et al. 2019), most of them focused on adults. Since immature stages develop in habitats that can substantially differ from those where the adults might be found (Schulze et al. 2001), knowledge about the vertical niche partitioning of caterpillars remains incomplete. Adults can be found in environments that do not provide the conditions for a successful larval development, especially during migration, while seeking a mate and food sources. In addition, bait and light traps were most often used to study vertical stratification in adult butterflies and moths. These methods, however, could easily be biased by attracting species into strata that they usually do not inhabit.

The few available studies on stratification patterns of caterpillar assemblages focused either on focal plant species (Wagner et al. 1995, Le Corff & Marquis 1999) or examined vertical changes in their parasitism (Connahs et al. 2011, Šigut et al. 2018). Despite contrary findings, they indicate, at least partially, that forest caterpillar assemblages are vertically structured in terms of density, composition, and diversity (Le Corff & Marquis 1999, Šigut et al. 2018). However, the presented information often differed, depending on the aim of the study, or revealed inconsistencies due to different sampling systems (i.e., target host plant species). This prevents general conclusions from being made and invokes further investigation.

## HOW PLANT TRAITS STRUCTURE CATERPILLAR ASSEMBLAGES

Properties of caterpillar assemblages such as density, richness, composition, and specialisation are unequally distributed within and among co-occurring plant species (Le Corff & Marquis 1999, Novotny et al. 2002b, Summerville et al. 2003, Šigut et al. 2018). Besides top-down control by natural enemies (Lill et al. 2002, Singer et al. 2012, Singer et al. 2017), bottom-up forces by plants are generally considered the main driver behind these variations (Campos et al. 2016, Vidal & Murphy 2018). Caterpillar assemblages are therefore structured by a range of plant traits which either act as defence mechanisms or influence insect development, fitness, and reproduction (Lill et al. 2009, Marquis & Lill 2010, Carmona et al. 2011, War et al 2018). These traits include defence mechanisms, nutritional quality (primary and secondary nutrients) as well as life history and plant architecture (Agrawal 2007, Carmona et al. 2011).

Due to their function as feeding deterrents or toxins, plant defences (e.g., secondary chemistry, latex, trichomes) are undoubtedly the most important traits structuring caterpillar assemblages (Agrawal & Fishbein 2006, Agrawal 2007). Pellissier et al. (2012), for instance, showed that butterfly assemblages at lower altitudes are more specialised than those found at higher elevations where plants are less well-defended. Further studies revealed that investment in defence mechanisms by plants negatively affected the abundance, density and richness of associated caterpillar assemblages (Diniz et al. 1999, Lill et al. 2009). In addition, several studies indicated that leaf manipulation by endophagous and shelter-building caterpillars allowed them to avoid chemical and physical plant defences (Cornell et al. 1989, Sandberg & Berenbaum 1989, Sagers 1992). Thus, variation in plant defences might further lead to changes in guild composition with lower proportions of exposed feeders on highly protected plants. While most defensive traits directly affect insect herbivores, some traits such as extrafloral nectaries and volatile organic compounds (VOCs) structure assemblages indirectly by attracting parasitoids and predators and thus strengthen top-down pressure (Diniz et al. 2012, Agrawal 2007).

Besides defence mechanisms, nutritional quality is another crucial parameter as it influences caterpillar development and performance. Caterpillars feeding on poor leaf quality plants need longer for development and thus are exposed to potential enemies for longer (Stamp & Bowers 1990, Coley et al. 2006, Bede et al. 2007). The positive correlation between host plant quality and caterpillar density was confirmed by various studies and seems to be a common pattern (e.g., Marquis & Lill 2010, Singer et al. 2012, Whitfeld et al. 2012). A study by Forbes et al. (2017) further indicated positive effects of specific nutrients on herbivore richness. These quality-dependent richness and abundance patterns could be partially explained by female oviposition preference (Baylis & Pierce 1991) and the fact that generalist caterpillar species tend to favour nutrient-rich plants (Lee et al. 2003). Further traits such as phenology, architecture, and a plant's ontogenetic stage were also shown to influence caterpillar assemblages (Marquis et al. 2002, Barrett & Agrawal 2004, Donaldson & Lindroth 2008, Carmona et al. 2011, Zvereva et al. 2014), generally because they reflect changes in plant defences and resource quality.

A range of plant traits, which were shown to structure caterpillar assemblages, are phylogenetically conserved, implying that trait similarity decreases with increasing phylogenetic distance of the plant species (Ackerly 2003, Agrawal 2007, Whitfeld et al. 2012, Davies et al. 2013). Thus, closely related plant species should affect herbivore assemblages in a more similar way than distantly related plant taxa (Ødegaard et al. 2005, Vialatte et al. 2010, Grandez-Rios et al. 2015). Phylogenetic metrics indicating the relationships among co-occurring plant species might therefore provide useful measures to predict the assemblage structure of a host plant's caterpillar fauna in local communities and across larger scales.

## FEEDING GUILDS AND SPECIALISATION IN CATERPILLARS

Caterpillar species associated with plants represent a variety of guilds based on their feeding habits. Generally, they can be either categorised as internal (endophages) or external feeders (ectophages; Cornell 1989). Internal feeders (i.e., miners, borers, gall-inducers) live and feed inside plant organs (e.g., leaves, twigs, fruits), whereas external feeders comprise all taxa that live on the plant surface. In exceptional cases, some Lepidoptera species switch between categories during their larval development (mostly from internal to external feeding mode; Gaston et al. 1991). External feeders, however, do not necessarily need to live without any physical protection. Many species, commonly termed as shelter-builders, roll leaves or tie them together; others for example live in webs or construct cases from both organic and inorganic material (Gaston et al. 1992). Thus, external feeders can be further divided into two guilds: shelter builders and exposed feeders. The latter ones represent the guild of truly free-living caterpillar species. Feeding guilds, however, do not only reflect species-specific foraging behaviours, rather they have profound ecological implications. Shelters, for instance, protect against predation (Damman 1987, Connor & Taverner 1997, Tvardikova & Novotny 2012) and harsh environmental conditions by generating a beneficial microclimate (Henson 1958, Larsson et al. 1997, Fukui 2001). Shelter-building behaviour can further improve host plant quality by lowering chemical and physical defences (Sagers 1992). Because of their higher mobility, exposed feeders, in contrast, could optimize their diet by selective foraging, and lower their parasitism and predation rates by resting some distance away from the feeding site (Heinrich 1979). These differences between exposed feeders and shelter builders lead to guild-specific patterns in diet breadth, diversity, and composition (Menken et al. 2010, Connahs et al. 2011, Diniz et al. 2012, Hrcek et al. 2013). Shelter builders, for instance, were shown to be generally more specialised than exposed feeders (Gaston et al. 1992, Menken et al. 2010). Furthermore, shelter builders often represent the dominant feeding guild in local assemblages (Diniz et al. 2012, Hrcek et al. 2013), although this pattern is not always consistent (see for example Šigut et al. 2018). This underpins the need to treat and analyse feeding guilds separately when investigating assemblage structure and specialisation patterns of plant-caterpillar networks. Nevertheless, despite the general differences in specialisation patterns among exposed feeders and shelter builders, there is also high variability in diet breadth among species within individual feeding guilds.

Host plant specialisation is considered one of the most important drivers of the high diversity found in herbivorous insects. However, herbivore specialisation can be measured in various ways and many indices have been developed. While early indices were simple counts of host species, genera, or families that an insect species utilises, more advanced indices account fully, or at least partially, for host plant phylogeny, interaction strength, and resource availability (e.g., Symons & Beccaloni 1999, Blüthgen et al. 2006, Jorge et al. 2014). Some of these indices have become very popular and lend a more realistic perspective on specialisation patterns in herbivore assemblages.

It is assumed that increased specialisation leads to more finely partitioned food resources which in turn allows more herbivore species to coexist (Lewinsohn & Roslin 2008). Furthermore, evidence was found that host shifts followed by subsequent specialisation promotes speciation in Lepidoptera (Janz et al. 2006, Janz & Nylin 2008, Fordyce 2010). Thus, one would expect caterpillar assemblages to be more diverse the narrower their diet breadth. Indeed, several attempts have been made to investigate whether increased species richness in caterpillar assemblages is a result of overall higher specialisation or caused by greater resource diversity (e.g., Novotny et al. 2002a, Novotny et al. 2006, Dyer et al. 2007, Pellissier et al. 2012, Forister et al. 2015). While some of those studies revealed a positive relationship between richness and specialisation (Dyer et al. 2007, Pellissier et al. 2012, Forister et al. 2015), Novotny et al. (2002a, 2006) reported no significant differences in host specificity between the caterpillars of a species-poor temperate forest and its tropical counterpart. The reasons for the contrasting results are not clear and still under debate (Stork 2007). Studies investigating both richness/ diversity and specialisation concomitantly are therefore essential to understand how these components are linked in local assemblages and how they are structured among and within plant species.

## DIETARY DIVERSITY OF FOREST CATERPILLARS – A BRIEF OUTLINE

Forest ecosystems harbour an outstanding diversity of butterfly and moth species. A vast majority of those species are associated with the foliage of woody plants, while the summed fraction of grass and herb feeders is generally lower (Heinrich 1993, Hammond & Miller 1998, Summerville & Crist 2002). Furthermore, lepidopteran larvae represent the largest proportion of leaf-chewing insects in forest habitats (e.g., Novotny et al. 2010, Šigut et al. 2018) and thus contribute greatly to overall herbivory in these ecosystems. Especially during outbreaks, folivorous caterpillars can reach high densities resulting in severe impacts on trees by defoliating focal host species or even whole forest stands (Myers 1993, Myers 1998, Kamata 2002).

Besides these ‘classical’ herbivores, a smaller proportion of caterpillars do not consume the living tissue of vascular plants (Tracheophyta), but feed on other substrate such as dead plant material, lichens, algae, bryophytes, or fungi (Powell et al. 1998, Bodner et al. 2015, Adams et al. 2016). A few species even reveal a parasitic or predatory feeding habit (see Pierce 1995, Powell et al. 1998). These ‘alternative feeders’ (i.e., all dietary guilds besides those of ‘classical’ herbivores) represent a minority of Lepidoptera species and are mostly found in basal lineages (Powell et al. 1998, Menken et al. 2010).

As caterpillars are typically used to study interactions between insects and vascular plants, dietary guilds of ‘alternative feeders’ are often neglected leading to deficient knowledge about their role in forest ecosystems. Particularly in tropical forests and other regions where information about utilized food sources is scarce, the fraction of these ‘alternative feeders’ in local caterpillar assemblages is largely unknown. A recent study by Bodner et al. (2015) in a montane rainforest, for instance, revealed that ‘alternative feeders’ made up a substantial proportion of caterpillars sampled from woody plant species. The rarity of such studies, however, illustrates that we need more comprehensive information about these ‘alternative feeding’ habits in local caterpillar assemblages to draw concise conclusions about specialisation patterns and niche partitioning of co-existing species. This goal can only be reached by direct observations in the field and/or by feeding trials during rearing in the laboratory.

## METHODS TO STUDY PLANT-ARTHROPOD INTERACTIONS IN FOREST CANOPIES

Forest canopies are hotspots of biodiversity (Nakamura et al. 2017) and provide habitats for an exceptionally large number of arthropods (Basset et al. 2015). Although ecologists have always been fascinated by canopies and their associated biota, the upper canopy layers have been neglected for a very long time in ecological studies due to limited access techniques and logistics (Lowman 2009). Canopy research is thus a relatively young ecological discipline, which mostly evolved during the last four decades due to the development of suitable sampling methods. Specialised methods of canopy sampling include fogging as well as sampling from cranes, walkways, and towers (see Barker & Pinard 2001, Lowman 2009, Gottsberger 2017, Nakamura et al. 2017). Although these methods enabled valuable insights into the richness and composition of canopy arthropods, our knowledge about their functional role and trophic position in interaction networks is still limited. Many studies, for instance, focused either on certain plant taxa, randomly selected tree individuals, or sampled merely small parts of the tree crown. Such methods are rather 'selective' as, independent from sampling effort, they capture only a limited fraction of the occurring species and their trophic interactions in a given forest stand. This could lead to an overestimation of specialisation and provide fragmentary insights into local species richness. 'Selective' methods are therefore not ideal when studying plant-arthropod interaction networks. Another problem in canopy arthropod research is that many different sampling protocols were used, which either hinders direct comparisons among forest sites and regions, or even makes them impossible.

The necessity for standardized protocols in canopy research was formulated nearly 20 years ago (Barker & Pinard 2001), however, no comprehensive guidelines for arthropod sampling are currently available.

Considering the aforementioned limitations in canopy arthropod research, we need quantitative sampling strategies that reflect the tree composition realistically and include entire tree crowns (Godfray et al. 1999, Šigut et al. 2018, Redmond et al. 2019). In addition, observed trophic associations between plants and arthropods should be corroborated by rearing, literature searches, and/or the barcoding of gut contents (see Zhu et al. 2019, Hausmann et al. 2020). These approaches would provide more detailed information and holistic insights into plant-arthropod interactions. Furthermore, well-written sampling protocols and guidelines for sample processing must allow for rigorous comparisons among forest sites - even if the applied sampling techniques differ.

## AIMS AND SCOPE

The structure of insect herbivore assemblages varies substantially within and among forest habitats and ecosystems. As pointed out in the previous paragraphs, the underlying mechanisms are complex yet poorly understood. Only comprehensive sampling of plant-herbivore interactions in forests from a variety of biogeographic regions can shed more light into the mechanisms structuring their communities. Especially in regions where host plant information is scarce or the insect taxa poorly known, rigorous sampling and rearing is the best way to compile solid data on trophic interactions and local host plant preferences.

The aim of this dissertation is to provide deeper insights in how herbivore assemblages are spatially, compositionally, and functionally structured in forest ecosystems by using caterpillars as a highly diverse model organism group. Potential drivers are considered from an ecological as well as from an evolutionary perspective.

Particularly, we aim to study if caterpillar assemblages in temperate forests are vertically structured and if metrics derived from the plant phylogeny can help to predict their compositional changes and variation in assemblage characteristics. We further aim to investigate if caterpillars on plants meet the assumption to be generally classified as ‘classical’ herbivores sensu stricto. In addition, the present thesis provides guidelines to gather comparable and reproducible data on plant-herbivore interactions based on results and experiences of a well-established and promising sampling approach.

**CHAPTER I** While several studies documented stratification patterns of adult Lepidoptera, vertical niche partitioning of their immature stages received comparatively little investigation. Here, we study the vertical structuring of an arboreal caterpillar community in a temperate deciduous forest in eastern North America. We used a plot-based sampling method to gather plant – caterpillar interaction networks from the understory, midstory, and canopy of a whole 0.2 ha forest stand. Despite overall caterpillar density, we found pronounced stratification patterns in guild composition, taxonomic composition, and specialisation. We showed that the canopy unveiled a distinctly different caterpillar assemblage, while understory and midstory revealed the highest caterpillar richness, highlighting their importance in maintaining the diversity of arboreal caterpillar faunas.

**CHAPTER II** Assemblages of insect herbivores are structured by plant traits of which a considerable proportion are phylogenetically conserved. Plant phylogenetic metrics indicating distances and relationships could thus serve as 'synthetic similarity measure' of conserved traits and might predict variation in caterpillar assemblages among co-occurring plant species. In this chapter we investigate, based on a comprehensive cross-continental dataset of plant-caterpillar interactions, how phylogenetic distance among host trees and their phylogenetic isolation explains species turnover and variations in assemblage characteristics of associated caterpillars. By using plot-based sampling approaches, we show that distance metrics obtained from the host plant phylogeny could be useful predictors explaining compositional changes among hosts as well as host-specific variation in richness and mean specialisation of associated caterpillar assemblages. The study demonstrates that metrics obtained from plant phylogenies appear to be a promising tool in predicting the assemblage characteristics of insect herbivores within their respective communities.

**CHAPTER III** Folivorous caterpillars are widely considered as 'classical' herbivores feeding on living leave tissue. However, especially in tropical regions where host plant information is scarce, few attempts have been made to prove this general assumption based on feeding trials. In this study we focused on caterpillar assemblages associated with the bamboo genus Chusquea KUNTH in montane rainforest and elfin forest of the south Ecuadorian Andes. Specific emphasis was put on caterpillar feeding guilds, which were defined by foliage-quality preferences of individual species. Based on feeding trials we found that a substantial fraction of the caterpillar assemblages are not strict herbivores and that elevation, leaf area, and foliage quality further shape guild composition. Our findings lead to the general assumption that in tropical forests caterpillars, although associated with 'putative' host plants, might play a larger role as detritivores than in temperate forest ecosystems.

**CHAPTER IV** Various methods have been previously used to study plant – arthropod networks in forest ecosystems. However, focusing merely on selected tree species or parts of their canopy might lead to erroneous conclusions and misinterpretations. Here, we present reproducible guidelines for a plot-based sampling approach with the aim of gathering comprehensive plant – arthropod interaction data, hence enabling the reconstruction of whole-forest canopy networks. We compare three alternative approaches of this method that were previously applied in various forest ecosystems worldwide. In addition, we compare network properties derived from plot-based sampling with those derived from simulations of non-plot-based sampling data. We subsequently discuss the advantages of the plot-based sampling method in general and advertise its further use to acquire comparable datasets of plant-arthropod interactions. This would allow for rigorous comparisons across larger geographic scales and thus provide deeper insights in how networks are structured and change among sites and regions.

## REFERENCES


Ackerly, D.D., 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. Int. J. Plant Sci. 164, 165–184.

Adams, M.-O., Seifert, C.L., Lehner, L., Truxa, C., Wanek, W., Fiedler, K., 2016. Stable isotope signatures reflect dietary diversity in European forest moths. Front. Zool. 13, 1–10.

Agrawal, A.A., 2007. Macroevolution of plant defense strategies. Trends Ecol. Evol. 22, 103–109.

Agrawal, A.A., Fishbein, M., 2006. Plant defense syndromes. Ecology 87, S132–S149.

Ashton, L.A., Nakamura, A., Basset, Y., Burwell, C.J., Cao, M., Eastwood, R., Odell, E., de Oliveira, E.G., Hurley, K., Katabuchi, M., Maunsell, S., Mcbroom, J., Schmidl, J., Sun, Z., Tang, Y., Whitaker, T., Laidlaw, M.J., Mcdonald, W.J.F., Kitching, R.L., 2016. Vertical stratification of moths across elevation and latitude. J. Biogeogr. 43, 59–69.

Barker, M.G., Pinard, M.A., 2001. Forest canopy research: sampling problems, and some solutions. Plant Ecol. 153, 23–38.

Barrett, R.D.H., Agrawal, A.A., 2004. Interactive effects of genotype, environment, and ontogeny on resistance of cucumber (Cucumis sativus) to the generalist herbivore, Spodoptera exigua. J. Chem. Ecol. 30, 37–51.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A.K., Schmidl, J., Winchester, N.N., Roubik, D.W., Aberlenc, H.P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte Da Rocha, W., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., Gama De Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.B., Sørensen, L., Lewinsohn, T.M., Leponce, M., 2015. Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. PLoS One 10, 1–22. e0144110

Basset, Y., Hammond, P.M., Barrios, H., Holloway, J.D., Miller, S.E., 2003. Vertical stratification of arthropod assemblages. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (eds.) Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy, 1st edn. Cambridge University Press, Cambridge, pp. 17–27.

Baylis, M., Pierce, N.E., 1991. The effect of host-plant quality on the survival of larvae and oviposition by adults of an ant-tended lycaenid butterfly, Jalmenus evagoras. Ecol. Entomol., 16: 1-9.

Bede, J.C., McNeil, J.N., Tobe, S.S., 2007. The role of neuropeptides in caterpillar nutritional ecology. Peptides 28, 185–196.

Bell, J.R., Blumgart, D., Shortall, C.R., 2020. Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. Insect Conserv. Divers. https://doi.org/10.1111/icad.12412

Bodner, F., Brehm, G., Fiedler, K., 2015. Many caterpillars in a montane rain forest in Ecuador are not classical herbivores. J. Trop. Ecol. 31, 473–476.

Blüthgen, Nico, Menzel, F., Blüthgen, Nils, 2006. Measuring specialization in species interaction networks. BMC Ecol. 6, 1–12.

Brehm, G., 2007. Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest. Basic Appl. Ecol. 8, 44–54.

Coley, P.D., Bateman, M.L., Kursar, T.A., 2006. The effects of plant quality on caterpillar growth and defense against natural enemies. Oikos 115, 219–228.

Campos, W.G., Teixeira, N.C., Valim, J.O.S., Guedes, R.N.C., Oliveira, M.G.A., 2016. Bottom-up mechanisms generate the same temporal pattern of attack by a specialist and a generalist caterpillar on short-lived plants. Environ. Entomol. 45, 550–558.

Carmona, D., Lajeunesse, M.J., Johnson, M.T.J., 2011. Plant traits that predict resistance to herbivores. Funct. Ecol. 25, 358–367.

Connahs, H., Aiello, A., Van Bael, S., Rodríguez-Castañeda, G., 2011. Caterpillar abundance and parasitism in a seasonally dry versus wet tropical forest of Panama. J. Trop. Ecol. 27, 51–58.

Connor, E.F., Taverner, M.P., 1997. The evolution and adaptive significance of the leaf-mining habit. Oikos 79, 6–25.

Cornell, H.V., 1989. Endophage-ectophage ratios and plant defense. Evol. Ecol. 3, 64–76.

Damman, H., 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology 68: 88–97.

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., Betancourt, J.L., Bolmgren, K., Cleland, E.E., Cook, B.I., Crimmins, T.M., Mazer, S.J., Mccabe, G.J., Pau, S., Regetz, J., Schwartz, M.D., Travers, S.E., 2013. Phylogenetic conservatism in plant phenology. J. Ecol. 101, 1520–1530.

De Smedt, P., Vangansbeke, P., Bracke, R., Schauwvliege, W., Willems, L.U.C., Mertens, J.A.N., Forest, K.V., 2019. Vertical stratification of moth communities in a deciduous forest in Belgium. Insect Conserv. Divers. 12, 121–130.

De Vries, P.J., 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. J. Res. Lepid. 26, 98–108.

Di Giovanni, F., Cerretti, P., Mason, F., Minari, E., Marini, L., 2015. Vertical stratification of ichneumonid wasp communities: the effects of forest structure and life-history traits. Insect Sci. 22, 688–699.

Diniz, I.R., Hay, J.D., Greeney, H.F., Morais, H.C., 2012. Shelter-building caterpillars in the cerrado: seasonal variation in relative abundance, parasitism, and the influence of extra-floral nectaries. Arthropod. Plant. Interact. 6, 583–589.

Diniz, I.R., Morais, H.C., Botelho, A.M., Venturoli, F., Cabral, B.C., 1999. Lepidopteran caterpillar fauna on lactiferous host plants in the central Brazilian cerrado. Rev. Bras. Biol. 59, 627–635.

Donaldson, J.R., Lindroth, R.L., 2008. Effects of variable phytochemistry and budbreak phenology on defoliation of aspen during a forest tent caterpillar outbreak. Agric. For. Entomol. 10, 399–410.

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.

Fiedler, K., 2001. Ants that associate with Lycaeninae butterfly larvae: diversity, ecology and biogeography. Divers. Distrib. 7, 45–60.

Floren, A., Schmidl, J. 2008. Canopy arthropod research in Europe. Basic and applied studies from the high frontier, 1st edn. Bioform Entomology, Nuremberg.

Forbes, R.J., Watson, S.J., Steinbauer, M.J., 2017. Multiple plant traits influence community composition of insect herbivores: a comparison of two understorey shrubs. Arthropod. Plant. Interact. 11, 889–899.

Fordyce, J.A., 2010. Host shifts and evolutionary radiations of butterflies. Proc. R. Soc. B Biol. Sci. 277, 3735–3743.

Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y., Butterill, P.T., Cizek, L., Coley, P.D., Dem, F., Diniz, I.R., Drozd, P., Fox, M., Glassmire, A.E., Hazen, R., Hrcek, J., Jahner, J.P., Kaman, O., Kozubowski, T.J., Kursar, T. a, Lewis, O.T., Lill, J., Marquis, R.J., Miller, S.E., Morais, H.C., Murakami, M., Nickel, H., Pardikes, N. a, Ricklefs, R.E., Singer, M.S., Smilanich, A.M., Stireman, J.O., Villamarín-Cortez, S., Vodka, S., Volf, M., Wagner, D.L., Walla, T., Weiblen, G.D., Dyer, L. a, 2015. The global distribution of diet breadth in insect herbivores. PNAS 112, 442–447.

Fukui, A., 2001. Indirect interactions mediated by leaf shelters in animal-plant communities. Popul. Ecol. 43, 31–40.

Gaston, K.J., Reavey, D., Valladares, G.R., 1991. Changes in feeding habit as caterpillars grow. Ecol. Entomol. 16, 339-344.

Gaston, K.J., Reavey, D., Valladares, G.R., 1992. Intimacy and fidelity: internal and external feeding by the British microlepidoptera. Ecol. Entomol. 17, 86–88.

Godfray, H.C.J., Lewis, O.T., Memmott, J., 1999. Studying insect diversity in the tropics. Philos. Trans. R. Soc. B Biol. Sci. 354, 1811–1824.

Gottsberger, G., 2017. Canopy operation permanent access system: a novel tool for working in the canopy of tropical forests: history, development, technology and perspectives. Trees 31, 791–812.

Grandez-Rios, J.M., Bergamini, L.L., Araújo, W.S. De, 2015. The effect of host-plant phylogenetic isolation on species richness, composition and specialization of insect herbivores: a comparison between native and exotic hosts. PLoS One 1–14.

Hacker, H., Müller, J., 2008. Stratification of ‘Macro-Lepidoptera’ (Insecta) in northern Bavarian forest stands dominated by different tree species. In: Floren A., Schmidl, J. (eds.) Canopy arthropod research in Europe. Basic and applied studies from the high frontier, 1st edn. Bioform Entomology, Nuremberg, pp. 355–382.

Hahn, M., Brühl, C.A., 2016. The secret pollinators: an overview of moth pollination with a focus on Europe and North America. Arthropod. Plant. Interact. 10, 21–28.

Hammond Paul, C., Miller Jeffrey, C., 1998. Comparison of the biodiversity of Lepidoptera within three forested ecosystems. Ann. Entomol. Soc. Am. 91, 323–328.

Hausmann, A., Diller, J., Moriniere, J., Höcherl, A., Floren, A., Haszprunar, G., 2020. DNA barcoding of fogged caterpillars in Peru: a novel approach for unveiling host-plant relationships of tropical moths (Insecta, Lepidoptera). PLoS One 15, 1–20. e0224188

Heinrich, B., 1979. Foraging strategies in caterpillars. Oecologia 42, 325–337.

Heinrich, B., 1993. How avian predators constrain caterpillar foraging. In: Stamp, N.E, Casey, T.M. (eds.) Caterpillars – ecological and evolutionary constraints on foraging. Chapman & Hall, New York – London, pp. 224-247.

Henson, W. R., 1958. Some ecological implications of the leaf rolling habit in Compsolechia niveopulvella. Can. J. Zool. 36, 809–818.

Hirao, T., Murakami, M., Kashizaki, A., 2009. Importance of the understory stratum to entomofaunal diversity in a temperate deciduous forest. Ecol. Res. 24, 263–272.

Hrcek, J., Miller, S.E., Whitfield, J.B., Shima, H., Novotny, V., 2013. Parasitism rate, parasitoid community composition and host specificity on exposed and semi-concealed caterpillars from a tropical rainforest. Oecologia 173, 521–532.

Janson, E.M., Stireman, J.O., Singer, M.S., Abbot, P., 2008. Phytophagous insect-microbe mutualisms and adaptive evolutionary diversification. Evolution 62, 997–1012.

Janz, N. & Nylin, S., 2008 The oscillation hypothesis of host- plant range and speciation. In: Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects (ed. K. J. Tilmon), pp. 203–215. Los Angeles, CA: University of California Press.

Janz, N., Nylin, S., Wahlberg, N., 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects 10, 1–10.

Jorge, L.R., Prado, P.I., Almeida-Neto, M., Lewinsohn, T.M., 2014. An integrated framework to improve the concept of resource specialisation. Ecol. Lett. 17, 1341–1350.

Kalka, M., Kalko, E.K. V., 2005. Gleaning bats as underestimated predators of herbivorous insects: diet of Micronycteris microtis (Phyllostomidae) in Panama. J. Trop. Ecol. 22, 1–10.

Kamata, N., 2002. Outbreaks of forest defoliating insects in Japan, 1950 – 2000. Bull. Entomol. Res. 92, 109–117.

Kristensen, J., Rousk, J., Metcalfe, D.B., 2019. Below-ground responses to insect herbivory in ecosystems with woody plant canopies: a meta-analysis. J. Ecol. 1–14.

Kristensen, N.P., Scoble, M.J., Karsholt, O., 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa 1668, 699–747.

Larsson, S.H.D., Haggstrom, H.E., Denno, R.F., 1997. Preference for protected feeding sites by larvae of the willow-feeding leaf beetle Galerucella lineola. Ecol. Entomol. 22, 445–452.

Le Corff, J., Marquis, R.J., 1999. Differences between understorey and canopy in herbivore community composition and leaf quality for two oak species in Missouri. Ecol. Entomol. 24, 46–58.

Lee, K.P., Raubenheimer, D., Behmer, S.T., Simpson, S.J., 2003. A correlation between macronutrient balancing and insect host-plant range: evidence from the specialist caterpillar Spodoptera exempta (Walker). J. Insect Physiol. 49, 1161–1171.

Lewinsohn, T.M., Novotny, V., Basset, Y., 2005. Insects on plants: diversity of herbivore assemblages revisited. Annu. Rev. Ecol. Evol. Syst. 36, 597–620.

Lewinsohn, T.M., Roslin, T., 2008. Four ways towards tropical herbivore megadiversity. Ecol. Lett. 11, 398–416.

Lill, J.T., Marquis, R.J., Ricklefs, R.E., 2002. Host plants influence parasitism of forest caterpillar. Nature 417, 170–173.

Lill, J.T., Marquis, R.J., Forkner, R.E., Le Corff, J., Holmberg, N., Barber, N.A., 2009. Leaf pubescence affects distribution and abundance of generalist slug caterpillars (Lepidoptera: Limacodidae). Environ. Entomol. 35, 797–806.

Lowman, M.D., 2009. Canopy research in the twenty-first century: a review of arboreal ecology. Trop. Ecol. 50, 125–136.

Marquis, R.J., Lill, J.T., 2010. Impact of plant architecture versus leaf quality on attack by leaf-tying caterpillars on five oak species. Oecologia 163, 203–213.

Marquis, R.J., Lill, J.T., Piccinni, A., 2002. Effect of plant architecture on colonization and damage by leaftying caterpillars of Quercus alba. Oikos 99, 531–537.

Mcart, S.H., Halitschke, R., Salminen, J.P., Thaler, J.S., 2013. Leaf herbivory increases plant fitness via induced resistance to seed predators. Ecology 94, 966–975.

Menken, S.B.J., Boomsma, J.J., Nieukerken, E.J. Van, 2010. Large-scale evolutionary patterns of host plant associations in the Lepidoptera. Evolution (N. Y). 64, 1098–1119.

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. Ecol. Lett. 17, 324–32.

Mitter, C., Davis, D.R., Cummings, M.P., 2017. Phylogeny and evolution of Lepidoptera. Annu. Rev. Entomol. 62, 265–283.

Montgomery, G.A., Dunn, R.R., Fox, R., Jongejans, E., Leather, S.R., Saunders, M.E., Shortall, C.R., Tingley, M.W., Wagner, D.L., 2020. Is the insect apocalypse upon us? How to find out. Biol. Conserv. 241. https://doi.org/10.1016/j.biocon.2019.108327

Murakami, M., 2002. Foraging mode shifts of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest. Ornithol. Sci. 1, 63–69.

Myers, J.H., 1993. Population outbreaks in forest Lepidoptera. Am. Sci. 81, 240–251.

Myers, J.H., 1998. Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. Ecology 79, 1111–1117.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C.N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H., Ashton, L.A., 2017. Forests and their canopies: achievements and horizons in canopy science. Trends Ecol. Evol. 32, 438–451.

Nice, C.C., Fordyce, J.A., Bell, K.L., Forister, M.L., Gompert, Z., Devries, P.J., Nice, C.C., 2019. Vertical differentiation in tropical forest butterflies: a novel mechanism generating insect diversity? Biol. Lett. 15.

Novotny, V., Basset, Y., 2005. Host specificity of insect herbivores in tropical forests. Proc. Biol. Sci. 272, 1083–90.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L., Drozd, P., 2002a. Low host specificity of herbivorous insects in a tropical forest. Nature 416, 841–844.

Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y., Weiblen, G.D., 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313, 1115–1118.

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, Samuelson, G.A., Weiblen, G.D., 2010. Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. J. Anim. Ecol. 79, 1193–203.

Novotny, V., Miller, S.E., Basset, Y., Cizek, L., Drozd, P., Darrow, K., Leps, J., 2002b. Predictably simple: Assemblages of caterpillars (Lepidoptera) feeding on rainforest trees in Papua New Guinea. Proc. R. Soc. B Biol. Sci. 269, 2337–2344.

Ødegaard, F., Diserud, O.H., Engen, S., Aagaard, K., 2000. The magnitude of local host specificity for phytophagous insects and its implications for estimates of global species richness. Conserv. Biol. 14, 1182–1186.

Ødegaard, F., Diserud, O.H., Østbye, K., 2005. The importance of plant relatedness for host utilization among phytophagous insects. Ecol. Lett. 8, 612–617.

Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The Structure, Distribution, and Biomass of the World's Forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622.

Pearson, D.L., 1971. Vertical stratification of birds in a tropical dry forest. Condor 73, 46–55.

Pellissier, L., Fiedler, K., Ndribe, C., Dubuis, A., Pradervand, J.N., Guisan, A., Rasmann, S., 2012. Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. Ecol. Evol. 2, 1818–1825.

Pierce, N.E., 1995. Predatory and parasitic Lepidoptera: carnivores living on plants. J. - Lepidoterists' Soc. 49, 412–453.

Powell, J.A., Mitter, C., Farrell, B., 1998. Evolution of larval food preferences in Lepidoptera. In: Kristensen, N.P. (ed.) Lepidoptera: moths and butterflies, Vol. 1: Evolution, systematics, and biogeography. Handb. Zool., 35, Berlin, De Gruyter, pp. 403-422.

Redmond, C.M., Auga, J., Gewa, B., Segar, S.T., Miller, S.E., Molem, K., Weiblen, G.D., Butterill, P.T., Maiyah, G., Hood, A.S.C., Volf, M., Jorge, L.R., Basset, Y., Novotný, V., 2019. High specialization and limited structural change in plant-herbivore networks along a successional chronosequence in tropical montane forest. Ecography 42, 162–172.

Ribeiro, D.B., Williams, M.R., Specht, A., Freitas, A.V.L., 2016. Vertical and temporal variability in the probability of detection of fruit-feeding butterflies and moths (Lepidoptera) in tropical forest. Austral Entomol. 55, 112–120.

Sagers, C.L., 1992. Manipulation of host plant quality: herbivores keep leaves in the dark. Funct. Ecol. 6, 741–743.

Sandberg, S.L., Berenbaum, M.R., 1989. Leaf-tying by tortricid larvae as an adaptation for feeding on phototoxic Hypericum perforatum. J. Chem. Ecol. 15, 875–885.

Schulze, C.H., Linsenmair, K.E., Fiedler, K., 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain. Plant Ecol. 153, 133–152.

Šigut, M., Šigutová, H., Šipoš, J., Pyszko, P., Kotásková, N., Drozd, P., 2018. Vertical canopy gradient shaping the stratification of leaf- ¬ chewer – parasitoid interactions in a temperate forest. Ecol. Evol. 8, 7297–7311.

Singer, M.S., Clark, R.E., Lichter-Marck, I.H., Johnson, E.R., Mooney, K.A., 2017. Predatory birds and ants partition caterpillar prey by body size and diet breadth. J. Anim. Ecol. 86, 1363–1371.

Singer, M.S., Farkas, T.E., Skorik, C.M., Mooney, K.A., 2012. Tritrophic interactions at a community level: effects of host plant species quality on bird predation of caterpillars. Am. Nat. 179, 363–374.

Solis, M.A. 2008. Aquatic Lepidoptera. In: Merritt, R.W., Cummins, K.W., and Berg, M.B. (eds.) Aquatic Insects of North America. Dubuque, Iowa, Kendall/Hunt Publishing Company, pp. 553-569.

Stamp, N.E., Bowers, M.D., 1990. Phenology of nutritional differences between new and mature leaves and its effect on caterpillar growth. Ecol. Entomol. 15: 447-454.

Stireman, J.O., Cerretti, P., Whitmore, D., Hardersen, S., Gianelle, D., 2012. Composition and stratification of a tachinid (Diptera: Tachinidae) parasitoid community in a European temperate plain forest. Insect Conserv. Divers. 5, 346–357.

Stork, N.E., 2007. Biodiversity - World of insects World of insects. Nature 448, 657–658.

Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest Lepidoptera: community, guild, and species responses. Ecol. Appl. 12, 820.

Summerville, K.S., Crist, T.O., Kahn, J.K., Gering, J.G., 2003. Community structure of arboreal caterpillars within and among four tree species of the eastern deciduous forest. Ecol. Entomol. 28, 747–757.

Symons, F.B., Beccaloni, G.W., 1999. Phylogenetic indices for measuring the diet breadths of phytophagous insects. Oecologia 119, 427–434.

Tvardikova, K., Novotny, V., 2012. Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. J. Trop. Ecol. 28, 331–341.

Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. For. Ecol. Manage. 261, 1479–1489.

van Nieukerken, E.J., Kaila, L., Kitching, I.J., Kristensen, N.P., Lees, D.C., Minet, J., Mitter, C., Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.H, Zahiri, R., Adamski, D., Baixeras, J., Bartsch, D., Bengtsson, B.A., Brown, J.W., Bucheli, S.R., Davis, D.R., De Prins, J., De Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A., Holloway, J.D., Kallies, A., Karsholt, O., Kawahara, A.Y., Koster, S., Kozlov, M.V., Lafontaine, J.D., Lamas, G., Landry, J.-F., Lee, S., Nuss, M., Park, K.T., Penz, C., Rota, J., Schintlmeister, A., Sschmidt, B.C., Sohn, J.C., Solis, M.A., Tarmann, G.M., Warren, A.D., Weller, S., Yakovlev, R.V., Zolotuhin, V.V., Zwick, A., 2011. Order Lepidoptera Linnaeus, 1758. In: Zhang, Z.-Q. (ed.), Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148, pp. 212–221.

Vialatte, A., Bailey, R.I., Vasseur, C., Matocq, A., Gossner, M.M., Everhart, D., Vitrac, X., Belhadj, A., Ernoult, A., Prinzing, A., 2010. Phylogenetic isolation of host trees affects assembly of local Heteroptera communities. Proc. R. Soc. B Biol. Sci. 277, 2227–2236.

Vidal, M.C., Murphy, S.M., 2018. Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. Ecol. Lett. 21, 138–150.

Visser, M.E., Holleman, L.J.M., Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172.

Wagner, D.L., 2020. Insect declines in the Anthropocene. Annu. Rev. Entomol. 65, 457-480.

Wagner, D.L., Peacock, J.W., Carter, J.L. & Talley, S.E., 1995. Spring caterpillar fauna of oak and blueberry in a Virginia deciduous forest. Ann. Entomol. Soc. Am, 88, 416-426.

War, A.R., Taggar, G.K., Hussain, B., Taggar, M.S., Nair, R.M., Sharma, H.C., 2018. Plant defence against herbivory and insect adaptations. AoB Plants 10, 1–19.

Wardhaugh, C.W., 2014. The spatial and temporal distributions of arthropods in forest canopies: Uniting disparate patterns with hypotheses for specialisation. Biol. Rev. 89, 1021–1041.

Whitfeld, T.J.S., Novotny, V., Miller, S.E., Hrcek, J., Klimes, P., Weiblen, G.D., 2012. Predicting tropical insect herbivore abundance from host plant traits and phylogeny. Ecology 93, S211-S222.

Wiens, J.J., Lapoint, R.T., Whiteman, N.K., 2015. Herbivory increases diversification across insect clades. Nat. Commun. 6, 1–7.

Zhu, C., Gravel, D., He, F., 2019. Seeing is believing? Comparing plant–herbivore networks constructed by field co-occurrence and DNA barcoding methods for gaining insights into network structures. Ecol. Evol. 9, 1764–1776.

Zvereva, E.L., Zverev, V., Kozlov, M. V., 2014. High densities of leaf-tiers in open habitats are explained by host plant architecture. Ecol. Entomol. 39, 470–479.

# ~ CHAPTER I ~

Vertical stratification of a temperate forest caterpillar community in eastern North America

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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

# Vertical stratification of a temperate forest caterpillar community in eastern North America

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## Abstract

Vertical niche partitioning might be one of the main driving forces explaining the high diversity of forest ecosystems. However, the forest's vertical dimension has received limited investigation, especially in temperate forests. Thus, our knowledge about how communities are vertically structured remains limited for temperate forest ecosystems. In this study, we investigated the vertical structuring of an arboreal caterpillar community in a temperate deciduous forest of eastern North America. Within a 0.2-ha forest stand, all deciduous trees ≥ 5 cm diameter at breast height (DBH) were felled and systematically searched for caterpillars. Sampled caterpillars were assigned to a specific stratum (i.e. understory, midstory, or canopy) depending on their vertical position and classified into feeding guild as either exposed feeders or shelter builders (i.e. leaf rollers, leaf tiers, webbers). In total, 3892 caterpillars representing 215 species of butterflies and moths were collected and identified. While stratum had no effect on caterpillar density, feeding guild composition changed significantly with shelter-building caterpillars becoming the dominant guild in the canopy. Species richness and diversity were found to be highest in the understory and midstory and declined strongly in the canopy. Family and species composition changed significantly among the strata; understory and canopy showed the lowest similarity. Food web analyses further revealed an increasing network specialization towards the canopy, caused by an increase in specialization of the caterpillar community. In summary, our study revealed a pronounced stratification of a temperate forest caterpillar community, unveiling a distinctly different assemblage of caterpillars dwelling in the canopy stratum.

**Keywords** Feeding guilds · Food web · Forest canopy · Lepidoptera · Specialization

## Introduction

Forests represent complex and heterogenous habitats (Basset et al. 2003; Floren and Schmidl 2008; Ulyshen 2011). Their canopies are often considered as hotspots for arthropods, especially in tropical regions, where they often harbour unique species (Nakamura et al. 2017). Accordingly, vertical changes in species communities and their interactions can be

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# ~ CHAPTER II ~

Plant phylogeny structures arboreal caterpillar assemblages in temperate deciduous forests of three continents.

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[Manuscript]

# Plant phylogeny structures arboreal caterpillar assemblages in temperate deciduous forests of three continents

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**Abstract**

1. Assemblages of insect herbivores are structured by plant traits such as nutrient content, secondary metabolites, physical traits, and phenology. These traits are often phylogenetically conserved, implying a decrease in trait similarity with increasing phylogenetic distance of the host plant taxa. A metric of phylogenetic distances and relationships among co-occurring plant species can be thus considered as '*proxy measure*' for phylogenetically conserved plant traits and might be used to predict variation in herbivorous insect assemblages among co-occurring plant species.
2. We analysed a Holarctic dataset of caterpillars and their host associations to study if the phylogenetic distances among host plants explain the compositional changes and assemblage characteristics of their insect herbivores.
3. Our plant – caterpillar network data derived from plot-based sampling from three different continents included >28,000 individual caterpillar – host tree interactions. We tested if increasing phylogenetic distance of the host plants leads to a decrease in caterpillar assemblage overlap. We further investigated to what degree phylogenetic isolation of a host tree species explains abundance, density, richness and mean specialisation of their caterpillar assemblages.
4. We found that overlap of caterpillar assemblages decreased with increasing phylogenetic distance among the host tree species. Phylogenetic isolation of the host plant within its plant community

was correlated with lower species richness and lower mean specialisation of their caterpillar assemblages. We found no effect of phylogenetic isolation on caterpillar abundance or density per leaf area. Although abundance, density, richness, and mean specialisation of the exposed feeding and shelter-building caterpillar guilds varied among our study sites, plant phylogeny affected both guilds in the same direction.

5. Our study revealed that distance metrics obtained from host plant phylogeny could be useful predictors to explain compositional changes among hosts as well as host-specific variations in richness and mean specialisation of associated insect herbivore assemblages. While some characteristics are mainly driven by resource availability, phylogeny-based methods provide a promising tool for global studies investigating changes in herbivore assemblages, especially now that phylogenetic information of host plants is becoming increasingly available.

**Key words**

Exposed feeders, guilds, herbivorous insects, Lepidoptera, phylogenetic isolation, specialisation, shelter builders, species richness

# ~ CHAPTER III ~

Caterpillar assemblages on *Chusquea* bamboos in southern Ecuador: abundance, guild structure, and the influence of host plant quality

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# Caterpillar assemblages on *Chusquea* bamboos in southern Ecuador: abundance, guild structure, and the influence of host plant quality

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**Abstract.** 1. Information on the guild structure of foliage-associated tropical insects is scarce, especially as caterpillars are mostly considered only as herbivores feeding on living leaves. However, many caterpillar species display alternative trophic associations, feeding on dead or withered leaves or epiphylls ('non-herbivores').

2. To determine the contribution of these non-herbivores, caterpillar communities associated with *Chusquea* Kunth (Poaceae) in the Andes of southern Ecuador were investigated. Caterpillars were collected at two elevation levels (montane rainforest ~2000 m and elfin forest at ~3000 m a.s.l.) and assigned to three feeding guilds (strict herbivores, non-herbivores, and switchers) based on feeding trials. Foliage quality and leaf area were recorded to test for their influence on guild composition and caterpillar density.

3. Three hundred and eighty-nine individuals belonging to 175 Lepidoptera species associated with *Chusquea* bamboos were found. The species richness of caterpillars was similarly high at both elevation levels but varied between feeding guilds. Approximately half (46.5%) displayed an alternative feeding association, i.e. were non-herbivores (31.1%) or switchers (15.4%).

4. Caterpillar density was nearly two-fold higher in the elfin forest, but only strict herbivores and switchers increased significantly with elevation. Leaf area positively influenced the density of strict herbivores and switchers; foliage quality only affected strict herbivores. The density of non-herbivores did not differ significantly between the forest types and was not related to leaf area or foliage quality.

5. The present study underpins that non-herbivores make up a considerable fraction of caterpillar communities in tropical mountain ecosystems and demonstrates that elevation, foliage quality and available plant biomass further shape feeding guild composition.

**Key words.** Bamboo, feeding guild, Lepidoptera, montane rainforest, non-herbivores, strict herbivores.

## Introduction

Comprehensive knowledge of insect–plant relationships in tropical regions is essential to understand specialisation patterns, diversification processes, insect species richness, and herbivore pressure (e.g. Novotny *et al.*, 2010; Salazar & Marquis, 2012; Wilson *et al.*, 2012; Neves *et al.*, 2014; Novotny & Miller, 2014). Studies dealing with foliage-associated insects usually focus on 'classic' herbivore communities, i.e. those feeding on living tissue of their host plant (hereafter referred to as 'strict herbivores'). This is the ecological role for which Lepidopteran caterpillars are generally well known (Johns *et al.*, 2016), but species representing unusual feeding guilds, e.g. feeding on dead or withered foliage or on associated organisms such as

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# ~ CHAPTER IV ~

Quantitative assessment of plant-arthropod interactions in forest canopies: a plot-based approach

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RESEARCH ARTICLE

# Quantitative assessment of plant-arthropod interactions in forest canopies: A plot-based approach

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**Data Availability Statement:** We provide the data used in the analyses in S1 Table. The data on Yawan dataset that were used for the comparison of plot-based and non-plot-based analyses of herbivore-plant interaction networks were taken from Redmond et al. 2019 [20]. The publicly available sequences on insect DNA barcodes can be accessed from The Barcode of Life Data System (http://www.boldsystems.org) as DS-LANZMIK (Mikulcice and Lanzhot sites; [21]), TLR (Tomakomai), DS-CATS1, DS-SEGAR16, and

## Abstract

Research on canopy arthropods has progressed from species inventories to the study of their interactions and networks, enhancing our understanding of how hyper-diverse communities are maintained. Previous studies often focused on sampling individual tree species, individual trees or their parts. We argue that such selective sampling is not ideal when analyzing interaction network structure, and may lead to erroneous conclusions. We developed practical and reproducible sampling guidelines for the plot-based analysis of arthropod interaction networks in forest canopies. Our sampling protocol focused on insect herbivores (leaf-chewing insect larvae, miners and gallers) and non-flying invertebrate predators (spiders and ants). We quantitatively sampled the focal arthropods from felled trees, or from trees accessed by canopy cranes or cherry pickers in 53 0.1 ha forest plots in five biogeographic regions, comprising 6,280 trees in total. All three methods required a similar sampling effort and provided good foliage accessibility. Furthermore, we compared interaction networks derived from plot-based data to interaction networks derived from simulated non-plot-based data focusing either on common tree species or a representative selection of tree families. All types of non-plot-based data showed highly biased network structure

# ~ SUMMARY ~

## SUMMARY

Vertical niche partitioning, plant traits, resource availability, and specialisation are considered important drivers in structuring communities of insect herbivores. This thesis aims to provide deeper insights into how caterpillar assemblages are structured in temperate and tropical forest ecosystems. To that end, the thesis focuses on externally feeding, folivorous caterpillars. We used a quantitative sampling approach to investigate the vertical structure of an arboreal caterpillar assemblage in eastern North America. Furthermore, by including quantitative interaction networks from the Czech Republic and Japan, we extended this dataset to answer the question of whether host plant phylogeny is a useful predictor of variation in caterpillar assemblages among co-occurring tree species. In another study, we asked whether folivorous caterpillars associated with bamboo in two tropical forest habitats fulfilled the criteria to be considered 'classical' herbivores, or whether there was need for further precision regarding their trophic associations. The thesis ends with a methodological study in which we compared various approaches to plot-based sampling, discuss their advantages over alternative approaches, and provide comprehensive guidelines for replication. In the following paragraphs, I summarise the main findings of my thesis, draw some conclusions, and provide potential directions for further investigation.

## MAIN FINDINGS AND CONCLUSION

In **CHAPTER I**, the vertical stratification of a temperate forest caterpillar assemblage was investigated by defining three equally sized forest strata. We hereby extended previous attempts (e.g., Wagner et al. 1995, Le Corff & Marquis 1999) by shifting from focal host plant species to a quantitative approach where trees within a 0.2 ha forest stand were entirely sampled.

Overall, we observed a pronounced stratification with differences in guild structure, taxonomic composition, diversity, and specialisation across the forest strata. By and large, our study thus contradicts the perceived wisdom that stratification patterns of arthropod assemblages in temperate forests are weakly developed (Lowman et al. 1993, Basset et al. 2003). We found that the lower forest strata, i.e., understory and midstory, harboured a large fraction of the caterpillar species and was dominated by exposed feeders. In contrast, the canopy was species-poor but with a caterpillar community that was more host specific. Based on these findings, we conclude that taxonomic composition, life history traits (e.g., feeding guild), and specialisation are closely linked and strongly influence vertical niche partitioning. We further interpret the increased species richness found in the lower strata and the lack of exclusively canopy-dwelling species as an indicator of the high conservation value of understory and midstory strata in maintaining caterpillar diversity in temperate forests. Caterpillar density did not differ significantly across the forest strata, which suggests that variation in vertical abundance is mainly driven by resource availability (i.e., leaf area). Besides resource availability, the biotic and abiotic factors shaping the vertical stratification of forest arthropods are complex and their relative importance may differ among taxonomic and functional groups (Ulyshen 2011, Nakamura et al. 2017). As insect herbivores are strongly influenced by their resources (Vidal & Murphy 2018), we speculate that vertical changes in plant traits such as toughness, nutritional quality and secondary metabolites may play an important role (Dominy et al. 2003, Murakami et al. 2005). Understanding the relative importance of such traits as drivers of caterpillar vertical niche partitioning would thus be a crucial step forward. Vertical variation in abundance, guild composition, and restrictions of certain caterpillar species to a particular stratum could have cascading effects on the vertical distribution and foraging behaviours of their antagonists such as insectivorous birds and parasitoids. Therefore, the examination of tri-trophic interaction networks, especially those including parasitoids, might be a worthy direction for future studies on vertical stratification. These interaction networks could help us to understand the high richness and abundance of tachinid flies and ichneumonid wasps found in the understory of temperate forests and might further explain their compositional turnover among the forest strata (Stireman et al. 2012, Di Giovanni 2015).

Besides vertical niche partitioning, host plant traits also play a crucial role in structuring herbivore assemblages (Agrawal 2007, Carmona et al. 2011). These traits, such as nutritional quality, secondary metabolites, and phenology, are to a certain degree phylogenetically conserved (Agrawal 2007, Davies et al. 2013). In **CHAPTER II**, we explored whether or not metrics derived from plant phylogeny could be used as predictors that explain the changes in caterpillar assemblages among co-occurring plant species. More than 28,000 single host plant interactions from three different continents were analysed. We achieved this through an extension of the dataset used in chapter I by including additional data derived from plot-based sampling in the Czech Republic and Japan.

We found that the compositional similarity of caterpillar assemblages declined with increasing phylogenetic distance of the host plant species. Moreover, species richness and mean specialisation of the caterpillar assemblage were observed to decline with increasing phylogenetic isolation of the host plant. Our findings thus clearly demonstrated that plant metrics indicative of phylogenetic relatedness could be useful measures to predict changes in community structure among coexisting plant species. Plant traits which directly or indirectly structure caterpillar assemblages, therefore, may exhibit a considerable degree of phylogenetic conservatism. In addition, our results reveal that highly isolated plant species are mostly exploited by species-poor assemblages of less specialised caterpillar taxa. However, the study also suggested that resource availability plays a crucial role in the structure of caterpillar assemblages. Species richness, for instance, was positively affected by resource availability suggesting that caterpillar diversity in temperate forests is primarily maintained by plant species that are common and have close relatives within the community. Furthermore, caterpillar abundance and density were primarily driven by available foliage area rather than by plant phylogeny, which is in accordance with previous studies from tropical forests (Whitfeld et al. 2012). These findings underpin the need to account for both host plant phylogeny and resource availability when predicting assemblage characteristics of insect herbivores. Our study focused on the effects of plant phylogeny on the consumer level (i.e., insect herbivores). Several studies, however, reported variations in top-down effects on caterpillars mediated by host plant traits (Lill et al. 2002, Singer et al. 2012). It would thus be an interesting opportunity for further research to test if host plant phylogenies could also be used to predict host plant specific variations in predation pressure and compositional changes in parasitoid communities. As phylogentic information is becoming increasingly widespread, metrics derived from host plant phylogeny might thus not only provide a promising tool to study insect herbivore assemblages but also to investigate and predict tri-trophic interactions.

In chapter I and II, we specifically focused on caterpillar species feeding exclusively on living leaf tissue of temperate forest trees. However, some caterpillar species might not consume the living foliage of a particular plant species, but feed on its dead or withered leaves that may be already infested by other organisms such as fungi. In **CHAPTER III**, we were particularly interested in these 'alternative feeders' (i.e., those caterpillars which do not exclusively feed on fresh, living foliage tissue) and aimed to determine their prevalence. We therefore investigated the trophic associations of caterpillars associated with the bamboo genus Chusquea KUNTH in a montane rainforest ecosystem in the south Ecuadorian Andes. Based on feeding trials, caterpillars were segregated into three trophic guilds, i.e., strict herbivores, non-herbivores, and switchers. Surprisingly, nearly half of all sampled caterpillar individuals (46.5%) and species (41.7%) fed either exclusively on dead or withered leaves or switched between fresh and dead leaf material during their development. The proportion of non-herbivorous caterpillars was about one third (~31% of all individuals and species, respectively). This fraction of alternative feeders was even higher than reported for caterpillar assemblages associated with shrubs of Piperaceae and Asteraceae within the same study area (22%; Bodner et al. 2015). Our findings thus strengthened former assumptions that the proportion of caterpillars taking part in alternative trophic associations is much higher in tropical rainforest ecosystems than is known from temperate forests (Bodner et al. 2015). Furthermore, we found the fraction of non-herbivores to be lower in elfin forest than in montane forest, while those of “switchers” and strict herbivores increased. To feed exclusively on dead plant material, therefore, might be a disadvantage in environments of lower temperature and generally harsher environment. This would further suggest that in lowland rainforests, the proportion of caterpillars feeding on dead plant material might be even higher than for the studied forest habitats of higher elevation. Comparable studies from tropical lowlands would be needed to verify or reject this assumption.

Caterpillar densities of non-herbivores and switchers were not significantly influenced by foliage quality of the host plant. Furthermore, positive effects of resource availability were only observed for those guilds that feed at least partially during their development on living leaf tissue (i.e., strict herbivores and switchers). We therefore conclude that predicting caterpillar densities based on the availability of living foliage is only a reliable method if the caterpillar guilds rely at least to some extent on this food source. Overall, our findings demonstrated that in ecological studies, trophic associations should be always clarified prior to further analyses to avoid misinterpretations about 'putative' resources used for caterpillar development. This is particularly the case when plant-caterpillar interactions are used to study antagonistic networks. Although barcoding methods are nowadays available to reveal host plant information (Zhu et al. 2018, Hausmann et al. 2020), their ability to detect trophic associations is limited in cases where the food substrate (e.g., leaf tissue), originated from the same host plant species. Traditional rearing methods including food-choice tests and stable isotope analyses as suggested by Adams et al. (2016) may provide suitable alternatives.

In the first two chapters of this thesis, we employed different approaches of plot-based sampling to study quantitative interaction networks in forest ecosystems, i.e., cherry picker, canopy crane, and tree felling. In **CHAPTER IV**, we compared the efficiency of these three methods and contrasted plant-caterpillar networks derived from plot-based sampling with those derived from simulated non plot-based approaches. We found that sampling effort (person-hours) did not differ among the three techniques, but was dependent on forest type. Forest habitats with higher stem densities generally demanded greater sampling effort. Although all three methods provided access to >80% of the foliage, sampling by cherry picker performed slightly better in terms of foliage accessibility than sampling by crane or tree felling. However, especially in forest sites that are difficult to access, felling or the use of established canopy cranes might be the methods of choice. Apart from method-specific advantages and limitations, all three approaches turned out to be well-suited for studying endophytic and exophytic species of non-flying arthropods such as externally feeding insect larvae, miners, and gallers. Furthermore, since plant-arthropod interactions are completely censused for a standardised forest area, the networks derived from plot-based sampling allow rigorous comparisons across sites, regions, and ecosystems (e.g., Volf et al. 2017, Redmond et al. 2019, Plowman et al. 2020). Additonally, we showed that commonly used network metrics derived from simulated non plot-based samplings revealed bias in the results, irrespective of whether the plant selection was based on taxonomy or abundance. The significance of this finding goes far beyond those studies investigating interaction networks of canopy arthropods. It clearly demonstrates the importance of reflecting plant composition realistically when studying plant-arthropod interaction networks, regardless of habitat and functional plant group. The comparability of the tested approaches and the striking advantages of the interaction networks over those derived from non plot-based samplings are convincing arguments to follow our introduced sampling guidelines in further research.

## FUTURE DIRECTIONS

The present thesis reveals new insights in the factors shaping caterpillar assemblages in forest ecosystems. However, further investigations across a broader selection of forest types, successional stages, and ecosystems are needed to clarify if the observed patterns are valid generally (see Volf et al. 2017, Redmond et al. 2019). As mentioned before, expanding the scope of investigation from bipartite to tri-trophic interaction networks by including parasitoids would allow for studying both bottom-up and top-down forces simultaneously. This would provide new insights as their relative contributions in structuring caterpillar communities could be thoroughly evaluated. The inclusion of additional information on the life history, behaviour, and morphology of interacting taxa may further reveal how and to what extent functional traits shape the structure of interaction networks. Our research focused on two major guilds of external feeding caterpillar assemblages, while internal leaf feeders (i.e., miners and gall-inducers) were not considered. Internal leaf feeders, however, experience a completely different environment during their larval development and are capable of feeding on specific leaf tissue. Thus, it would be worthy to include these guilds in future studies to examine if their assemblages are similarly structured as those of external feeding guilds, or to what degree they behave differently.

Most importantly, the methodology for the future sampling of forest caterpillars and their trophic interactions should ideally be standardised to enable spatial and temporal comparisons. The guidelines presented in chapter IV represent an auspicious starting point to build up a global network of forest plots in which to study trophic interactions between plants, caterpillars and their natural enemies in a comparable way. Realising the establishment of such a global network of standardised forest plots would provide the opportunity to study macroecological patterns in species diversity, specialisation, and community structure. Additionally, it would allow the monitoring of temporal dynamics and long-term changes in arthropod communities and their interaction networks and thus yield essential information for conservation management.

## REFERENCES


Adams, M.-O., Seifert, C.L., Lehner, L., Truxa, C., Wanek, W., Fiedler, K., 2016. Stable isotope signatures reflect dietary diversity in European forest moths. Front. Zool. 13, 1–10.

Agrawal, A.A., 2007. Macroevolution of plant defense strategies. Trends Ecol. Evol. 22, 103–109.

Basset, Y., Hammond, P.M., Barrios, H., Holloway, J.D., Miller, S.E., 2003. Vertical stratification of arthropod assemblages. In: Basset Y., Novotny V., Miller S.E., Kitching R.L. (eds.) Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy, 1st edn. Cambridge University Press, Cambridge, pp. 17–27.

Bodner, F., Brehm, G., Fiedler, K., 2015. Many caterpillars in a montane rain forest in Ecuador are not classical herbivores. J. Trop. Ecol. 31, 473–476.

Carmona, D., Lajeunesse, M.J., Johnson, M.T.J., 2011. Plant traits that predict resistance to herbivores. Funct. Ecol. 25, 358–367.

Davies, T.J., Wolkovich, E.M., Kraft, N.J.B., Salamin, N., Allen, J.M., Ault, T.R., Betancourt, J.L., Bolmgren, K., Cleland, E.E., Cook, B.I., Crimmins, T.M., Mazer, S.J., Mccabe, G.J., Pau, S., Regetz, J., Schwartz, M.D., Travers, S.E., 2013. Phylogenetic conservatism in plant phenology. J. Ecol. 101, 1520–1530.

Di Giovanni, F., Cerretti, P., Mason, F., Minari, E., Marini, L., 2015. Vertical stratification of ichneumonid wasp communities: The effects of forest structure and life-history traits. Insect Sci. 22, 688–699.

Dominy, N.J., Lucas, P.W., Wright, S.J., 2003. Mechanics and chemistry of rain forest leaves: canopy and understorey compared. J. Exp. Bot. 54, 2007–2014.

Hausmann, A., Diller, J., Moriniere, J., Höcherl, A., Floren, A., Haszprunar, G., 2020. DNA barcoding of fogged caterpillars in Peru: a novel approach for unveiling host-plant relationships of tropical moths (Insecta, Lepidoptera). PLoS One 15, 1–20. e0224188

Le Corff, J., Marquis, R.J., 1999. Differences between understorey and canopy in herbivore community composition and leaf quality for two oak species in Missouri. Ecol. Entomol. 24, 46–58.

Lill, J.T., Marquis, R.J., Ricklefs, R.E., 2002. Host plants influence parasitism of forest caterpillar. Nature 417, 170–173.

Lowman, M., Taylor, P., Block, N., 1993. Vertical stratification of small mammals and insects in the canopy of a temperate deciduous forest: a reversal of tropical forest distribution? Selbyana 14, 25.

Murakami, M., Yoshida, K., Hara, H., 2005. Spatio-temporal variation in Lepidopteran larval assemblages associated with oak, Quercus crispula: the importance of leaf quality. Ecol. Entomol. 30, 521–531.

Nakamura, A., Kitching, R.L., Cao, M., Creedy, T.J., Fayle, T.M., Freiberg, M., Hewitt, C.N., Itioka, T., Koh, L.P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C.M.P., Song, L., Wang, H., Ashton, L.A., 2017. Forests and their canopies: achievements and horizons in canopy science. Trends Ecol. Evol. 32, 438–451.

Plowman, N.S., Mottl, O., Novotny, V., Idigel, C., Philip, F.J., Rimandai, M., Klimes, P., 2020. Nest microhabitats and tree size mediate shifts in ant community structure across elevation in tropical rainforest canopies. Ecography 43, 431–442.

Redmond, C.M., Auga, J., Gewa, B., Segar, S.T., Miller, S.E., Molem, K., Weiblen, G.D., Butterill, P.T., Maiyah, G., Hood, A.S.C., Volf, M., Jorge, L.R., Basset, Y., Novotný, V., 2019. High specialization and limited structural change in plant-herbivore networks along a successional chronosequence in tropical montane forest. Ecography 42, 162–172.

Singer, M.S., Farkas, T.E., Skorik, C.M., Mooney, K.A., 2012. Tritrophic interactions at a community level: effects of host plant species quality on bird predation of caterpillars. Am. Nat. 179, 363–374.

Stireman, J.O., Cerretti, P., Whitmore, D., Hardersen, S., Gianelle, D., 2012. Composition and stratification of a tachinid (Diptera: Tachinidae) parasitoid community in a European temperate plain forest. Insect Conserv. Divers. 5, 346–357.

Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. For. Ecol. Manage. 261, 1479–1489.

Vidal, M.C., Murphy, S.M., 2018. Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. Ecol. Lett. 21, 138–150.

Volf, M., Pyszko, P., Abe, T., Libra, M., Kot, N., Sigut, M., Kumar, R., Butterill, P.T., Sipo, J., Abe, H., Fukushima, H., Drozd, P., Kamata, N., Murakami, M., Novotny, V., 2017. Phylogenetic composition of host plant communities drives plant-herbivore food web structure. J. Anim. Ecol. 86, 556–565.

Wagner, D.L., Peacock, J.W., Carter, J.L. & Talley, S.E., 1995. Spring caterpillar fauna of oak and blueberry in a Virginia deciduous forest. Ann. Entomol. Soc. Am, 88, 416-426.

Whitfeld, T.J.S., Novotny, V., Miller, S.E., Hrcek, J., Klimes, P., Weiblen, G.D., 2012. Predicting tropical insect herbivore abundance from host plant traits and phylogeny. Ecology 93, S211-S222.

Zhu, C., Gravel, D., He, F., 2019. Seeing is believing? Comparing plant–herbivore networks constructed by field co-occurrence and DNA barcoding methods for gaining insights into network structures. Ecol. Evol. 9, 1764–1776.

# ~ CURRICULUM VITAE ~

# CURRICULUM VITAE

## Carlo L. Seifert

| | |
|---|---|
| **Date of birth** | 29.12.1988 |
| **Place of birth** | Borna, Germany |
| **Nationality** | German |

### ACADEMIC EDUCATION

| | | |
|---|---|---|
| **2016 – pres.** | | **University of South Bohemia, Ceske Budejovice, Czech Republic** |
| | 2016 – pres. | Study of PhD curriculum 'Entomology'<br>supervisor: prof. RNDr. Vojtěch Novotný, CSc. |
| | 10/ 2019 | RNDr. in Zoology/ Entomology |
| **2010 – 2016** | | **University of Vienna, Vienna, Austria** |
| | 06/ 2014 | M.Sc. in ‘Conservation Biology and Biodiversity Management’ (Graduation with distinction) at the Dept. of Tropical Ecology & Animal Biodiversity<br>supervisor: Univ.-Prof. Mag. Dr. Konrad Fiedler |
| | 2014 – 2016 | Studies within following curricula: ‘Biology’ (B.Sc. curriculum), 'Ecology and Ecosystems' (M.Sc. curriculum), and ‘Conservation Biology and Biodiversity Management’ (M.Sc. curriculum) |
| **2007 – 2010** | | **Anhalt University of Applied Sciences, Bernburg, Germany** |
| | 09/ 2010 | B.Sc. in ‘Nature Conservation and Landscape Planning’, supervisor: Prof. Dr. Klaus Richter |
| | 2007-2010 | Study of 'Nature Conservation and Landscape Planning' |

## CURRENT PROJETCS

- Ecological determinants of tropical-temperate trends in insect diversity (Lead PI: Vojtěch Novotný)
- Barcoding trophic interactions in ForestGEO Lepidoptera (Lead PIs: Scott E. Miller, Jeremy deWaard)
- Why is there such a high diversity of chemical defences: the role of insect herbivory in promoting chemical diversity in willows (Lead PI: Martin Volf)

## STAYS ABROAD & PROFESSIONAL APPOINTMENTS

- 2018/ 2019 — **Germany**, German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Lab of Molecular Interaction Ecology, *Visiting researcher*.
- 2016/ 2017 — (**USA**: SCBI & **Panama**: STRI) Smithsonian Institution, *Predoctoral fellow*.
- 2014 — **French Guiana** - 'Nouragues Nature Reserve', Nouragues Travel Grant 2014 (C.H. Schulze), *Research assistant*.
- 2014 — **Costa Rica** - Golfo Dulce region, Tropical Field Station 'La Gamba', *Research assistant*.
- 2013 — **Indonesia** - 'Training in Tropical Ecology and Rapid Biodiversity Assessment' in the Krakatau archipelago, Indonesia. University of Vienna and Bogor Agricultural University, *Student*.
- 2012/ 2013 — **Ecuador** - 'Reserva Biológica San Francisco', DFG project: FOR 816, *Student*.

## REVIEWS

Entomol. Exp. Appl., PLOS ONE, Sci. Rep., Funct. Ecol

## TEACHING EXPERIENCE

- 10/ 2019 Teaching assistant: "Community Ecology", University of South Bohemia. Lectures/ practical seminars
- 09/ 2017 Teaching assistant: "Community Ecology", University of South Bohemia. Field excursion
- 03 – 05/ 2013 Teaching assistant: "Species - Diversity, Ecology and Conservation Needs", University of Vienna. Field excursion

## PUBLICATIONS & MANUSCRIPTS

### Peer-reviewed articles

***Seifert, C.L.**, Lamarre, G.P.A., Volf, M., Jorge, L.R., Miller, S.E., Wagner, D.L., Anderson-Teixeira K.J. & Novotný, V. (2020) Vertical stratification of a temperate forest caterpillar community in eastern North America. *Oecologia*, **192**, 501-514.

*Volf, M., Klimeš, P., Lamarre, G.P.A., Redmond, C.M., **Seifert, C.L.**, [...], Weiblen, G.D. & Novotný, V. (2019) Quantitative assessment of arthropod-plant interactions in forest canopies: a plot-based approach. *Plos One*, **14**, 1-20.

Strutzenberger, P., Brehm, G., Gottsberger, B., Bodner, F., **Seifert, C.L.** & Fiedler, K. (2017) Diversification rates, host plant shifts and an updated molecular phylogeny of Andean *Eois* moths (Lepidoptera: Geometridae). *Plos One*, **12**, 1-22.

Adams, M.-O., **Seifert, C.L.**, Lehner, L., Truxa, C., Wanek, W. & Fiedler, K. (2016) Stable istotope signatures reflect dietary diversity in European forest moths. *Frontiers in Zoology*, **13**, 1-10.

***Seifert, C.L.**, Lehner, L., Bodner, F. & Fiedler, K. (2016) Caterpillar assemblages on *Chusquea* bamboos in southern Ecuador: abundance, guild structure, and the influence of host plant quality. *Ecological Entomology*, **41**, 698-706.

Mahr, K., **Seifert, C.L.** & Hoi, H. (2016) Female and male Blue Tits (*Cyanistes caeruleus*) sing in response to experimental predator exposition. *Journal of Ornithology*, **157**, 907-911.

**Seifert, C.L.**, Schulze, C.H., Dreschke, T.C.T., Frötscher, H. & Fiedler, K. (2016) Day vs. night predation on artificial caterpillars in primary rainforest habitats – an experimental approach. *Entomologia Experimentalis et Applicata*, **158**, 54-59.

**Seifert, C.L.**, Bodner, F., Brehm, G. & Fiedler, K. (2015) Host plant associations and parasitism of south Ecuadorian *Eois* species (Lepidoptera: Geometridae) feeding on *Peperomia* (Piperaceae). *Journal of Insect Science,* **15**, 1-7.

**Seifert, C.L.**, Lehner, L., Adams, M.-O. & Fiedler, K. (2015) Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south- western Costa Rica. *Journal of Tropical Ecology*, **31**, 281-284.

## Other publications

**Seifert, C.L.** (2011) 10 Jahre Libellenmonitoring im FND "Kuhbergbruch". *Naturschutz und Landschaftspflege in Thüringen*, **48**, 70-82.

## Manuscripts submitted

***Seifert, C.L.**, Volf, M., Jorge, L.R., Abe, T., Carscallen, G., Drozd, P., Kumar, R., Lamarre, G.P.A., Libra, M., Losada, M.E., Miller, S.E., Murakami, M., Nichols, G., Pyszko, P., Šigut, M., Wagner, D.L. & Novotný, V. (submitted) Plant phylogeny structures arboreal caterpillar assemblages in temperate deciduous forests of three continents. *Journal of Animal Ecology*

Mottl, O., Fibich, P., Klimeš, P., Volf, M., […], **Seifert, C.L.**, Vrána, J., Weiblen, G. & Novotný, V. (submitted) Spatial covariance of herbivorous and predatory guilds of forest canopy arthropods along a latitudinal gradient. *Ecology Letters*

***** Publications/ manuscripts included in this PhD thesis.

Cover image: *Eacles imperialis* (photo by Michael Thomas)



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