Stephanie Stiegel

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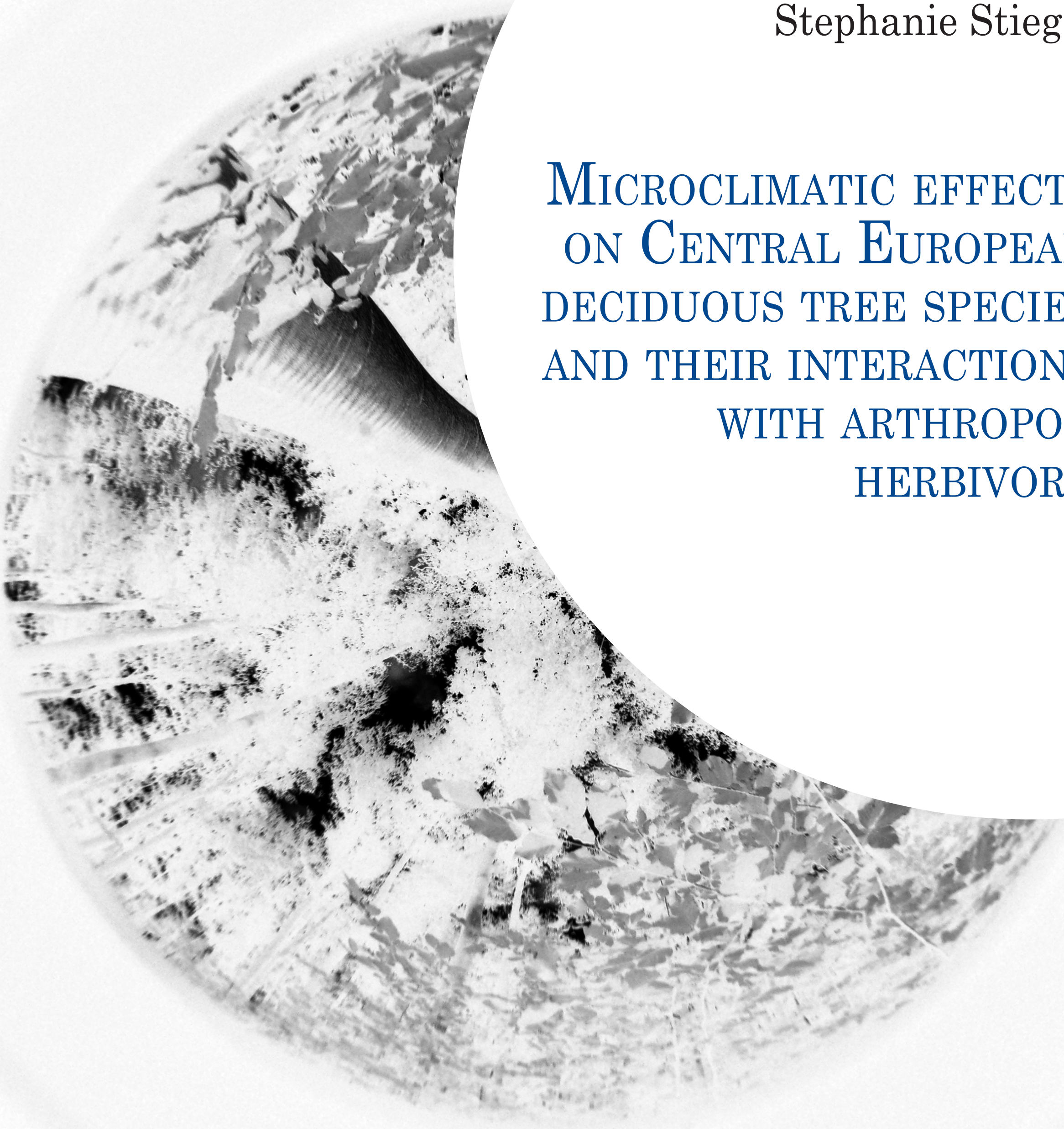

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Stephanie Stiegel

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SUMMARY

Arthropod herbivores act as mediators for effects that cascade up and down the trophic chain. Therefore, herbivory plays an important role for driving ecosystem processes and influencing ecosystem structures and functions. Generally, ecosystem processes are mediated by interactions between organisms. The plant community composition is influenced by competitive interactions among plants, which is affected by herbivore species. Leaf area loss to insects can reduce tree growth, but alters material flows from canopies to forest soils. Therefore, the chemical quality of litter is changed (increases in nitrogen content) through enhanced nutrient cycling rates caused by herbivory.

Climate and microclimate can affect insect physiology and behaviour directly or indirectly through climate-induced changes of host plants. Temperature determines the geographical range, site and timing of activities, success of oviposition and hatching, and the duration of developmental stages of arthropod herbivores. The activity of poikilothermic insects increases with temperature, and therefore growth and consumption rates are enhanced. However, morphological and functional leaf traits that determine host plant palatability often mediate indirect environmental effects on herbivory. Leaf palatability is determined by leaf toughness, nutrients, and defence compounds. In warm environments, expected high rates of arthropod herbivory can then be suppressed by negative changes of leaf traits.

Microclimate gradients are found across the different strata of forest ecosystems. Abiotic factors change vertically between forest layers due to a micro-environmental gradient. Along the vertical gradient, microclimate is affected by the light regime, with increasing temperatures and decreasing humidity from understorey to upper canopies. Various organisms are distributed along the vertical forest gradient based on changes in environmental conditions and in the quality and quantity of available resources. Temperate deciduous forests reveal highly stratified arthropod communities with vertical and horizontal distribution patterns. Microclimatic requirements and the availability of food resources along the vertical forest gradient can reflect spatial distributions and preferences of arthropods.

This research study investigated arthropod herbivory on leaves of deciduous tree species along the vertical gradient of temperate forests. A field study with ten forests sites in Central Germany and an experimental study in greenhouses were conducted, addressing effects of microclimate and leaf traits on arthropod herbivory. Juvenile and adult individuals of *Fagus sylvatica* L. (European beech), the dominant deciduous tree species in Central Europe, were chosen as main research subjects. Furthermore, *Acer pseudoplatanus* L. (Sycamore maple) and *Carpinus betulus* L. (hornbeam), two frequent tree species in the forest understorey, were also surveyed. The aim of the study was to detect patterns of herbivory along the vertical forest gradient, and if they are dependent on different feeding guilds like leaf-chewing, sap-sucking, leaf-mining, and gall-inducing. Herbivory patterns were tried to link to microclimate and leaf trait factors.

Leaf damaged on *F. sylvatica*, caused by leaf-chewing insects, decreased from the understorey to upper canopies, along with changes towards unfavourable leaf trait characteristics for insect herbivores (tough leaves, low nitrogen and high carbon content). Changes of leaf traits along the vertical forest gradient were in accordance with effects of the light-induced microclimatic gradient of forest stands. Furthermore, herbivory differences between juvenile tree species in the understorey, with highest levels found on *A. pseudoplatanus* and *C. betulus* compared to *F. sylvatica*, seemed to be in accordance with patterns of defensive traits (indicated by carbon content).

In addition, arthropod herbivores also showed variability in their preferences for plant ontogenetic stages, because the distribution of identified feeding traces revealed distinct patterns with differences between juvenile and adult *F. sylvatica* individuals. Herbivory of gall-inducing species was increased on adult compared to juvenile trees. The distribution of galls is strongly linked to the theory of harsh environment, which is based on top-down control through predation. Further impact on arthropod herbivores was detected for decreasing herbivory with an increase in phytodiversity.

In conclusion, the choice of quantitative measure is essential for determining and comparing herbivory, and differs between distinct feeding guilds. Along the vertical forest gradient, herbivory patterns can be linked to environmental and ontogenetic processes, and microclimate essentially affects herbivory intensities, patterns, and processes. Despite direct impacts on arthropod herbivores, the environment influences herbivory through effects on leaf traits and the top-down control by predators. In addition, plant ontogeny affects herbivory indirectly through alterations of leaf traits and top-down processes of predation.

ZUSAMMENFASSUNG

Herbivore Arthropoden fungieren als Mediatoren für Effekte entlang der Nahrungskette (trophische Kaskade). Daher spielt Herbivorie eine wichtige Rolle für die Lenkung von Ökosystemprozessen und beeinflusst Struktur sowie Funktionen von Ökosystemen. Die Zusammensetzung der Pflanzengesellschaft entsteht beispielsweise durch kompetitive Interaktion zwischen Pflanzen, die wiederum von herbivoren Arten beeinflusst wird. Der Blattflächenverlust durch Insekten kann einerseits das Wachstum der Bäume reduzieren. Andererseits verändert Herbivorie die Materialflüsse von den Kronen zum Waldboden und erhöht dadurch die Geschwindigkeit des Nährstoffkreislaufs, wodurch die Streuqualität verändert wird (Erhöhung des Stickstoffgehalts).

Klima und Mikroklima können die Physiologie und das Verhalten von Insekten direkt oder indirekt durch klimatisch induzierte Veränderungen der Wirtspflanze beeinflussen. Temperatur entscheidet über die geographische Verbreitung, den Ort und das Timing von Aktivitäten, den Erfolg der Eiablage und des Schlüpfens und die Dauer der Entwicklungsstadien von herbivoren Arthropoden. Die Aktivität der poikilothermen Insekten wächst mit der Temperatur, wodurch die Wachstums- und Konsumraten gesteigert werden. Jedoch vermitteln morphologische und funktionale Blattmerkmale (*leaf traits*), die die Schmackhaftigkeit der Wirtspflanze bestimmen, indirekte Umwelteffekte auf Herbivorie. Die Schmackhaftigkeit von Blättern wird bestimmt durch Festigkeit, sowie Nähr- und Abwehrstoffe. In warmer Umgebung können dadurch erwartet hohe Raten von Herbivorie durch negative Veränderungen der Blattmerkmale unterdrückt werden.

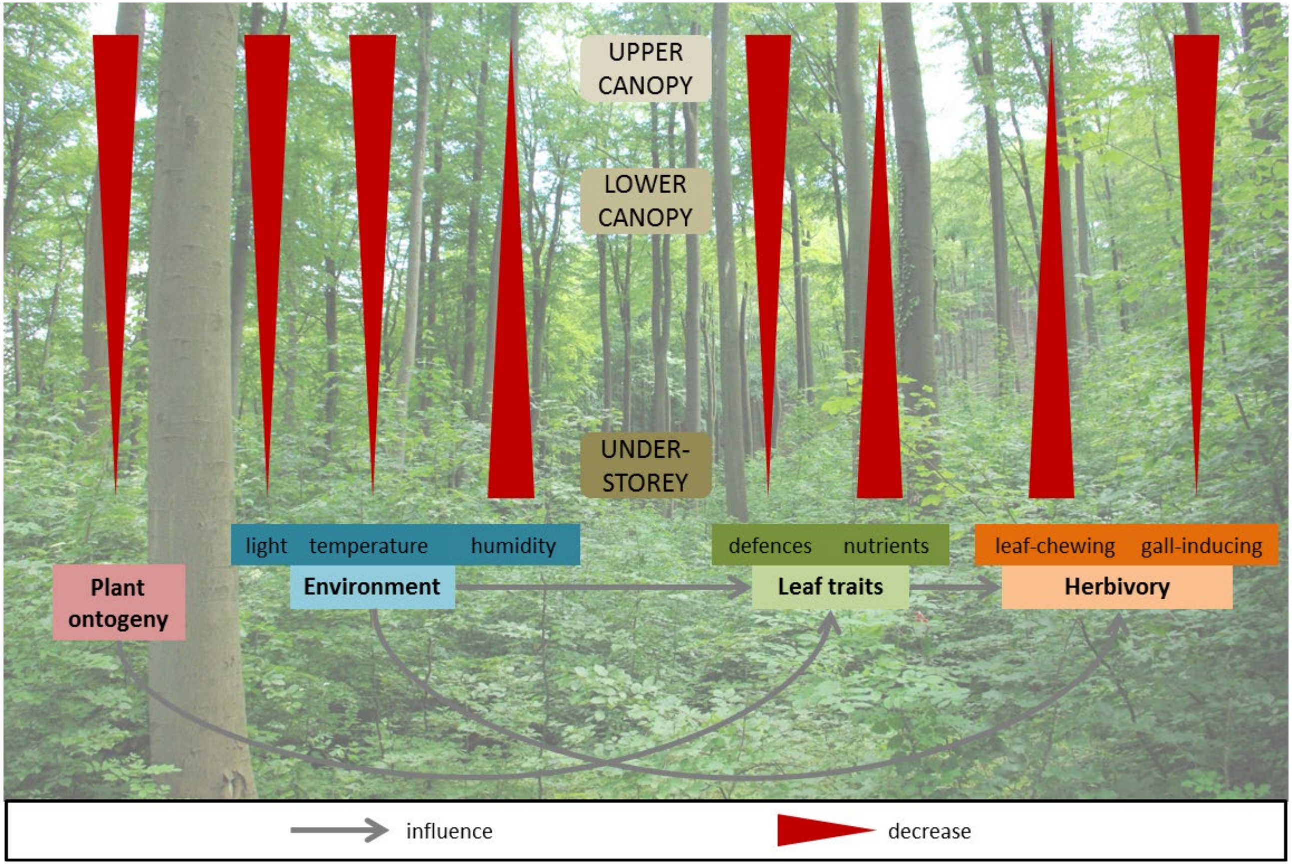
Mikroklimatische Gradienten existieren entlang der verschiedenen Straten von Waldökosystemen, wodurch sich abiotische Faktoren vertikal zwischen den Waldschichten verändern. Das Mikroklima des vertikalen Waldgradienten ist durch das Lichtregime beeinflusst und äußert sich durch steigende Temperaturen und abnehmende Luftfeuchtigkeit vom Unterwuchs zur Sonnenkrone. Diverse Organismen sind aufgrund der Veränderung der Umweltbedingungen sowie der Qualität und Quantität der verfügbaren Ressourcen entlang des vertikalen Waldgradienten verbreitet. Temperate Laubwälder zeigen hoch stratifizierte Gemeinschaften von Arthropoden mit vertikalen und horizontalen Verteilungsmustern. Mikroklimatische Anforderungen und die Verfügbarkeit von Nahrungsressourcen können dabei die räumliche Verteilung und Präferenzen von Arthropoden wiederspiegeln.

Die vorliegende Dissertation befasste sich mit der Blattherbivorie an Laubbäumen entlang des vertikalen Waldgradienten von temperaten Wäldern. Eine Feldstudie an zehn Waldstandorten in Mitteldeutschland und eine experimentelle Studie in Gewächshäusern adressierten die Effekte von Mikroklima und Blattmerkmale auf Herbivorie. Juvenile und adulte Individuen von *Fagus sylvatica* L. (Rotbuche) wurden als Hauptuntersuchungsgegenstand ausgewählt und juvenile Individuen von *Acer pseudoplatanus* L. (Bergahorn) und *Carpinus betulus* L. (Hainbuche) zusätzlich im Unterwuchs untersucht. Die Analyse von Herbivoriemustern entlang des vertikalen Waldgradienten und deren Abhängigkeit von verschiedenen Herbivoriegilden (Blattfresser, Saftsauger, Minierer und Gallbildner) war Ziel der Studie. Verursachende Faktoren des Mikroklimas und der Blattmerkmale für die Herbivoriemuster sollten identifiziert werden.

Schäden bei *F. sylvatica*, die durch Blattfressende Insekten verursacht wurden, nahmen vom Unterwuchs zur Sonnenkrone hin parallel zur Veränderung in Richtung ungünstiger Blattmerkmale ab (feste Blätter, niedriger Stickstoff- und hoher Kohlenstoffgehalt). Die Veränderungen der Blattmerkmale entlang der Waldschichten waren in Übereinstimmung mit den Effekten des Licht-induzierten Mikroklimagradienten der Waldbestände. Die Herbivorieunterschiede zwischen den juvenilen Baumindividuen im Unterwuchs, mit höchsten Werten bei *A. pseudoplatanus* und *C. betulus* im Vergleich zu *F. sylvatica*, schienen mit den Mustern von Abwehrstoffen übereinzustimmen. Zusätzlich zeigte die Herbivorie identifizierter Fraßspuren unterschiedliche Präferenzen zwischen juvenile und adulte Individuen von *F. sylvatica* (Effekt der Pflanzenontogenie). Die Herbivorie von Gallbildenden Arten war bei adulten im Vergleich zu juvenilen Bäumen erhöht. Die Verteilung von Gallen ist verbunden mit der *harsh environment* Theorie, die auf der top-down Kontrolle durch Prädation beruht.

Die Wahl der quantitativen Messmethode, die sich für verschiedene Gilden unterscheidet, ist essentiell für die Bestimmung und Vergleiche von Herbivorie. Die Herbivoriemuster entlang des vertikalen Waldgradienten stehen in direktem Zusammenhang mit umweltbedingten und ontogenetischen Prozessen und das Mikroklima beeinflusst essentiell die Intensitäten, Muster und Prozesse von Herbivorie. Neben direkten Auswirkungen auf herbivore Arthropoden beeinflusst die Umwelt die Herbivorie durch Effekte auf Blattmerkmale und top-down Kontrolle durch Prädatoren. Die Pflanzenontogenie beeinflusst Herbivorie indirekt durch Veränderungen der Blattmerkmale und top-down Prozesse der Prädation.

GRAPHICAL ABSTRACT



CHAPTER 1

GENERAL INTRODUCTION

1.1 Arthropod herbivory in forest ecosystems

Orders of arthropod herbivores and feeding guilds

More than three-quarter of all insect species in Central Europe are related to plants (Zwölfer, 2010). Insect herbivores occur in various orders and families with some of them harbouring a high diversity (e.g. Coleoptera: Curculionidae). Some orders consist of insect species that live as herbivores without exception (e.g. Auchenorrhyncha and Sternorrhyncha) or with few exceptions (e.g. Thysanoptera and larvae of Lepidoptera). Furthermore, 30% and 35% larvae of beetles (Coleoptera) and flies (Diptera) are herbivores, respectively (Zwölfer, 2010). Taxa of hemimetabolic insect herbivores occupy the same ecological niche on their host plants. In contrast, insects with complete metamorphosis have different niches for larval and imaginal stages with mostly larvae living as herbivores.

Generally, different arthropod herbivore species feed on several parts of plants on above- and below-ground organs, e.g. leaves, stems, and roots. They have a different range of host plants with most insect species being monophagous (specialists on one plant species/ genus) or oligophagous (within one plant family), and few species are polyphagous (generalists on various plant species and families). Arthropod herbivores can be classified into guilds according to their feeding mode (chewing or sucking), developmental stage (larva or adult), on the basis of the plant part used for feeding (leaves, flowers, fruits, xylem, and phloem tissue), and whether feeding internally or externally on the plant (Tab. 1.1). Typical herbivore damages on leaves (folivory) are defined as follows based on illustrations in Cranshaw & Shetlar (2017):

- Leaf-chewing leads to missing leaf area at the edge, as a hole in the interior of the leaf, or skeletonized leaves that are recognized as a network of veins remaining with the intervening tissue eaten (including epidermis);
- Leaf-mining causes a papery area, often with curving surface, where the leaf tissue has been eaten, but leaving the epidermis intact;
- Galls are lumps of many different forms, resulting from insects or mites laying eggs, which results in the leaf tissue growing to envelop the herbivore.

Table 1.1: Feeding guilds of arthropod herbivores. Classification is based on the feeding mode, developmental stage, feeding location of the herbivore, and the plant part (changed after Novotny *et al.*, 2010). Guilds with underline were investigated in this study.

Plant part	Feeding mode, development stage, feeding location			
	chewing, larva, internal	chewing, larva, external	chewing, adult, external	sucking, larva + adult, external
leaf	leaf miners	leaf chewers	leaf chewers	leaf suckers
xylem, above-ground	xylem chewers	stem chewers	stem chewers	xylem suckers
xylem, below-ground	xylem chewers	root chewers	not applicable	xylem suckers
phloem, above-ground	phloem chewers	stem chewers	stem chewers	phloem suckers
phloem, below-ground	phloem chewers	root chewers	not applicable	phloem suckers
flower	flower chewers	flower chewers	flower chewers	flower suckers
fruit	fruit chewers	fruit chewers	fruit chewers	fruit suckers
induced gall tissue	chewing gallers	not applicable	not applicable	sucking gallers

Relevance of arthropod herbivores for ecosystems

Arthropods are an important component of biodiversity in ecosystems worldwide dominating with species, individuals, and biomass. Ecosystems are maintained by insects through their roles as prey, decomposers, pollinators, and predators (Wilson, 1987; Price, 2002; Losey & Vaughan, 2006). Therefore, insect herbivores can affect the structure and function of ecosystems (Crawley, 1983; Mulder *et al.*, 1999; Weisser & Siemann, 2008). Nutrient dynamics are accelerated and the relative competitive balance among trees in the community is altered by herbivory (Schowalter *et al.*, 1986). Leaf area loss to insects has direct negative and indirect positive effects for the host plant. On the one hand, folivory damages reduce important photosynthetic tissue of the plant. But on the other hand, insect herbivores change material flows from the canopy to the forest soil (Hunter, 2001; Hartley & Jones, 2004). Herbivory seems to enhance nutrient cycling rates through an increase of nitrogen (N) content that changes the chemical quality of litter (Chapman *et al.*, 2003). Leaf damage is variable between broadleaved temperate forest sites worldwide and ranges between 1–20% (Kozlov, 2008; Adams & Zhang, 2009; Schowalter, 2011). Herbivory is generally lower in temperate forest canopies than in tropical canopies (Adams *et al.*, 2009; Moles *et al.*, 2011). Lower insect herbivory in temperate forest canopies reaches up to 7.5% of missing leaf area (Franklin, 1973; Coley & Aide, 1991). However, in outbreak situations rates of herbivory can increase dramatically. Studies about influences of insect herbivory on nutrient cycling have often focused on outbreaks (Brown, 1994; Lovett & Ruesink, 1995), which is a natural dynamic of some arthropod populations. Intense negative effects on forests are caused by severe outbreaks of short-lived herbivory. However, less intense and persistent insect herbivory plays an important role in driving forest ecosystem processes (de Mazancourt *et al.*, 2001).

Vertical stratification of arthropod herbivores in forests

Forest ecosystems have a changing vertical structure with different strata from the understorey to upper canopies (Fig. 1.1). Various organisms are distributed along the vertical forest gradient (ground, shrub, and tree layer) based on changes in environmental conditions like microclimate and in the quality and quantity of available resources (Novotny *et al.*, 2003; Grimbacher & Stork, 2007). Therefore, herbivory can be highly heterogeneous along the vertical forest gradient. In the past, canopies were quite unexplored habitats because of access difficulties. Canopy research is essential for acquiring the holistic perspective that is needed to optimize conservation and management strategies (Moffett, 2000, 2001; Didham & Fagan, 2004). Crane and climbing techniques have improved the access to canopies, which supports research projects.

Temperate deciduous forests are widespread and vary strongly worldwide. Nonetheless, tropical forests have historically been focused stronger for canopy research and associated organisms. Therefore, vertical patterns of herbivory and herbivore abundance in temperate forests are less clear (Le Corff & Marquis, 1999). Studies have suggested a weak vertical stratification of arthropod herbivore communities in temperate forests compared to the tropics (Lowman *et al.*, 1993; Basset *et al.*, 2003b). However, a review about studies on vertical distribution patterns of arthropods in temperate deciduous forests has revealed highly stratified communities (Ulyshen, 2011). In German temperate forests, different strata of forest ecosystems are inhabited by distinct arthropod communities showing vertical and horizontal distribution patterns (Gruppe *et al.*, 2008). Important resources for folivorous arthropod herbivores are leaves and their palatability, which is dependent on leaf traits.

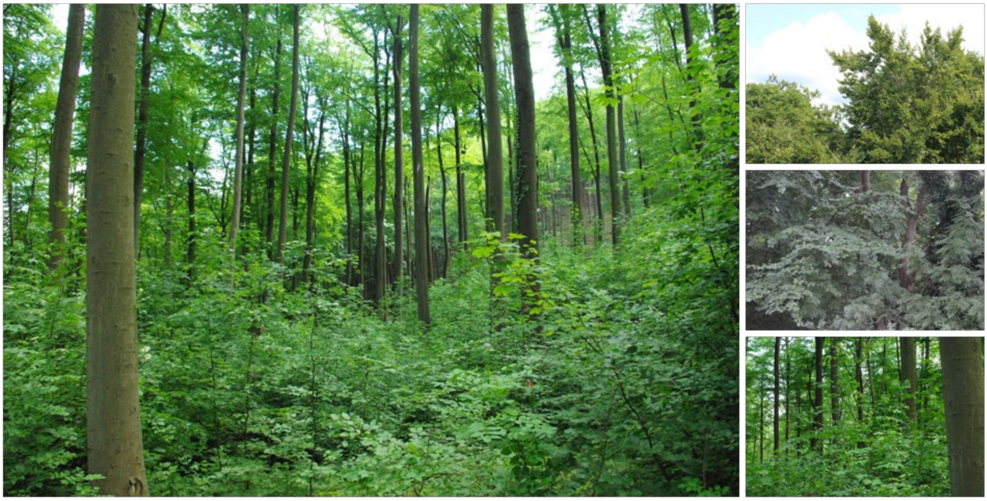


Figure 1.1: Example of a temperate forest site in Lower Saxony, Central Germany (left side), with the vertical gradient from bottom to top represented by the understorey, lower canopy, and upper canopy (right side).

1.2 Leaf traits affecting arthropod herbivory

Leaf traits determining leaf palatability

Herbivory can be affected by morphological and functional leaf traits like toughness, defence compounds, or nutrients (Stamp, 2003). These leaf traits differ among but also within host individuals of a given tree species (Laitinen *et al.*, 2000; Osier *et al.*, 2000), representing varying quality of plant resources (Dudt & Shure, 1994; Henriksson *et al.*, 2003). Differences of leaf traits lead to distinct feeding behaviour and development of insect herbivores (Osier & Lindroth, 2001; Fortin & Mauffette, 2002). On the one hand, positive effects on herbivore insects can refer to leaf nutrients (e.g. N). On the other, hand negative effects are represented by defensive leaf traits. Leaf palatability for arthropod herbivores is correlated with plant nutritional quality that is determined by the concentration of macronutrients (Marschner, 2011; Joern *et al.*, 2012), as well as secondary plant metabolites (Felton *et al.*, 1992; Summers & Felton, 1994; Steinbauer *et al.*, 2015). A variety of defensive leaf traits aims to avoid herbivory. Plant strategies and defensive leaf traits can be divided into structural (spines and thorns, trichomes, and toughened or hardened leaves), chemical (defence compounds), and phenological types (e.g. life-history of plants). In conclusion, various arthropod herbivores prefer to feed on soft leaves, which contain high protein and water content combined with low concentrations of phenolic compounds (Feeny, 1992).

Leaf toughness

Structural defensive traits include the toughness of leaves. Physical properties of leaves are important determinants of palatability and plant defence for herbivores (Agrawal & Fishbein, 2006). In general, leaf toughness is a common and effective defence feature of protecting leaves against a wide range of physical disturbances and herbivores (Edwards, 1989; Choong *et al.*, 1992; Lucas *et al.*, 2000; Sanson *et al.*, 2001; Peeters *et al.*, 2007). Herbivore damage has been shown to correlate with leaf toughness (Feeny, 1970). The palatability of leaves for arthropod herbivores is decreased through leaf toughness and folivory rates decline as leaf toughness increases in mature foliage (Coley *et al.*, 1985; Brunt *et al.*, 2006; Zehnder *et al.*, 2009). Expanding leaves are less tough due to constraints of cell expansion and cell-wall development. Fibre and lignin contents are correlated with leaf toughness that can be predicted by measurements of the force needed to penetrate a leaf sample (Arsuffi & Suberkropp, 1984), or the force that is necessary to tear apart a leaf sample (Graça *et al.*, 1993). Carbon-based physical traits (cellulose and lamina density) enhance leaf fracture toughness that can explain differences in herbivory and leaf lifespan of distinct plant species (Kitajima *et al.*, 2012).

An important morphological leaf trait is the leaf mass per area (LMA). Generally, the LMA is correlated with leaf toughness, and may also enhance leaf lifespan (Hanley *et al.*, 2007; Kitajima & Poorter, 2010; Onoda *et al.*, 2011). Long leaf lifespan requires the robustness and low palatability associated with high LMA (Reich *et al.*, 1997; Wright & Westoby, 2002). Leaf mass per area measures the leaf dry-mass that is invested per unit of light-intercepting leaf area. Leaves with high LMA are characterized by a thicker blade, a denser tissue, or both combined. For the calculation of LMA (g m^{-2}), the product of lamina density (LamD, g m^{-3}) and lamina thickness (LamT, m) is used to represent the ratio between leaf dry mass and leaf area (Witkowski & Lamont, 1991; Poorter *et al.*, 2009). It can be also used as its inverse, the specific leaf area (SLA, m^2 g^{-1}).

Defence compounds

Secondary metabolites produced by plants can influence behaviour, growth, and survival of herbivores. Chemical defence effects are repellent, toxic, or act as a reduction of plant digestibility for arthropod herbivores. These defence compounds can be always present in the plant (constitutive defences) or synthesized after initial herbivore damage (induced defences) (McKey, 1979). A great variety of defence compounds is synthesized by plants, which can be either present in many species or restricted to families, genus, or single species. Chemical plant defences include for example non-protein amino acids, phenolics, cyanogenic glycosides, glucosinolates, terpenoids, and alkaloids (Rosenthal & Berenbaum, 2012). Especially, non-protein amino acids and phenolics are directly effective against insect herbivores (Lattanzio *et al.*, 2006; Huang *et al.*, 2011). Volatile terpenoids are induced indirect plant defences that attract predators and parasitoids for herbivore insects (Mumm *et al.*, 2008). Glucosinolates even act as stimulants for oviposition and feeding of some coleopteran, lepidopteran, and dipteran insect species (Hopkins *et al.*, 2009). Some mechanism of plant toxins are revealed while many other modes of action still need to be understood (Wittstock & Gershenzon, 2002).

Tannins and lignins are phenolic defence compounds with high concentrations in all vascular plants. While tannins show a high structural diversity, lignins have a relatively restricted variation in structural features (Hagerman & Butler, 2012). Tannins are soluble components in the sap of living cells and reduce the availability of plant macronutrients (proteins and polysaccharides) and the activity of digestive enzymes of herbivores. Lignins are associated with polysaccharides of the cell wall and increase leaf toughness, which leads to limiting the digestibility of plants for herbivores.

Nutrients

Nutrients, which are obtained from host plants by arthropod herbivores, are essential for survival. Feeding on plants is a rather restricted diet and difficult to digest. Endosymbionts are necessary to compensate for vitamin deficiencies and to supply arthropod herbivores with enzymes and amino acids (Zwölfer, 2010). Furthermore, it is important for arthropod herbivores to obtain sufficient organically bonded N from plants. Biological molecules (e.g. proteins and nucleic acids) are built-on N and phosphorus (P) as important components (Marschner, 2011). Leaf N is essential for proteins of the photosynthetic machinery, particularly

Rubisco (Lambers *et al.*, 2008). Herbivory increases with leaf N content because higher concentrations have been linked to increased insect density, shorter development time, higher survival rates, and higher fecundity (Cisneros & Godfrey, 2001; Nevo & Coll, 2001; Huberty & Denno, 2006; Burns *et al.*, 2011).

Phosphorus is found in nucleic acids, lipid membranes, and bioenergetic molecules (e.g. ATP). It could be another limiting macronutrient because concentrations of plant P are significantly lower than insect P levels (Elser *et al.*, 2000). The survival (Clancy & King, 1993), development (Perkins *et al.*, 2004), and growth rates of herbivores (Watts *et al.*, 2006) are influenced by P. Furthermore, the insect herbivore performance can be optimized through an uptake of other macronutrients, supplementary to N and P (Behmer & Joern, 2008). Potassium, calcium, and magnesium are important for physiological processes (Marschner, 2011), but few research has studied their significance for insect herbivores.

1.3 Environmental effects on arthropod herbivory

Climate effects on arthropod herbivores

Climate is an important factor for insects with different impacts of temperature, air humidity, and precipitation. It determines their geographical range, the site and timing of activities, the success of oviposition and hatching, and the duration of developmental stages (Willmer, 1982). Insects can live in a wide range of thermal climates with maximum temperature reaching 40–50°C (Heinrich, 1981). They can survive extreme temperatures and are rather limited by sufficient summer heat (Bale *et al.*, 2002). Temperature influences developmental rates, voltinism, and population density. The activity of poikilothermic insects increases with temperature, and therefore growth and consumption rates are enhanced (Levesque *et al.*, 2002).

Air humidity is closely related to temperature and increases with precipitation. But limited and inconsistent results are found for direct effects of humidity on insects. On the one hand, dehydration of insects could be expected at dry conditions. On the other hand, pathogen infestation could increase with rising humidity. But studies have shown that there is no optimal level of humidity for insect development. Nymphal stages can survive and develop under a wide range of humidity conditions without optimal levels (Chiarelli *et al.*, 2011). In addition, insects can buffer humidity fluctuations with evolutionary adaptations, e.g. co-

coons and galls (Danks, 2002). Nonetheless, there is a possibility that high humidity supports fungal infection of insects (Wraight *et al.*, 2000).

Few studies have researched effects of changing precipitation on insects but rainfall generally increases mortality rates (Thacker *et al.*, 1997; Dixon, 1998; Bale *et al.*, 2002). In conclusion, insect life-history characteristics and distributions depend on climatic factors. Direct influences of climate on insects determine growth rates and development or act as a mortality factor. A successful adaptation to host plants and the climatic environment allows insect herbivores to complete their life cycles.

Climate effects on leaf traits

Life-forms and characteristics of plants are essentially influenced by climate factors. Climatic habitat conditions affect important leaf traits such as nutrient concentrations, leaf lifespan, and SLA (Wright *et al.*, 2004). In general, high temperature leads to an increase in SLA, but it strongly depends on higher soil moisture content and lower CO_2-concentration (Tjoelker *et al.*, 1999; Xu & Zhou, 2006). Plant species of arid and semi-arid regions tend to have tough leaves (low SLA), and leaves with thinner and larger lamina (high SLA) are typical features for plants in humid environments (Cunningham *et al.*, 1999; Fonseca *et al.*, 2000; Niinemets, 2001). Climatic conditions of xeric habitats lead to plants with sclerophyllous leaves. Dry environmental conditions that are based on low precipitation and air humidity, eventually combined with higher temperatures, cause stress situations for plants. In return, water stress can lead to sclerophylly, which is based in the accumulation of phenolics and lignification of leaf tissues (Bussotti *et al.*, 1997; Grossoni *et al.*, 1998).

Leaf nutrient concentrations and chlorophyll content both depend on moisture conditions. In general, drought stress can cause variations of chlorophyll content, respiration, and nutrient metabolism, which influences plant growth (Jaleel *et al.*, 2008). Low soil moisture conditions of dry environments, representing water stress for plants, lead to an increase of N content in plant tissues (Rouault *et al.*, 2006). Furthermore, the physiological state of plants is strongly affected by water supply, which influences photosynthetic processes. Generally, chlorophyll content decreases significantly through drought stress situations (Mafakheri *et al.*, 2010; Gholamin & Khayatnezhad, 2011; Aref *et al.*, 2013).

Along the vertical forest gradient, microclimate changes with increasing temperature and decreasing air humidity from the understorey to the upper canopy. This microclimatic pattern, caused by the light gradient, is visible during daylight along the growing season of temperate deciduous forests and can be reversed, weakened, or even disappear during the night (Parker, 1995; Tal *et al.*, 2008). Leaves of the same tree species differ along the vertical forest gradient. The development of sun and shade leaves is based on the adaptation to environmental conditions. Leaves of *Fagus sylvatica* L. (European beech; Fagaceae) show different leaf traits along the vertical forest gradient, with largest and toughest leaves in lower and upper canopies, respectively (Fig. 1.2).

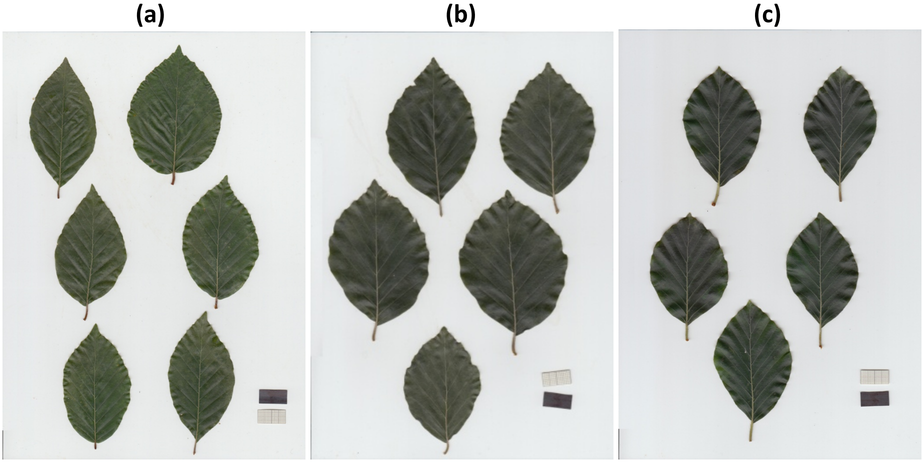


Figure 1.2: Leaves of *Fagus sylvatica* from the **(a)** understorey, **(b)** lower canopy, and **(c)** upper canopy.

1.4 Research question

Changing climatic conditions occur along the vertical micro-environmental gradient of forest stands. Based on the light exposure gradient, temperature and relative air humidity vary from upper canopies to lower canopies and the understorey. Furthermore, arthropod communities show a vertical stratification in forest layers. Contrasting results have been found for vertical patterns of insect herbivory with higher intensities in upper canopies or the understorey. Furthermore, most canopy research has been conducted in tropical forests which strongly differ in their ecological characteristics compared to temperate forest ecosystems.

Expected positive influences of temperature on herbivory could be reversed by unfavourable changes of important leaf characteristics, which are effected by temperature, too. This study investigated arthropod herbivory on leaves of deciduous tree species along the vertical gradient of temperate forests and consisted of a field study and an additional experimental study. Indirect climate effects on herbivory intensities were analyzed through measurements of leaf traits. The study was conducted addressing the following research questions:

1) What patterns of herbivory are present along the vertical gradient of temperate deciduous forests in Central Germany?
2) Do indirect effects via the host plant interfere with direct influences of climate on herbivory?
3) Does the herbivory pattern along the vertical forest gradient vary between different feeding guilds?

CHAPTER 2

METHODOLOGICAL RESEARCH CONCEPTION

2.1 Introduction

This chapter provides a general overview of the methods that were applied in the study. The research study investigated arthropod herbivory on leaves of deciduous tree species along the vertical gradient of temperate deciduous forests. A field study in 2012 and an experimental study with greenhouses in 2014 were used to address the research questions regarding the effects of microclimate and leaf traits on herbivory.

Generally, plant traits and herbivory are determined by a multitude of environmental and inter- or intraspecific interactions. Moreover, herbivory can be extremely variable on small spatial scales between individual leaves and branches (Lowman, 1985). The field study was undertaken across multiple forest sites to overcome the influence of small spatial scale differences on herbivory, and to obtain data with general patterns and validity.

The experimental study was additionally carried out to exclude factors of forest layers potentially influencing herbivory, which interfere with effects of microclimate on important leaf traits for herbivory. Different forest layers along the vertical forest gradient, representing distinct microclimates, vary in regard to further environmental factors (e.g. light condition and wind exposure). Outer canopies are characterized by increased wind exposure and higher irradiances compared to the understorey (Parker, 1995; Tal *et al.*, 2008). The experimental study provided consistent conditions for light and wind exposure, and enabled a research focus on the interaction between microclimate and leaf traits.

Furthermore, most leaf traits are dependent on seasonal and developmental stages, e.g. defence compounds increase with ontogeny (Boege & Marquis, 2005). Along the vertical forest gradient of the field study, the understorey and canopies were represented by juvenile and adult individuals, respectively. The ontogenetic effect was overcome in the experimental study using juvenile tree individuals of the same age.

Finally, soil fertility also influences leaf traits. Increases in specific leaf area (SLA) and leaf nitrogen (N) concentrations are connected to an increased soil fertility (Ordoñez *et al.*, 2009). Most study sites, with three exceptions, occurred on the same geological substrate (lower Trias sandstone). However, differences of soil conditions like fertility possibly exist between the ten studied forest sites and potentially influence the analyzed leaf traits. In the experimental study, any influence of soil fertility on analyzed leaf traits was avoided by applying a standard substrate to all trial pots.

2.2 Field study

Study area and subject

The study area was located in Central Germany within the federal states of Thuringia, Lower Saxony, and Hesse. Ten study sites were selected at mixed deciduous forest stands along a 140 km east–west transect (Chap. 3: Fig. 3.1; Chap. 4: Fig. 4.1). Elevations varied between the study sites and ranged between 140 and 444 m.a.s.l. Mean annual precipitation ranged from 474 mm to 874 mm based on data from the German Weather Service (reference period from 1961–1990). The geological substrate of the forest sites was mostly lower Trias sandstone, with exceptions of upper Trias sandstone at one site (Bocksbühl) and middle Triassic limestone at two sites (Feuerkuppe and Heidelberg).

Fagus sylvatica L. (European beech; Fagaceae) is the most common deciduous tree species in German forests (BMEL, 2016). The selected mixed deciduous forest sites for the research study were also dominated by *F. sylvatica*. Within the forests sites, adult and juvenile individuals of *F. sylvatica* were chosen for the investigation along the vertical forest gradient from the understorey to upper canopy. *Acer pseudoplatanus* L. (sycamore maple; Sapindaceae) and *Carpinus betulus* L. (hornbeam; Betulaceae) were frequent tree species in the understorey. Both deciduous tree species were selected for analyses of leaf traits and herbivory within the same microclimate (presented by the understorey).

Methods

Lower and upper canopies of adult *F. sylvatica* tree individuals were accessed with a climbing rope. A number of methods were applied for measurements of environmental parameters, leaf traits, biodiversity, and herbivory (Fig. 2.1). Microclimate (temperature and relative air humidity) was recorded with data loggers in the understorey, lower and upper canopy. Leaf traits were analyzed and represented by SLA, leaf N, leaf carbon (C), and chlorophyll content. Single methods are described in detail in Chapter 3.3 and 4.3. At all forest sites, biodiversity was measured for flora and fauna. The phytodiversity was assessed with vegetation surveys (number of plant species and abundances). Insect diversity was surveyed with window traps for flying insects, which were installed

Figure 2.1: Methods that were applied for the field study (clockwise starting top left): access of canopies with rope climbing, recording microclimate with data loggers, collecting insect samples with window traps in lower canopy and beating nets in all forest layers, vegetation survey, and collecting foliage samples.

in lower canopies of adult *F. sylvatica*. Sampled insects were sorted and counted on the level of orders. Methods applied for the biodiversity assessment are described in detail in Chapter 5.2.

This research study focused on herbivory as leaf damage caused by different arthropod herbivores. Exophagous (leaf-chewing and sap-sucking; Fig. 2.2a–b) and endophagous (leaf-mining and gall-inducing; Fig. 2.2c–d) feeding guilds distinguish the arthropod herbivores, which feed externally or internally on leaves, respectively. Herbivory was analyzed based on feeding traces on collected leaf material, and investigated in a qualitative and quantitative way along the vertical forest gradient. On the one hand, sampled foliage material was analyzed regarding the quantitative leaf area loss. On the other hand, feeding traces were identified and investigated concerning their distributions (number of attacked leaves). Arthropod

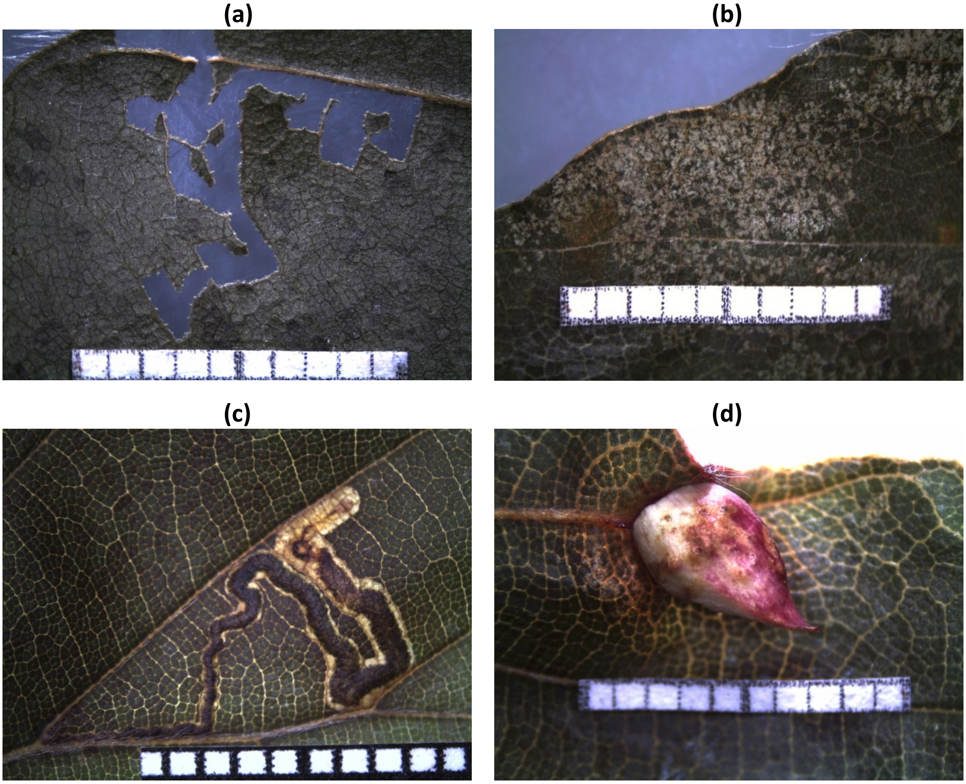


Figure 2.2: Feeding guilds of arthropod herbivores that were used in this research study represented by feeding traces of **(a)** leaf-chewing, **(b)** sap-sucking, **(c)** leaf-mining, and **(d)** gall-inducing species. One small square represents 1 mm^2.

herbivore species that probably caused the feeding traces were identified for *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* (App. A: Tab. 1A). Methods for the herbivory assessment are described in detail in Chapter 3.3 and Chapter 4.3.

2.3 Experimental study

Set up

The greenhouse experiment was carried out at the Samelsonplatz in Hildesheim, Germany. An old schoolyard behind the main building of the University of Hildesheim provided enough open space for the installation of two greenhouses (size: 6x28 m). The experimental design aimed to imitate the different microclimatic conditions from understorey and canopy with cooler and warmer temperatures as well as higher and lower air humidity, respectively. Random effects (light conditions, wind exposure, and soil fertility) from the field study were controlled and uniform factors in the greenhouses. Furthermore, investigated juvenile tree individuals of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* had the same age.

Methods

Manipulations of microclimate (type of greenhouse) and soil moisture (irrigation levels) were used as treatments for the trial pots with juvenile tree individuals. In the greenhouses, microclimatic conditions (temperature and relative air humidity) were recorded with data loggers. Soil moisture was measured with a soil moisture sensor. Leaf traits were analyzed and represented by SLA (indicator for leaf toughness) and chlorophyll content (indicator for N content). Leaf samples of tree individuals were taken to determine SLA. The chlorophyll content was directly measured in the greenhouses. A detailed description of the methods used in the experimental study is given in Chapter 6.3.

CHAPTER 3

READING THE LEAVES' PALM:
LEAF TRAITS AND HERBIVORY ALONG THE MICROCLIMATIC GRADIENT OF FOREST LAYERS

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3.1 Abstract

Microclimate in different positions on a host plant has strong direct effects on herbivores. But little is known about indirect effects due to changes of leaf traits. We hypothesized that herbivory increase from upper canopy to lower canopy and understorey due to a combination of direct and indirect pathways. Furthermore, we hypothesized that herbivory in the understorey differs between tree species in accordance with their leaf traits. We investigated herbivory by leaf chewing insects along the vertical gradient of mixed deciduous forest stands on the broad-leaved tree species *Fagus sylvatica* L. (European beech) with study sites located along a 140 km long transect. Additionally, we studied juvenile *Acer pseudoplatanus* L. (sycamore maple) and *Carpinus betulus* L. (hornbeam) individuals within the understorey as a reference of leaf traits in the same microclimate. Lowest levels of herbivory were observed in upper canopies, where temperatures were highest. Temperature was the best predictor for insect herbivory across forest layers in our study. However, the direction was opposite to the generally known positive relationship. Herbivory also varied between the three tree species with lowest levels for *F. sylvatica*. Leaf C content was highest for *F. sylvatica* and probably indicates higher amounts of phenolic defence compounds. We conclude that the effect of temperature must have been indirect, whereby the expected higher herbivory was suppressed due to unfavourable leaf traits (lower nitrogen content, higher toughness and carbon content) of upper canopy leaves compared to the understorey.

3.2 Introduction

Insect herbivores play an important role in ecosystems and affect their structure and function (Crawley, 1983; Mulder *et al.*, 1999). Leaf area loss to insects reduces tree growth (Marquis & Whelan, 1994; Wagner *et al.*, 2008), and redirects primary production into the herbivore food chain (McNaughton *et al.*, 1989; Cebrian, 1999), altering material flows from canopies to forest soils (Hunter, 2001; Hartley & Jones, 2004). These interactions are influenced by the environment, essentially by climatic conditions (temperature and air humidity). Effects of climate on insect herbivory are complex because any factor can affect the insect and the plant at the same time, sometimes with opposite consequences for herbivory.

For example, temperature can affect insect physiology and behaviour directly or indirectly through climate-induced changes of host plants (Bale *et al.*, 2002).

Temperature determines herbivore growth and development (Simonet *et al.*, 1981; Levesque *et al.*, 2002), movement or activity rates (Wiktelius, 1981), and distribution (Strathdee *et al.*, 1993; Whittaker & Tribe, 1998), and therefore influences the feeding intensity.

Developmental rates of insect herbivores increase with temperature. In contrast, limited and inconsistent results are found for direct effects of humidity (Chiarelli *et al.*, 2011). Unlike temperature, under a wide range of humidity conditions there is no optimal level and insect herbivores can buffer humidity fluctuations (Danks, 2002). Low levels of humidity leading to water stress of host plants can benefit defoliators through increased nitrogen (N) content in plant tissue as an indirect effect (Rouault *et al.*, 2006). Nonetheless, a meta-analysis revealed inconsistent responses of plant water stress for leaf-chewers and miners (Huberty & Denno, 2004).

Indirect effects of microclimate on herbivory can also be mediated by morphological and functional leaf traits like toughness, nutrients, or defence compounds (Stamp, 2003). Carbon (C) and N content of leaves are important predictors for herbivory levels (Mattson, 1980). Herbivory increases with leaf N, which has been linked to increased insect density, shorter development time, higher survival rates, and higher fecundity (Cisneros & Godfrey, 2001; Stiling & Moon, 2005; Huberty & Denno, 2006). Carbon content is negatively correlated to leaf palatability (Schädler *et al.*, 2003) because mechanical or chemical defences are often carbon-based (Feeny, 1970; Southwood *et al.*, 1986). Also leaf toughness negatively influences the palatability for insect herbivores (Brunt *et al.*, 2006; Zehnder *et al.*, 2009). Negative changes of leaf traits for insect herbivores can suppress expected high rates of herbivory in warm environments (Niesenbaum & Kluger, 2006). Therefore, it is essential for research to consider the indirect effects of leaf traits besides direct effects of microclimate.

On a local scale, microclimate gradients are found across the different strata of forests. Abiotic factors change between layers within forest stands due to the vertical micro-environmental gradient (Eliáš *et al.*, 1989; Ellsworth & Reich, 1993). Along the vertical gradient, microclimate is affected by the light regime, with increasing temperature and decreasing humidity from understorey to outer canopies, especially during sunshine. Outer canopies of trees experience high irradiances, vapour pressure deficits, and temperature fluctuations (Parker, 1995). The understorey of forests is characterized by low light, damped temperature fluctuations and generally high air humidity. Existing studies have evidenced variable patterns of herbivory for sun and shade leaves. Sun leaves of slow-growing species are either less attractive for insect herbivores (Mole & Waterman, 1988; Dudt & Shure, 1994), or reveal higher herbivory (Futuyma & Saks, 1981; Lincoln & Mooney, 1984; Harrison, 1987; Louda & Rodman, 1996). Under standardized temperatures, leaves from the outer canopy show higher palatability for herbivores (Fortin & Mauffette, 2002), or no consistent difference compared to leaves from lower forest layers (Ruhnke *et al.*, 2009). In contrast, under field conditions lower herbivory is observed on outer canopy leaves of *Fagus crenata* (Yamasaki & Kikuzawa, 2003). Few studies have focused on effects of leaf spatial location within tree canopies on herbivore insects. They reveal preference of shade leaves close to ground level for grazing (Lowman, 1985), higher aggregation and feeding of beetles in upper canopies (Rowe & Potter, 1996), and that the difference in herbivory of upper and lower canopies varies in direction and magnitude depending on tree species (Ruhnke *et al.*, 2009). This complicates generalizations about the responses of insect herbivores and patterns of herbivory to different microclimates on the same host plant.

Few studies include the whole vertical forest gradient. They show migration of moth larvae from canopies to understorey seedlings due to changes in leaf quality (Murakami & Wada, 1997), and higher herbivore performance in upper canopies with leaves containing more total N (Fortin & Mauffette, 2002). In this study, we investigated levels of herbivory caused by leaf-chewing insects (leaf damage as percentage of missing leaf area) along the whole vertical gradient of forest stands on the broad-leaved tree species *Fagus sylvatica* L. (European beech; Fagaceae). We compared leaf damage between different microclimates (understorey, lower and upper canopy) of mature *F. sylvatica* individuals. Patterns of herbivory were analyzed with respect to abiotic factors (microclimate, leaf toughness and leaf nutrients) determining interactions and main predicting parameters for herbivory levels along the vertical forest gradient. Additionally, we studied juvenile *Acer pseudoplatanus* L. (sycamore maple; Sapindaceae) and *Carpinus betulus* L. (hornbeam; Betulaceae) individuals within the understorey as a reference of leaf traits in the same microclimate. We tested the following alternative hypotheses for the vertical forest gradient: 1) herbivory increases towards upper canopies of *F. sylvatica* through higher temperatures (direct effect of microclimate) or 2) oppositely, herbivory may be decreased in upper canopies through a shift of leaf traits towards lower palatability (indirect effect of microclimate with low leaf N content as well as high leaf C content and leaf toughness). Furthermore, we hypothesized that 3) herbivory in the understorey differs between tree species in accordance with their leaf traits, i.e. increases with leaf N content and decreases with leaf C content and leaf toughness.

3.3 Materials and methods

Ethics statement

Field work permits were issued by the responsible forestry offices Leinefelde (Winkelberg and Hubenberg), Neuhaus (Tiefentals Ebene), Münden (Klingenberg/Vaaker Berg), Wehrtal (Schieferstein), Hessisch-Lichtenau (Heiligenberg), Reinhausen (Bocksbühl), Michael Wienrich (Feuerkuppe), and Oldisleben (Heidelberg and Eichleite). The study sites comprise state forests and private forest. During this study no species that are protected by European or national laws were sampled. Jasmin Mantilla-Contreras received financial support from the University of Hildesheim. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Study area

The study was conducted in the centre of the distribution range of *F. sylvatica* within the hill and mountain region of Central Germany. We selected ten study sites with mixed deciduous forest stands in Thuringia, Lower Saxony and Hesse at elevations between 140 and 444 m.a.s.l. (Fig. 3.1). Study sites were located along a 140 km long transect with increasing annual precipitation from east to west. According to the German Weather Service, mean annual precipitation ranges from 474 mm (Artern, Thuringia) to 874 mm (Herzberg, Lower Saxony) based on the reference period from 1961–1990 (Fig. 3.1). Mean annual temperature in the study area was similar among the different forest sites, and has increased from about 8 °C to 9 °C until the beginning of the 21th century (App. B: Tab. 2A).

Most study sites occurred on the same geological substrate (lower Trias sandstone), with exceptions of Bocksbühl (upper Trias sandstone), Feuerkuppe, and Heidelberg (middle Triassic limestone). Our stand selection criteria were (i) closed canopy without major gaps, (ii) no significant presence of coniferous tree species, and (iii) stem circumference of adult beech individuals >1 m (average circumference: 1.80 m).

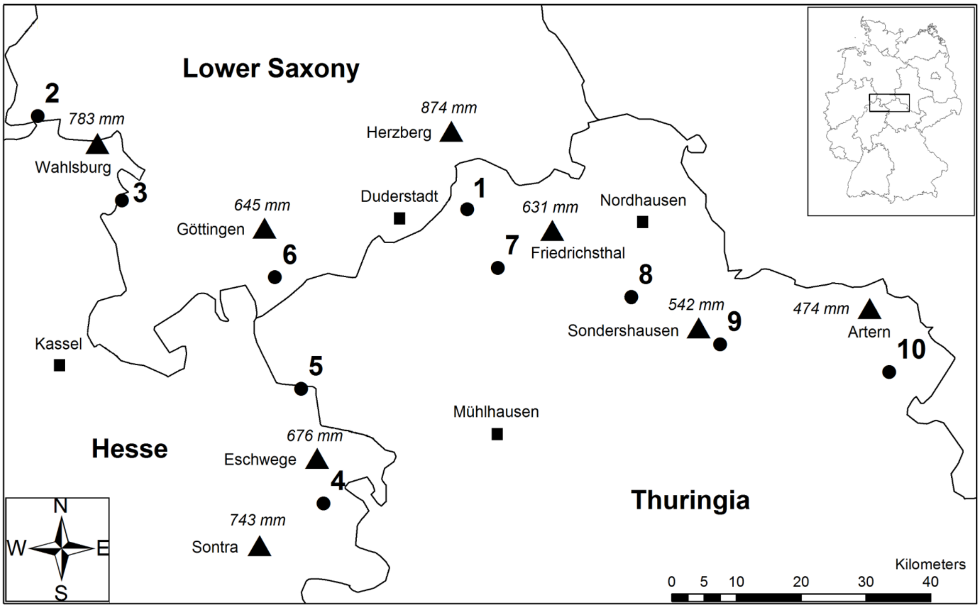

Figure 3.1: Overview of the ten forest study sites (circles) in Thuringia, Lower Saxony and Hesse. Weather stations (triangles) present mean annual precipitation (italic values) from reference period 1961–90 (German Weather Service). Forest sites: **(1)** Winkelberg; **(2)** Tiefentals Ebene; **(3)** Klingenberg/Vaaker Berg; **(4)** Schieferstein; **(5)** Heiligenberg; **(6)** Bocksbühl; **(7)** Hubenberg; **(8)** Feuerkuppe; **(9)** Heidelberg; and **(10)** Eichleite. Reprinted from BKG under a CC BY license, with permission from Bundesamt für Kartographie und Geodäsie, original copyright GeoBasis-DE / BKG 2015 (data changed).

Sampling trees

We selected most common tree species found in forest stands of the study area. Within the study area, *F. sylvatica* was the dominant broad-leaved tree species in mixed deciduous forests and therefore chosen as main object of focus. *Acer pseudoplatanus* and *C. betulus* were frequent in the understorey at nine forest sites and included into the study to investigate differences and influences of leaf traits within the same forest layer. Within the ten forest sites, we undertook a random selection of juvenile and adult study tree individuals with north as well as south exposition. At each of the 20 exposition sites, three juvenile individuals (if available) of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* were selected in the understorey for further analysis (App. C: Fig. 1A). Additionally, we surveyed three adult individuals of *F. sylvatica* at the lower and upper canopy at each sample site. Selection of sample individuals at north and south exposition and in different forest layers represented a variation of microclimatic conditions. We selected a total of 60 adult and juvenile *F. sylvatica*, 41 juvenile *A. pseudoplatanus*, and 27 juvenile *C. betulus* individuals.

Data collection

Microclimatic data (air temperature and relative air humidity) were measured every hour with data loggers (iButton, Model DS1923, Maxim Integrated, San Jose, CA, USA) for two months (July–August 2012). Data loggers were installed within the understorey (about 1 m height), as well as in lower (about 18 m height) and upper canopies (about 35 m height) of adult beech trees per sample site. We accessed the (inner) lower and (outer) upper canopy of adult beech trees by rope climbing. Foliage material was collected in June 2012 at each sample site and analyzed according to LEDA trait standards (Cornelissen *et al.*, 2003). Single foliage samples of all available individuals were randomly taken within the layers of selected trees for analysis of specific leaf area (SLA), as an indicator for toughness, nutrients (C and N), and herbivory (samples of twigs). All collected material was deep frozen until analyses were carried out. At some sample sites, juvenile tree individuals of *A. pseudoplatanus* and *C. betulus* were too small for harvesting enough foliage sample material. In this case, one sample consisted of several individuals. Given that chlorophyll content correlates with N content (van den Berg & Perkins, 2004), measures of chlorophyll content index (CCI) were estimated with a CCM-200 plus Chlorophyll Content Meter (Opti-Sciences Inc., Hudson, NH, USA). For each tree individual, we took ten values directly in the field in June 2012.

Analyses

Microclimatic data of the three forest layers (understorey, lower and upper canopy) were used as average daily values (6 am to 9 pm) from 01-July-2012 to 31-August-2012, based on the higher variation of temperature and humidity during day and its influence on plant-insect interactions. Specific leaf area was calculated for ten leaves of each tree individual (five leaves for *A. pseudoplatanus*). We scanned all fresh leaves with a flat-bed scanner and analyzed their areas with the computer image analysis system WinFOLIA (Régent Instruments Inc., Ville de Québec, QC, Canada). Then, we dried (70 °C, 48 h) and weighed foliage samples.

We conducted nutritional analyses with mixed samples consisting of 10 (*F. sylvatica* and *C. betulus*) and 5 (*A. pseudoplatanus*) leaves per individual.

Grounded samples were analyzed for total C and N content with a C/N elemental analyzer (Department of Plant Ecology and Ecosystem Research, University of Göttingen, Göttingen, Germany). As a combination of positive indicator for nutrients and negative indicator for defence compounds we used the C/N ratio. Specific leaf area, nutrient, and chlorophyll parameters were used as mean values for each species and forest layer at the 20 sampled exposition sites.

We determined herbivory as the percent area of missing leaf tissue. Therefore, we scanned leaves of collected twigs with a flat-bed scanner (n(*F. sylvatica* understorey) = 1801; n(*F. sylvatica* lower canopy) = 1120; n(*F. sylvatica* upper canopy) = 1425; n(*A. pseudoplatanus*) = 528; n(*C. betulus*) = 628) and then analyzed them with the computer image analysis system WinFOLIA (Régent Instruments Inc., Ville de Québec, QC, Canada). Leaf damage, including area of missing leaf edges, along the forest layer gradient was calculated for all species at the 20 exposition sites with the potential leaf size (existing plus missing leaf area) and the missing leaf area. Most leaf-chewing insect species that feed on leaves in temperate broadleaved forests are polyphagous (Kimber, 2017; Rennwald & Rodeland, 2017). Based on the feeding traces on *F. sylvatica*, some herbivore insect species that cause loss of leaf tissue were identified, all of which are polyphagous (*Diurnea fagella* D. & S., *Orchestes fagi* L., and *Phyllobius argentatus* L.).

For significant comparison of measured parameters and leaf damage along the vertical forest gradient and the three tree species in the understorey, we performed statistical analyses in R (R development core team 2013, version 3.0.2). Normal statistical distribution for temperature, air humidity, SLA, leaf N and C content, C/N ratio, and chlorophyll content was assessed with Shapiro-Wilk test and further tests were performed with ANOVA or Kruskal-Wallis and post-hoc tests, depending on the statistical distribution.

Determining parameters for herbivory were tested with linear mixed models. For herbivory of *F. sylvatica*, model comparison was conducted for effects of forest layer, microclimate (2 parameters) and leaf traits (5 parameters) with a model specification (Equation 3.1).

$$\begin{aligned}\mathrm{lmer}(&\mathrm{herbivory} \sim \mathrm{forest\ layer} + \mathrm{temperature} + \mathrm{air\ humidity}\\ &+ \mathrm{N\ content} + \mathrm{C\ content} + \mathrm{chlorophyll} + \mathrm{C/N\ ratio}\\ &+ \mathrm{SLA} + (1|\mathrm{site}), \mathrm{REML} = \mathrm{FALSE})\end{aligned} \tag{3.1}$$

Model comparison for the three tree species in the understorey was assessed for effects of species, microclimate (2 parameters) and leaf traits (5 parameters) with a model specification (Equation 3.2).

$$\begin{aligned}\mathrm{lmer}(&\mathrm{herbivory} \sim \mathrm{species} + \mathrm{temperature} + \mathrm{air\ humidity} \\ &+ \mathrm{N\ content} + \mathrm{C\ content} + \mathrm{chlorophyll} + \mathrm{C/N\ ratio} \\ &+ \mathrm{SLA} + (1|\mathrm{site}), \mathrm{REML} = \mathrm{FALSE})\end{aligned} \tag{3.2}$$

Herbivory was square-root transformed and all models contained study site as a random effect. Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016). We selected the best model based on the Bayesian Information Criterion (BIC). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Linear regressions for herbivory and the best determining parameter were calculated (Equation 3.3).

$$\mathrm{lm}(\mathrm{herbivory} \sim \mathrm{parameter}) \tag{3.3}$$

3.4 Results

Microclimate

Neither temperature nor relative air humidity showed significant differences between north (e.g. understorey: 17.8 °C ± 0.2 SD; 84.5% ± 3.3 SD) and south expositions (e.g. understorey: 18.1 °C ± 0.6 SD; 81.8% ± 5.3 SD). Thus, we excluded exposition as a parameter from further analyses. In contrast, microclimatic conditions varied significantly between the three forest layers across all sample sites. Average temperature increased from understorey (17.9 °C ± 0.5 SD) to lower canopy (18.8 °C ± 0.5 SD) and upper canopy (20.1 °C ± 0.8 SD) (Fig. 3.2a). Air humidity and temperature showed a strong negative correlation (rho = -0.87; $p<0.001$) (App. C: Tab. 3A and Fig. 2A). Accordingly, average air humidity decreased from understorey (83.1% ± 4.5 SD) to lower canopy (74.1% ± 2.8 SD) and upper canopy (69.2% ± 2.2 SD) (Fig. 3.2b). Therefore, forest layers represented different microclimates and were further investigated.

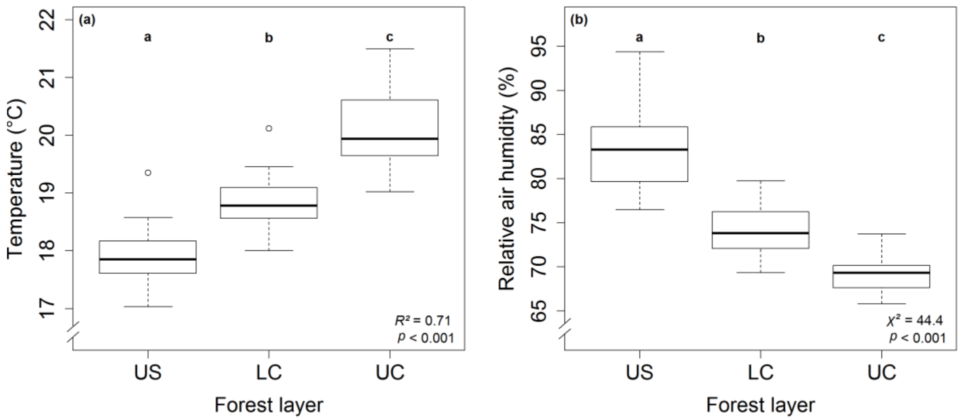

Figure 3.2: Microclimate along the vertical forest gradient. Microclimatic conditions for understorey (n = 20), lower (n = 20) and upper canopy (n = 17) represented by **(a)** temperature and **(b)** relative air humidity. Boxplots with lowercase letters indicate significant differences using **(a)** ANOVA and Tukey's HSD (p<0.05; df = 2) and **(b)** Kruskal-Wallis and post-hoc test (p<0.05; df = 2). US = understorey; LC = lower canopy; UC = upper canopy.

Leaf parameters

Specific leaf area of *F. sylvatica* differed significantly between forest layers and decreased from understorey to lower and upper canopy (Fig. 3.3a). Leaves of upper canopies were thicker than in the understorey. Total leaf C content increased on average from 474 mg g^{-1} ± 4 SD to 484 mg g^{-1} ± 5 SD along the forest layer gradient (Fig. 3.3b). Average total leaf N content was significantly reduced in upper canopies (20.9 mg g^{-1} ± 2.1 SD) compared to lower canopies (23.1 mg g^{-1} ± 2.9 SD) and the understorey (22.4 mg g^{-1} ± 2.8 SD) (Fig. 3.3c). Patterns of C and N content resulted in significantly augmented C/N ratio in upper canopies (23.3 g g^{-1} ± 2.3 SD) versus lower canopies (21.0 g g^{-1} ± 2.4 SD) and understorey (21.6 g g^{-1} ± 3.0 SD) (Fig. 3.3d). Values for chlorophyll content did not vary significantly along the vertical forest gradient and ranged on average between 13.2 CCI ± 1.8 SD (upper canopy), 13.4 CCI ± 1.7 SD (understorey), and 14.2 CCI ± 2.2 SD (lower canopy).

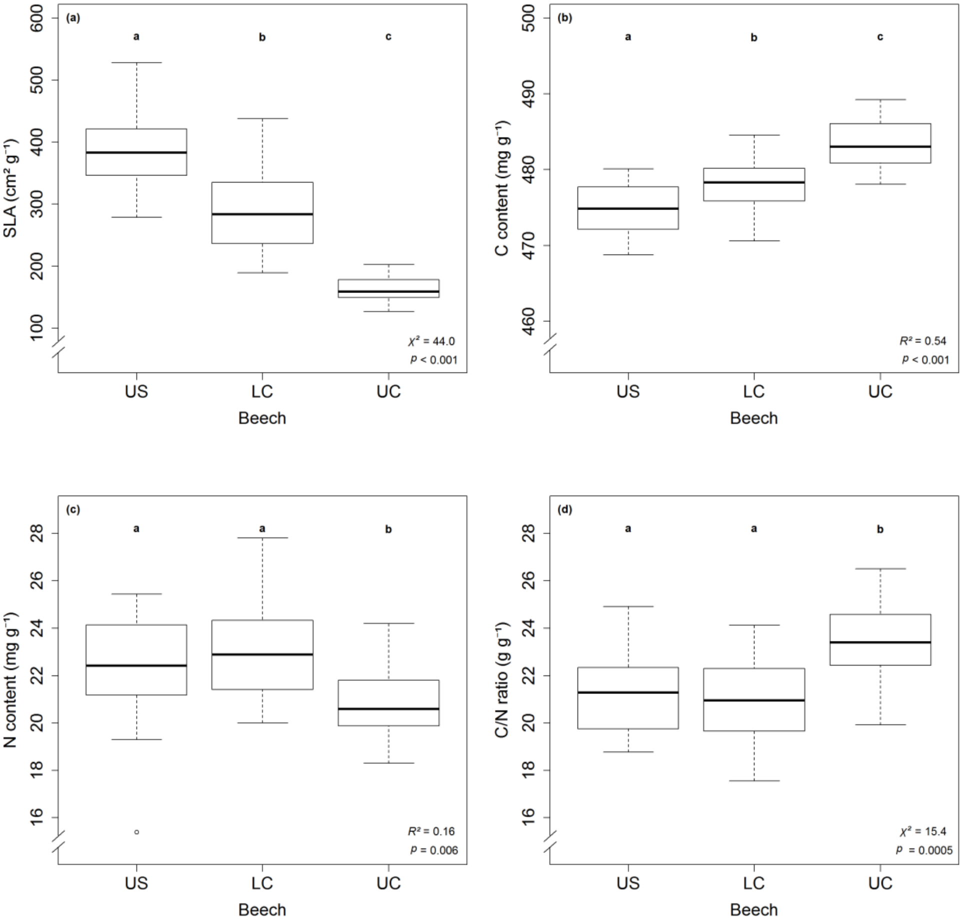

Figure 3.3: Leaf parameters for *Fagus sylvatica* (n = 60) are represented by **(a)** specific leaf area (SLA), **(b)** total carbon (C) content, **(c)** total nitrogen (N) content, and **(d)** C/N ratio along the forest layers. Boxplots with lowercase letters indicate significant differences using **(b)–(c)** ANOVA and Tukey's HSD ($p<0.05$; df = 2) and **(a)** and **(d)** Kruskal-Wallis and post-hoc test ($p<0.05$; df = 2). US = understorey; LC = lower canopy; UC = upper canopy.

Leaf traits were strongly correlated to microclimate (App. C: Tab. 3A and Fig. 2A). With increasing temperature, C content increased (rho = 0.59; $p<0.001$) and SLA decreased (rho = -0.78; $p<0.001$) resulting in a converse correlation pattern for air humidity with C content (rho = -0.65; $p<0.001$) and SLA (rho = 0.89; $p<0.001$). Further correlations were found between N content and SLA (rho = 0.55; $p<0.001$), C/N ratio and SLA (rho = -0.60; $p<0.001$) as well as N and chlorophyll content (rho = 0.26; $p<0.0429$).

Within the same microclimate, leaf parameters were less variable between *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* in the understorey. Average values for SLA did not vary significantly due to high standard deviations (Tab. 3.1). Carbon content of *F. sylvatica* leaves was significantly higher than for leaves of *A. pseudoplatanus* and *C. betulus*. Other leaf parameters like N content, C/N ratio, and chlorophyll content did not vary significantly between the three species in the understorey. Chlorophyll content of *A. pseudoplatanus* leaves was on average highest but with higher variation of values (Tab. 3.1).

Table 3.1: Leaf parameters of juvenile *Fagus sylvatica* (n = 20), *Acer pseudoplatanus* (n = 14), and *Carpinus betulus* (n = 10) individuals represented by specific leaf area (SLA), carbon (C) and nitrogen (N) content, C/N ratio, and chlorophyll content in the understorey. Presented are mean values with standard deviation.

Species	**SLA** ($cm^2\ g^{-1}$)	**C** ($mg\ g^{-1}$)	**N** ($mg\ g^{-1}$)	**C/N ratio** ($g\ g^{-1}$)	**Chlorophyll** (CCI)
Fagus sylvatica	388 ± 64^a	474 ± 4^a	22.4 ± 2.8^a	21.6 ± 3.0^a	13.4 ± 1.7^a
Acer pseudoplatanus	345 ± 52^a	456 ± 5^b	23.0 ± 4.3^a	20.6 ± 4.1^a	15.1 ± 4.0^a
Carpinus betulus	353 ± 35^a	457 ± 6^b	22.4 ± 2.8^a	20.7 ± 2.5^a	13.4 ± 2.4^a

Lowercase letters indicate significant differences using Kruskal-Wallis and post-hoc test ($p<0.05$; df = 2).

Herbivory patterns

Overall, leaf damage of *F. sylvatica*, *A. pseudoplatanus* and *C. betulus* due to insect herbivores showed low values between 1.4% and 5.5% on average. For *F. sylvatica*, leaf damage differed between forest layers and showed highest values in the understorey (Fig. 3.4a). Differences were significant between upper canopy (1.5% ± 1.6 SD) and understorey (2.9% ± 1.3 SD). Within the understorey, leaf damage varied between the three species with significant differences between *F. sylvatica* (2.9% ± 1.3 SD) and *C. betulus* (5.5% ± 2.5 SD) (Fig. 3.4b). *Acer pseudoplatanus* showed highest variation of herbivory (4.6% ± 2.8 SD) and ranged between *F. sylvatica* and *C. betulus* with no significant differences to them.

Based on the BIC, herbivory of *F. sylvatica* across forest layers was slightly better explained by temperature than by humidity or leaf traits (App. C: Tab. 4A). Herbivory decreased with increasing temperature from the understorey to upper canopies. Within the understorey, herbivory of juvenile individuals was better

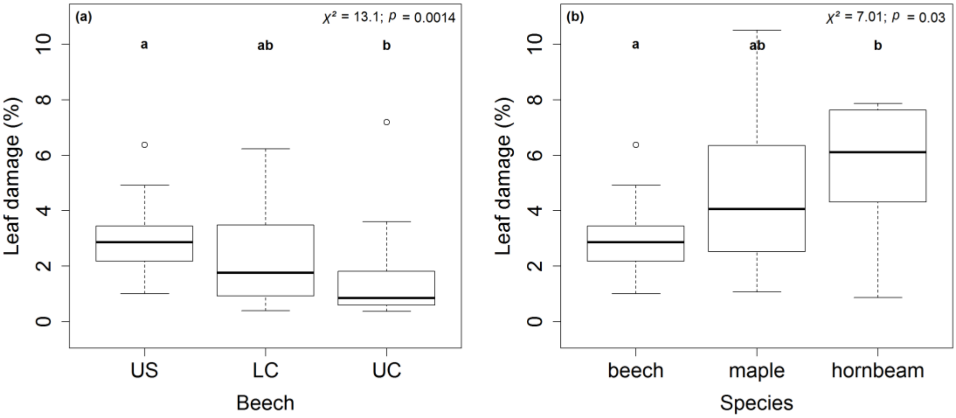

Figure 3.4: Herbivory patterns along the vertical forest gradient. Leaf damage (missing leaf area) of **(a)** *Fagus sylvatica* (beech; n = 60) in different forest layers and **(b)** the three tree species (*F. sylvatica*: n = 20; *Acer pseudoplatanus* (maple): n = 14; *Carpinus betulus* (hornbeam): n = 10) in the understorey. Boxplots with lowercase letters indicate significant differences using Kruskal-Wallis and post-hoc test ($p<0.05$; df = 2). US = understorey; LC = lower canopy; UC = upper canopy.

explained by tree species, followed by leaf C content as the second best model (App. C: Tab. 5A). Linear regressions based on the selected predictors for herbivory of *F. sylvatica* (Fig. 3.5a) and the juvenile tree individuals (Fig. 3.5b) showed significant relations.

3.5 Discussion

Leaf traits along the vertical forest gradient

All measured leaf traits of *F. sylvatica*, except chlorophyll content, changed significantly along our vertical forest gradient. Leaves in upper canopies showed lower SLA and leaf N content as well as higher leaf C content and C/N ratio than in the understorey. The strongest difference was observed in SLA, where the values dropped by half from understorey to upper canopy. In general, high temperature leads to an increase in SLA, but it strongly depends on higher soil moisture content and lower CO_2-concentration (Tjoelker *et al.*, 1999; Xu & Zhou, 2006). Photosynthesizing leaves in the understorey experience higher CO_2-concentrations (a result of plant and soil respiration) than leaves of upper canopies (Bazzaz & Williams, 1991; Brooks *et al.*, 1997; Koike *et al.*, 2001), suggesting lower SLA in the

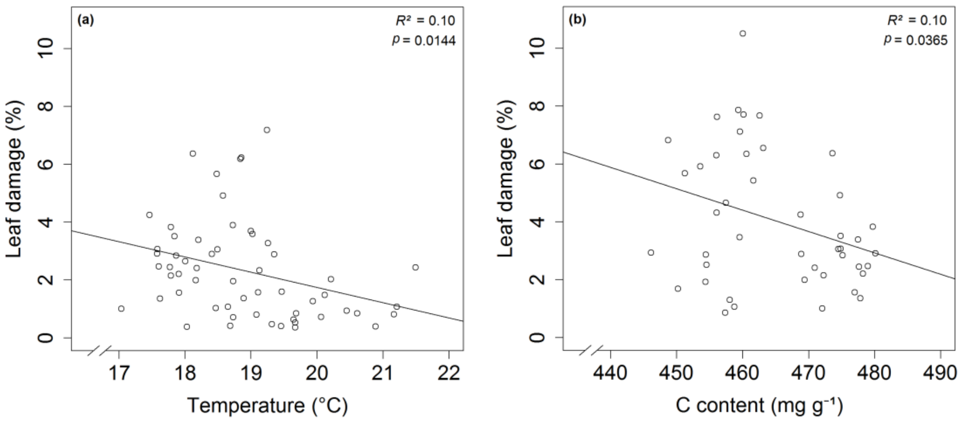

Figure 3.5: Linear regressions for herbivory with selected predictors from the model comparison. Presented are leaf damage (missing leaf area) of **(a)** *Fagus sylvatica* according to temperature along the vertical forest gradient (n = 57) and **(b)** based on leaf carbon (C) content for *F. sylvatica*, *Acer pseudoplatanus* and *Carpinus betulus* in the understorey (n = 44).

understorey. However, air humidity also plays an important role for leaf trait characteristics, e.g. leaf length (Kessler *et al.*, 2007). Our pattern of decreasing SLA from understorey to upper canopy coincides with other studies (Ellsworth & Reich, 1993; Koike *et al.*, 2001; Afas *et al.*, 2007). The formation of thinner and larger leaf lamina (high SLA values) is a common response to a humid environment (Cunningham *et al.*, 1999; Niinemets, 2001; Sellin *et al.*, 2013). This finding supports a stronger influence of humidity than temperature on the characteristic of SLA.

Nutritional quality of plant material with higher N concentrations is usually increased in sun-exposed leaves (Fortin & Mauffette, 2002; Levesque *et al.*, 2002). However, leaf N concentration of *F. crenata* decreases as light availability increases (Yamasaki & Kikuzawa, 2003). We found a similar pattern for *F. sylvatica* with lower N concentration in upper canopy leaves compared to the understorey. Since *F. sylvatica* is a shade-tolerant tree species, higher leaf N concentration in lower light environment is a strategy of N partitioning for more efficient light harvesting (Niinemets, 1995). Therefore, higher nutritional quality leaves of *F. sylvatica* are found in the understorey.

Generally, sun leaves of slow growing species produce more carbon-based secondary defence compounds than shade leaves (Mole & Waterman, 1988; Dudt & Shure, 1994). Chemical defences of woody plants also vary by growth stage, increasing from juveniles to adults (Bryant *et al.*, 1991). According to the C/N balance hypothesis (Coley *et al.*, 1985), an increase in C/N ratio positively correlates with levels of defence compounds. Our pattern of leaf C content along the vertical forest gradient is plausible, because concentrations were highest in sun-exposed leaves of adult *F. sylvatica* individuals. Furthermore, increased leaf C content and C/N ratio in leaves of upper canopies of *F. sylvatica* suggest higher amounts of carbon-based defence compounds.

In our study, a trend of positive correlation between chlorophyll and leaf N content was visible. Chlorophyll content is certainly dependent on light conditions through its regulating influence on photosynthesis. Studies have presented contrary results with sun leaves of *F. sylvatica* showing higher chlorophyll content than shade leaves (Lichtenthaler *et al.*, 2000), while in other tree species shade leaves contain more chlorophyll than sun leaves (Matyssek *et al.*, 2010). Measurements of chlorophyll are easy to conduct and a non-destructive method is possible. But since the amount of chlorophyll does not account for the total leaf N content, it appears to be a weak parameter for herbivory levels.

Growing in the same microclimate, SLA, leaf N content, C/N ratio, and chlorophyll content did not differ significantly between the three tree species in the understorey. Only leaf C content was significantly higher for *F. sylvatica* compared to *A. pseudoplatanus* and *C. betulus*. A defence index based on leaf size, chemical and mechanical defence for large mammalian herbivores rates all our studied tree species with no defensive traits (Borchard *et al.*, 2011). However, it is known that *F. sylvatica* trees typically have the highest amount of phenols compared to co-occurring species in mixed beech forests (Bussotti *et al.*, 1998). Therefore, increased leaf C content of *F. sylvatica* suggests higher amounts of phenolic defence compounds against insect herbivores compared to *A. pseudoplatanus* and *C. betulus*, in line with the lower herbivory observed on juvenile *F. sylvatica*.

Forest-layer and species-specific herbivory

Arthropod herbivory is considered to be generally low in temperate forest tree canopies (i.e. up to 7.5% of leaf area eaten), except in outbreak situations (Franklin, 1973; Coley & Aide, 1991). Leaf area loss to insects accumulates over time, although the highest damage rates occur on young, high-quality leaves. Folivory rates decline as nutritional quality like N content decreases and leaf toughness increases in mature foliage (Feeny, 1970; Coley *et al.*, 1985; Brunt *et al.*, 2006; Zehnder *et al.*, 2009). Also, percentages of leaf area removed from lower canopies are significantly greater compared to upper canopies (Reynolds & Crossley, 1997). Typical leaf damage is determined about 6% for *F. sylvatica* in late summer (Gossner *et al.*, 2014). Herbivory levels of our study were somewhat below this range for *F. sylvatica* at all forest layers. Highest rates (2.9% ± 1.3 SD) occurred in the understorey and where significantly lower than herbivory levels of *C. betulus* and *A. pseudoplatanus*. Greater herbivory on *A. pseudoplatanus* compared to *F. sylvatica*, with leaf area loss reaching 7.6% (Sobek *et al.*, 2009b), is known from other studies, too (Modrý *et al.*, 2004). Highest rates of consumed leaf area show similar values around 3.3% for *F. crenata* in spring and a further increase in loss of leaf area occurs in lower parts of the canopy after June (Yamasaki & Kikuzawa, 2003). Since our field work was done in June, herbivory levels in lower canopies and the understorey might have still increased towards the end of the growing season.

Indirect effects interfere with temperature influence

According to model comparisons, temperature was the best predictor for insect herbivory across forest layers in our study. However, the direction was opposite to the generally known positive relationship between herbivory and temperature: lowest levels of herbivory were observed in upper canopies, where temperatures were highest. Thus, the effect of temperature must have been indirect, either through reduced humidity or through reduced palatability of leaves in the upper canopy. If reduced herbivory in upper canopies is related to higher C content, then the mechanism for higher herbivory levels of *A. pseudoplatanus* and *C. betulus* compared to *F. sylvatica* in the understorey could be the same as for herbivory of *F. sylvatica* along the vertical forest gradient. However, further study is needed to differentiate between air humidity, SLA and leaf chemical composition.

Leaves in upper canopies of *F. sylvatica* were tougher and showed lower leaf N content as well as higher leaf C content and C/N ratio than in the understorey. This pattern is linked to increasing light conditions (Yamasaki & Kikuzawa, 2003). There is a strong relationship between light and leaf quality that determines herbivory levels (Louda & Rodman, 1996; Jansen & Stamp, 1997). Habitat conditions (microclimate and light) influence leaf traits like foliage lifespan, SLA, and nutrient concentrations (Reich *et al.*, 1997; Wright *et al.*, 2004), which are relevant to plant-insect interactions (Landsberg & Ohmart, 1989; Dirzo & Boege, 2008). Specific leaf area increases in response to shading (Wuytack *et al.*, 2011), because light affects leaf thickness (Yun & Taylor, 1986). Furthermore, light increases or decreases leaf N content depending on plant species (Fortin & Mauffette, 2002; Yamasaki & Kikuzawa, 2003) and increases carbon-based defence compounds of leaves (Dudt & Shure, 1994; Crone & Jones, 1999; Roberts & Paul, 2006). Example linkages between habitat conditions (microclimate and light) with leaf traits are found in the literature and in our correlations of microclimate (temperature and humidity) with SLA and leaf C content. Based on these findings, regulation of our studied leaf traits by given habitat conditions is supported.

Since light and temperature are generally expected to be strongly correlated, direct effects of light and temperature on herbivory are likely to be confounded (Niesenbaum & Kluger, 2006). Light is certainly the most obvious environmental factor which changes along the vertical forest gradient. It is well known that light is reduced from the outer canopy until the forest floor as a result to an increasing tree and shrub cover. Light intensity from upper canopy to the forest floor decreases by 20 times (Fortin & Mauffette, 2002). Therefore, outer canopies of trees experience high irradiances whereas the understorey of forests is characterized by low light (Parker, 1995). The light regime directly affects plants by changes of leaf traits (e.g. formation of sun and shade leaves), growth, and physiology (e.g. transpiration and nutrient uptake). Microclimate is also directly influenced by light, creating higher temperatures at the outer canopies and lower temperatures (with less fluctuation) in the understorey. Eventually, herbivory is indirectly affected by light due to leaf based changes of host plants or changes in microclimate. Light based variation in leaf nutritional quality and defence compounds might for example account for the suppression of expected high rates of herbivory in warmer habitats (Niesenbaum & Kluger, 2006). The exact role of light for measured leaf traits and herbivory levels remains unclear because it has not been evaluated in our study[1]. Nonetheless, the effect of temperature on herbivory in our study probably represents indirect effects based on the light regime along the vertical

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[1] Conclusions for the effect of light can be drawn from the experimental study in Chapter 6 and is discussed in Chapter 7.1.

forest gradient. The involved direct and indirect pathways are summarized in Figure 3.6.

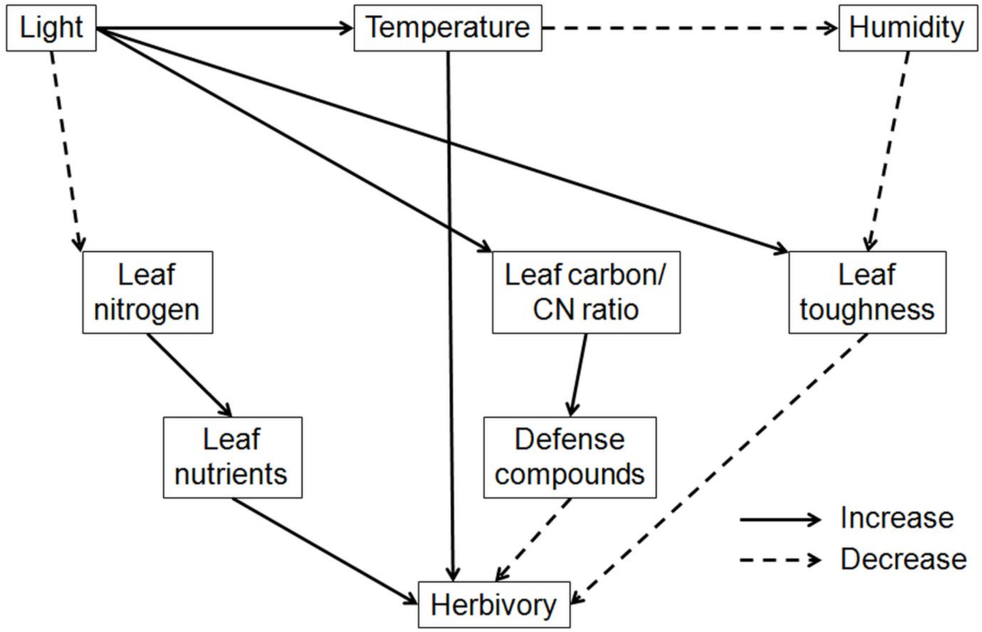

Figure 3.6: Effects of temperature determining herbivory through direct and indirect pathways and the influence of light on leaf traits along the vertical forest gradient. Data are based on our research and other studies (Dudt & Shure, 1994; Crone & Jones, 1999; Fortin & Mauffette, 2002; Schädler *et al.*, 2003; Yamasaki & Kikuzawa, 2003; Roberts & Paul, 2006; Wuytack *et al.*, 2011).

Carbon content increases with light and lowers levels of herbivory presumably due to higher amounts of carbon-based defence compounds. For *Fagus* species, light also decreases nutritional quality (N content) of leaves, which can lower herbivory levels. Higher temperatures in upper canopies go along with decreasing humidity, which lowers SLA and causes tougher leaves that are less palatable for herbivore insects. In our study, low SLA and leaf N content as well as high leaf C content of upper canopy leaves of *F. sylvatica* seem to account for reduced herbivory levels. Overall, we believe that the general positive influence of temperature on herbivory in upper canopies is suppressed due to these unfavourable leaf trait changes for insect herbivores.

Due to repetition across a wide geographical range (140 km transect) of ten different forest sites, our results are representative for a large area. Leaf-chewing herbivory can be extremely variable on small spatial scales between individual leaves and branches (Lowman, 1985). Our study shows that a clear overall pattern emerges where hundreds of leaves were pooled on larger scales between individual canopies and among geographically different sites. Therefore, differences of herbivory levels in our study design reflect variation of habitat conditions along the vertical forest gradient and its influences on leaf traits avoiding small-scale patterns between individual leaves and branches.

Overall, the pattern both along the vertical gradient on *F. sylvatica* and between three tree species in the understorey is in accordance with high C content (likely in the form of phenols) limiting herbivory. However, more detailed studies are needed to confirm this mechanism. The same mechanism is expected to underlie a decrease in herbivory with leaf age (seasonal patterns of leaf traits), which was not investigated in the current study.

CHAPTER 4

ENVIRONMENT VS. PLANT ONTOGENY: ARTHROPOD HERBIVORY PATTERNS ON EUROPEAN BEECH LEAVES ALONG THE VERTICAL GRADIENT OF TEMPERATE FORESTS IN CENTRAL GERMANY

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4.1 Abstract

Environmental and leaf trait effects on herbivory are supposed to vary among different feeding guilds. Herbivores also show variability in their preferences for plant ontogenetic stages. Along the vertical forest gradient, environmental conditions change, and trees represent juvenile and adult individuals in the understorey and canopy, respectively. This study was conducted in ten forests sites in Central Germany for the enrichment of canopy research in temperate forests. Arthropod herbivory of different feeding traces was surveyed on leaves of *Fagus sylvatica* L. (European beech; Fagaceae) in three strata. Effects of microclimate, leaf traits, and plant ontogenetic stage were analyzed as determining parameters for herbivory. The highest herbivory was caused by exophagous feeding traces. Herbivore attack levels varied along the vertical forest gradient for most feeding traces with distinct patterns. If differences of herbivory levels were present, they only occurred between juvenile and adult *F. sylvatica* individuals, but not between the lower and upper canopy. In contrast, differences of microclimate and important leaf traits were present between the lower and upper canopy. In conclusion, the plant ontogenetic stage had a stronger effect on herbivory than microclimate or leaf traits along the vertical forest gradient.

4.2 Introduction

Arthropod herbivores influence the structure and functioning of plant diversity and ecosystem processes (Crawley, 1983; Mulder *et al.*, 1999), with different effects depending on the feeding guild. Effects of leaf-chewing insects on ecosystems include influencing the composition and productivity of plant communities, as well as carbon and nutrient cycling (reviewed by Kozlov & Zvereva, 2017). Sap-feeding insects significantly reduce plant growth, reproduction, and photosynthesis (reviewed by Zvereva *et al.*, 2010), which is important for forest ecosystems. To date, most studies about herbivory in canopies have been published for tropical forests, whereas temperate forests have received less attention. However, temperate deciduous forests reveal an uneven vertical distribution of arthropod communities in different strata (Tal *et al.*, 2008; Ulyshen, 2011). Along this vertical gradient of temperate forest stands, environmental changes occur with increasing temperature and decreasing air humidity from understorey to upper canopies (Wilmers & Ellenberg, 1986; Tal *et al.*, 2008). Spatio-temporal changes of the environment are expected to alter interactions between plants and herbivores

(Tylianakis *et al.*, 2008). Nonetheless, ontogenetic changes are also present along the vertical forest gradient since juvenile and adult trees occupy the understorey and canopies, respectively. Insect herbivores show a variability in their preferences for plant ontogenetic stages (Fowler, 1985; Kearsley & Whitham, 1989). Varying frequencies of insect herbivores have been documented for some feeding guilds being more abundant either on saplings or mature plants (Lowman, 1992; Basset, 2001). Possible causes for this variation are differences in plant chemistry, leaf palatability, and local microclimate (Coley & Barone, 1996). These parameters are connected to the development of plants, which can be generally categorized into ontogenetic and physiological or environmental processes (Lawson & Poethig, 1995).

Ontogenetic processes on plant development arise from alterations in plant meristem gene expression (Poethig, 1990). The changes in vegetative structure are widespread and occur across whole plant gradients (Jones, 1999). Many plant traits including those involved in defences against herbivores vary between different plant ontogenetic stages. Variations among plant ontogenetic stages have been found amongst others in leaf toughness (Kearsley & Whitham, 1989; Loney *et al.*, 2006) and chemical defences, such as phenolics (Donaldson *et al.*, 2006; Neilson *et al.*, 2006; Elger *et al.*, 2009). Boege and Marquis (2005) have proposed a pattern for plant ontogenetic changes in herbivory defence and tolerance with increasing levels until reaching an optimum as plants further develop. In woody plants, chemical and physical defences increase during seedling and vegetative juvenile stages, respectively, but no differences in plant defences (physical defence traits and secondary chemistry) are found between juvenile and mature individuals (Barton & Koricheva, 2010). Furthermore, a comparison of insect herbivores revealed no preferences for juvenile or mature individuals of woody species (Barton & Koricheva, 2010). Clearly, the great diversity of insect herbivores and feeding guilds cannot lead to one general plant ontogenetic pattern.

Environmental processes on plant development are based on factors such as shading, water, and nutrient relations, resulting in alterations of the local meristem environment. Morphological and functional leaf traits (e.g. toughness, nutrients, or defence compounds) often mediate indirect environmental effects on herbivory (Stamp, 2003). Based on the variation of environmental conditions, the above-ground strata of forest ecosystems represent different microclimates. Microclimatic requirements and the availability of food resources within the tree canopies can reflect spatial distributions and preferences of arthropods (Basset, 1992). For European beech (*Fagus sylvatica* L.; Fagaceae), leaf traits change along the vertical forest gradient with unfavourable conditions (e.g., lower nitrogen (N) content, higher carbon (C) content, and toughness) for leaf-chewing insects in upper canopy leaves (Chap. 3). However, a variation of arthropod herbivory patterns is expected between different feeding traces, especially between different feeding guilds.

Even though knowledge about interactions of herbivory and forest ecosystems has increased during the last years, several gaps remain, and particularly for temperate forests. Most research focuses only on a single type of insect herbivore (Ali & Agrawal, 2012), or the distribution of different herbivore feeding guilds on juvenile and mature leaves (Peeters, 2002; Andrew & Hughes, 2005). Only few studies have surveyed the whole vertical forest gradient for herbivory research (Murakami & Wada, 1997; Fortin & Mauffette, 2002), especially few include several feeding guilds (Horchler & Morawetz, 2008). Furthermore, galls have rarely been studied in upper canopies of mesic forests (Price *et al.*, 1998). This study attempts to elucidate the distribution patterns of arthropod herbivory on leaves of the broad-leaved tree species *F. sylvatica*, focussing on the whole vertical forest gradient for comparisons between different microclimates, as well as between juvenile and adult *F. sylvatica* individuals. Herbivory was investigated for distinct arthropod feeding traces within four feeding guilds (leaf-chewing, sap-sucking, leaf mining, and gall-inducing). Patterns of herbivory were analysed with respect to microclimate (temperature and relative air humidity), leaf traits (toughness, N and C content), and plant ontogenetic stage (juvenile and adult tree individuals) determining the main predicting parameters. Based on the knowledge that levels of herbivory differ between distinct feeding guilds, as well as within feeding guilds and species along environmental gradients, two contrasting hypotheses were tested: patterns of herbivore attacks along the vertical forest gradient are (1) caused indirectly by changing leaf traits (toughness, nutrients, and defence compounds) induced by distinct environmental conditions (temperature and air humidity); or (2) determined by the plant ontogenetic stage (juvenile and adult trees).

4.3 Materials and methods

Study site

The research study was conducted in the hill and mountain region of Central Germany, within the federal states Thuringia, Lower Saxony, and Hesse (Fig. 4.1). Ten forest sites with mixed deciduous tree species were selected along a 140 km long west–east transect (altitude: 140–444 m.a.s.l.). The criteria for the forest stand selection were (i) closed canopy without major gaps; (ii) no significant presence of coniferous tree species; and (iii) a stem circumference of adult beech individuals >1 m. In the study area, mean annual temperature was about 9 °C and annual precipitation ranged from 474–874 mm (German Weather Service, reference period 1961–1990). The geological substrate of the forest sites was lower Trias sandstone, except for Bocksbühl (upper Trias sandstone), Feuerkuppe, and Heidelberg (middle Triassic limestone).

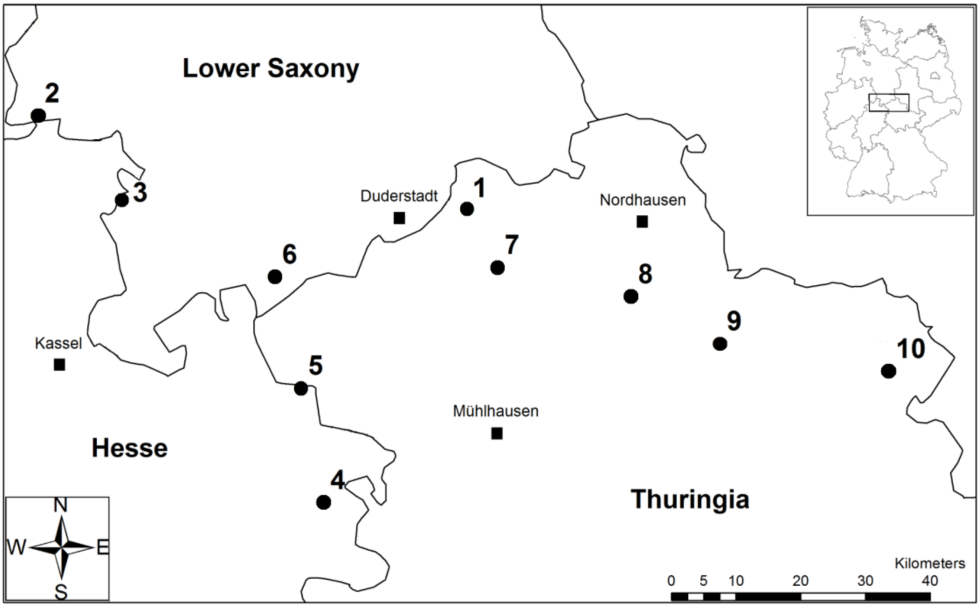

Figure 4.1: Study region in Thuringia, Lower Saxony, and Hesse with ten forest sites (black circles). Forest sites: **(1)** Winkelberg; **(2)** Tiefentals Ebene; **(3)** Klingenberg/Vaaker Berg; **(4)** Schieferstein; **(5)** Heiligenberg; **(6)** Bocksbühl; **(7)** Hubenberg; **(8)** Feuerkuppe; **(9)** Heidelberg; and **(10)** Eichleite. Original copyright: GeoBasis-DE/BKG 2015, data changed with permission from *Bundesamt für Kartographie und Geodäsie*.

Within the studied forest sites, *F. sylvatica* was the dominant broad-leaved tree species. At each of the ten forest sites, a random selection of juvenile and adult tree individuals was undertaken at two different spots resulting in 20 sample sites. Three adult individuals of *F. sylvatica* were surveyed at the lower and upper canopy (average height: 18 and 35 m, respectively), as well as three juvenile indi-viduals of *F. sylvatica* in the understorey (average height: 1 m) at all sample sites. Lower and upper canopies of adult beech trees were accessed with rope climbing. A total of 60 adult and 60 juvenile *F. sylvatica* individuals were selected for the study.

Microclimate and leaf trait data

Microclimate (air temperature and relative air humidity) was measured hourly with data loggers (iButton, Model DS1923, Maxim Integrated, San Jose, CA, USA). Data loggers were installed in the understorey (about 1 m height), as well as in lower and upper canopies of adult *F. sylvatica* trees (about 18 and 35 m height, respectively) at each sample site. Complete data were available from July–August 2012 for all sample sites. Average day values from sunrise to sunset (6 am to 9 pm) were used for further analyses with temperature and air humidity. Night values for microclimate were excluded for two reasons. On the one hand, the microclimatic pattern along the vertical forest gradient is most present during daylight and can be reversed, weakened, or even disappear during the night (Parker, 1995; Tal *et al.*, 2008). On the other hand, insect herbivores show a greater activity during the day than at night (Basset *et al.*, 2003a).

Foliage material was collected in June 2012. Despite the guidelines for specific leaf area (SLA) measurements (Cornelissen *et al.*, 2003), foliage material had to be deep frozen due to logistical constraints during the field work until analyses of leaf traits (toughness and nutrients) and herbivory could be carried out at the university. If collected leaves could not be measured within 24 h they were stored between moist filter paper in sealed plastic bags in the freezer (−18 to −35 °C) according to the data standards protocols of the LEDA Traitbase (data*base* of the life-history *traits* of Northwest European flora) (Kleyer *et al.*, 2008). The sampling period was kept as short as possible (one month) to minimize a variation of leaf traits and herbivory caused by seasonal changes (leaf age). Specific leaf area (m^2 kg^{-1}) was used as an indicator for toughness. It relates the area of a fresh leaf to its dry mass, and low SLA values are linked to structural defences (Cornelissen *et al.*, 2003). Five to ten leaves were collected per tree individual in the understorey, lower, and upper canopy for analysis of SLA. The collecting time was either in the morning or the afternoon and deviated from the recommended time after sunset or before sunset (Cornelissen *et al.*, 2003) based on logistical constraints (access to the canopy with climbing rope). The variation of leaf sample amount was dependent on the availability of fully developed leaves without obvious symptoms of pathogens or herbivore attacks. Any petiole and all veins were considered as part of the leaf for standardised SLA (Cornelissen *et al.*, 2003), and were included in the SLA measurement. All frozen leaves were defrosted and scanned with a flat-bed scanner to obtain their leaf area using the computer image analysis system WinFOLIA (Régent Instruments Inc., Ville de Québec, QC, Canada). Afterwards, leaves were dried in an oven (48 h at 70 °C) and weighed to calculate SLA values (Equation 4.1). For further analyses with SLA, the mean value was used for each forest layer per sample site.

$$\mathrm{SLA} = \text{leaf area }(\mathrm{m}^2)/\text{leaf dry mass }(\mathrm{kg}) \tag{4.1}$$

Leaf N and C concentrations represent the total contents of N and C per unit of dry leaf mass (mg g^{-1}). Nutritional analyses were conducted with mixed samples consisting of ten fully-developed leaves per forest layer for each sample site. Leaves without petioles were dried in an oven (72 h at 60 °C) and ground afterwards. Total N and C contents were obtained with a C/N elemental analyser (Department of Plant Ecology and Ecosystem Research, University of Göttingen, Göttingen, Germany). The N and C contents for the C/N ratio (g g^{-1}) were calculated for all samples (Equation 4.2). The C/N ratio connects N content, an important macronutrient, as a positive indicator for leaf nutritional quality with C content, an indicator for phenolics (quantitative defence compound), as a negative indicator for leaf palatability. According to the carbon-nutrient balance hypothesis (Coley *et al.*, 1985), an increase in C/N ratio positively correlates with levels of defence compounds. For further nutritional analyses, the mean values were used for each forest layer per sample site.

$$\mathrm{C/N\ ratio} = \text{C content (g)}/\text{N content (g)} \tag{4.2}$$

The chlorophyll content of leaves correlates with leaf N content (van den Berg & Perkins, 2004), because up to 75% of N content is located in chloroplasts (Peoples & Dalling, 1988). Measurements of chlorophyll content index (CCI) were conducted with a CCM-200 plus Chlorophyll content meter (Opti-Sciences Inc., Hudson, NH, USA). The CCI increases with the chlorophyll content of leaves. Ten CCI values were taken directly in the field in June 2012 for each individual tree and forest layer at all sample sites. The mean values of chlorophyll were used of each forest layer per sample site for further analyses.

Herbivory data

Arthropod herbivory was assessed with a visual inspection of adaxial and abaxial sides of leaf samples. Therefore, foliage material was defrosted and all leaves from two 30 cm long branches (starting at the tip of the branch) per tree individual and forest layer were surveyed (1799 understorey leaves, 2158 lower canopy leaves, and 2665 upper canopy leaves). All leaves were checked for all four classes of herbivore feeding traces (leaf-chewing, sap-sucking, leaf-mining, and gall-inducing). A species level identification for the feeding traces was reduced, because an unequivocal attribution of damage to a particular arthropod species, especially belonging to exophagous feeding guilds, is often impossible. Feeding traces were sorted into groups of homogeneous appearance and considered as recognizable taxonomic units (RTUs). Ecological research often uses RTUs for indices of abundances (Kozlov *et al.*, 2009; Kozlov & Zvereva, 2014; Smith *et al.*, 2016; Vanbergen *et al.*, 2017). Overall, 15 feeding traces were identified (App. D: Fig. 3A–5A), and voucher specimens were stored at the Department of Biology, University of Hildesheim, Hildesheim, Germany.

For every detected feeding trace, the number of attacked leaves was counted and used as the percentage of the total amount of leaves per sample, representing the herbivore attack levels. For each feeding trace, the associated arthropod species, probably causing the feeding trace, was determined with identification databases and literature (Alford, 2012; Ellis, 2017; Hochschule Weihenstephan-Triesdorf, 2017; Kimber, 2017; Pitkin *et al.*, 2017; Rennwald & Rodeland, 2017). Most of the feeding traces were also analysed in a study written by Gossner *et al.* (2014) and are in accordance with the associated arthropod herbivore species in this study. Larvae of endophagous arthropod species were found within the herbivore feeding traces on leaf samples. Additionally, insect samples were taken in the understorey, lower and upper canopy at all forests sites with a beating net for the identification of the probable exophagous insect herbivore species. Voucher specimens of *Orchestes fagi* L. (Coleoptera: Curculionidae), *Phyllobius argentatus*

L. (Coleoptera: Curculionidae), *Fagocyba cruenta* H.-S. (Hemiptera: Cicadellidae), and *Phyllaphis fagi* L. (Hemiptera: Callaphididae) were stored at the Department of Biology, University of Hildesheim, Hildesheim, Germany. Since about two thirds of the feeding traces belonged to endophagous leaf-mining and gall-inducing feeding guilds, their feeding traces were more suitable for the identification than those of exophagous feeding guilds. Due to a high specialization of endophagous arthropod herbivores by internal interactions with the host plant physiology, feeding traces were well distinguishable based on special differences in form and appearance of galls and mines.

Statistical analyses

Eight feeding traces that occurred at all forest sites (App. D: Tab. 6A) were further investigated concerning their distribution along the vertical forest gradient. The selection included two leaf-chewing, one sap-sucking, one leaf-mining, and four gall-inducing feeding traces. Herbivory was regarded as herbivore attack level, measured as the numbers of leaves bearing the feeding trace (as percentage of the sample). The spatial distribution of oviposition can result in clumping of mines and galls. Single occasions of mine and gall clumping were averaged using the 20 sample sites to overcome the influence of clumping on the data set. Herbivore attack levels of all eight feeding traces were compared between juvenile and adult *F. sylvatica* along the vertical forest gradient. An adequate comparison of leaf herbivory between individual plants would necessarily rely on similar leaf sizes. Leaf size was higher for leaves in lower canopies compared to similar average values of leaves in the understorey and upper canopies (App. D: Tab. 7A). However, leaf size had no overall effect on herbivore attack levels ($F_{1478} = 0.693$, $p = 0.405$), neglecting an influence for the comparison of herbivore attack levels between different plant individuals. Statistical analyses for significant comparison were performed with the R version 3.4.1 (R Development Core Team, 2017). The statistical distribution of the data (microclimate, leaf traits, and herbivory) was assessed with the Shapiro-Wilk test, which was necessary to select between ANOVA or Kruskal-Wallis tests for analyses of variance. Based on the nonparametric data for herbivore attack levels, significant comparisons were performed with Kruskal-Wallis and post-hoc tests for all eight feeding traces on juvenile and adult *F. sylvatica* along the vertical forest gradient (Equations 4.3 and 4.4):

$$\mathrm{kruskal.test(herbivore\ attack\ level \sim forest\ layer)} \tag{4.3}$$

$$\text{kruskalmc(herbivore attack level} \sim \text{forest layer)} \tag{4.4}$$

With eight dependent variables for herbivory (number of feeding traces) and seven independent variables for microclimate and leaf traits (temperature, relative air humidity, SLA, N and C content, C/N ratio, and chlorophyll content) multivariate statistics was firstly chosen for analysis. The aim was to illustrate the ecological and environmental (dis)similarities between the occurrence of feeding traces in terms of microclimate, leaf trait parameters, and plant ontogenetic stage along the vertical forest gradient (App. D: Tab. 8A). On the basis of nonparametric data for herbivore attack levels, the ordination was generated using non-metric multidimensional scaling (NMDS) (Legendre & Legendre, 1998). Calculations were done with the R packages *vegan* and *goeveg* based on the Bray-Curtis dissimilarity (Friedmann & Schellenberg, 2017; Oksanen *et al.*, 2017). For constructing the ordination, the *dimcheckMDS* function was used for detecting the best dimensionality in NMDS. The *dimcheckMDS* function provided a diagnostic plot of stress values for six tested dimensions in NMDS (App. D: Fig. 6A), showing the decrease in ordination stress with an increase in the number of ordination dimensions. Based on the diagnostic plot, two dimensions were used for the ordination. The NMDS was calculated with data of herbivore attack levels for all eight feeding traces. Sample sites along the vertical forest gradient (corresponding to juvenile and adult *F. sylvatica*) were plotted onto the ordination. Arthropod herbivory was interpreted based on post-hoc correlations with microclimate (temperature and relative air humidity) and leaf trait parameters (SLA, N and C content, C/N ratio, and chlorophyll content). Significant parameters were fitted onto the biplot (App. D: Tab. 8A).

Effects of parameters on arthropod herbivory along the vertical forest gradient were determined with linear mixed models (LMM) and a following model selection. Calculations were done using the R libraries *lme4* for LMM and *MuMIn* for the model selection (Bartoń, 2016; Bates *et al.*, 2017). Herbivore attack levels were either square-root transformed (small circles and whitish spots) or log-transformed (labyrinth, tubular mine, leaf edge gall, haired vein gall, pannose spot, and ovate gall), depending on the best reduction for skewed statistical distributions of the nonparametric data. All models contained the study site as a random effect. For the herbivore attack levels on *F. sylvatica* leaves caused by the eight feeding traces, model comparisons were conducted for effects of microclimate (temperature and relative air humidity), leaf traits (SLA, N and C content, and C/N ratio), and plant ontogenetic stage with a full model specification. The best models were selected based on the Bayesian Information Criterion (BIC) (App. D: Fig. 9A–16A). Linear regressions for herbivore attack levels and the determining parameters of the best models, preferring single parameters, were calculated for all eight feeding traces.

4.4 Results

Herbivore feeding traces

Overall, 15 different feeding traces were identified for *F. sylvatica* (Tab. 4.1 and App. D: Fig. 3A–5A). Identified feeding traces belonged to leaf-chewing (3), sap-sucking (2), leaf-mining (5), and gall-inducing (7) feeding guilds. Ubiquitous feeding traces, like small circles and whitish spots, were found in all three forest layers at all sample sites, and haired vein galls and pannose spots were found on almost all juvenile and adult *F. sylvatica* samples (App. D: Fig. 6A).

Along the vertical forest gradient, patterns of herbivore attack levels differed between the eight feeding traces (Fig. 4.2 and 4.3). On the one hand, herbivore attack levels on *F. sylvatica* leaves were higher on juveniles compared to adults for labyrinths, whitish spots, and tubular mines (Fig. 4.2b–d). On the other hand, *F. sylvatica* leaves of adults were more often attacked than leaves of juveniles by leaf edge galls, haired vein galls, and pannose spots (Fig. 4.3a–c). Herbivore attack levels for small circles and whitish spots did not vary significantly between the two ontogenetic stages of *F. sylvatica* (Fig. 4.2a and 4.3d).

Overall, the herbivore attack levels on leaves varied between different feeding traces (Tab. 4.2). Herbivore attack levels on *F. sylvatica* leaves were the highest for small circles (leaf-chewing) and whitish spots (sap-sucking), intermediate for all galls, and low for labyrinths (leaf-chewing) and tubular mines. The highest herbivore attack levels on juvenile *F. sylvatica* individuals were also found for small circles and whitish spots, with percentages much higher than all other feeding traces. On adult *F. sylvatica* individuals, herbivore attack levels of pannose spots between veins (galls) reached the high magnitude of small circles and whitish spots. Feeding traces of labyrinths and tubular mines were rarely seen on leaves of adult *F. sylvatica* individuals.

Table 4.1: List of 15 identified arthropod herbivore feeding traces (recognizable taxonomic unit = RTU) on leaves of *Fagus sylvatica*. Presented are feeding traces for **(a)** exophagous and **(b)** endophagous feeding guilds. Images of all feeding traces are available in Appendix D (Fig. 3A–5A).

Feeding trace[1]	**Description**	**Guild**[2]	**Leaf side**[3]	**Probable arthropod species**[1]
(a) exophagous:				
windows	scraping damage on leaf surface	ch		*Diurnea fagella* (Denis & Schiffermüller, 1775)
small circles	missing leaf area as small circles	ch		*Orchestes fagi* (Linnaeus, 1758)
labyrinth	missing leaf area in form of labyrinths	ch		*Phyllobius argentatus* (Linnaeus, 1758)
whitish spots	leaf flecked with whitish spots	s	ADS	*Fagocyba cruenta* (Herrich-Schäffer, 1838)
wax wool	waxed threads on leaf surface	s	ABS	*Phyllaphis fagi* (Linnaeus, 1767)
(b) endophagous:				
tubular mine	tubular shaped mine between lateral veins	m	ABS	*Phyllonorycter maestingella* (Müller, 1764)
oval mine	oval shaped mine between lateral veins	m	ABS	*Phyllonorycter messaniella* (Zeller, 1846)
line crossing veins	wide corridor mine crossing lateral veins	m		*Stigmella hemargyrella* (Kollar, 1832)
line between veins	zigzag mine between lateral veins	m		*Stigmella tityrella* (Stainton, 1854)
leaf edge gall	gall causing rolled-up leaf edges	g		*Acalitus stenaspis* (Nalepa, 1891)
haired vein gall	haired gall along lateral leaf veins	g	ADS	*Aceria nervisequa* (Canestrini, 1891)
pannose spot	pannose spot between lateral veins	g	ABS	*Aceria nervisequa faginea* (Nalepa, n.d.)
haired brownish gall	cylindrical, haired brownish gall	g	ADS	*Hartigiola annulipes* (Hartig, 1839)
ovate gall	ovate, acuminated gall (green to red)	g	ADS	*Mikiola fagi* (Hartig, 1839)
pleated gall	swollen, pleated leaf tissue forming a pouch	g	ADS	*Phegomyia fagicola* (Kieffer, 1901)

[1] Feeding traces were identified as RTUs and assigned to the probably responsible arthropod herbivore species using identification databases and literature (Alford, 2012; Ellis, 2017; Hochschule Weihenstephan-Triesdorf, 2017; Kimber, 2017; Pitkin *et al.*, 2017; Rennwald & Rodeland, 2017). Feeding traces with underline: distributions of herbivory were analysed along the vertical forest gradient.

[2] ch = leaf-chewing; s = sap-sucking; m = leaf-mining; g = gall-inducing.

[3] ADS = adaxial side; ABS = abaxial side.

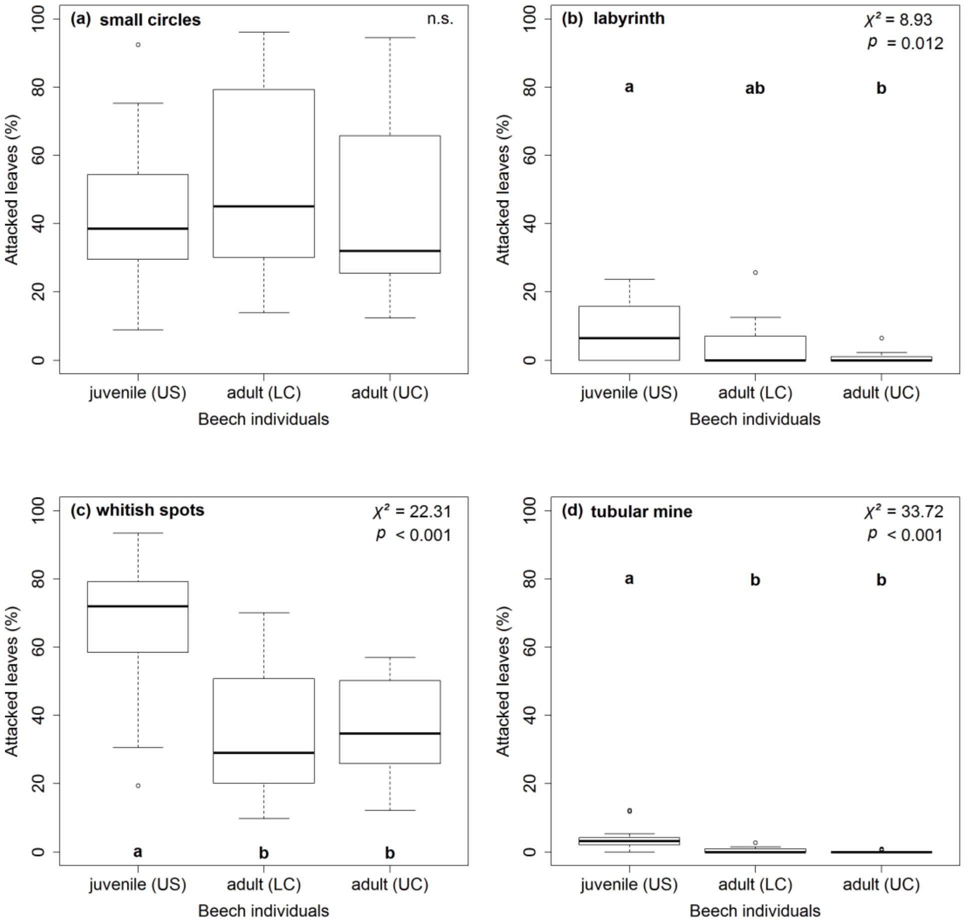

Figure 4.2: Distributions of herbivore attack levels for identified feeding traces along the vertical forest gradient. Percentages of attacked leaves on juvenile (US = understorey) and adult (LC = lower canopy; UC = upper canopy) *Fagus sylvatica* (n = 60) are presented for the leaf-chewing feeding guild **(a)** small circles and **(b)** labyrinth, the sap-sucking feeding guild **(c)** whitish spots, and the leaf-mining feeding guild **(d)** tubular mine. Boxplots are marked with lowercase letters indicating significant differences using Kruskal-Wallis and post-hoc test (p≤0.05; df = 2) or with "n.s." for non-significant differences.

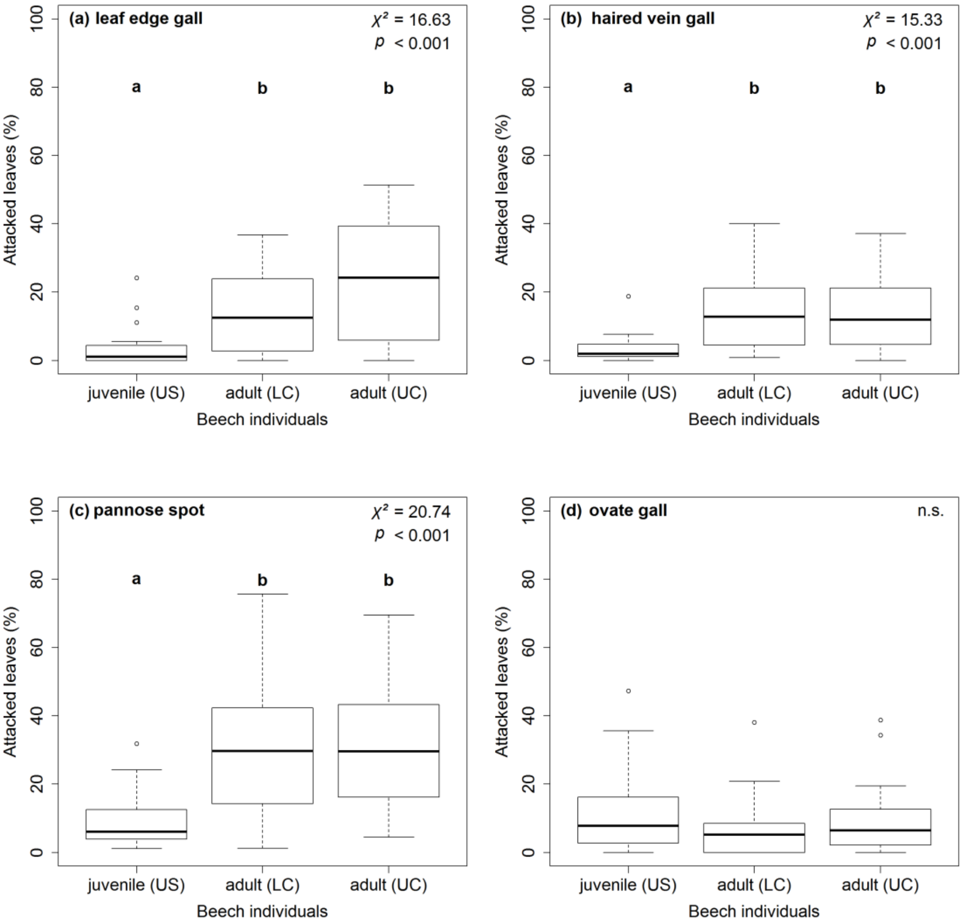

Figure 4.3: Distributions of herbivore attack levels for identified feeding traces along the vertical forest gradient. Percentages of attacked leaves on juvenile (US = understorey) and adult (LC = lower canopy; UC = upper canopy) *Fagus sylvatica* (n = 60) are presented for the gall-inducing feeding guild **(a)** leaf edge gall, **(b)** haired vein gall, **(c)** pannose spot, and **(d)** ovate gall. Boxplots are marked with lowercase letters indicating significant differences using Kruskal-Wallis and post-hoc test ($p \leq 0.05$; df = 2) or with "n.s." for non-significant differences.

Table 4.2: Herbivore attack levels (percentage of attacked leaves) of feeding traces on leaves of *Fagus sylvatica* (n = 60). Comparisons are shown for leaves along the vertical forest gradient, as well as for leaves of juvenile and adult *F. sylvatica*. Values represent the median and interquartile ranges (IQR = first quartile, third quartile). Lowercase letters indicate significant differences for overall attacks and the comparison within juvenile and adult *F. sylvatica* using Kruskal-Wallis and post-hoc test ($p \leq 0.05$; df = 7).

Feeding guild	Feeding trace	Attacked leaves (%)		
		overall	juvenile beech	adult beech
leaf-chewing	small circles	36 (29,65)^{a}	39 (30,54)^{a}	35 (28,72)^{a}
leaf-chewing	labyrinth	0 (0,7)^{b,c}	6 (0,13)^{b}	0 (0,2)^{b,d}
sap-sucking	whitish spots	41 (27,60)^{a}	72 (59,78)^{a}	32 (23,49)^{a}
leaf-mining	tubular mine	0 (0,2)^{c}	3 (2,4)^{b}	0 (0,0)^{b}
gall-inducing	leaf edge gall	9 (1,24)^{d,e}	1 (0,4)^{b}	19 (3,32)^{c,d,e}
gall-inducing	haired vein gall	7 (2,16)^{d}	2 (1,4)^{b}	12 (5,21)^{e}
gall-inducing	pannose spot	18 (7,35)^{e}	6 (4,12)^{b}	30 (15,42)^{a,c}
gall-inducing	ovate gall	6 (2,13)^{b,d}	8 (3,15)^{b}	13 (4,21)^{d,e}

Feeding trace composition

Herbivore attack levels of the eight feeding traces, as well as forest layer sample sites (representing juvenile and adult *F. sylvatica*), were ordinated in a biplot with NMDS along the environmental and leaf trait parameter axes (Fig. 4.4). The stress value was 0.187 and goodness of NMDS was determined with the category “usable” (stress value < 0.20) following the guidelines for acceptable stress values (Clarke, 1993). A Shepard diagram is available in Appendix D (Fig. 6A). Temperature, relative air humidity, SLA, leaf C content, leaf N content, and C/N ratio axes were significant parameters for the NMDS ordination (post-hoc correlations). The chlorophyll parameter was deleted due to non-significance ($R^2 = 0.054$; $p = 0.234$). Data for microclimate and leaf traits of juvenile and adult *F. sylvatica* along the vertical forest gradient are available in Appendix D (Tab. 7A). The NMDS showed a complete overlap of feeding trace compositions for lower and upper canopy leaves, and also a slight overlap for juvenile and adult *F. sylvatica* individuals. Along environmental and leaf trait parameter axes, the orientation varied between the three forest layers. Sample sites with juveniles of *F. sylvatica* were orientated towards increasing air humidity, SLA and, to a lesser degree, towards leaf N content. In contrast to juveniles, adult *F. sylvatica* exhibited an orientation towards increasing temperature, leaf C content, and C/N ratio. Lowest distances for the feeding traces existed between leaf edge gall, haired vein gall, and pannose spot (ordinated within adults), as well as between small circles, whitish spots, and ovate gall (ordinated within the overlap of juveniles and adults). Labyrinth and tubular mine feeding traces showed the greatest distances to the other feeding traces.

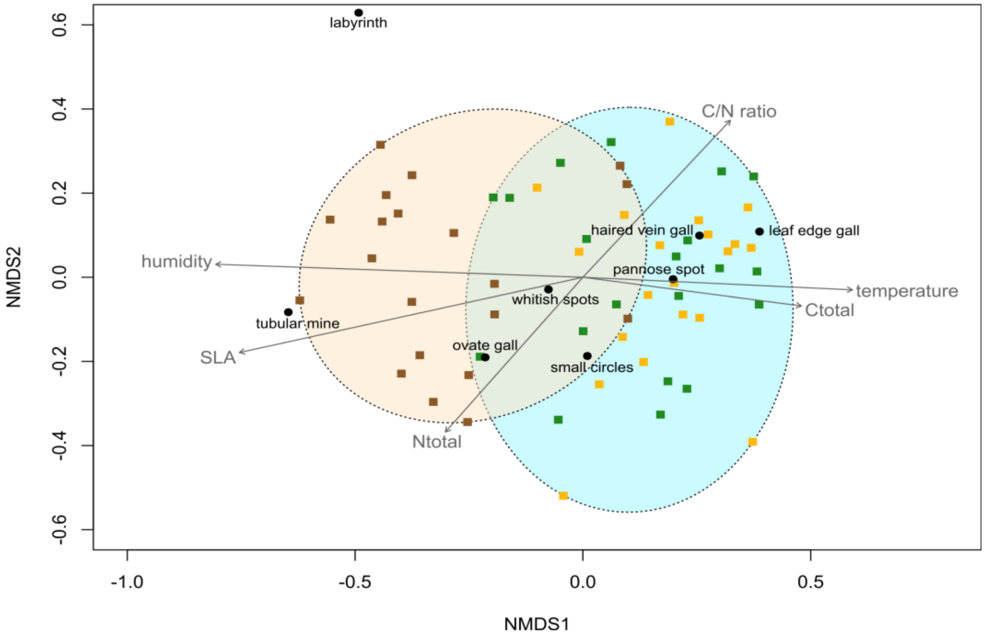

Figure 4.4: Ordination of samples and arthropod herbivore attack levels in a biplot with non-metric multidimensional scaling (NMDS). Each point of a sample site represents the composition of herbivore attack levels. Herbivore attack levels caused by identified feeding traces (black circles) are orientated along microclimate (temperature, humidity) and leaf traits (SLA, Ctotal, Ntotal, C/N ratio) parameter axes (post-hoc correlations). Sample sites along the vertical forest gradient are presented for the understorey (brown squares), lower canopy (green squares), and upper canopy (yellow squares), representing juvenile (beige ellipse) and adult (blue ellipse) *Fagus sylvatica*. Non-metric multidimensional scaling is based on Bray-Curtis dissimilarity (stress = 0.187 (usable)). Temperature (R^2 = 0.249; p = 0.002), humidity (R^2 = 0.461; p = 0.001), SLA (R^2 = 0.426; p = 0.001), Ctotal (R^2 = 0.167; p = 0.007), Ntotal (R^2 = 0.161; p = 0.009), and C/N ratio (R^2 = 0.173; p = 0.005) parameters represent significant axes for the NMDS ordination. Temperature = air temperature; humidity = relative air humidity; SLA = specific leaf area; Ctotal = leaf C content; Ntotal = leaf N content.

Effects of microclimate, leaf traits, and plant ontogenetic stage

Based on the BIC, herbivore attack levels of the eight feeding traces on juvenile and adult *F. sylvatica* along the vertical forest gradient were best explained by different parameters (Tab. 4.3, App. D: Fig. 9A–16A). The best predicting parameters were relative air humidity, N content, C/N ratio, and plant ontogenetic stage. Linear regressions based on the best predictors for herbivore attack levels on *F. sylvatica* showed significant effects, except for small circles and ovate galls (Tab. 4.3). The plant ontogenetic parameter significantly explained all other feeding traces. Effects of C/N ratio were positive on whitish spots and tubular mine, or negative on leaf edge gall, haired vein gall, and pannose spot (App. D: Fig. 11A–15A). In contrast, effects of N content were negative on tubular mine or positive on leaf edge gall, haired vein gall, and pannose spot.

4.4 Discussion

This study revealed varying herbivore attack levels between (overall values) and within (values along the vertical forest gradient) different feeding traces. A majority of feeding traces occupied different layers in forest stands, with distinct preferences for juvenile or adult trees of *F. sylvatica*. In addition, patterns of herbivore attack levels also differed within feeding guilds. Highest herbivore attack levels were found for small circles and whitish spots (Tab. 4.2), both belonging to the exophagous feeding guild. Gall-inducing feeding traces revealed herbivore attack levels lying in between the highest and lowest herbivore attack levels. Lowest herbivore attack levels were caused by one exophagous and endophagous feeding trace (labyrinth and tubular mine, respectively). These findings are in accordance with other studies. For *Acer pseudoplatanus* (sycamore maple), levels of herbivory (proportion of attacked leaves) for sap-sucking, leaf-mining, and gall-inducing feeding guilds show the same differences (Horchler & Morawetz, 2008), comparable to the values on *F. sylvatica* in this study. Leaf-mining often forms only a minor component of herbivore damage due to low levels of abundance (Pritchard & James, 1984). Overall, differences in herbivory levels are based on the mobile ability of exophagous insects to exploit many leaves on various plants. In contrast, single individuals of arthropod herbivore species belonging to the endophagous feeding guild are naturally restricted to one leaf of a plant individual.

Table 4.3: Effects of microclimate, leaf trait parameters, and plant ontogenetic stage on arthropod herbivore attack levels (linear regressions) based on the best calculated models compared with the Bayesian Information Criterion (App. D: Fig. 9A–16A). The preference was set on models with the lowest number of parameters, resulting in choices of single parameters or the combination of two parameters (without interaction). The effect of the plant ontogenetic stage was tested for all exophagous and endophagous feeding traces. Herbivore attack levels on *Fagus sylvatica* (n = 57) were square-root transformed (small circles and whitish spots) or log-transformed (labyrinth, tubular mine, leaf edge gall, haired vein gall, pannose spot, and ovate gall), depending on the best reduction for skewed statistical distributions of the nonparametric data.

Model parameters[1]	**d.f.**		***F*-values**[2]							
			exophagous			endophagous				
	n.	d.	small circles	labyrinth	whitish spots	tubular mine	leaf edge gall	haired vein gall	pannose spot	ovate gall
humidity	1	55								1.29
N content	1	55	0.98							
N content + stage	2	54				20.50***	16.99***	14.62***	18.15***	
C/N ratio + stage	2	54			17.72***	21.08***	16.31***		17.25***	
stage	1	55	0.19	9.79**	30.85***	37.25***	17.96***	18.64***	27.56***	1.33

[1] humidity = relative air humidity; N content = leaf nitrogen content; stage = plant ontogenetic stage.

[2] *F*-values with underline: best models are based on the BIC (ΔBIC = 0–2). * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; n. = numerator; d. = denominator.

In this study, six out of eight feeding traces showed differences along the vertical forest gradient concerning herbivore attack (Fig. 4.2–4.3). However, levels of herbivore attack only differed significantly between juvenile and adult *F. sylvatica*, but not within the canopy. On the one hand, three out of four feeding traces of the gall-inducing feeding guild (probably acari) showed increased herbivore attack levels on adult *F. sylvatica* compared to juveniles. On the other hand, herbivore attack levels of labyrinth and whitish spots (leaf-chewing and sap-sucking feeding guild, respectively) were higher on juveniles compared to adult *F. sylvatica*. The distinct patterns are the same for gall-inducing and sap-sucking feeding traces on leaves of *A. pseudoplatanus* (Horchler & Morawetz, 2008). Differences along the whole vertical gradient, even between lower and upper canopies, are present for microclimate (temperature and relative air humidity) and leaf traits (SLA and C content; N content and C/N ratio only differ within the canopy) for *F. sylvatica* (App. D: Tab. 7A). Therefore, distribution patterns of herbivore attack levels in the understorey and canopy do not seem to be driven by microclimate and leaf trait parameters. Instead, the plant ontogenetic stage had a stronger effect on herbivore attack levels than microclimate or leaf traits (Tab. 4.3). This leads to the predominate role of plant ontogeny, not the environment, affecting herbivory on *F. sylvatica* along the vertical forest gradient. The remaining question is the underlying cause behind the plant ontogenetic effect on preferences of arthropod herbivores for juvenile or adult *F. sylvatica*.

The ontogenetic variation of leaf toughness (Kearsley & Whitham, 1989; Loney *et al.*, 2006) is linked to the accumulation of phenolic compounds and lignifications of leaf tissues (Bussotti *et al.*, 1997). Furthermore, phenolic compounds are indicated by leaf C content because mechanical or chemical defences are often carbon-based (Feeny, 1970; Southwood *et al.*, 1986). Despite the absence of differences in plant defences between juvenile and mature woody species (Barton & Koricheva, 2010), leaves of juvenile and adult *F. sylvatica* in this study differed in toughness (indicated by SLA) and C content. Since these differences were also present between the lower and upper canopy, a potential effect on herbivory could only be applied to a non-linear relationship. In this case, values for leaf C content and toughness would cross a threshold from juvenile to adult *F. sylvatica* individuals that could cause the existing herbivory shift. Another possible reason for distinct preferences of some feeding guilds for juvenile or mature plants can also be enemy-free space (Coley & Barone, 1996). Predation by birds (Van Bael *et* *al.*, 2003), predatory wasps (Domínguez *et al.*, 1989), and parasitoids (Boege, 2005a) is higher in mature compared to juvenile trees. According to the hypothesis of harsh environment, herbivory of galls is higher in xeric compared to mesic habitats, which is explained by different mortality rates through parasitoids and fungi (Fernandes & Price, 1992). The lower top-down control by parasitoids also affects gall patterns along the vertical gradient in mesic tropical rainforests (Ribeiro & Basset, 2007). Testing the hypothesis of a harsh environment as an example of an enemy-free space along the vertical gradient of temperate forests would require counting the galls and separating them into dead and living galls. This represents a different measure of herbivory than that used in this study and could lead to different results for herbivory levels.

Feeding traces of small circles (leaf-chewing) did not show significantly distinct herbivore attack levels along the vertical forest gradient in this study. However, using a different measure for herbivory caused by the leaf-chewing feeding guild, quantifying the missing leaf area, leads to an increased herbivory in the understorey compared to upper canopies (Chap. 3). This pattern seems to be driven by indirect effects of environmental conditions, causing leaves in the understorey to be more palatable for leaf-chewing insect herbivores. The natural movement of the leaf-chewing weevil *Phyllobius argentatus* L., which is more active in the understorey, from one tree species to another, depends on the palatability of the leaves (Stork *et al.*, 2001). Patterns of leaf palatability for *F. sylvatica* along the vertical forest gradient can be adapted to general differences between young and mature leaves. Peak densities of exophagous feeding guilds are associated with new leaf samples on most plant species (Peeters *et al.*, 2001). Many structural features develop with increasing leaf age that makes feeding on mature leaves more difficult for exophagous herbivore insects (Peeters, 2002). Features include tougher leaves and higher defence compounds that are also caused in *F. sylvatica* leaves by environmental conditions (light, microclimate, and water stress) along the vertical forest gradient.

4.5. Conclusions

Despite the overall high levels of herbivory caused by exophagous feeding traces, patterns of herbivore attack levels vary within different feeding traces between juvenile and adult *F. sylvatica*. In addition, levels and distribution patterns of herbivore attacks are even distinct between different feeding traces within one feeding guild. Therefore, general conclusions on herbivory patterns can hardly be drawn at the species level, but are rather possible as averages for whole feeding guilds. This would be in accordance with the assumption that the type of damage is more important than the identity of the causer from the plant's perspective (Kozlov *et al.*, 2017). Furthermore, the great diversity of arthropod herbivores and feeding guilds cannot lead to one general plant ontogenetic pattern. This study presents findings for the importance to differentiate between distinct feeding guilds of insect herbivores for research about plant ontogenetic effects on herbivory. The underlying causes for ontogenetic preferences need to be addressed in future studies. Changes in leaf traits affecting herbivory are found between the ontogenetic stages of juvenile and adult *F. sylvatica* along the vertical forest gradient. However, if these leaf traits represent underlying causes for plant ontogenetic preferences of insect herbivores, relationships cannot be linear, since important leaf traits also change between lower and upper canopies of adult *F. sylvatica*.

CHAPTER 5

EFFECTS OF PHYTODIVERSITY ON INSECT DIVERSITY AND HERBIVORY

5.1 Introduction

Biodiversity has become an important focus for research and nature conservation that is certainly motivated by reports about a numerous loss of species. Unfortunately, a global decline in biodiversity becomes increasingly evident (e.g. Pimm & Raven, 2000; Singh, 2002). Reasons for biodiversity declines worldwide are divers but generally relate to anthropogenic activities. In Europe, the main drivers for biodiversity loss are agricultural and forest policies, EU directives, recreation and hunting (reviewed by Young *et al.*, 2005). Changing human demands concerning forests and forestry with increasingly multi-purpose roles produce conflicts for the protection of forest biodiversity. Silvicultural systems have changed with intensive harvesting methods, including a wider use of machinery, the shortening of crop rotation times, and plantation forestry. Biodiversity loss reduces the efficiency of ecological communities to capture essential resources, produce biomass, decompose and recycle nutrients (Cardinale *et al.*, 2012). Amongst other ecosystems, these results have been documented for forests (Piotto, 2008; Zhang *et al.*, 2012). A firm evidence base exists that demonstrates the importance of biodiversity to ecosystem functioning. Therefore, the concept of biodiversity leading to the stability of ecosystems is an ongoing focus of ecological debates (McCann, 2000), and biodiversity is often used as a measure for ecological studies.

Phytodiversity is supposed to be an important factor for arthropod diversity in forest ecosystems (Erwin, 1982). Along the food chain, plants as primary producers are the important basic resource for other trophic levels. According to predicted models, a greater number of resources should support a greater number of consumer species (Tilman, 1986; Rosenzweig, 1995). This relationship could be applied on the diversity and abundance of species. In experimental forest habitats, tree diversity has positively affected general arthropod species richness (Vehviläinen *et al.*, 2008). As an example, forests with plant species richness harbour a greater diversity of beetle species based on their host specificity (Erwin, 1982; Stork, 1988). Since most arthropod herbivores are also specialized species and restricted to one or a few host plants, a positive relation between the number of plant species and arthropod herbivore diversity seems logical. Further correlative studies and experimental studies have shown increases in arthropod herbivore diversity through increasing phytodiversity (e.g. Niemelä *et al.*, 1996; Siemann, 1998). If the arthropod herbivore diversity increases, the remaining question is how herbivory intensity changes. For plants, better resource exploitation is considered to be a main driver that leads to the greater productivity of diverse communities (Tilman, 1996; Loreau *et al.*, 2001). If the same principle is applied to herbivores, it would result in increased plant consumption (Mulder *et al.*, 1999; Cardinale *et al.*, 2006).

Forest canopies are a major source of global insect diversity (Erwin, 1982; Stork, 1988; Novotny & Basset, 2005). For temperate deciduous forests, canopy research is still scarce. However, the importance of tree species, season, and spatial variability for structuring species richness and abundance patterns of beetles has been demonstrated for temperate forest canopies (Gering & Crist, 2000). *Fagus sylvatica* L. (European beech; Fagaceae), the dominant deciduous tree species in Central Europe, should have a special research interest concerning its contribution to arthropod diversity.

This research study investigated arthropod herbivory on leaves of *F. sylvatica* along the vertical gradient of temperate forests, as well as *Acer pseudoplatanus* L. (sycamore maple; Sapindaceae) and *Carpinus betulus* L. (hornbeam; Betulaceae) in the understorey. This research study investigated the plant and insect diversity of forest sites in Central Germany. The aim was exploring differences of diversity between the sample sites and the identification of parameters (precipitation, exposition, and microclimate) determining the diversity. Furthermore, effects of phytodiversity on insect diversity and herbivory on *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* were analyzed. The following hypotheses were tested: (1) phytodiversity increases the abundance and diversity of insects and (2) herbivory intensity (leaf area loss) increases with phytodiversity.

5.2 Materials and methods

Study area

Ten study sites were selected along a 140 km east–west transect with locations in Central Germany within the federal states of Thuringia, Lower Saxony, and Hesse (Chap. 3: Fig. 3.1; Chap. 4: Fig. 4.1). Mixed deciduous tree species dominated the forest stands. At each forest stand, sample sites were selected facing northern and southern exposition (n = 20). Elevations varied between the study sites (140–444 m.a.s.l.) and mean annual precipitation ranged from 474 mm to 874 mm (German Weather Service, reference period from 1961–1990). Lower Trias sandstone was mostly the geological substrate of the forest sites, with exceptions of upper Trias sandstone at one site (Bocksbühl) and middle Triassic limestone at two sites (Feuerkuppe and Heidelberg).

Environmental data

Precipitation data for the forest sites based on the reference period from 1961–1990 were obtained from the Germen Weather Service (App. B: Tab. 2A). Microclimate (air temperature and relative air humidity) was measured hourly with data loggers (iButton, Model DS1923, Maxim Integrated, San Jose, CA, USA). Data loggers were installed in the understorey (about 1 m height) and in lower canopies of adult *F. sylvatica* trees (about 18 m height) at each sample site. Complete data were available from July–August 2012 for all sample sites. Average day values from sunrise to sunset (6 am–9 pm) were used for further analyses with microclimate.

Biodiversity data

Phytodiversity was assessed with vegetation surveys that were conducted at each sample site. Plant species of angiosperms were recorded for the ground, shrub, and tree layer. Their abundances in each layer were estimated with the Londo scale (Londo, 1976) in a 10 x 10 m square (vegetation plot) representing the vegetation cover of the forest sample site. Based on the vegetation data, phytodiversity was represented as the number of plant species per vegetation plot (species richness) and the Shannon index (Equation 5.1), which includes the abundance of each plant species representing the value of species.

$$\text{Shannon index} = -\sum_{i=1}^{s} \frac{n_i}{N} \times \ln \frac{n_i}{N} \tag{5.1}$$

$s = \text{sum of species};\ n_i = \text{value of species i};\ N = \text{sum of values of all species}$

Insect diversity was surveyed for all forest sites. Window traps were used for capturing flying insects (Fig. 5.1). A window trap was installed at each sample site in lower canopies of three adult *Fagus sylvatica* individuals (average height: 18 m). Selected *F. sylvatica* trees were identical to the individuals that were used for the assessment of leaf traits and herbivory (Chap. 3–4). Saturated saline solution with a drop of rinsing detergent was used as catch liquid in one-litre-sized containers.

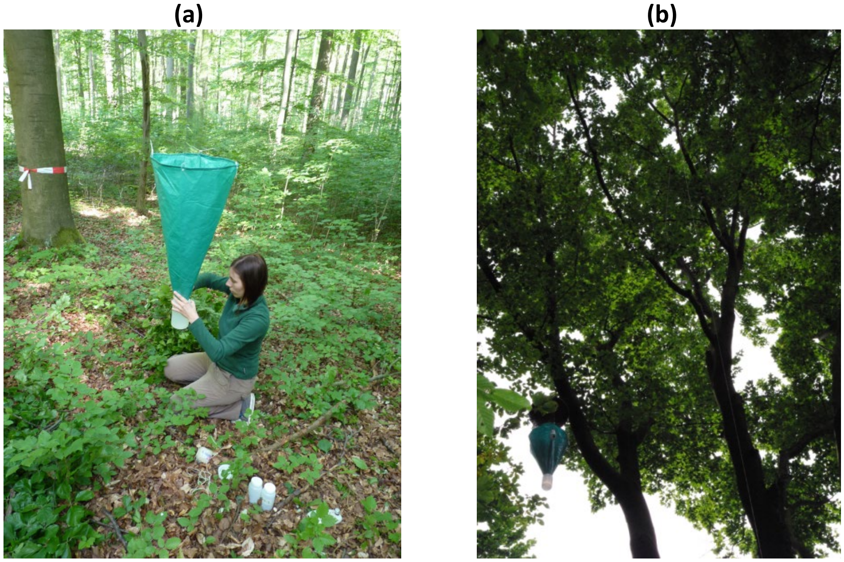

Figure 5.1: **(a)** Window traps installed in **(b)** lower canopies (average height: 18 m) of *Fagus sylvatica* for the collection of flying insects.

The sample period started in June 2012 and ended at the beginning of August 2012. Storms caused some fall outs of window traps. Each window trap was active for about three weeks with three rounds after changing the catch liquid. Insect individuals were transferred from the window trap container to tubes with ethanol (70%). For further analyses, the insect abundance per sample site was calculated as an average (Equation 5.2). The Shannon index for insect diversity was calculated based on the insect abundance as percentages for each order, which stand for the value of order (Equation 5.3).

$$\text{abundance of insects} = \text{number of insects/number of traps} \tag{5.2}$$

$$\text{Shannon index} = -\sum_{i=1}^{s} \frac{n_i}{N} \times \ln \frac{n_i}{N} \tag{5.3}$$

s = sum of orders; n_i = value of orders i; N = sum of values of all orders

Herbivory data

Arthropod herbivory intensities on leaves were assessed for *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus*. At each of the 20 sample sites, three juvenile individuals (if available) of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* were selected in the understorey, and three adult individuals of *F. sylvatica* were additionally surveyed at the lower and upper canopy. Canopies were accessed with rope climbing. A total of 60 adult and juvenile *F. sylvatica*, 41 juvenile *A. pseudoplatanus*, and 27 juvenile *C. betulus* individuals were selected for analyses. Foliage material (twigs) of all tree individuals was randomly collected in June 2012 and stored deep frozen. Herbivory was determined as the percent area of missing leaf tissue. Therefore, all leaves of collected twigs were defrosted and scanned with a flat-bed scanner (n(*F. sylvatica* understorey) = 1801; n(*F. sylvatica* lower canopy) = 1120; n(*F. sylvatica* upper canopy) = 1425; n(*A. pseudoplatanus*) = 528; n(*C. betulus*) = 628), and then analyzed with the computer image analysis system WinFOLIA (Régent Instruments Inc., Ville de Québec, QC, Canada). Leaf damage, including area of missing leaf edges, was calculated with the potential leaf size (existing plus missing leaf area) and the missing leaf area.

Statistical analyses

Statistical analyses were performed with the R version 3.4.1 (R Development Core Team, 2017). Statistical distributions of the data (precipitation, microclimate, phytodiversity, insect abundances and diversity, and herbivory) was assessed with the Shapiro-Wilk test. Based on the statistical distributions, differences of plant species richness (ground layer) and insect abundance as well as differences of the Shannon index for plants (ground layer) and insects between expositions of sample sites were tested with the *t* test and Mann-Whitney *U* test, respectively.

With four independent variables (exposition, precipitation, temperature, and relative air humidity) multivariate statistics was chosen for analyses of plant and insect diversity of the sample sites. The aim was to illustrate (dis)similarities between the composition of plants and insects in terms of environmental conditions. On the basis of nonparametric data for plant species and insect order abundances, non-metric multidimensional scaling (NMDS) was used to generate the ordination (Legendre & Legendre, 1998). Calculations were done with the R packages *vegan* (Oksanen *et al.*, 2017) and *goeveg* (Friedmann & Schellenberg, 2017) based on the Bray-Curtis dissimilarity. For constructing the ordination, the *dimcheckMDS* function was used for detecting the best dimensionality in NMDS. The *dimcheckMDS* function provided a diagnostic plot of stress values for six tested dimensions in NMDS (App. E: Fig. 7A–8A), showing the decrease in ordination stress with an increase in the number of ordination dimensions. Based on the diagnostic plot, three and two dimensions were used for the ordination based on plant species and insect order compositions, respectively. The NMDS for plant species composition was calculated with vegetation data of the ground layer. Sample sites were plotted onto the ordination. Plant species and insect order compositions of the sample sites were tried to interpret with independent variables (exposition, precipitation, temperature, and relative air humidity of lower canopies and the understorey) based on post-hoc correlations. Significant parameters would be fitted onto the ordination plot (App. E: Tab. 17A).

Linear regressions were conducted for effects of phytodiversity (species richness and Shannon index) of tree, shrub, and ground layers on insect abundance and diversity, as well as for effects of phytodiversity on leaf damage (leaf area loss) of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus*.

5.3 Results

Overall, the composition of plant species and insect orders differed between the sample sites. Eight different tree species were found in the tree and shrub layer (App. E: Tab. 18A–19A) and the ground layer harboured 66 plant species across all sample sites (App. E: Tab. 20A). *Fagus sylvatica* was present at all samples sites and layers. Insect catches with flight traps revealed individuals belonging to 13 different insect orders with a range of 10–12 orders per sample site (App. E: Tab. 21A). The number of plant species and the diversity of plants and insects also varied between and within the studied forest sites (Tab. 5.1). Minimum and maximum numbers of plant species in the ground layer and insect individuals ranged from 3–26 and 47–265, respectively.

The species richness and Shannon index for plants showed a tendency of lower values on sample sites with southern exposition compared to northern exposition (Fig. 5.2a–b). However, neither differences of species richness nor Shannon index were significant. Insect abundances and diversity showed tendencies of lower and higher values on sample sites with southern compared to northern exposition, respectively (Fig. 5.2c–d). Once again, differences were not significant.

Sample sites were ordinated with NMDS according to their plant species and insect order composition (Fig. 5.3a–b). The stress values were 0.133 and 0.184 for NMDS based on plant species and insect order composition, respectively. Following the guidelines for acceptable stress values (Clarke, 1993), goodness of NMDS was determined with the category “usable” (stress value < 0.20). Shepard dia-

Table 5.1: Plant and insect diversity of all sample sites. Phytodiversity is represented as species richness and the Shannon index in tree, shrub, and ground layer. Insect diversity is represented as the number of insect orders, insect individuals, and the Shannon index. Lists of plant species and insect orders are available in Appendix E (Tab. 18A–20A).

Site[1]	Exposition	Plants						Insects		
		tree layer		shrub layer		ground layer				
		species richness	Shannon-index[2]	species richness	Shannon-index[2]	species richness	Shannon-index[2]	# orders	# Individuals[3]	Shannon-index[2]
WB	north	3	0.44	3	0.38	19	2.19	11	118	1.16
	south	2	0.26	3	0.65	6	1.19	10	81	1.36
TE	north	1	0.00	1	0.00	7	1.55	10	93	1.24
	south	2	0.22	1	0.00	7	1.64	11	76	1.47
KBVB	north	3	0.82	1	0.00	5	1.43	10	95	1.28
	south	3	0.48	2	0.24	3	0.96	10	47	1.51
SS	north	3	0.56	1	0.00	6	0.75	11	103	1.24
	south	5	0.97	1	0.00	14	2.06	11	72	1.34
HGB	north	1	0.00	1	0.00	22	1.54	10	56	1.21
	south	2	0.39	3	0.35	13	1.89	11	90	1.11
BB	north	1	0.00	4	0.73	12	1.77	11	98	1.32
	south	1	0.00	4	0.54	9	1.90	10	172	1.01
HB	north	1	0.00	2	0.39	21	2.56	12	110	1.18
	south	3	0.85	2	0.47	11	1.76	10	126	1.09
FK	north	1	0.00	4	0.26	8	1.42	11	138	1.14
	south	1	0.00	3	0.68	18	1.40	10	62	1.55
HDB	north	1	0.00	3	0.60	26	2.53	11	59	1.47
	south	4	0.93	1	0.00	11	1.47	10	85	1.37
EL	north	3	0.38	4	0.30	15	1.60	11	265	0.88
	south	2	0.23	2	0.01	4	1.10	11	124	1.37

[1] WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite.

[2] The Shannon index was calculated based on plant species abundances or based on insect abundances as percentages for each order.

[3] Insect individuals were calculated as the number of insect individuals per trap.

grams are available in Appendix E (Fig. 7A–8A). Neither exposition nor environmental factors (precipitation, temperature, and relative air humidity) were significant parameters as axes for the NMDS ordination (App. E: Tab. 17A). The NMDS showed varying ordination distances between forest and exposition sites based on plant species and insect order compositions, and no clear pattern emerged.

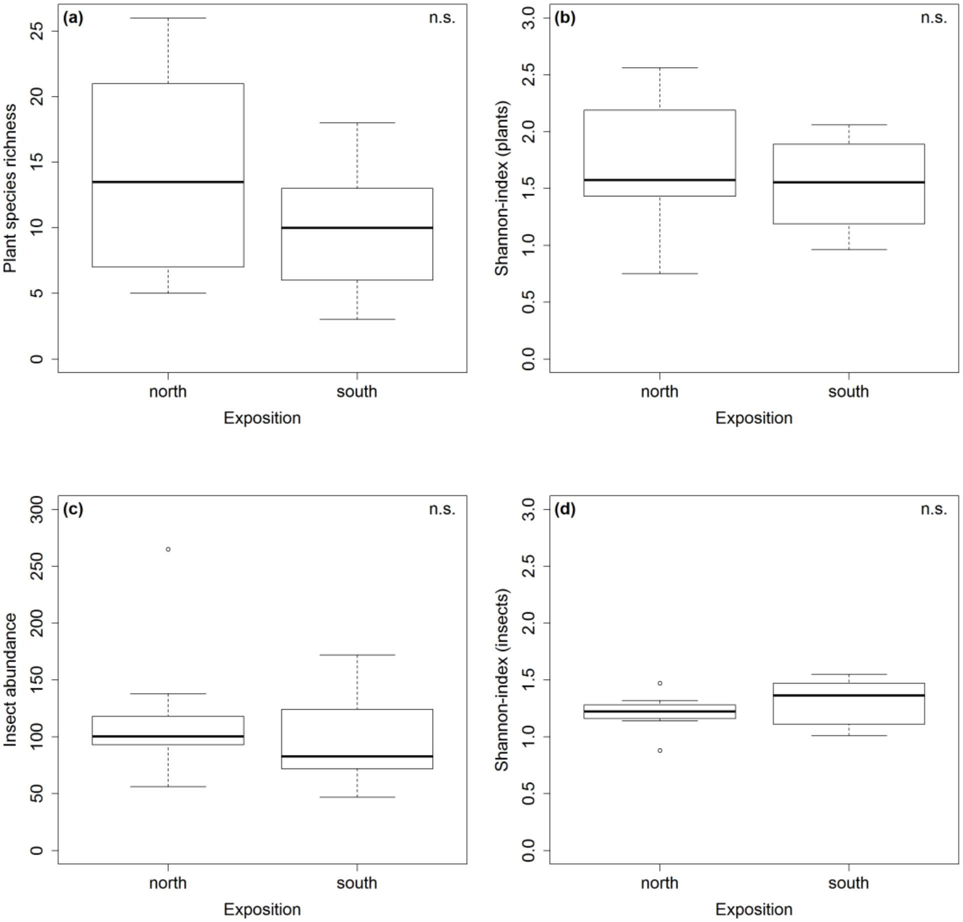

Figure 5.2: Diversity of plants and insects according to the northern and southern exposition of sample sites. Presented are **(a)** species richness (number of species per vegetation plot) and **(b)** Shannon index (based on species abundances) for plants in the ground layer, as well as the **(c)** insect abundance (number of individuals per window trap) and **(d)** Shannon index for insects (based on abundances of orders). Boxplots are marked with "n.s." for non-significant differences ($p>0.05$) using Mann-Whitney *U* test for **(a)** and **(c)** and *t* test for **(b)** and **(d)** depending on the statistical distributions.

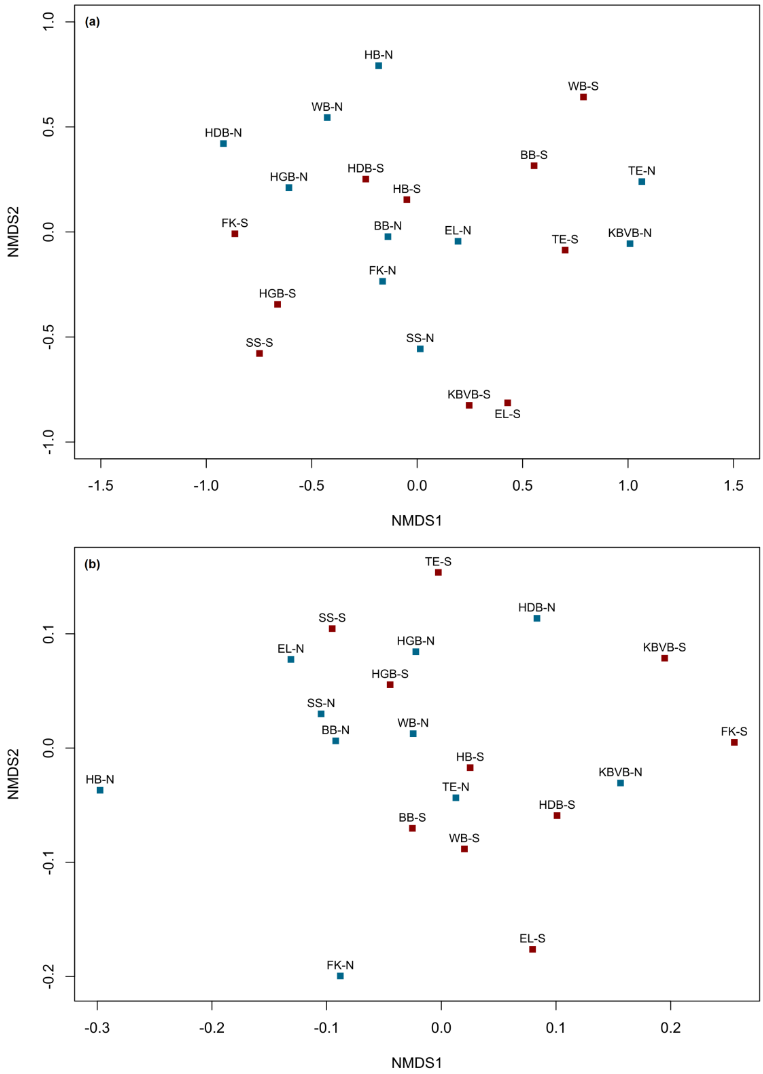

Figure 5.3: Ordination of sample sites with non-metric multidimensional scaling (NMDS). Each square (blue = northern exposition; red = southern exposition) represents a sample site according to the composition of **(a)** plant species (based on abundances) and **(b)** insect orders (based on individual abundances). Non-metric multidimensional scaling is based on the Bray-Curtis dissimilarity with stress values of **(a)** 0.133 and **(b)** 0.184. WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite; N = north exposition; S = south exposition.

Effects of phytodiversity in the tree, shrub, and ground layer on insect abundance and diversity, as well as on herbivory (leaf area loss) were surveyed. On the one hand, phytodiversity revealed almost no significant interactions with insect abundance and diversity or herbivory (Tab. 5.2–5.3). On the other hand, plant species richness in the shrub layer showed a positive effect on insect abundance (Fig. 5.4a), and a negative effect on herbivory in lower canopies of *F. sylvatica* (Fig. 5.4b). Furthermore, a negative trend of increasing plant diversity (Shannon index) in the shrub layer with decreasing herbivory of *F. sylvatica* in lower canopies was identified. In contrast, a positive trend was found for increasing phytodiversity with herbivory on *A. pseudoplatanus* in the understorey (Tab. 5.3).

Table 5.2: Effects of phytodiversity in the tree, shrub, and ground layer on insect abundance and diversity (n = 20).

Parameter[1]	**d.f.**		***F*-values**[2]	
	n.	d.	insect abundance	insect diversity
(a) Tree layer				
species richness	1	18	0.03	<0.01
Shannon index	1	18	0.01	0.01
(b) Shrub layer				
species richness	1	18	6.31*	2.27
Shannon index	1	18	0.14	0.01
(c) Ground layer				
species richness	1	18	0.08	0.12
Shannon index	1	18	0.05	0.81

[1] The species richness represents the number of plant species per vegetation plot and the Shannon index is based on the abundance of each plant species.

[2] The insect abundance represents the number of individuals per window trap, and insect diversity (Shannon index) is based on insect abundances as percentages per order. * = $p<0.05$; n. = numerator; d. = denominator.

5.4 Discussion

Tree diversity included a total of eight species and Shannon indices between 0–1. While the number of tree species (11) is similar, the range of the Shannon index is higher with values between 0–2 in a study by Sobek *et al.* (2009c). Neither exposition and precipitation, nor microclimate could be linked to the diversity of plant species in the present study. The diversity of plant species was heterogeneous within and between the mixed deciduous forest sites. Therefore, no clusters of study sites were identified based on the plant species composition in the

Table 5.3: Effects of phytodiversity in the tree, shrub, and ground layer on herbivory (leaf area loss) of *Fagus sylvatica* (beech; n = 20), *Acer pseudoplatanus* (maple; n = 14), and *Carpinus betulus* (hornbeam; n = 10).

Parameter[1]	***F*-values**[2]				
	beech (UC)	beech (LC)	beech (US)	maple (US)	hornbeam (US)
(a) Tree layer					
species richness	0.01	1.17	0.07	0.12	1.35
Shannon index	0.01	0.62	0.03	0.05	0.57
(b) Shrub layer					
species richness	1.21	5.33*	0.86	0.52	0.41
Shannon index	1.28	4.38^t	0.58	0.29	0.19
(c) Ground layer					
species richness	2.39	0.03	0.03	3.65^t	0.21
Shannon index	0.45	<0.01	0.02	1.13	1.00
d.f. n.	1	1	1	1	1
d.	18	18	18	12	8

[1] The species richness represents the number of plant species per vegetation plot and the Shannon index is based on the abundance of each plant species.

[2] UC = upper canopy; LC = lower canopy; US = understorey; * = $p<0.05$; t = $p<0.1$; n. = numerator; d. = denominator.

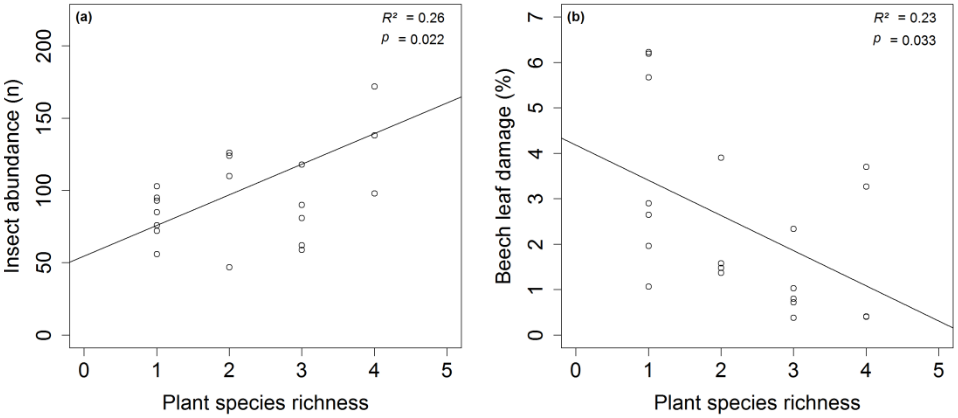

Figure 5.4: Positive and negative effect of phytodiversity in the shrub layer on **(a)** insect abundance (n = 20) and **(b)** herbivory (leaf area loss) of *Fagus sylvatica* (beech) in lower canopies (n = 20), respectively. Insect abundance represents the mean number of individuals per window trap.

understorey. Greater differences of plant diversity appeared when abundances of plant species were taken into account, i.e. study sites with similar numbers of plants species showed distinct diversity based on the Shannon index. Comparisons of phytodiversity between the three forest layers have not been conducted. However, the dominant role of tree species in forests is expected to influence understorey diversity and composition (Bratton, 1976; Palik & Engstrom, 1999). Changes in resource availability, e.g. understorey light and soil nutrients, physical effects of litter, and phytotoxic compounds are responsible mechanisms for the impact of trees on understorey diversity (reviewed by Barbier *et al.*, 2008). Indeed, the understorey of temperate deciduous forests in Germany shows higher abundances and species richness of herbaceous plants along a tree diversity gradient (Mölder *et al.*, 2008). Furthermore, environmental variables like humus layer mass and pH also affect the herb layer species richness and cover (Vockenhuber *et al.*, 2011). Generalizing the impacts is difficult because varying forest management practices affecting the understorey vegetation interfere with the effects of trees. Potentially, different forest management practices within the study region and other site attributes could have contributed to the phytodiversity and composition differences of the study sites.

Insect abundances did vary to different extents between and within the forest sites. However, the variation of insect diversity was low concerning the number of orders. Since biodiversity was not the main research focus of the dissertation, the Shannon index was only based on individual abundances of orders and has a lower informative value compared to a diversity index based on actual insect species. The identification of insect species is an enormous work and would be necessary to explore more adequately the interaction of insect and plant diversity. Relating to the first hypothesis of this study, effects on insect abundance but not insect diversity were identified with a positive relation based on the number of plant species in the shrub layer. The shrub layer consisted mostly of tree species that also occurred in the tree layer. An increase in insect diversity based on insect species can be expected with increasing tree diversity for the studied forest sites. In general, habitat heterogeneity is supposed to be the driving force of animal species richness across various ecosystems and taxonomic groups (Tews *et al.*, 2004). For arthropod communities, varying architectures of different tree species can determine the availability of ecological niches and an associated diversity (Southwood *et al.*, 1982; Halaj *et al.*, 2000; Gossner & Ammer, 2006). In temperate deciduous forests of Germany, the species richness of beetles increases across a tree diversity (Sobek *et al.*, 2009c). This represents more diverse ecological resources, which the increasing number of plant species offer for insects. Potentially, plant abundances could also be related to insect abundances (number of individuals). This would be a quantitative measure representing the resources supporting a certain amount of insect abundances.

Corresponding to the second hypothesis, herbivory intensity increases with phytodiversity. However, leaf area loss of *F. sylvatica* leaves in lower canopies decreased with the number of plant species in the shrub layer. The same trend was visible with the diversity of shrub species based on their abundances (Shannon index). No effects of phytodiversity on herbivory were found for *A. pseudoplatanus* (except for one trend) and *C. betulus*. Both species were only sampled in the understorey, resulting in a potential lack of impact on herbivory caused by tree species in the shrub layer. The effect of shrub species might be in accordance with a quantitative review showing that tree herbivory is decreased in mixed species stands compared to pure stands (Jactel & Brockerhoff, 2007). According to the resource concentration hypothesis, insects can locate host plants better in species-poor compared to plant species-rich environments (Root, 1973). Furthermore, the relationship between plant and herbivore diversity may be nonlinear. The diversity of higher trophic levels could also be increased by phytodiversity because many arthropod parasites and predators are dependent on floral resources (Powell, 1986; Jervis *et al.*, 1993). Despite the positive relationship between plant and arthropod diversity, local herbivore diversity is also maintained by a diversity of parasites and predators (Siemann, 1998). In polycultures, effects of parasites and predators often reduce herbivory intensity compared to monocultures (reviewed by Andow, 1991). Indeed, herbivore and predator species richness are both positively related to plant species richness (Knops *et al.*, 1999; Haddad *et al.*, 2009). As an example, herbivore parasitoids exist within the hymenopteran order. In the present study, insect herbivores are for instance represented by the order of Hemiptera (sap-sucking feeding guild) and parasitoids could be present in the order of Hymenoptera. Both orders would need to be analyzed in detail concerning the nonlinear relationship between phytodiversity and herbivory.

CHAPTER 6

EXPERIMENTAL STUDY OF ENVIRONMENTAL EFFECTS: LEAF TRAITS OF JUVENILE *FAGUS SYLVATICA*, *ACER PSEUDOPLATANUS*, AND *CARPINUS BETULUS* ARE COMPARABLE TO LEAVES OF MATURE TREES IN UPPER CANOPIES

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6.1 Abstract

Morphological and functional leaf traits like leaf toughness and nutrient content are essentially influenced by the environment, especially through light and climatic conditions. Varying light conditions have been identified as a significant predictor for the variation of many leaf traits. However, the leaf acclimation to light is suggested to be of secondary importance. The aim of the experimental study was to analyse environmental effects (microclimate and soil moisture), which are present in upper canopies of forest stands, on leaf traits of juvenile *Fagus sylvatica* L. (European beech; Fagaceae), *Acer pseudoplatanus* L. (sycamore maple; Sapindaceae), and *Carpinus betulus* L. (hornbeam; Betulaceae). The experimental design managed to imitate two distinct microclimates causing different temperature and air humidity conditions. Furthermore, the irrigation treatment with different levels of applied water caused distinct soil moisture conditions in the trial pots. As a result of the treatments, leaves of C. betulus showed a tendency of decreased specific leaf area (SLA) caused by the treatment with warmer and drier microclimate. The environmental effect on SLA was even stronger with lower soil moisture conditions. Chlorophyll content showed lower values in treatments with higher soil moisture conditions in both greenhouses for *F. sylvatica* and *A. pseudoplatanus*. The trends are in accordance with combined effects of temperature, air humidity, and soil moisture on SLA, and increased leaf chlorophyll content caused by slight drought stress. Plants in the greenhouses were exposed to full sunlight indicating a microclimatic environment comparable to upper canopies in forest stands. The comparable SLA and chlorophyll content between leaves of mature *F. sylvatica* trees in upper canopies and juvenile trees of the greenhouses suggest similar environmental conditions instead of ontogenetic effects that are responsible for the formation of leaf trait characteristics.

6.2 Introduction

Morphological and functional leaf traits are essentially influenced by the environment, especially through light and climatic conditions. Changes in climate (temperature and air humidity) and light can affect leaf toughness and leaf nutrient content like nitrogen (N) and carbon (C) concentrations. While leaves of tree seedlings and saplings grow in a similar environment of the understorey, large trees need to develop leaves with a distinct development of traits that are acclimated to different environmental conditions in the canopy.

The formation of softer leaves with a thinner and larger leaf lamina, represented by high specific leaf area (SLA), is a common response to humid environments (Cunningham *et al.*, 1999; Niinemets, 2001; Sellin *et al.*, 2013). In addition, high temperatures can also lead to an increase in SLA, but it strongly depends on sufficient soil moisture (Xu & Zhou, 2006). Low soil moisture leads to water stress situations for plants. In return, water stress can cause sclerophylly (Bussotti *et al.*, 1995), resulting in thickened and hardened foliage that resists loss of moisture. Sclerophylly is based in an accumulation of phenolic compounds and lignification of leaf tissues (Bussotti *et al.*, 1997; Grossoni *et al.*, 1998).

Leaf N concentrations are especially influenced by light conditions (Reich *et al.*, 1997; Wright *et al.*, 2004). Sun-exposed leaves usually show increased leaf N concentrations compared to shade leaves (Fortin & Mauffette, 2002; Levesque *et al.*, 2002). Nonetheless, patterns of leaf N content also depend on the shade tolerance of tree species. In lower light environments, increasing the leaf N concentration is a strategy of N partitioning for more efficient light harvesting (Niinemets, 1995). Furthermore, levels of humidity can also affect leaf nutrient concentrations. Low soil moisture conditions of dry environments, causing water stress of host plants, increase the N content in plant tissues (Rouault *et al.*, 2006).

Varying light conditions have been identified as a significant predictor for the variation of many leaf traits within forest canopies (e.g. Rijkers *et al.*, 2000; Leal & Thomas, 2003). Leaf trait trends identified by Thomas (2010) are likely to be influenced by the leaf acclimation both to environmental conditions (light) and to plant ontogeny (tree size). However, the leaf acclimation to light is suggested to be of secondary importance. Studies with a controlled light effect (e.g., comparison between leaves of open-grown saplings and upper canopy trees) indicate that ontogenetic changes in leaf toughness and herbivory cannot be fully accounted by environmental acclimation responses to sun and shade (Thomas & Winner, 2002; Thomas *et al.*, 2010). Strong effects of tree size on leaf toughness are found independently of crown exposure (Thomas, 2010). Decreases in SLA and related leaf features (leaf tissue density and lignifications) at the end of tree ontogeny are also noted to be independent of sun and shade acclimation (Day *et al.*, 2001; Niinemets, 2002; Nabeshima & Hiura, 2004; England & Attiwill, 2006). Furthermore, the magnitude of ontogenetic changes in traits is larger than what is documented for studies of light acclimation responses (Ellsworth & Reich, 1992a, 1992b; Sipe & Bazzaz, 1994; Beaudet *et al.*, 2000; Thomas *et al.*, 2010).

The aim of the experimental study was to analyse environmental effects, which are present in upper canopies of forest stands (Chap. 3–5), on leaf traits of juvenile *Fagus sylvatica* L. (European beech; Fagaceae), *Acer pseudoplatanus* L. (sycamore maple; Sapindaceae), and *Carpinus betulus* L. (hornbeam; Betulaceae). The two following hypotheses were tested: (1) higher temperatures (and lower air humidity) and lower soil moisture conditions increase leaf toughness, and (2) lower soil moisture conditions increase the leaf N content.

6.3 Materials and methods

Set up

Plant individuals of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus* with an age of 2 years old and a height about 50–80 cm (Müller Münchehof, Seesen, Germany) were planted in trial pots in August 2013 (Fig. 6.1a). A mixture of 50% soil (Fruhstorfer Erde Typ T, HAWITA, Vechta, Germany) and 50% sand (Estrich sand, grain size = 0–2 mm, Tönsmeier, Hildesheim, Germany) was used as substrate. Two greenhouses (size: 6x28 m) were installed with different UV permeable greenhouse films (FVG EURO 4 and FVG Sun 5 Clear ST, FVG Professional Gardening, Dernbach, Germany) in March 2014, creating distinct climatic conditions (Fig. 6.1b). A plant protection product (Micula, Biofa AG, Münsingen, Germany) was applied to the trees in April 2014 against eggs and individuals of sap-sucking insects that potentially occurred on the tree individuals avoiding herbivory on the experimental foliage material. All trial pots were protected against insect herbivores with mosquito nets.

Figure 6.1: Experimental study with the **(a)** trail pots harbouring *Fagus sylvatica*, *Acer pseudoplatanus*, and *Carpinus betulus* tree individuals **(b)** in the greenhouses 1 (left) and 2 (right) at the installation site at the Samelsonplatz, Hildesheim.

The experimental design consisted of 10 trial pots for each tree species in greenhouse 1 and 2. Manipulations of microclimate and soil moisture were used as treatments for the trial pots. Trial pots in the greenhouses 1 and 2 were labelled with the code LT (lower temperature) and HT (higher temperature) for the microclimate treatment, respectively. Irrigation codes LW (lower water amount) and HW (higher water amount) were added to the trial pots in each greenhouse according to the soil moisture treatment. Overall, four different treatments with five replicates existed for each tree species (Tab. 6.1).

Table 6.1: Treatment codes representing the combination of temperature and irrigation level that were used in the experimental study.

Treatment	Lower irrigation	Higher irrigation
Lower temperature	LTLW	LTHW
Higher temperature	HTLW	HTHW

Trial pots were irrigated two or three times a week. The different amounts of irrigation levels were orientated to maximum and minimum values of the precipitation gradient of the field study (Chap. 3–5; Artern: 59 l/m²; Wahlsburg: 75 l/m²). The area of a trial pot was 0.03 m². Therefore, the amount of water was adapted to the size of the trial pot resulting in 1.77 l and 2.25 l per month for lower and higher water irrigation treatments, respectively. Based on tougher conditions in the trial pots compared to forest sites, trees were always irrigated when soil was dry to avoid withering of individuals. A total amount of 4.96 l and 7.08 l water (about three times higher than at the forest sites) was used for the irrigation of each trial pot with lower and higher water irrigation, respectively.

Measurements

Greenhouse measurements took place in June 2014. Microclimate was assessed as air temperature and relative air humidity. Microclimatic data were measured every hour with data loggers (iButton, Model DS1923, Maxim Integrated, California, USA). Data loggers were installed in the centres at about 1.5 m height in both greenhouses. Soil moisture was measured as volumetric water content (% v v^{-1}) with a soil moisture sensor (FieldScout TDR 100 Soil Moisture Meter, Aurora, Illinois, USA) using 7.5 cm long rods. Five measurements of soil moisture were taken for every trial pot during the experimental period to calculate mean values for statistical analyses.

Specific leaf area (cm² g^{-1}) was assessed as an indicator for leaf toughness. It relates the area of a fresh leaf to its dry mass, and low SLA values are linked to structural defences (Cornelissen *et al.*, 2003). Fully developed leaves were collected for all tree individuals in June 2014 (four leaves of *F. sylvatica* and *C. betulus*, and three leaves of *A. pseudoplatanus*). All fresh leaves were scanned with a flat-bed scanner (CanoScan LiDE 110, Canon, Krefeld, Germany), analyzing their areas with the computer image analysis system WinFOLIA (Régent Instruments Inc., Ville de Québec, QC, Canada). Then, each foliage sample was dried (70 °C, 48 h) and weighed for calculation of SLA that was used as the mean per individual for further analyses of leaf toughness. Since *A. pseudoplatanus* did not survive the treatment with higher temperature and lower water irrigation, no SLA values could be assessed.

The chlorophyll content of leaves correlates with leaf N content (van den Berg & Perkins, 2004), because up to 75% of N content is located in chloroplasts (Peoples & Dalling, 1988). Chlorophyll content, as an indicator for leaf N content, was measured with a CCM-200 plus Chlorophyll Content Meter (Opti-Sciences Inc., Hudson, NH, USA). From each tree individual, four chlorophyll values as chlorophyll content index (CCI) were taken in June 2014. Average values were calculated for each treatment per tree species (n = 20). Since *A. pseudoplatanus* did not survive the treatment with higher temperature and lower water irrigation, no chlorophyll content could be assessed.

Statistics

For significant comparisons of measured parameters (microclimate, soil moisture conditions, and leaf traits) in the greenhouses, statistical analyses were performed with the R Version 3.4.1 (R Development Core Team, 2017). Statistical distributions of the parameters were assessed with the Shapiro-Wilk test. Depending on the statistical distributions, further tests for microclimate and soil moisture were performed with Mann-Whitney *U* and *t* test, respectively. Comparisons of SLA and chlorophyll content between the treatments were performed with ANOVA or Kruskal-Wallis and suitable post-hoc tests using the R package *pgirmess* (Giraudoux, 2017).

6.4 Results

Climatic conditions represented by temperature and relative air humidity differed between the two greenhouses (Tab. 6.2). On average, temperature was increased about 1.3 °C and 2.8 °C, and relative air humidity decreased about 3% and 4% in greenhouse 2 compared to greenhouse 1 during day and midday, respectively. Humidity was only significantly distinct between the two greenhouses considering midday values.

Table 6.2: Climatic conditions represented by temperature and relative air humidity during day (5 am – 9 pm; n = 1020) and midday (11 am – 2 pm; n = 60) in the greenhouses 1 and 2 in June 2014. Values represent the median and interquartile ranges (IQR = first quartile, third quartile).

Greenhouse	**Temperature** (°C)		**Relative air humidity** (%)	
	day	midday	day	midday
1	21.4 (16.7,27.9)^{a}	26.5 (22.3,31.5)^{a}	58 (40,80)^{a}	41 (33,52)^{a}
2	22.7 (17.2,30.0)^{b}	29.3 (24.1,35.9)^{b}	55 (37,79)^{a}	37 (28,49)^{b}

Lowercase letters indicate significant differences of temperature and relative air humidity between the greenhouses using Mann-Whitney *U* test (p<0.05; df = 1).

Soil moisture conditions were increased through the treatment of higher irrigation for all tree species in both greenhouses. Average values of soil moisture were increased about 6%, 4%, and 3% in the higher irrigated trial pots of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus*, respectively. Statistical analyses revealed significant differences for trial pots containing *F. sylvatica* and *A. pseudoplatanus* trees (Tab. 6.3).

Table 6.3: Comparisons of soil moisture conditions in the trial pots between lower and higher irrigation treatments for all three tree species (n = 10, per species). Presented are mean values with standard deviation.

Soil moisture (%)	**Trial pot species**		
	Fagus sylvatica	*Acer pseudoplatanus*	*Carpinus betulus*
lower irrigation	18.9 (± 2.2)^{a}	21.6 (± 3.9)^{a}	19.6 (± 2.4)^{a}
higher irrigation	24.6 (± 4.3)^{b}	25.3 (± 3.0)^{b}	22.4 (± 4.3)^{a}

Lowercase letters indicate significant differences using *t* test (*F. sylvatica*: p = 0.003, df = 13; *A. pseudoplatanus*: p = 0.028, df = 18; *C. betulus*: p = 0.079, df = 18).

Average SLA values were highest for *F. sylvatica* (173 cm² g^{-1} ± 25.9 SD), intermediate for *A. pseudoplatanus* (167 cm² g^{-1} ± 20.3 SD), and lowest for

C. betulus (155 cm² g^{-1} ± 20.8 SD). Differences of SLA between the treatments (microclimate and soil moisture) were only present for *C. betulus* but not for *F. sylvatica* and *A. pseudoplatanus* (Fig. 6.2). Specific leaf area of *C. betulus* was decreased in warmer temperatures of greenhouse 2 compared to greenhouse 1, but only differed significantly with the lower irrigation treatment compared to the other three treatment combinations.

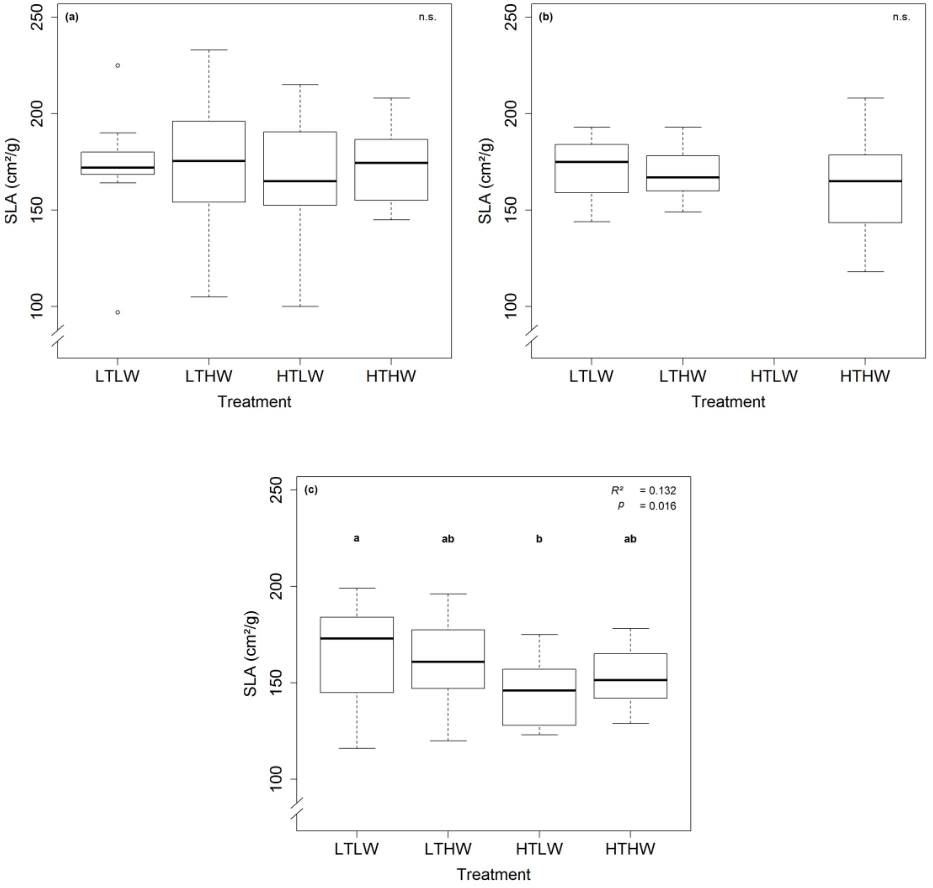

Figure 6.2: Specific leaf area (SLA) of **(a)** *Fagus sylvatica* (n = 20), **(b)** *Acer pseudoplatanus* (n = 15), and **(c)** *Carpinus betulus* (n = 18) for the different treatments. Boxplots are marked with lowercase letters indicating significant differences or with "n.s." for non-significant differences using **(a)** Kruskal-Wallis and post-hoc test ($p<0.05$; df = 3), and **(b–c)** ANOVA and Tukey's HSD ($p<0.05$; df = 3). Treatments: LTLW = lower temperature/ lower irrigation; LTHW = lower temperature/ higher irrigation; HTLW = higher temperature/ lower irrigation; HTHW = higher temperature/ higher irrigation.

Chlorophyll content was on average similar for all tree species with values ranging between 7.1 CCI ± 2.7 SD (*A. pseudoplatanus*), 7.4 CCI ± 2.7 SD (*C. betulus*), and 8.2 CCI ± 2.0 SD (*F. sylvatica*). Depending on the experimental irrigation treatment, leaf chlorophyll content differed significantly for *F. sylvatica* and *A. pseudoplatanus* but not for *C. betulus* (Fig. 6.3). *Carpinus betulus* leaves showed lower chlorophyll content in treatments with higher soil moisture conditions in both greenhouses. Chlorophyll content of trees with the same irrigation treatment did not significantly differ between the two greenhouses.

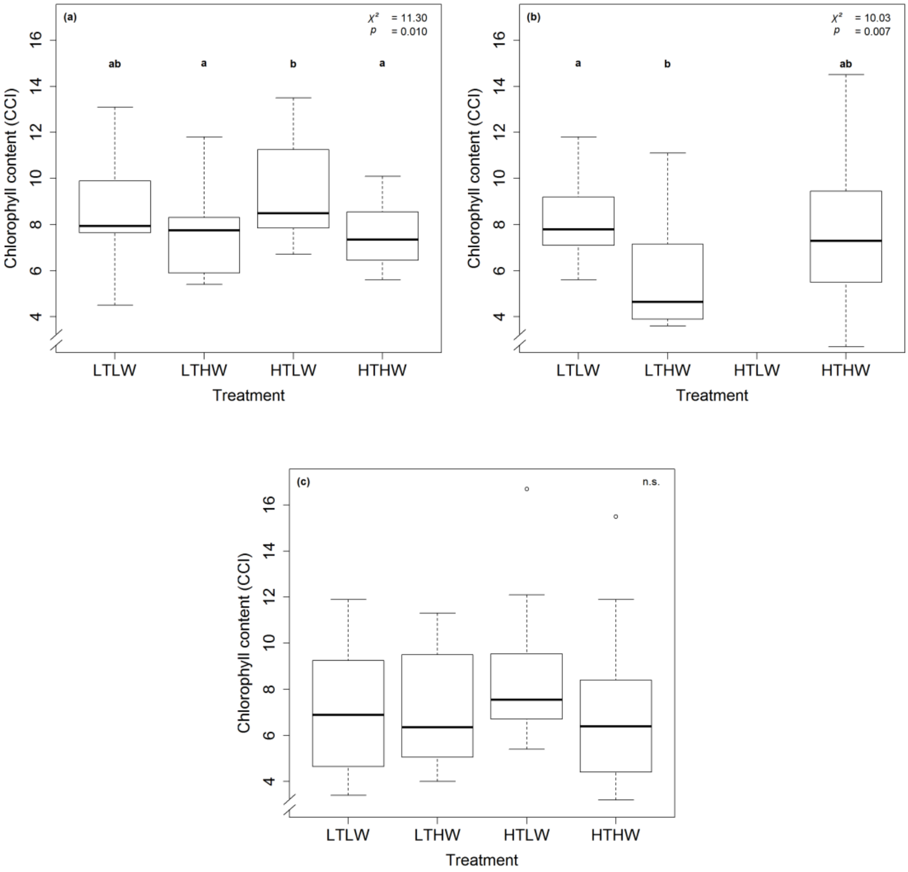

Figure 6.3: Chlorophyll content of **(a)** *Fagus sylvatica* (n = 20), **(b)** *Acer pseudoplatanus* (n= 15), and **(c)** *Carpinus betulus* (n = 20) for the different treatments. Boxplots are marked with uppercase letters indicating significant differences using Kruskal-Wallis and post-hoc test ($p<0.05$; df = 3) or with "n.s." for non-significant differences. Treatments: LTLW = lower temperature/ lower irrigation; LTHW = lower temperature/ higher irrigation; HTLW = higher temperature/ lower irrigation; HTHW = higher temperature/ higher irrigation.

6.5 Discussion

The experimental design managed to imitate two distinct microclimates causing different temperature and air humidity conditions. Thereby, random effects (light conditions, soil moisture, and fertility) of the field study were controlled factors for studying environmental effects on leaf traits of *F. sylvatica*, *A. pseudoplatanus*, and *C. betulus*. Furthermore, the irrigation treatment with different levels of applied water caused distinct soil moisture conditions in the trial pots. Different soil moisture conditions implicated varying water availability for the tree individuals. As a result of the treatments, *C. betulus* showed varying leaf toughness (indicated by SLA) and *F. sylvatica* and *A. pseudoplatanus* differed in chlorophyll content (indicating leaf N content).

Plants in the greenhouses were exposed to full sunlight indicating a microclimatic environment comparable to upper canopies of mixed deciduous forest stands in Central Germany (Chap. 3–4). Average day temperatures in upper canopies of the field study are 1.5 and 2.8°C lower and relative air humidity conditions are 11 and 14% higher compared to greenhouses 1 and 2 of this experimental study, respectively. The magnitude of differences in temperature and relative air humidity between lower and upper canopies (1.1°C and 5%, respectively) of the forest stands (Chap. 3–4) is comparable to the difference between the two greenhouses of this study (1.3°C and 3%, respectively).

The SLA of all three juvenile tree species (*F. sylvatica*, *A. pseudoplatanus*, and *C. betulus*) in this experimental greenhouse study is similar to SLA values of mature F. sylvatica in upper canopies, representing less than half of the SLA values that were found for the tree species in the understorey of forest stands (Chap. 3–4). The comparable leaf toughness between upper canopies (mature trees) and the greenhouses (juvenile trees) suggests similar environmental conditions instead of ontogenetic effects that are responsible for the formation of leaf trait characteristics. Upper canopies and the greenhouses were both exposed to full sunlight, and leaves of juvenile trees in the greenhouses with low SLA values exhibit the typical pattern of sun leaves. Generally, a decline of SLA can be induced by light conditions because light increases the leaf thickness (Yun & Taylor, 1986). Thicker sun leaves of *F. sylvatica* are characterized by a lower SLA compared to the much thinner blades of shade leaves (Lichtenthaler *et al.*, 2007).

Leaf chlorophyll content was decreased about 50% in the experimental study compared to values that were measured in the field study (Chap. 3–4). As part of the photosynthesis, chlorophyll content is dependent on the regulating influence of light conditions. Studies present contrasting results concerning patterns of chlorophyll content based on light conditions. Sun leaves of *F. sylvatica* show higher chlorophyll content than shade leaves (Lichtenthaler *et al.*, 2000), in contrast to shade leaves of other tree species that contain more chlorophyll than sun leaves (Matyssek *et al.*, 2010). High light conditions in the greenhouses might have caused the low chlorophyll content in leaves of the three tree species. In addition, this effect of decreasing chlorophyll content can be enhanced through impacts of water supply.

Leaves of *C. betulus* showed a tendency of decreased SLA caused by the treatment with warmer and drier microclimate. The environmental effect on SLA was even stronger with lower soil moisture conditions, thus supporting the first hypothesis. This trend is in accordance with combined effects of temperature and air humidity on SLA (Cunningham *et al.*, 1999; Niinemets, 2001; Sellin *et al.*, 2013), considering also the important factor of soil moisture (Xu & Zhou, 2006). According to basic plant physiology, drought experiments with potted tree seedlings or saplings show a reduction in SLA with decreasing water supply (Kozlowski & Pallardy, 1997; Otieno *et al.*, 2005). In contrast, *F. sylvatica* and *A. pseudoplatanus* did not demonstrate significant changes in SLA caused by the experimental treatments. While *F. sylvatica* and *A. pseudoplatanus* are most abundant in forest communities where soil drought is rare, *C. betulus* grows also in regions with regular or episodic summer drought (Ellenberg & Leuschner, 2010). *Carpinus betulus* is known to have smaller water flux levels per tree in contrast to greater water flux levels encountered in *F. sylvatica* and *A. pseudoplatanus* (Hölscher *et al.*, 2005).

Generally, drought sensitivity varies between different tree species. Indeed, *C. betulus* reveals lower drought sensitivity compared to *F. sylvatica* and *A. pseudoplatanus* (Hölscher *et al.*, 2005). Potentially, *C. betulus* reacted as an adaptation strategy with lower SLA, leading to an increase in leaf toughness, for the survival in a warm and dry environment, which was manipulated by the experimental treatments. This would also be in accordance with the range for SLA, which increases in the sequence *A. pseudoplatanus* < *F. sylvatica* < *C. betulus* (Legner *et al.*, 2014). Regarding *A. pseudoplatanus*, the fact that tree individuals grown under the treatment with lower water supply in the warmer and drier greenhouse did not survive has to be taken into account. Compared to the other two tree species, leaves of *A. pseudoplatanus* had the largest size, which potentially resulted in a higher water demand leading to the desiccation of the tree individuals.

In the experimental study, differences of chlorophyll content did not exist between the two greenhouses but regarding the irrigation treatment, leaves showed lower chlorophyll content in treatments with higher soil moisture conditions in both greenhouses. Significant differences were identified for the chlorophyll content of *F. sylvatica* and *A. pseudoplatanus*. The physiological state of plants, which influences photosynthetic processes, is strongly affected by the water supply. Impacts of drought stress on the variation of chlorophyll content have been well studied. Generally, drought stress can limit plant growth through variations of chlorophyll content, respiration, and nutrient metabolism (Jaleel *et al.*, 2008). Chlorophyll content decreases significantly through drought stress situations (Mafakheri *et al.*, 2010; Gholamin & Khayatnezhad, 2011; Aref *et al.*, 2013). However, a slight drought stress can increase leaf chlorophyll content (Mensah *et al.*, 2006). Potentially, the lower irrigation treatment caused minor drought stress conditions for the tree individuals of *F. sylvatica* and *A. pseudoplatanus* reacting with increased chlorophyll content. This is also in accordance with a higher drought sensitivity of *F. sylvatica* and *A. pseudoplatanus* compared to *C. betulus* (Hölscher *et al.*, 2005). In conclusion, the patterns of chlorophyll content, indicating leaf N concentrations, would support the second hypothesis for *F. sylvatica* and *A. pseudoplatanus* that lower soil conditions lead to an increase in leaf N content.

6.6 Conclusions

The comparable specific leaf area and chlorophyll content between leaves of mature *F. sylvatica* trees in upper canopies of forest stands and juvenile trees of the experimental greenhouse study suggest similar environmental conditions instead of ontogenetic effects that are responsible for the formation of leaf trait characteristics.

CHAPTER 7

SYNOPSIS

7.1 Environmental and plant ontogenetic effects on herbivory along the vertical forest gradient

Changes of environmental conditions and the plant ontogeny of woody species occur along the vertical forest gradient. Environmental conditions are especially altered through the light gradient, and plant ontogeny is present as different developmental stages occupying the forest strata. While seedlings are restricted to the ground layer, saplings can be found in the ground and shrub layer. Mature trees form the canopy, which can be divided into the upper canopy (leaves exposed to full sunlight) and the lower canopy (leaves shadowed by the upper canopy). These environmental (abiotic) and ontogenetic (biotic) factors have impacts through direct and indirect pathways on arthropod herbivores and herbivory intensities. A variety of studies have evidenced different patterns of herbivory in the understorey and the canopies of tropical and temperate forests (e.g. Lowman, 1992; Basset, 2001; Horchler & Morawetz, 2008). Underlying causes for the variation of herbivory intensities between the understorey and canopy can be differences in plant chemistry, leaf palatability, and local microclimate (Coley & Barone, 1996). The development of plants is connected to these parameters, which can be categorized as ontogenetic and physiological or environmental processes (Lawson & Poethig, 1995).

Environmental processes for plant development are essentially influenced by light. Light conditions change strongly along the vertical forest gradient because light is absorbed by the vegetation. While large trees need to develop distinct leaves that are acclimated to different light conditions, leaves of seedlings and small saplings in the understorey experience more or less the same light environment. The tree and shrub cover can lead to a decrease in light intensities from upper canopy to the understorey by 20 times (Fortin & Mauffette, 2002), and internal shading increases with tree size (Niinemets, 1995). Along this light-induced micro-environmental gradient, temperature increases and air humidity decreases from understorey to upper canopies (Wilmers & Ellenberg, 1986; Parker, 1995; Tal *et al.*, 2008). Although light conditions were not measured in this study, the light-induced micro-environmental gradient was visible as an increase in temperature and a decrease in relative air humidity along the vertical forest gradient from bottom to top (Chap. 3.4: Fig. 3.2).

Leaf traits that are relevant for arthropod herbivores, e.g. leaf nutrients and defences, are affected by light. Specific leaf area (SLA) increases with shading

(Wuytack *et al.*, 2011), because light is known to affect leaf thickness (Yun & Taylor, 1986). Therefore, leaf toughness generally differs between sun and shade leaves. Furthermore, light conditions also alter the leaf nitrogen (N) content. Patterns of varying leaf N content depend on the shade tolerance of plant species. While N content is increased in sun leaves compared to shade leaves of *Acer saccharinum*, a tree species with intermediate shade tolerance (Fortin & Mauffette, 2002), the opposite is found for *Fagus crenata*, a shade-tolerant species (Yamasaki & Kikuzawa, 2003). For the shade-tolerant *Fagus sylvatica*, N content was also highest in shade leaves of the understorey and lower canopy compared to sun leaves of upper canopies (Chap. 3.4: Fig. 3.3). In addition, carbon-based defence compounds of leaves generally increase with light (Dudt & Shure, 1994; Crone & Jones, 1999; Roberts & Paul, 2006). This pattern was also found in the field study with sun leaves of *F. sylvatica* (upper canopy) containing highest carbon (C) concentrations (Chap. 3.4: Fig. 3.3). An increase in leaf C content indicates higher mechanical or chemical defences like carbon-based phenolic compounds (Feeny, 1970; Southwood *et al.*, 1986).

Temperature and air humidity also influence leaf toughness and nutrients. While leaves of plants in arid and semi-arid regions are typically tough with low SLA values, plants in humid regions have thinner and larger lamina with high SLA values (Cunningham *et al.*, 1999; Fonseca *et al.*, 2000; Niinemets, 2001). High temperatures can also lead to an increase in SLA, but this effect is highly dependent on sufficient soil moisture contents (Xu & Zhou, 2006). According to basic plant physiology, drought experiments with potted tree seedlings or saplings show a reduction in SLA with decreasing water supply (Kozlowski & Pallardy, 1997; Otieno *et al.*, 2005). In this study, highest SLA values were found for leaves of *F. sylvatica* in the understorey, a cooler and more humid environment compared to upper canopies (Chap. 3.4: Fig. 3.2 and Fig. 3.3). Finally, an increase in temperature can also lead to a decrease in leaf N content and an increase in carbon-based phenolic compounds (Dury *et al.*, 1998). This is also in accordance with patterns of leaf N and C content of *F. sylvatica*, and temperature along the vertical forest gradient (Chap. 3.4: Fig. 3.2 and Fig. 3.3).

Physiological processes of plant development occur along the ontogeny. During the development from seedlings and saplings (juvenile stages) to mature trees (adult stage), woody species undergo physiological and morphological changes. Ontogenetic processes emerge as alterations in plant meristem gene expression, which are responsible for the plant development (Poethig, 1990). Despite increases in structural complexity with plant ontogeny and an inherent increase in plant size (Langellotto & Denno, 2004), different ontogenetic stages exhibit varying leaf traits. Leaf traits that are associated with growth performance (e.g. leaf size and leaf N content) show hump-shaped patterns with peak values at an intermediate ontogenetic stage (Thomas, 2010). Along the vertical forest gradient of this study, leaf size of *F. sylvatica* revealed a hump-shaped pattern with peak values in lower canopies, too (App. D: Tab. 7A).

Many leaf traits that vary with ontogeny are involved in defences against herbivores. As an example, variations of leaf toughness and chemical defences are found in different ontogenetic stages (Kearsley & Whitham, 1989; Loney *et al.*, 2006; Neilson *et al.*, 2006; Elger *et al.*, 2009). Ontogenetic switches are detected as changes from chemical to physical defences or between distinct classes of chemical defences from early to late ontogenetic stages (Donaldson *et al.*, 2006; Webber & Woodrow, 2009). This reflects varying patterns of herbivore defences among species and traits in woody species (Boege *et al.*, 2011). Overall, plant ontogenetic changes are supposed to lead to an increase in herbivory defence and tolerance levels until reaching an optimum as plants further develop (Boege & Marquis, 2005). While plant defences in tree species increase through secondary chemistry in seedlings followed by physical defences in saplings, the transition from juvenile to mature trees reveals no significant effect on physical defences, constitutive chemical defences, or tolerance (reviewed by Barton & Koricheva, 2010). However, juvenile and mature *F. sylvatica* individuals of the field study differed in herbivore defences like leaf toughness and phenolic compounds, which was indicated by SLA and C content, respectively (Chap. 3.4: Fig. 3.3a–b).

Generally, angiosperms show monotonous increases in leaf toughness, indicated by leaf mass area (the inverse of SLA), with increasing tree size that correlates with plant development (Nabeshima & Hiura, 2004; England & Attiwill, 2006). This ontogenetic decrease in SLA is found in all reviewed studies by Thomas & Winner (2002). Monotonous decreases in SLA are linked to related morphological parameters like leaf thickness, tissue density, and C content (Thomas, 2010). The accumulation of phenolic compounds and lignifications of leaf tissues is the underlying cause for the ontogenetic variation of leaf toughness (Kearsley & Whitham, 1989; Bussotti *et al.*, 1997; Loney *et al.*, 2006). This is in accordance with results for SLA and C content of juvenile and mature *F. sylvatica* trees of this study (Chap. 3.4: Fig. 3.3a–b).

A review study compared preferences by insect herbivores for juvenile or mature tree individuals and revealed no general pattern (Barton & Koricheva, 2010). However, in this study differences in herbivory intensities were either found along the whole vertical forest gradient (Chap. 3.4: Fig. 3.4a), or between juvenile and mature *F. sylvatica* trees depending on the feeding guild or arthropod species (Chap. 4.4: Fig. 4.2–4.3). Most feeding traces showed significant differences in herbivory intensities only between juvenile (understorey) and mature trees (lower and upper canopies) but not within the canopy. These findings suggest that ontogenetic effects are responsible for herbivory patterns along the vertical forest gradient. Since leaf traits showed distinct patterns (Chap. 3.4: Fig. 3.3), in contrast to herbivory patterns of identified feeding traces (Chap. 4.4: Fig. 4.2–4.3), they could not be detected as determining factors for arthropod herbivore preferences between juvenile and mature trees. Other factors than leaf traits, e.g. top-down effects by predation, might be responsible as underlying causes for ontogenetic effects on herbivory (Chap. 7.3).

Generalisations of environmental and ontogenetic effects on herbivory intensities along the vertical forest gradient seem to be difficult to draw. Leaf area loss showed a different pattern compared to environmental and leaf trait conditions, or plant ontogeny (Chap. 3.4: Fig. 3.3–3.4a). Significant differences of leaf area loss were present between the understorey and upper canopies with intermediate levels for lower canopies. On the one hand, a comparison between bottom and top of the vertical forest gradient leads to the conclusion that leaf area loss, caused by leaf-chewing insects, decreases towards upper canopies with unfavourable leaf quality for insect herbivores despite higher temperatures, which is generally known as a positive influence on herbivory. The herbivory pattern of leaf area loss in this study is in accordance with light-based variations in leaf nutritional quality and defence compounds accounting for the suppression of expected high rates of herbivory in warmer habitats (Niesenbaum & Kluger, 2006). On the other hand, the intermediate leaf area loss in lower canopies might suggest common features, which are important for determining herbivory, of lower canopies with both the understorey (minor differences between leaf traits) and upper canopy (identical ontogenetic stage).

Based on the literature and the results of the present study, the environment and plant ontogeny both affect significantly arthropod herbivory. Most of the leaf traits, which are important for arthropod herbivores, change both with the environment and plant ontogeny. The design of the field study does not allow distinguishing completely between environmental and ontogenetic effects leading to a complex interpretation about impacts on leaf traits and herbivory. Conclusions for the importance of environmental effects can be derived from the field and experimental study of this research project.

Plants in the greenhouses were exposed to full sunlight indicating a microclimatic environment comparable to upper canopies of the field study. Overall, microclimate of the greenhouses (Chap. 6.4: Tab. 6.2) showed higher temperature and lower relative air humidity conditions compared to the field study (Chap. 3.4: Fig. 3.2). Microclimatic values are most likely comparable to upper canopies, where average day temperatures were 1.5 and 2.8 °C lower and relative air humidity conditions 11 and 14% higher compared to greenhouses 1 and 2, respectively. The magnitude of differences in average temperature and relative air humidity between the two greenhouses (1.3 °C and 3%, respectively) is comparable to the difference between lower and upper canopies (1.1 °C and 5%, respectively) of the field study. Similar values of leaf traits (toughness and N content) can be expected for upper canopies and the greenhouses.

The SLA of all three juvenile tree species in the experimental study (*F. sylvatica*, *Acer pseudoplatanus*, and *Carpinus betulus*) is indeed comparable to values of mature *F. sylvatica* in upper canopies of the field study (Chap. 3.4: Fig. 3.3; Chap. 6.4: Fig. 6.2). These values represent less than half of the SLA values that were found for the tree species in the understorey of the field study (Chap. 3.4: Tab. 3.1). The comparable leaf toughness between upper canopies (mature trees) and the greenhouses (juvenile trees) suggest similar environmental conditions instead of ontogenetic effects that are responsible for the formation of leaf trait characteristics. Upper canopies and the greenhouses were both exposed to full sunlight, and leaves of juvenile trees in the greenhouses with low SLA values exhibit the typical pattern of sun leaves. Generally, a decline of SLA can be caused through light conditions because light increases the leaf thickness (Yun & Taylor, 1986). Thicker sun leaves of *F. sylvatica* are characterized by a lower SLA compared to the much thinner blades of shade leaves (Lichtenthaler *et al.*, 2007).

Within the two greenhouses, only *C. betulus* showed a tendency of decreased SLA values caused by the treatment with warmer and drier microclimate (Chap. 6.4: Fig. 6.2). This effect was even stronger and significant with lower soil moisture conditions. The trend that was found for *C. betulus* is in accordance with combined effects of temperature, air humidity, and soil moisture conditions on leaf toughness. Therefore, the results for SLA of *C. betulus* support the dependency on environmental conditions for the pattern of leaf trait characteristics, which was found along the vertical forest gradient, despite ontogenetic influences on leaf toughness. The magnitude of changes in SLA, indicating leaf toughness, was greater between lower and upper canopy compared to changes between the two greenhouses, although the magnitude of altered microclimatic conditions was similar. The differences in SLA can be linked to reduced light conditions in lower canopies compared to the greenhouses, because shading increases SLA (Wuytack *et al.*, 2011).

Leaf chlorophyll content was decreased about 50% in the experimental study compared to values that were measured in the field study (Chap. 3.4: Tab. 3.1; Chap. 6.4: Fig. 6.3). As part of the photosynthesis, chlorophyll content is dependent on the regulating influence of light conditions. Studies present contrasting results concerning patterns of chlorophyll content based on light conditions. On the one hand, no significant differences of chlorophyll content were found along the vertical forest gradient with changing light conditions in the field study (Chap. 3.4). On the other hand, sun leaves of *F. sylvatica* show higher chlorophyll content than shade leaves (Lichtenthaler *et al.*, 2000), in contrast to shade leaves of other tree species that contain more chlorophyll than sun leaves (Matyssek *et al.*, 2010). High light conditions in the greenhouses might have caused the low chlorophyll content in leaves of the three tree species. In addition, this effect of decreasing chlorophyll content could be enhanced through impacts of water supply.

No differences of chlorophyll content existed between the two greenhouses, representing the microclimate effect. However, leaves showed lower chlorophyll contents in treatments with higher soil moisture conditions in both greenhouses with significant differences for *F. sylvatica* and *A. pseudoplatanus* (Chap. 6.4: Fig. 6.3). Although leaf chlorophyll content is generally decreased by increasing drought stress (Mafakheri *et al.*, 2010; Gholamin & Khayatnezhad, 2011; Aref *et al.*, 2013), a slight drought stress can in contrast increase leaf chlorophyll content

(Mensah *et al.*, 2006). On the one hand, *F. sylvatica* and *A. pseudoplatanus* potentially underwent minor drought stress conditions in the lower irrigation treatment, reacting with increased chlorophyll content. On the other hand, trail pots in the experimental study possibly caused greater drought stress situations compared to the natural growth habitat in forests sites of the field study that could explain the generally lower leaf chlorophyll content.

Depending on the positive relationship between chlorophyll and leaf N content (van den Berg & Perkins, 2004), lower chlorophyll content would potentially be a disadvantage for arthropod herbivores through a decrease of the leaf palatability. However, such a link was not identified along the vertical forest gradient in the field study. While no significant changes existed in chlorophyll content, leaf N content was decreased in upper canopies compared to lower canopies and the understorey (Chap. 3.4: Fig. 3.3). On the one hand, chlorophyll content might not sufficiently indicate leaf N content. On the other hand, Rouault *et al.* (2006) identified increased N content in plant tissue through water stress of host plants caused by low levels of humidity. Therefore, measurements of leaf N content would have been necessary to determine effects of microclimate and soil moisture on the palatability of leaves for arthropod herbivores in the experimental study. In addition, the increase in leaf toughness of *C. betulus* (indicated by SLA) would also imply a decrease in the palatability for insect herbivores. Further investigations would have been necessary to analyze the underlying cause for the increase in leaf toughness. As an example, measurements of leaf C content could shed light on changes of carbon-based physical traits, indicating phenolic compounds (e.g. lignins).

In conclusion, leaf traits of juvenile trees in the experimental study exhibited similar values like leaves of mature *F. sylvatica* in upper canopies of the field study. These results show how the environment determines leaf traits despite ontogenetic effects. Further conclusions for the importance of environmental effects on leaf traits can be derived from the field study. Differences in SLA, N and C content within the same ontogenetic stage reveal adaptations of sun and shade leaves to environmental conditions (Chap. 3.4: Fig. 3.3). Varying light conditions have been identified as a significant predictor for the variation of many leaf traits within forest canopies (e.g. Rijkers *et al.*, 2000; Leal & Thomas, 2003). Leaf trait trends identified by Thomas (2010) are likely to be influenced by both the leaf acclimation to environmental conditions (light) as well as to plant ontogeny (tree size). Along the vertical forest gradient of this study, leaf traits are certainly affected by both environmental and ontogenetic effects. However, the leaf acclimation to light is suggested to be of secondary importance. Studies with a controlled light effect (e.g. comparison between leaves of open-grown saplings and upper canopy trees) indicate that ontogenetic changes in leaf toughness and herbivory cannot be fully accounted by environmental acclimation responses to sun and shade (Thomas & Winner, 2002; Thomas *et al.*, 2010). Strong effects of tree size on leaf toughness are found independently of crown exposure (Thomas, 2010). Decreases in SLA and related leaf features (tissue density and lignifications) at the end of tree ontogeny are also noted to be independent of sun and shade acclimation (Day *et al.*, 2001; Niinemets, 2002; Nabeshima & Hiura, 2004; England & Attiwill, 2006). Furthermore, the magnitude of ontogenetic changes in leaf traits is larger than documented for studies of light acclimation responses (Ellsworth & Reich, 1992a, 1992b; Sipe & Bazzaz, 1994; Beaudet *et al.*, 2000; Thomas *et al.*, 2010). In contrast, the magnitude of leaf trait changes was grater within the same ontogenetic stage of mature trees (lower and upper canopy) compared to changes between juvenile and mature trees (understorey and lower canopy, respectively) in this study (Chap. 3.4: Fig. 3.3). This finding might be connected to environmental adaptations to light and microclimate because the magnitude of temperature changes was also greater within the canopy (Chap. 3.4: Fig. 3.2).

7.2 Explanations for contradictory results on herbivory

In this study, varying patterns for herbivory have been found for distinct feeding guilds. While leaf area loss (leaf-chewing) was higher on shade leaves in the understorey compared to sun leaves in upper canopies (Chap. 3.4: Fig. 3.4a), gall-inducing herbivory was increased in the canopies (Chap. 4.4: Fig. 4.3a–c). Further contradictory results about herbivory have been revealed by a series of research studies. Especially studies, which compare sun and shade leaves, report higher herbivory on both types of leaves. Therefore, a literature review was conducted during this study to detect and discuss factors that are responsible for contradictory results on arthropod herbivory on sun and shade leaves. The use of selected keywords for the literature review (“arthropod herbivory”, “woody plants”, and “sun/ shade leaves”) resulted in 35 studies concentrating on herbivory caused by arthropod species on sun and shade leaves of trees and shrubs in forest ecosystems (App. E: Tab. 22A). Insights are given as an overview about important factors for herbivory patterns to shed light on contradictory results.

Overall, studies have been conducted in many regions of the world, from the Palearctic, Nearctic, Neotropic, Indomalayan to the Australasian realm, covering temperate, dry, and rain forests in lowland and montane sites. Study designs differ also in the study type (theory, field or laboratory study) and assessment methods for herbivory. Herbivory on sun and shade leaves can be derived from comparisons between understorey and canopy or gaps with plant individuals of different or the same ontogenetic stage, respectively. Furthermore, herbivory patterns are dependent on plant and insect species.

Generally, comparisons between temperate and tropical forests are crucial. In temperate forests, leaf area loss is generally higher on shade leaves than sun leaves (Larsson *et al.*, 1986; Niesenbaum, 1992; Dudt & Shure, 1994; Yamasaki & Kikuzawa, 2003; Niesenbaum & Kluger, 2006; Oishi *et al.*, 2006; Muth *et al.*, 2008; Żmuda *et al.*, 2008; Karolewski *et al.*, 2013). Maiorana (1981) discusses two theories for higher herbivory on shade leaves compared to sun leaves, based on the hypotheses that sun leaves are more toxic and shade is a shelter for herbivores. Exceptions with greater herbivory on sun leaves are found for single plant species (Żmuda *et al.*, 2008; Mooney *et al.*, 2009; Gossner *et al.*, 2014), feeding experiments in the laboratory and field (Fortin & Mauffette, 2002; Mooney *et al.*, 2009), or measurements of beetle mass and larval development (Łukowski *et al.*, 2015). Studies conducted as laboratory experiments, which have found higher area loss on sun leaves than shade leaves (Futuyma & Saks, 1981; Fortin & Mauffette, 2002; Niesenbaum & Kluger, 2006; Łukowski *et al.*, 2015), potentially reproduce results that cannot be transferred to field conditions. The herbivory pattern could be connected to an exclusion of the predation effect on insect herbivores, an important top-down control, which is present in forests sites of field studies.

Further variable features for highest herbivory on sun leaves are found in studies of tropical regions. First of all, highest leaf area losses have been found on sun leaves in the canopy (Basset, 1991; Nichols-Orians, 1991; Neves *et al.*, 2014). This pattern is linked to the higher availability and predictability of young foliage in the canopies for leaf-chewing insects compared to the understorey (Basset, 1996). This is an important ecological difference based on evergreen instead of deciduous tree species in temperate forests. In addition, the interpretation on herbivory intensities is dependent on the assessment methods. Many studies of tropical rainforest insects have evidenced higher abundances, activity, or diversity of insect herbivores in the upper canopy compared to the understorey (Basset, 1991, 2001; Basset *et al.*, 1992; Medianero *et al.*, 2003; Charles & Basset, 2005). However, greater insect species richness in the canopy does not necessarily lead to higher herbivory because apparent leaf damage can still be higher in the shrub layer compared to the canopy (Basset *et al.*, 1992). A review on tropical forests revealed that herbivory is actually greater in the understorey compared to the canopy (Coley & Barone, 1996).

Inconsistent results for herbivory intensity patterns on sun and shade leaves can be further connected to the type of arthropod species, different recording years, and seasons. Herbivory patterns on sun and shade leaves varied depending on the feeding guild (Nielsen & Ejlersen, 1977; Le Corff & Marquis, 1999; Forkner *et al.*, 2004; Hirao *et al.*, 2009). In the present study, distinct patterns of herbivory were also found between the understorey and the canopy of temperate forest sites depending on the feeding guild. While leaf area loss caused by leaf-chewing species was highest on shade leaves in the understorey (Chap. 3.4: Fig. 3.4a), herbivory of gall-inducing species was increased in the canopy (Chap. 4.4: Fig. 4.3). Other studies in temperate and tropical forests have found similar patterns with higher rates of herbivory caused by gall-inducing and exophagous arthropods on sun leaves and shade leaves, respectively (Kampichler & Teschner, 2002; Ribeiro & Basset, 2007; Thomas *et al.*, 2010; Ribeiro *et al.*, 2014). Differences in leaf area loss between lower and upper canopies also vary in direction and magnitude depending on tree species and year, including resource heterogeneity among-tree individuals (Ruhnke *et al.*, 2009). This suggests that tree populations in a habitat are heterogeneous resources for insect herbivores due to the variability within and among host individuals. Finally, herbivory on leaves occurs mainly during their earliest lifetime (Coley & Barone, 1996), although herbivory intensity patterns can change along the season. As an example, moth larvae on *Quercus crispula* (Mongolian oak) migrate from upper canopies to the understorey in late spring based on changes in leaf quality (Murakami & Wada, 1997).

Overall, studies on herbivory have tried to connect the intensity patterns to different determining factors. Even if the same variables were used, results are inconsistent. While leaf quality along the vertical forest gradient seems to be reasonable for patterns of leaf area loss on *F. sylvatica* (Chap. 3) and *Q. crispula* (Murakami & Wada, 1997), Ruhnke *et al.* (2009) could not relate leaf traits to leaf area losses in the field. First of all, the consumed leaf area was corrected by tree-specific conversion factors taking into account the thickness of leaves based on variations of specific leaf weight between lower and upper canopies (Ruhnke *et al.*, 2009). This complicates comparisons with other studies that have not used conversion factors. Furthermore, contradicting results also appear for comparisons of herbivory intensities between field studies and experimental feeding trials in laboratories. Even if sun leaves reveal better leaf qualities for leaf-chewing insects than shade leaves, resulting in better insect performance, the pattern cannot simply be transferred to forest sites. Despite the palatability of leaves, other factors influence herbivory in the field and can confound expected high rates on sun leaves. Since natural enemies are key participants in plant defences (Coley & Barone 1996), an important factor is the top-down control by predators and parasites (Stamp & Bowers, 1988; Dicke & Grostal, 2001), with additional migration activities of insect herbivores (Batzer *et al.*, 1995; Magalhães *et al.*, 2002). Therefore, actual leaf palatability measured in the laboratory can be a weak determinant for herbivory.

Despite contradicting results on herbivory intensities, previous reviews have tried to generate general patterns. However, the reviews focused on tropical forests (Coley & Barone, 1996; Rinker & Lowman, 2004) or included studies on different life forms of herbaceous and woody plants (Roberts & Paul, 2006). A literature review focussing on woody species and including studies about temperate forests might detect and elucidate general underlying causes for herbivory patterns on sun and shade leaves. The factors that are discussed above should be carefully considered for comparisons of herbivory patterns (Fig. 7.1).

7.3 Bottom-up and top-down processes affecting herbivory

Plant-insect interactions are affected by bottom-up and top-down processes in ecosystems. While top-down processes control structure and dynamics of arthropod herbivore populations by predator activities, bottom-up processes in ecosystems refer to nutrient supply and productivity of plants (primary producers). Both effective directions, the top-down influence of predation (Chap. 4.4) and phytodiversity as a bottom-up process (Chap. 5), are discussed concerning their effects on herbivory intensity patterns.

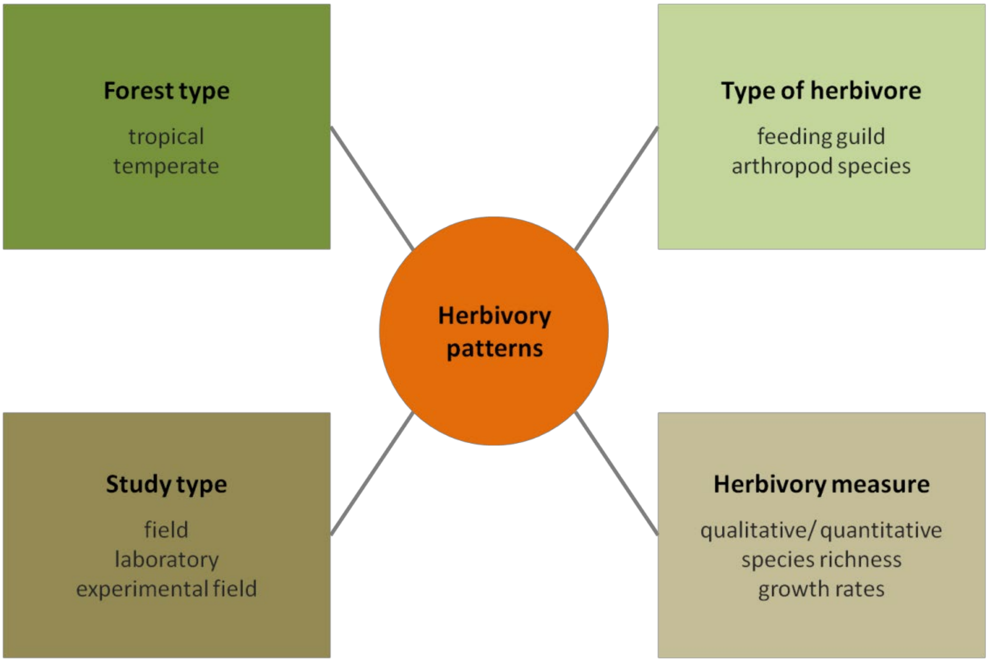

Figure 7.1: Overview of factors that influence results about arthropod herbivory.

Research studies have shown a positive link between plant and insect diversity, including insect herbivores. Distinct tree species in species-rich environments offer a variation of architecture that enhances the number of ecological niches, which in return increase the diversity of associated arthropod communities (Lawton, 1983). However, greater insect herbivore diversity does not simply lead to an increase in herbivory intensities. Interactions between plant abundances and diversity, based on the competition for necessary resources, have to be taken into account. Each plant species is relatively less abundant with a likely more patchy distribution in diverse plant communities (Kareiva, 1983; Yamamura, 2002). Therefore, the abundance of each plant species should decrease with increasing phytodiversity. In general, the relationship between plant and herbivore diversity may be nonlinear based on differences in the ability of herbivores to locate host plants, the suitability of different plant patch sizes, and/ or differences in the effects of parasites and predators (reviewed by Andow, 1991). The mechanisms responsible for the plant-herbivore relationship can be divided into bottom-up and top-down processes.

Bottom-up processes are linked to the resource concentration hypothesis (Root, 1973), which can explain the ability of herbivores to locate host plants. Increased host availability is often cited as the main reason for higher rates of herbivory in monocultures (Risch, 1981; Russell, 1989; Jones, 2001). The resource concentration hypothesis suggests that plants are more visible to insects in species-poor than in species-rich environments based on different visual and chemical stimuli from host plants. The stimuli are dependent on the density of host plants, the patch size, and the patch diversity (Kareiva, 1983). Therefore, foraging or dispersing herbivores encounter physical or chemical barriers for the host plant location by non-host plant species. According to the resource concentration hypothesis, herbivory would increase with decreasing plant diversity because insect herbivores could better locate their host plants. An increasing proportion of non-host trees reduces herbivory intensities on the host tree species in mixed stands (e.g. Katovich & Morse, 1992; Nichols *et al.*, 1999; Jactel *et al.*, 2006). In the present study, leaf herbivory intensity in lower canopies of *F. sylvatica* was negatively associated with the number of plant species and by trend with the diversity of species based on their abundances in the shrub layer (Chap. 5.3: Tab. 5.3). The results seem to be in accordance with the resource concentration hypothesis, depending on the abundance of host plants and the patch diversity. Plant abundances could also be related to insect abundances that would represent a quantitative measure for the necessary resources in a system.

Since a relationship was found between the shrub layer diversity and herbivory of *F. sylvatica* in lower canopies, it is not surprising that no effect was found for *A. pseudoplatanus* and *C. betulus*, which were only sampled in the understorey. However, herbivory intensity of *A. pseudoplatanus*, in contrast to *F. sylvatica*, increased by trend with the number of plant species in the ground layer. Generally, *A. pseudoplatanus* leaves show higher herbivory compared to *F. sylvatica* (Modrý *et al.*, 2004), and was also more variable (Chap. 3.4: Fig. 3.4). On the one hand *F. sylvatica* has a later appearance of leaf shoots than *A. pseudoplatanus*. Therefore, leaves of *A. pseudoplatanus* had a longer time period exposed to arthropod herbivores until the sampling time in June 2012. The longer herbivore exposure time could lead to differences in herbivory intensities between *F. sylvatica* and *A. pseudoplatanus*. On the other hand, highest damage rates occur on young leaves because leaf palatability (high N content and low toughness) decreases in mature foliage (Feeny, 1970; Coley *et al.*, 1985; Brunt *et al.*, 2006; Zehnder *et al.*, 2009). This would diminish the meaning of exposure time to arthropod herbivores for differences in herbivory intensities because highest damage rates on *F. sylvatica* leaves can be expected in May and June.

Presumably, lower herbivory on *F. sylvatica*, compared to *A. pseudoplatanus*, can be rather linked to higher leaf C contents suggesting greater amounts of phenolic defence compounds against insect herbivores (Chap. 3.4: Tab. 3.1). In mixed beech forests, *F. sylvatica* trees have typically the highest amount of phenols, compared to co-occurring species (Bussotti *et al.*, 1998). Furthermore, leaf size of *A. pseudoplatanus* is also larger compared to *F. sylvatica* leaves. According to the resource concentration hypothesis, leaves of *A. pseudoplatanus* would be more visible to insect herbivores than leaves of *F. sylvatica* or *C. betulus*. Moreover, leaves of *A. pseudoplatanus* might be better visible than plant species with smaller leaves even in species-rich environments. This could explain the trend of increasing herbivory on *A. pseudoplatanus* with an increase in phytodiversity of the ground layer.

Top-down processes for the relationship between plant and herbivore diversity can be described by effects of parasites and predators. According to the enemies hypothesis, natural enemies are more abundant in species-rich compared to species-poor environments, resulting in lower herbivore population densities (Root, 1973). In the present study, an increasing number of plant species in the shrub layer increased and decreased insect abundances and herbivory (leaf area loss) in lower canopies of *F. sylvatica*, respectively (Chap. 5.3: Tab. 5.2–5.3). Since only insect orders and not species were identified, the actual abundance and diversity of insect herbivores and predators remains unclear. A reliable determination of arthropod diversity for forest ecosystems and across habitat gradients needs extensive sampling effort including a variety of seasonal and spatial scales (Gering & Crist, 2000; Tylianakis *et al.*, 2005). However, insect herbivores were present as Hemiptera (sap-sucking larva and imago) and potentially existent within the order of Coleoptera (leaf-chewing imago and leaf-mining larvae), Lepidoptera (leaf-chewing and leaf-mining larvae), and Diptera (gall-inducing larvae) (Chap. 5; App. E: Tab. 21A). Insect predators were potentially present within the order of Hymenoptera that could contain parasitoid wasps, e.g. Ichneumonidae and Figitidae.

Other studies show that both herbivore and predator species richness are positively connected to plant species richness (Knops *et al.*, 1999; Haddad *et al.*, 2009). Therefore, herbivore abundances and diversity are also dependent on increased diversity of parasites and predators caused by phytodiversity (Siemann, 1998). Predators outnumber insect herbivore species and both guilds increase in species richness across a tree diversity gradient, resulting in constant relative proportions (Sobek *et al.*, 2009c). This pattern seems to be typical for forest habitats with different tree species harbouring consistent relative abundances of different feeding guilds (Moran & Southwood, 1982; Southwood *et al.*, 1982; Jukes *et al.*, 2002). Combining the bottom-up and top-down processes, which are connected to the relationship between plant and herbivore diversity, could explain the changes in herbivory intensities. Despite constant relative abundances of different feeding guilds with increasing phytodiversity in forest ecosystems, herbivory would still decrease through the impact of the resource concentration hypothesis.

The increase in herbivore species diversity, which is connected to plant species diversity, differs between distinct feeding types. According to the resource concentration and enemies hypotheses, fewer monophagous insect herbivores feed on plants in complex systems. Generalists have certainly advantages in diverse forests compared to specialists. In plant species-rich environments, generalist herbivores come across more suitable resources than specialized insect species that are restricted to one or a few host plant species. The patchy and less abundant distribution of single plant species in diverse plant communities results in a lower availability to specialist herbivores (Kareiva, 1983; Yamamura, 2002). Physical or chemical barriers that are associated with non-host plant species affect specialist herbivores more than generalist herbivores, especially if they are wind-dispersed. Furthermore, generalist natural enemies should be more abundant because they can utilize a greater variety and abundance of prey or hosts available in complex systems. In both herbivore and predator feeding guilds, the numbers of generalist species increases with phytodiversity (Sobek *et al.*, 2009c). In addition, herbivory caused by oligophagous species (specialists) is reduced, and responses of polyphagous species (generalists) are variable in plant species-rich forests (reviewed by Jactel & Brockerhoff, 2007).

In the present study, 15 arthropod herbivore species were identified that probably caused the analyzed feeding traces on *F. sylvatica* (Chap. 4; App. D: Fig. 3A–5A). Furthermore, four and one feeding traces were identified on *A. pseudoplatanus* and *C. betulus*, respectively (App. A: Tab. 1A). On the one hand, about one third of the arthropod herbivores were polyphagous (6 species), which belonged to exophagous feeding guilds (except for *Phyllonorycter messaniella:*

leaf-miner). These herbivore species would benefit of increases in phytodiversity according to the resource concentration hypothesis. On the other hand, a majority of the herbivores were monophagous (14 species) mainly belonging to endophagous feeding guilds, with one exception: 4 leaf-mining, 9 gall-inducing, and one sap-sucking arthropod species. Gall-inducing arthropod species are predominantly specialists and their diversity has been especially related to plant species richness (Wright & Samways, 1996, 1998; Oyama *et al.*, 2003). Nonetheless, these monophagous herbivore species would decrease in their abundance with increasing phytodiversity, according to the resource concentration hypothesis.

Abiotic factors (e.g. soil quality and water stress) and other biotic factors (e.g. life-form of host plant, plant age, plant density, and natural enemies) may also affect gall-inducing species richness and abundance. Three out of four analyzed gall-inducing feeding traces, probably belonging to the order of acari, showed increased herbivore attack levels on mature *F. sylvatica* compared to juveniles (Chap. 4.4: Fig. 4.3a–c). Generally, herbivory of galls is higher in xeric compared to mesic habitats, which is explained by different mortality rates through parasitoids and fungi according to the hypothesis of harsh environment (Fernandes & Price, 1992). The survivorship of gall-inducing arthropods is linked to decreased predation and disease risks through desiccating conditions. The lower top-down control by parasitoids also affects gall patterns along the vertical gradient in mesic tropical rainforests, where gall-inducing arthropods are expected to increase in abundance with tree size and canopy height (Ribeiro & Basset, 2007). In terms of desiccation risks, the upper canopies of older trees present a particularly harsh environment with leaves showing sclerophyllous morphological features (Koch *et al.*, 2004). The top-down process related to the effect of parasites (enemy-free space) and predators is important for distinct preferences of juvenile or mature plants by arthropod herbivore feeding guilds (Coley & Barone, 1996). In the present study, only the number of attacked leaves by gall-inducing arthropods was surveyed. Since the number of galls per leaf can vary strongly, different results could emerge when counting the total number of galls along the vertical gradient. Additionally, galls need to be separated into dead and alive for testing the hypothesis of harsh environment. If upper canopies of *F. sylvatica* represent a harsh environment, different quantities of dead and living galls would be expected within the canopy of mature trees. Therefore, top-down effects could be also connected to the herbivory patterns between juvenile and mature trees of this study (Chap. 4: Fig. 4.2–4.3).

The patterns of enemy-free space differ between endophagous and exophagous herbivore species. Studies have also shown that predation of exophagous herbivores (e.g. lepidopteran larvae) by wasps and parasitoids increases from juvenile to mature trees (Domínguez *et al.*, 1989; Boege, 2005a). Leaf and branch morphology within plant species, which vary between canopy and understorey stages (Holmes & Schultz, 1988; Van Bael *et al.*, 2003), influence foraging strategies of insectivorous birds (Whelan, 2001). Furthermore, studies have shown important effects of leaf structure on bird foraging preferences among tree species (Robinson & Holmes, 1984). Lawton (1983) already proposed that architectural traits (plant height and branch length) influence the probability for natural enemies of herbivores to find a plant. Therefore, reproductive plants could be more noticeable than saplings to predators and parasitoids. A meta-analysis evidenced that a majority of natural enemy guilds become more abundant as structural complexity increases with plant ontogeny (Langellotto & Denno, 2004). This effect is important for exophagous insect herbivores.

In conclusion, phytodiversity plays a crucial role for herbivory and the impact pathways are linked to bottom-up and top-down processes (Fig. 7.2). On the one hand, the resource concentration hypothesis (bottom-up process) evidently explains increases in insect diversity (especially generalists) and decreases in herbivory intensities with phytodiversity. On the other hand, the enemies hypothesis (top-down process) cannot explain the decreasing herbivory, because herbivory intensity should be constant based on parallel increases in predator and herbivore species with phytodiversity. Instead of phytodiversity, other abiotic (e.g. micro-/climate) and biotic factors (e.g. ontogeny) are responsible for enemy-free spaces that cause different patterns of herbivory intensities along the vertical forest gradient for distinct arthropod herbivore species.

7.4 Importance of herbivory for nature conservation and forestry

Generally, herbivory is experienced as a negative impact on plant fitness (Crawley, 1983; Dirzo, 1984). In this study, leaf area loss to insect herbivores was rather low in temperate forests of Central Germany (Chap. 3.4: Fig. 3.4). This is in accordance with other studies, except for outbreak situations where herbivory increases dramatically (Franklin, 1973; Coley & Aide, 1991; Gossner *et al.*, 2014). However, important forest ecosystem processes are also driven by low but persistent insect herbivory (de Mazancourt *et al.*, 2001).

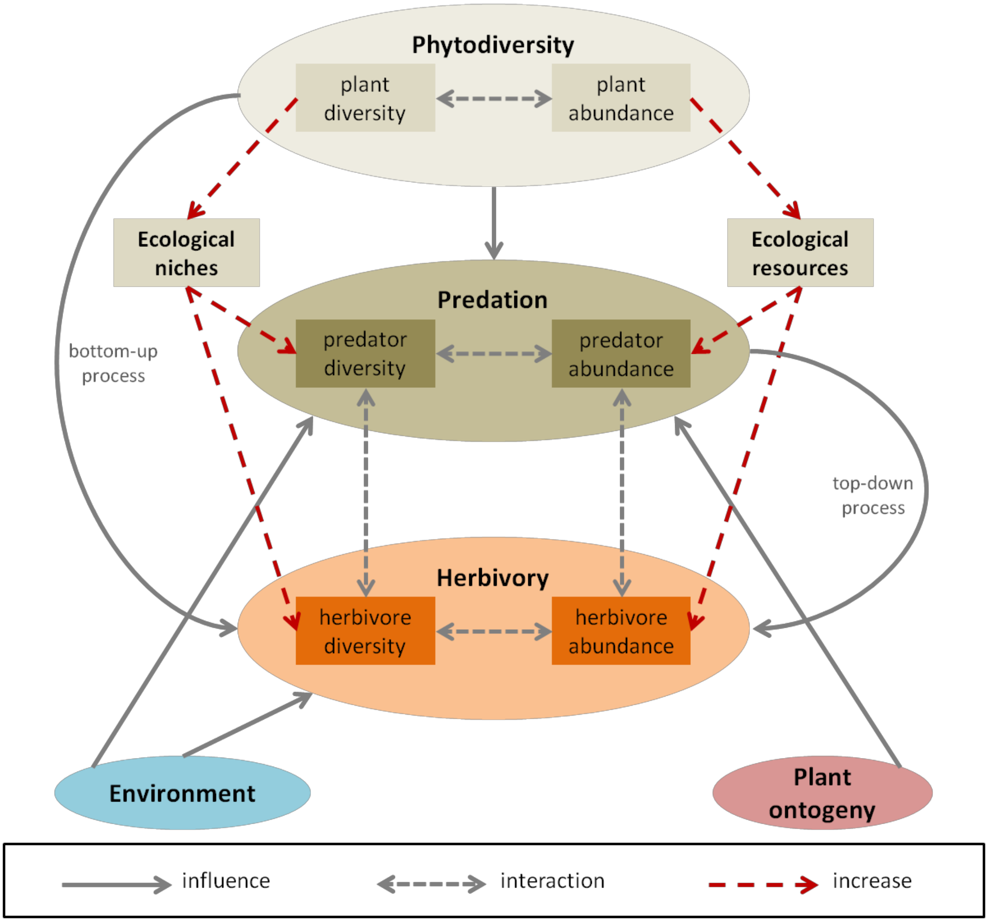

Figure 7.2: Impact of phytodiversity on herbivory with direct pathways (bottom-up process) and indirect pathways (top-down process). The top-down process is influenced by the environment and plant ontogeny.

The impact of herbivory varies between different plant ontogenetic stages of woody species (Weiner, 2004), with seedlings being especially vulnerable (Dirzo *et al.*, 2007). On mature trees, impact of herbivory becomes lower but can still cause reductions in their growth rates, survival, and reproduction (Marquis, 1984; Domínguez & Dirzo, 1994; Boege, 2005b). Nonetheless, arthropod herbivore species play an important role for ecosystem functioning. Nutrient dynamics and water movement from the soil to the atmosphere are affected by arthropod herbivory (Schowalter *et al.*, 1986; Loreau, 1995; Fonte & Schowalter, 2005; Cunningham *et al.*, 2009).

Generally, ecosystem processes are mediated by interactions between organisms. Any change in the biotic composition of forests might alter ecosystem processes mediated by complex species interactions (Sala *et al.*, 2000; Bailey & Whitham, 2003). As an example, the plant community composition is influenced by competitive interactions among plants, which is affected by herbivore species (Frost & Hunter, 2008). Furthermore, arthropod herbivores act as mediators for effects that cascade up and down the trophic chain (Schmitz, 2008). In conclusion, arthropod herbivores play a crucial role for forest ecosystem processes and biodiversity.

Germany harbours a forest area of about 32%, of which 98.6% is utilized for wood production, even in protected areas of different categories, and only 1.9% is managed with conservation standards (BMEL, 2017). According to the German National Strategy on Biological Diversity, forests with natural forest development should account for 10% of the forest area by 2020 (BMUB, 2007). Therefore, forestry has to play an important role for maintaining biodiversity in forest ecosystems.

The forest management includes several pathways for impacts on the arthropod community and herbivory. Management effects are supposed to be primarily mediated through a changing forest structure that is an important driver for herbivory (Schowalter *et al.*, 1986). Generally, management in forest stands leads to the removal of old and large trees (Franklin *et al.*, 2002). Therefore, forestry strongly affects tree age distribution (horizontal and vertical structures of forest stands), which influences the arthropod herbivore community through the provision of distinct ecological niches and a variety of resources (Schowalter *et al.*, 1986; Schowalter, 1995). Tree age-related changes in plant phenology and chemistry additionally affect arthropod herbivory (Coley, 1980; Donaldson *et al.*, 2006).

Another main factor, which is altered through forest management, is the tree species composition. The arthropod herbivore species community and composition of forests is essentially influenced by tree species richness and abundance (Sobek *et al.*, 2009a, 2009c; Boncina, 2011). In this study, species richness of shrub trees was also positively and negatively correlated with insect abundances and herbivory in lower canopies of *F. sylvatica*, respectively (Chap. 5.3: Tab. 5.2–5.3). Since forest management affects the diversity of plants and insects, forestry might also affect herbivory processes mediated by arthropod species (Jactel & Brockerhoff, 2007; Vehviläinen *et al.*, 2007; Sobek *et al.*, 2009b).

While effects of forest tree compositions have been found to be positive on the herbivore community, different management types in single-dominated forest stands reveal only minor differences in herbivory, with changing management effects on herbivory between regions, forest strata, and feeding guild (Gossner *et al.*, 2014). Abiotic factors that are relevant as habitat requirements for arthropod herbivores might be changed with forestry activities (De Cauwer *et al.*, 2006; Abrahamczyk *et al.*, 2011), which alter the light regime, precipitation, or temperature. Therefore, additional components of forest management (e.g. thinning regime, harvest tree age, and use of machinery) seem to be important, and environmental factors such as forest structure variables that are influencing microclimatic conditions might explain the variability in herbivory (Gossner *et al.*, 2014).

7.5 Conclusions

The environment, plant ontogeny, leaf traits, as well as phytodiversity and predation effects that represent bottom-up and top-down processes, respectively, influence herbivory through direct or indirect pathways (Fig. 7.3). The choice of qualitative measures is essential for determining and comparing herbivory, and differs between distinct feeding guilds. Mines and galls (living and dead) can be counted, leaf area loss through leaf-chewing can be calculated, but sap-sucking remains difficult to quantify. Depending on the type of herbivory or arthropod species, distinct intensities occur across different forest layers or between juvenile and adult trees, which can be partly linked to environmental and ontogenetic processes. Along the vertical forest gradient, microclimate essentially affects herbivory intensities, patterns, and processes. Despite direct impacts on arthropod herbivores, the environment influences herbivory through effects on leaf traits and the top-down control by predators. Plant ontogeny affects herbivory indirectly through alterations of leaf traits and top-down processes of predation. The arthropod herbivore diversity can be seen as an important part of biodiversity in forest ecosystems. Outbreak situations can be prevented because herbivory does not increase but rather decrease with phytodiversity. Since forest management strongly alters tree diversity and environmental conditions, forestry activities play a crucial role for keeping herbivory at equilibrium.

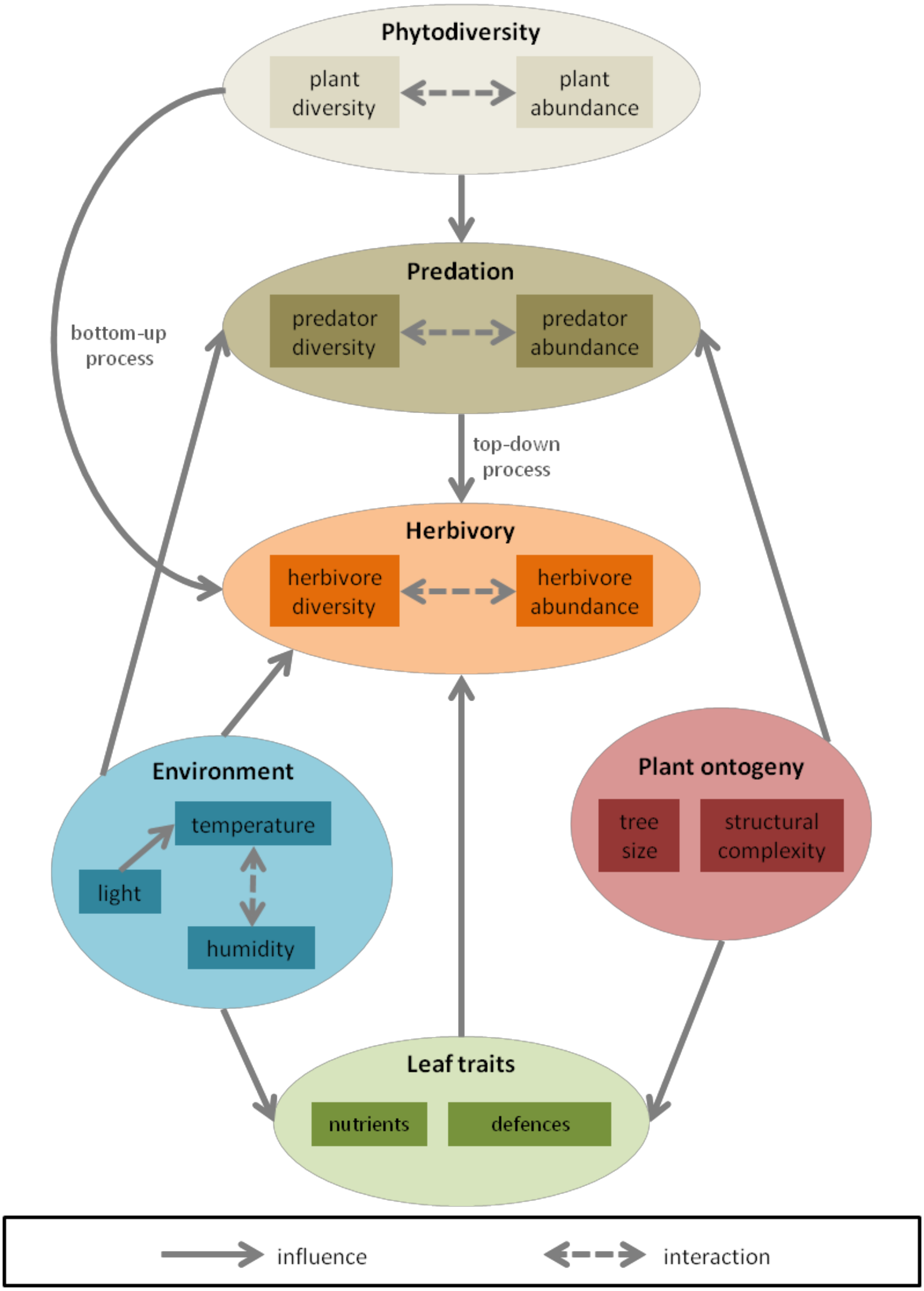

Figure 7.3: Overview of factors influencing herbivory with direct and indirect pathways. Presented interactions are based on effects caused by the environment (Chap. 3), plant ontogeny (Chap. 4), phytodiversity (Chap. 5), and leaf traits (Chap. 6). Herbivory is influenced by phytodiversity, representing ecological niches and resources for arthropods, through bottom-up and top-down processes, which are active in the ecosystem.

REFERENCES

Abrahamczyk, S., Gottleuber, P., Matauschek, C. & Kessler, M. (2011) Diversity and community composition of euglossine bee assemblages (Hymenoptera: Apidae) in western Amazonia. *Biodiversity and Conservation*, **20**, 2981–3001.

Adams, J.M. & Zhang, Y. (2009) Is there more insect folivory in warmer temperate climates? A latitudinal comparison of insect folivory in eastern North America. *Journal of Ecology*, **97**, 933–940.

Adams, J.M., Zhang, Y., Basri, M. & Shukor, N. (2009) Do tropical forest leaves suffer more insect herbivory? A comparison of tropical versus temperate herbivory, estimated from leaf litter. *Ecological Research*, **24**, 1381–1392.

Afas, N.A., Marron, N. & Ceulemans, R. (2007) Variability in *Populus* leaf anatomy and morphology in relation to canopy position, biomass production, and varietal taxon. *Annals of Forest Science*, **64**, 521–532.

Agrawal, A.A. & Fishbein, M. (2006) Plant defense syndromes. *Ecology*, **87**, S132–S149.

Alford, D.V. (2012) *Pests of ornamental trees, shrubs and flowers: a colour handbook*. second. Manson Publishing, London, UK.

Ali, J.G. & Agrawal, A.A. (2012) Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science*, Special Issue: Specificity of plant–enemy interactions, **17**, 293–302.

Andow, D.A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.

Andrew, N.R. & Hughes, L. (2005) Herbivore damage along a latitudinal gradient: relative impacts of different feeding guilds. *Oikos*, **108**, 176–182.

Aref, I., El Atta, H., El Obeid, M., Ahmed, A., Khan, P. & Iqbal, M. (2013) Effect of water stress on relative water and chlorophyll contents of *Juniperus procera* Hochst. ex Endlicher in Saudi Arabia. *Life Science Journal*, **10**, 681–685.

Arsuffi, T.L. & Suberkropp, K. (1984) Leaf processing capabilities of aquatic hyphomycetes: interspecific differences and influence on shredder feeding preferences. *Oikos*, **42**, 144–154.

Bailey, J.K. & Whitham, T.G. (2003) Interactions among elk, aspen, galling sawflies and insectivorous birds. *Oikos*, **101**, 127–134.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.

Barbier, S., Gosselin, F. & Balandier, P. (2008) Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. *Forest Ecology and Management*, **254**, 1–15.

Bartoń, K. (2016) *MuMIn: multi-model inference*. URL https://CRAN.R-project.org/package=MuMIn.

Barton, K.E. & Koricheva, J. (2010) The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. *The American Naturalist*, **175**, 481–493.

Basset, Y. (1991) The spatial distribution of herbivory, mines and galls within an Australian rain forest tree. *Biotropica*, **23**, 271–281.

Basset, Y. (1992) Influence of leaf traits on the spatial distribution of arboreal arthropods within an overstorey rainforest tree. *Ecological Entomology*, **17**, 8–16.

Basset, Y. (1996) Local Communities of Arboreal Herbivores in Papua New Guinea: Predictors of Insect Variables. *Ecology*, **77**, 1906–1919.

Basset, Y. (2001) Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia*, **129**, 253–260.

Basset, Y., Aberlenc, H.-P., Barrios, H. & Curletti, G. (2003a) Arthropod diel activity and stratification. In *Arthropods of tropical forests – spatio-temporal dynamics and resource use in the canopy* (ed. by Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.). University Press, Cambridge, UK, pp. 304–314.

Basset, Y., Aberlenc, H.-P. & Delvare, G. (1992) Abundance and stratification of foliage arthropods in lowland rain forest of Cameroon. *Ecological Entomology*, **17**, 310–318.

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

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., *et al.* (2017) *lme4: linear mixed-effects models using "Eigen" and S4*. URL https://CRAN.R-project.org/package=lme4.

Batzer, H.O., Martin, M.P., Mattson, W.J. & Miller, W.E. (1995) The forest tent caterpillar in aspen stands: distribution and density estimation of four life stages in four vegetation strata. *Forest Science*, **41**, 99–121.

Bazzaz, F.A. & Williams, W.E. (1991) Atmospheric CO_2 concentrations within a mixed forest: implications for seedling growth. *Ecology*, **72**, 12–16.

Beaudet, M., Messier, C., Hilbert, D.W., Lo, E., Wang, Z.M. & Lechowicz, M.J. (2000) Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. *Canadian Journal of Forest Research*, **30**, 390–404.

Behmer, S.T. & Joern, A. (2008) Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences*, **105**, 1977–1982.

Berg, A.K. van den & Perkins, T.D. (2004) Evaluation of a portable chlorophyll meter to estimate chlorophyll and nitrogen contents in sugar maple (*Acer saccharum* Marsh.) leaves. *Forest Ecology and Management*, **200**, 113–117.

BMEL. (2016) *Der Wald in Deutschland: ausgewählte Ergebnisse der dritten Bundeswaldinventur*. Bundesministerium für Ernährung und Landwirtschaft, Berlin, Germany.

BMEL. (2017) *Waldbericht der Bundesregierung 2017*. Bundesministerium für Ernährung und Landwirtschaft, Bonn, Germany.

BMUB. (2007) *Nationale Strategie zur biologischen Vielfalt*. Bundesministerium für Umwelt, Naturschutz, Bau und Reaktorsicherheit, Berlin, Germany.

Boege, K. (2005a) Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. *Oecologia*, **143**, 117–125.

Boege, K. (2005b) Influence of plant ontogeny on compensation to leaf damage. *American Journal of Botany*, **92**, 1632–1640.

Boege, K., Barton, K.E. & Dirzo, R. (2011) Influence of tree ontogeny on plant-herbivore interactions. In *Size- and age-related changes in tree structure and function*, Tree Physiology (ed. by Meinzer, F.C., Lachenbruch, B. & Dawson, T.E.). Springer, Dordrecht, Netherlands, pp. 193–214.

Boege, K. & Marquis, R.J. (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology & Evolution*, **20**, 441–448.

Boncina, A. (2011) Conceptual approaches to integrate nature conservation into forest management: a Central European perspective. *The International Forestry Review*, **13**, 13–22.

Borchard, F., Berger, H.-J., Bunzel-Drüke, M. & Fartmann, T. (2011) Diversity of plant-animal interactions: possibilities for a new plant defense indicator value? *Ecological Indicators*, **11**, 1311–1318.

Bratton, S.P. (1976) Resource division in an understory herb community: responses to temporal and microtopographic gradients. *The American Naturalist*, **110**, 679–693.

Brooks, J.R., Flanagan, L.B., Varney, G.T. & Ehleringer, J.R. (1997) Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO_2 within boreal forest canopies. *Tree Physiology*, **17**, 1–12.

Brown, D.G. (1994) Beetle folivory increases resource availability and alters plant invasion in monocultures of goldenrod. *Ecology*, **75**, 1673–1683.

Brunt, C., Read, J. & Sanson, G.D. (2006) Changes in resource concentration and defence during leaf development in a tough-leaved (*Nothofagus moorei*) and soft-leaved (*Toona ciliata*) species. *Oecologia*, **148**, 583–592.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., Toit, D., *et al.* (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, **22**, 431–446.

Burns, A.E., Cunningham, S.A. & Watson, D.M. (2011) Arthropod assemblages in tree canopies: a comparison of orders on box mistletoe (*Amyema miquelii*) and its host eucalypts. *Austral Entomology*, **50**, 221–230.

Bussotti, F., Bottacci, A., Bartolesi, A., Grossoni, P. & Tani, C. (1995) Morpho-anatomical alterations in leaves collected from beech trees (*Fagus sylvatica* L.) in conditions of natural water stress. *Environmental and Experimental Botany*, **35**, 201–213.

Bussotti, F., Gravano, E., Grossoni, P. & Tani, C. (1998) Occurrence of tannins in leaves of beech trees (*Fagus sylvatica*) along an ecological gradient, detected by histochemical and ultrastructural analyses. *New Phytologist*, **138**, 469–479.

Bussotti, F., Grossoni, P. & Bottacci, A. (1997) Sclerophylly in beech (*Fagus sylvatica* L.) trees: its relationship with crown transparency, nutritional status and summer drought. *Forestry*, 267–272.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M., *et al.* (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992.

Cebrian, null. (1999) Patterns in the fate of production in plant communities. *The American Naturalist*, **154**, 449–468.

Chapman, S.K., Hart, S.C., Cobb, N.S., Whitham, T.G. & Koch, G.W. (2003) Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology*, **84**, 2867–2876.

Charles, E. & Basset, Y. (2005) Vertical stratification of leaf-beetle assemblages (Coleoptera: Chrysomelidae) in two forest types in Panama. *Journal of Tropical Ecology*, **21**, 329–336.

Chiarelli, R.N., Pratt, P.D., Silvers, C.S., Blackwood, J.S. & Center, T.D. (2011) Influence of temperature, humidity, and plant terpenoid profile on life history characteristics of *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae), a biological control agent of the invasive tree *Melaleuca quinquenervia*. *Annals of the Entomological Society of America*, **104**, 488–497.

Choong, M.F., Lucas, P.W., Ong, J.S.Y., Pereira, B., Tan, H.T.W. & Turner, I.M. (1992) Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist*, **121**, 597–610.

Cisneros, J.J. & Godfrey, L.D. (2001) Midseason pest status of the cotton aphid (Homoptera: Aphididae) in California cotton – is nitrogen a key factor? *Environmental Entomology*, **30**, 501–510.

Clancy, K.M. & King, R.M. (1993) Defining the western spruce budworm’s nutritional niche with response surface methodology. *Ecology*, **74**, 442–454.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Coley, P.D. (1980) Effects of leaf age and plant life history patterns on herbivory. *Nature*, **284**, 545–546.

Coley, P.D. & Aide, T.M. (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In *Plant–animal interactions: Evolutionary ecology in tropical and temperate regions* (ed. by Price, P.W., Lewinsohn, T.M., Fernandes, G.W. & Benson, W.W). John Wiley & Sons, Newe York, USA, pp. 25**–**49.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.

Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Cranshaw, W. & Shetlar, D. (2017) *Garden insects of North America*. 2nd edn. Princeton University Press, Princeton, USA.

Crawley, M.J. (1983) Plant-herbivore dynamics. In *Plant ecology* (ed. by Crawley, M.J.). Blackwell Scientific Publications, Oxford, UK, pp. 401–474.

Crone, E.E. & Jones, C.G. (1999) The dynamics of carbon-nutrient balance: effects of cottonwood acclimation to short- and long-term shade on beetle feeding preferences. *Journal of Chemical Ecology*, **25**, 635–656.

Cunningham, S.A., Pullen, K.R. & Colloff, M.J. (2009) Whole-tree sap flow is substantially diminished by leaf herbivory. *Oecologia*, **158**, 633–640.

Cunningham, S.A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*, **69**, 569–588.

Danks, H.V. (2002) Modification of adverse conditions by insects. *Oikos*, **99**, 10–24.

Day, M.E., Greenwood, M.S. & White, A.S. (2001) Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiology*, **21**, 1195–1204.

De Cauwer, B., Reheul, D., De Laethauwer, S., Nijs, I. & Milbau, A. (2006) Effect of light and botanical species richness on insect diversity. *Agronomy for Sustainable Development*, **26**, 35–43.

Dicke, M. & Grostal, P. (2001) Chemical detection of natural enemies by arthropods: an ecological perspective. *Annual Review of Ecology Evolution and Systematics*, **32**, 1–23.

Didham, R.K. & Fagan, L.L. (2004) Forest canopies. In *Encyclopedia of forest sciences* (ed. by Burley, J., Evans, J. & Youngquist, J.). Academic Press, London, UK, pp. 68–80.

Dirzo, R. (1984) Herbivory: a phytocentric overview. In *Perspectives on plant population ecology* (ed. by Dirzo, R. & Sarukhan, J.). Sinauer, Sunderland, USA, pp. 141–165.

Dirzo, R. & Boege, K. (2008) Patterns of herbivory and defense in tropical dry and rain forests. In *Tropical forest community ecology* (ed. by Carson, W. & Schnitzer, S.). Wiley-Blackwell, Chichester, UK, pp. 63–78.

Dirzo, R., Mendoza, E. & Ortíz, P. (2007) Size-related differential seed predation in a heavily defaunated Neotropical rain forest. *Biotropica*, **39**, 355–362.

Dixon, A. (1998) *Aphid ecology - an optimization approach*. 2nd edn. Chapman and Hall, London, UK.

Dmitriev, D.A. (2017) 3I Interactive Keys and Taxonomic Databases [WWW Document]. URL http://dmitriev.speciesfile.org/index.asp [accessed on 2017].

Domínguez, C.A. & Dirzo, R. (1994) Effects of defoliation on *Erythroxylum havanese*, a tropical proleptic species. *Ecology*, **75**, 1896–1902.

Domínguez, C.A., Dirzo, R. & Bullock, S.H. (1989) On the function of floral nectar in *Croton suberosus* (Euphorbiaceae). *Oikos*, **56**, 109–114.

Donaldson, J.R., Stevens, M.T., Barnhill, H.R. & Lindroth, R.L. (2006) Age-related shifts in leaf chemistry of clonal aspen (*Populus tremuloides*). *Journal of Chemical Ecology*, **32**, 1415–1429.

Dudt, J.F. & Shure, D.J. (1994) The influence of light and nutrients on foliar phenolics and insect herbivory. *Ecology*, **75**, 86–98.

Dury, S.J., Good, J.E.G., Perrins, C.M., Buse, A. & Kaye, T. (1998) The effects of increasing CO_2 and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology*, **4**, 55–61.

Edwards, P.J. (1989) Insect herbivory and plant defence theory. In *Toward a more exact ecology* (ed. by Grubb, P.J. & Whittaker, J.B.). Blackwell Scientific Publications, Oxford, UK, pp. 275–297.

Elger, A., Lemoine, D.G., Fenner, M. & Hanley, M.E. (2009) Plant ontogeny and chemical defence: older seedlings are better defended. *Oikos*, **118**, 767–773.

Eliáš, P., Kratochvílová, I., Janouš, D., Marek, M. & Masarovičová, E. (1989) Stand microclimate and physiological activity of tree leaves in an oak-hornbeam forest. *Trees*, **3**, 227–233.

Ellenberg, H. & Leuschner, C. (2010) *Vegetation Mitteleuropas mit den Alpen*. 6th edn. Ulmer, Stuttgart, Germany.

Ellis, W.N. (2017) Leafminers and plant galls of Europe [WWW Document]. URL http://www.bladmineerders.nl/index.htm [accessed on 2017].

Ellsworth, D.S. & Reich, P.B. (1992a) Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. *Functional Ecology*, **6**, 423–435.

Ellsworth, D.S. & Reich, P.B. (1992b) Water relations and gas exchange of *Acer saccharum* seedlings in contrasting natural light and water regimes. *Tree Physiology*, **10**, 1–20.

Ellsworth, D.S. & Reich, P.B. (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia*, **96**, 169–178.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., *et al.* (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature*, **408**, 578–580.

England, J.R. & Attiwill, P.M. (2006) Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F. Muell. *Trees*, **20**, 79–90.

Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin*, **36**, 74–75.

Feeny, P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 565–581.

Feeny, P. (1992) The evolution of chemical ecology: contributions from the study of herbivorous insects. In *Herbivores: their interactions with secondary plant metabolites* (ed. by Rosenthal, G.A. & Berenbaum, M.R.). Academic Press, San Diego, USA, pp. 1–44.

Felton, G.W., Donato, K.K., Broadway, R.M. & Duffey, S.S. (1992) Impact of oxidized plant phenolics on the nutritional quality of dietar protein to a noctuid herbivore, *Spodoptera exigua*. *Journal of Insect Physiology*, **38**, 277–285.

Fernandes, G.W. & Price, P.W. (1992) The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. *Oecologia*, **90**, 14–20.

Fonseca, C.R., Overton, J.M., Collins, B. & Westoby, M. (2000) Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, **88**, 964–977.

Fonte, S.J. & Schowalter, T.D. (2005) The influence of a neotropical herbivore (*Lamponius portoricensis*) on nutrient cycling and soil processes. *Oecologia*, **146**, 423–431.

Forkner, R.E., Marquis, R.J. & Lill, J.T. (2004) Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of Quercus. *Ecological Entomology*, **29**, 174–187.

Fortin, M. & Mauffette, Y. (2002) The suitability of leaves from different canopy layers for a generalist herbivore (Lepidoptera: Lasiocampidae) foraging on sugar maple. *Canadian Journal of Forest Research*, **32**, 379–389.

Fowler, S.V. (1985) Differences in insect species richness and faunal composition of birch seedlings, saplings and trees: the importance of plant architecture. *Ecological Entomology*, **10**, 159–169.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., *et al.* (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and*

Management, Forest Ecology in the next Millennium : Putting the long view into Practice, **155**, 399–423.

Franklin, R.T. (1973) Insect Influences on the Forest Canopy. In *Analysis of Temperate Forest Ecosystems*. Springer, Berlin, Heidelberg, pp. 86–99.

Friedmann, G. & Schellenberg, J. (2017) *Functions for community data and ordinations*. R package version 0.3.3. URL https://CRAN.R-project.org/package=goeveg.

Frost, C.J. & Hunter, M.D. (2008) Insect herbivores and their frass affect *Quercus rubra* leaf quality and initial stages of subsequent litter decomposition. *Oikos*, **117**, 13–22.

Futuyma, D.J. & Saks, M.E. (1981) The effect of variation in host plant on the growth of an oligophagous insect, *Malacosoma americanum* and its polyphagous relative, *Malacosoma disstria*. *Entomologia Experimentalis et Applicata*, **30**, 163–168.

Gering, J.C. & Crist, T.O. (2000) Patterns of beetle (Coleoptera) diversity in crowns of representative tree species in an old-growth temperate deciduous forest. *Selbyana*, **21**, 38–47.

Gholamin, R. & Khayatnezhad, M. (2011) The effect of end season drought stress on the chlorophyll content, chlorophyll fluorescence parameters and yield in maize cultivars. *Scientific Research and Essays*, **6**, 5351–5357.

Giraudoux, P. (2017) *Miscellaneous functions for data analysis in ecology, with special emphasis on spatial data*. URL https://CRAN.R-project.org/package=pgirmess.

Gossner, M.M. & Ammer, U. (2006) The effects of Douglas-fir on tree-specific arthropod communities in mixed species stands with European beech and Norway spruce. *European Journal of Forest Research*, **125**, 221–235.

Gossner, M.M., Pašalić, E., Lange, M., Lange, P., Boch, S., Hessenmöller, D., *et al.* (2014) Differential responses of herbivores and herbivory to management in temperate European beech. *PLOS ONE*, **9**, e104876.

Graça, M. a. S., Maltby, L. & Calow, P. (1993) Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I: feeding strategies. *Oecologia*, **93**, 139–144.

Grimbacher, P.S. & Stork, N.E. (2007) Vertical stratification of feeding guilds and body size in beetle assemblages from an Australian tropical rainforest. *Austral Ecology*, **32**, 77–85.

Grossoni, P., Bussotti, F., Tani, C., Gravano, E., Santarelli, S. & Bottacci, A. (1998) Morpho-anatomical alterations in leaves of *Fagus sylvatica* L. and *Quercus ilex* L. in different environmental stress conditions. *Chemosphere*, **36**, 919–924.

Gruppe, A., Gossner, M.M., Engel, K. & Simon, U. (2008) Vertical and horizontal distribution of arthropods in temperate forests. In *Canopy arthropod research in Europe* (ed. by Floren, A. & Schmidl, J.). bioform entomology, Nürnberg, Germany, pp. 383–405.

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.

Hagerman, A.E. & Butler, L.G. (2012) Tannins and lignins. In *Herbivores: their interactions with secondary plant metabolites* (ed. by Rosenthal, G.A. & Berenbaum, M.R.). Academic Press, Michigan, USA, pp. 355–388.

Halaj, J., Ross, D.W. & Moldenke, A.R. (2000) Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos*, **90**, 139–152.

Hanley, M.E., Lamont, B.B., Fairbanks, M.M. & Rafferty, C.M. (2007) Plant structural traits and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 157–178.

Harrison, S. (1987) Treefall gaps versus forest understory as environments for a defoliating moth on a tropical forest shrub. *Oecologia*, **72**, 65–68.

Hartley, S.E. & Jones, T.H. (2004) Insect herbivores, nutrient cycling and plant productivity. In *Insects and ecosystem function*. Springer, Berlin-Heidelberg, Germany, pp. 27–52.

Heinrich, B. (1981) Ecological and evolutionary perspectives. In *Insect thermoregulation* (ed. by Heinrich, B.). Wiley, New York, USA, pp. 236–302.

Henriksson, J., Haukioja, E., Ossipov, V., Ossipova, S., Sillanpää, S., Kapari, L., *et al.* (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.

Hirao, T., Murakami, M. & Kashizaki, A. (2009) Importance of the understory stratum to entomofaunal diversity in a temperate deciduous forest. *Ecological Research*, **24**, 263–272.

Hochschule Weihenstephan-Triesdorf. (2017) ARBOFUX – Diagnose-Datenbank für Gehölze [WWW Document]. URL http://www.arbofux.de/ [accessed on 2017].

Holmes, R.T. & Schultz, J.C. (1988) Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology*, **66**, 720–728.

Hölscher, D., Koch, O., Korn, S. & Leuschner, C. (2005) Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. *Trees*, **19**, 628–637.

Hopkins, R.J., Dam, N.M. van & Loon, J.J.A. van. (2009) Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Annual Review of Entomology*, **54**, 57–83.

Horchler, P.J. & Morawetz, W. (2008) Canopy structure and its effect on canopy organisms: a generel introduction and some first findings of the Leipzig Canopy Crane Project with special reference to vertical stratification. In *Canopy arthropod research in Europe* (ed. by Floren, A. & Schmidl, J.). Bioform Entomology, Nürnberg, Germany, pp. 31–48.

Huang, T., Jander, G. & Vos, M. de. (2011) Non-protein amino acids in plant defense against insect herbivores: representative cases and opportunities for further functional analysis. *Phytochemistry*, Plant-Insect Interactions, **72**, 1531–1537.

Huberty, A.F. & Denno, R.F. (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, **85**, 1383–1398.

Huberty, A.F. & Denno, R.F. (2006) Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. *Oecologia*, **149**, 444–455.

Hunter, M.D. (2001) Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. *Agricultural and Forest Entomology*, **3**, 3–9.

Jactel, H. & Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters*, **10**, 835–848.

Jactel, H., Menassieu, P., Vetillard, F., Gaullier, A., Samalens, J.C. & Brockerhoff, E.G. (2006) Tree species diversity reduces the invasibility of maritime pine stands by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). *Canadian Journal of Forest Research*, **36**, 314–323.

Jaleel, C.A., Manivannan, P., Lakshmanan, G.M.A., Gomathinayagam, M. & Panneerselvam, R. (2008) Alterations in morphological parameters and photosynthetic pigment responses of *Catharanthus roseus* under soil water deficits. *Colloids and Surfaces B: Biointerfaces*, **61**, 298–303.

Jansen, M.P.T. & Stamp, N.E. (1997) Effects of light availability on host plant chemistry and the consequences for behavior and growth of an insect herbivore. *Entomologia Experimentalis et Applicata*, **82**, 319–333.

Jervis, M.A., Kidd, N.C.A., Fitton, M.G., Huddleston, T. & Dawah, H.A. (1993) Flower-visiting by hymenopteran parasitoids. *Journal of Natural History*, **27**, 67–105.

Joern, A., Provin, T. & Behmer, S.T. (2012) Not just the usual suspects: insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology*, **93**, 1002–1015.

Jones, C.S. (1999) An essay on juvenility, phase change, and heteroblasty in seed plants. *International Journal of Plant Sciences*, **160**, S105–S111.

Jones, R.E. (2001) Mechanisms for locating resources in space and time: impacts on the abundance of insect herbivores. *Austral Ecology*, **26**, 518–524.

Jukes, M.R., Ferris, R. & Peace, A.J. (2002) The influence of stand structure and composition on diversity of canopy Coleoptera in coniferous plantations in Britain. *Forest Ecology and Management*, **163**, 27–41.

Kampichler, C. & Teschner, M. (2002) The spatial distribution of leaf galls of *Mikiola fagi* (Diptera: Cecidomyiidae) and *Neuroterus quercusbaccarum* (Hymenoptera: Cynipidae) in the canopy of a Central European mixed forest. *European Journal of Entomology*, **99**, 79–84.

Kareiva, P. (1983) Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. In *Variable plants and herbivores in natural and managed systems* (ed. by Denno, R.F. & McClure, M.S.). Academic Press, New York, USA, pp. 259–289.

Karolewski, P., Giertych, M.J., Żmuda, M., Jagodziński, A.M. & Oleksyn, J. (2013) Season and light affect constitutive defenses of understory shrub species against folivorous insects. *Acta Oecologica*, **53**, 19–32.

Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773–795.

Katovich, S.A. & Morse, F.S. (1992) White pine weevil response to oak overstory girdling – results from a 16-year-old study. *Northern Journal of Applied Forestry*, **9**, 51–54.

Kearsley, M.J.C. & Whitham, T.G. (1989) Developmental changes in resistance to herbivory: implications for individuals and populations. *Ecology*, **70**, 422–434.

Kessler, M., Siorak, Y., Wunderlich, M. & Wegner, C. (2007) Patterns of morphological leaf traits among pteridophytes along humidity and temperature gradients in the Bolivian Andes. *Functional Plant Biology*, **34**, 963–971.

Kimber, I. (2017) UKMoths – guide to the moths of Great Britain and Ireland [WWW Document]. URL http://www.ukmoths.org.uk/ [accessed on 2017].

Kitajima, K., Llorens, A.-M., Stefanescu, C., Timchenko, M.V., Lucas, P.W. & Wright, S.J. (2012) How cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of shade-tolerant species. *The New Phytologist*, **195**, 640–652.

Kitajima, K. & Poorter, L. (2010) Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist*, **186**, 708–721.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., *et al.* (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., *et al.* (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 286–293.

Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. *Nature*, **428**, 851–854.

Koike, T., Kitao, M., Maruyama, Y., Mori, S. & Lei, T.T. (2001) Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. *Tree Physiology*, **21**, 951–958.

Kozlov, M.V. (2008) Losses of birch foliage due to insect herbivory along geographical gradients in Europe: a climate-driven pattern? *Climatic Change*, **87**, 107–117.

Kozlov, M.V., Zverev, V. & Zvereva, E.L. (2017) Combined effects of environmental disturbance and climate warming on insect herbivory in mountain birch in subarctic forests: results of 26-year monitoring. *The Science of the Total Environment*, **601**–**602**, 802–811.

Kozlov, M.V. & Zvereva, E.L. (2014) Variations in the effects of local foliar damage on life span of individual leaves of downy birch (*Betula pubescens*). *Botany*, **92**, 477–484.

Kozlov, M.V. & Zvereva, E.L. (2017) Background insect herbivory: impacts, patterns and methodology. In *Progress in botany Vol. 79*, Progress in Botany. Springer, Cham, Switzerland, pp. 313–355.

Kozlov, M.V., Zvereva, E.L. & Zverev, V. (2009) *Impacts of point polluters on terrestrial biota*. 1st edn. Springer, Netherlands.

Kozlowski, T.T. & Pallardy, S.G. (Eds.). (1997) *Physiology of woody plants*. Academic Press, San Diego, USA.

Laitinen, M.-L., Julkunen-Tiitto, R. & Rousi, M. (2000) Variation in phenolic compounds within a birch (*Betula pendula*) population. *Journal of Chemical Ecology*, **26**, 1609–1622.

Lambers, H., Chapin, F.S. & Pons, T.L. (2008) *Plant physiological ecology*. 2nd edn. Springer, New York, USA.

Landsberg, J. & Ohmart, C. (1989) Levels of insect defoliation in forests: patterns and concepts. *Trends in Ecology & Evolution*, **4**, 96–100.

Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1–10.

Larsson, S., Wirén, A., Lundgren, L. & Ericsson, T. (1986) Effects of Light and Nutrient Stress on Leaf Phenolic Chemistry in Salix dasyclados and Susceptibility to Galerucella lineola (Coleoptera). *Oikos*, **47**, 205–210.

Lattanzio, V., Lattanzio, V.M.T. & Cardinali, A. (2006) Role of phenolics in the resistance mechanisms of plants against fungal pathogens and insects. In *Phytochemistry: advances in research* (ed. by Imperato, F.). Research Signpost, Trivandrum, India, pp. 23–67.

Lawson, E.J.R. & Poethig, R.S. (1995) Shoot development in plants: time for a change. *Trends in Genetics*, **11**, 263–268.

Lawton, J.H. (1983) Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23–39.

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. *Ecological Entomology*, **24**, 46–58.

Leal, D.B. & Thomas, S.C. (2003) Vertical gradients and tree-to-tree variation in shoot morphology and foliar nitrogen in an old-growth *Pinus strobus* stand. *Canadian Journal of Forest Research*, **33**, 1304–1314.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*. 2nd edn. Elsevier, Amsterdam, Netherlands.

Legner, N., Fleck, S. & Leuschner, C. (2014) Within-canopy variation in photosynthetic capacity, SLA and foliar N in temperate broad-leaved trees with contrasting shade tolerance. *Trees*, **28**, 263–280.

Levesque, K.R., Fortin, M. & Mauffette, Y. (2002) Temperature and food quality effects on growth, consumption and post-ingestive utilization efficiencies of the forest tent caterpillar *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Bulletin of Entomological Research*, **92**, 127–136.

Lichtenthaler, H.K., Ač, A., Marek, M.V., Kalina, J. & Urban, O. (2007) Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. *Plant Physiology and Biochemistry*, **45**, 577–588.

Lichtenthaler, H.K., Babani, F., Langsdorf, G. & Buschmann, C. (2000) Measurement of differences in red chlorophyll fluorescence and photosynthetic activity between sun and shade leaves by fluorescence imaging. *Photosynthetica*, **38**, 521–529.

Lincoln, D.E. & Mooney, H.A. (1984) Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. *Oecologia*, **64**, 173–176.

Londo, G. (1976) The decimal scale for releves of permanent quadrats. *Vegetatio*, **33**, 61–64.

Loney, P.E., McArthur, C., Potts, B.M. & Jordan, G.J. (2006) How does ontogeny in a Eucalyptus species affect patterns of herbivory by brushtail possums? *Functional Ecology*, **20**, 982–988.

Loreau, M. (1995) Consumers as maximizers of matter and energy flow in ecosystems. *The American Naturalist*, **145**, 22–42.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., *et al.* (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.

Losey, J.E. & Vaughan, M. (2006) The economic value of ecological services provided by insects. *BioScience*, **56**, 311–323.

Louda, S.M. & Rodman, J.E. (1996) Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, bittercress). *Journal of Ecology*, **84**, 229–237.

Lovett, G.M. & Ruesink, A.E. (1995) Carbon and nitrogen mineralization from decomposing gypsy moth frass. *Oecologia*, **104**, 133–138.

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.

Lowman, M.D. (1985) Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology*, **10**, 7–24.

Lowman, M.D. (1992) Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica*, **24**, 263–272.

Lucas, P.W., Turner, I.M., Dominy, N.J. & Yamashita, N. (2000) Mechanical defences to herbivory. *Annals of Botany*, **86**, 913–920.

Łukowski, A., Giertych, M.J., Zadworny, M., Mucha, J. & Karolewski, P. (2015) Preferential feeding and occupation of sunlit leaves favors defense response and development in the flea beetle, *Altica brevicollis coryletorum* – a pest of *Corylus avellana*. *PLoS ONE*, **10**.

Mafakheri, A., Siosemardeh, A., Bahramnejad, B., Struik, P.C. & Sohrabi, Y. (2010) Effect of drought stress on yield, proline and chlorophyll contents in three chickpea cultivars. *Australian Journal of Crop Science*, **4**, 580–585.

Magalhães, S., Janssen, A., Hanna, R. & Sabelis, M.W. (2002) Flexible antipredator behaviour in herbivorous mites through vertical migration in a plant. *Oecologia*, **132**, 143–149.

Maiorana, V.C. (1981) Herbivory in sun and shade. *Biological Journal of the Linnean Society*, **15**, 151–156.

Marquis, R.J. (1984) Leaf herbivores decrease fitness of a tropical plant. *Science*, **226**, 537–539.

Marquis, R.J. & Whelan, C.J. (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, **75**, 2007–2014.

Marschner, H. (2011) *Marschner's mineral nutrition of higher plants*. 3rd edn. Academic Press, Amsterdam, Netherlands.

Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.

Matyssek, R., Fromm, J., Rennenberg, H. & Roloff, A. (2010) *Biologie der Bäume*. 1st edn. Ulmer, Stuttgart, Germany.

Mazancourt, C. de, Loreau, M. & Dieckmann, U. (2001) Can the evolution of plant defense lead to plant-herbivore mutualism? *The American Naturalist*, **158**, 109–123.

McCann, K.S. (2000) The diversity-stability debate. *Nature*, **405**, 228–233.

McKey, D. (1979) The distribution of secondary compounds within plants. In *Herbviores: Their interaction with secondary plant metabolites* (ed. by Rosenthal, G.A. & Janzen, D.H.). Academic Press, Orlando, USA, pp. 56–134.

McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, **341**, 142–144.

Medianero, E., Valderrama, A. & Barrios, H. (2003) Diversidad de insectos minadores de hojas y formadores de agallas en el dosel y sotobosque del bosque tropical. *Acta zoológica mexicana*, **89**, 153–168.

Mensah, J., Obadoni, B., Eruotor, P. & Onome-Irieguna, F. (2006) Simulated flooding and drought effects on germination, growth, and yield parameters of sesame (*Sesamum indicum* L.). *African Journal of Biotechnology*, **5**, 1249–1253.

Modrý, M., Hubený, D. & Rejšek, K. (2004) Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. *Forest Ecology and Management*, **188**, 185–195.

Moffett, M.W. (2000) What's "up"? A critical look at the basic terms of canopy Biology. *Biotropica*, **32**, 569–596.

Moffett, M.W. (2001) The nature and limits of canopy biology. *Selbyana*, **22**, 155–179.

Mölder, A., Bernhardt-Römermann, M. & Schmidt, W. (2008) Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? *Forest Ecology and Management*, Impacts of forest ecosystem management on greenhouse gas budgets, **256**, 272–281.

Mole, S. & Waterman, P.G. (1988) Light-induced variation in phenolic levels in foliage of rain-forest plants. *Journal of Chemical Ecology*, **14**, 23–34.

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.

Mooney, E.H., Tiedeken, E.J., Muth, N.Z. & Niesenbaum, R.A. (2009) Differential induced response to generalist and specialist herbivores by *Lindera benzoin* (Lauraceae) in sun and shade. *Oikos*, **118**, 1181–1189.

Moran, V.C. & Southwood, T.R.E. (1982) The guild composition of arthropod communities in trees. *Journal of Animal Ecology*, **51**, 289–306.

Mulder, C.P.H., Koricheva, J., Huss-Danell, K., Högberg, P. & Joshi, J. (1999) Insects affect relationships between plant species richness and ecosystem processes. *Ecology Letters*, **2**, 237–246.

Mumm, R., Posthumus, M.A. & Dicke, M. (2008) Significance of terpenoids in induced indirect plant defence against herbivorous arthropods. *Plant, Cell & Environment*, **31**, 575–585.

Murakami, M. & Wada, N. (1997) Difference in leaf quality between canopy trees and seedlings affects migration and survival of spring-feeding moth larvae. *Canadian Journal of Forest Research*, **27**, 1351–1356.

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.

Nabeshima, E. & Hiura, T. (2004) Size dependency of photosynthetic water- and nitrogen-use efficiency and hydraulic limitation in *Acer mono*. *Tree Physiology*, **24**, 745–752.

Neilson, E.H., Goodger, J.Q.D. & Woodrow, I.E. (2006) Novel aspects of cyanogenesis in *Eucalyptus camphora* subsp. *humeana*. *Functional Plant Biology*, **33**, 487–496.

Neves, F.S., Silva, J.O., Espírito-Santo, M.M. & Fernandes, G.W. (2014) Insect herbivores and leaf damage along successional and vertical gradients in a tropical dry forest. *Biotropica*, **46**, 14–24.

Nevo, E. & Coll, M. (2001) Effect of nitrogen fertilization on *Aphis gossypii* (Homoptera: Aphididae): variation in size, color, and reproduction. *Journal of Economic Entomology*, **94**, 27–32.

Nichols, J.D., Ofori, D.A., Wagner, M.R., Bosu, P. & Cobbinah, J.R. (1999) Survival, growth and gall formation by *Phytolyma lata* on *Milicia excelsa* established in mixed-species tropical plantations in Ghana. *Agricultural and Forest Entomology*, **1**, 137–141.

Nichols-Orians, C.M. (1991) The effects of light on foliar chemistry, growth and susceptibility of seedlings of a canopy tree to an attine ant. *Oecologia*, **86**, 552–560.

Nielsen, B.O. & Ejlersen, A. (1977) The distribution pattern of herbivory in a beech canopy. *Ecological Entomology*, **2**, 293–299.

Niemelä, J., Haila, Y. & Punttila, P. (1996) The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography*, **19**, 352–368.

Niesenbaum, R. (1992) The effects of light environment on herbivory and growth in the dioecious shrub *Lindera benzoin* (Lauraceae). *American Midland Naturalist*, **128**, 271–275.

Niesenbaum, R.A. & Kluger, E.C. (2006) When studying the effects of light on herbivory, should one consider temperature? The case of *Epimecis hortaria* F. (Lepidoptera: Geometridae) feeding on *Lindera benzoin* L. (Lauraceae). *Environmental Entomology*, **35**, 600–606.

Niinemets, Ü. (1995) Distribution of foliar carbon and nitrogen across the canopy of *Fagus sylvatica*: adaptation to a vertical light gradient. *Acta Oecologica*, **16**, 525–541.

Niinemets, Ü. (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, **82**, 453–469.

Niinemets, Ü. (2002) Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. *Tree Physiology*, **22**, 515–535.

Novotny, V. & Basset, Y. (2005) Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society of London B: Biological Sciences*, **272**, 1083–1090.

Novotny, V., Basset, Y. & Kitching, R. (2003) Herbivore assemblages and their food resources. In *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (ed. by Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.). University Press, Cambridge, UK, pp. 40–53.

Novotny, V., Miller, S.E., Baje, L., Balagawi, S., Basset, Y., Cizek, L., *et al.* (2010) Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. *The Journal of Animal Ecology*, **79**, 1193–1203.

Oishi, M., Yokota, T., Teramoto, N. & Sato, H. (2006) Japanese oak silkmoth feeding preference for and performance on upper-crown and lower-crown leaves. *Entomological Science*, **9**, 161–169.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., *et al.* (2017) *Vegan: an introduction to ordination*. R package version 2.4-2. URL https://CRAN.R-project.org/package=vegan.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., *et al.* (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, **14**, 301–312.

Ordoñez, J.C., Van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, **18**, 137–149.

Osier, T.L., Hwang, S.-Y. & Lindroth, R.L. (2000) Within- and between-year variation in early season phytochemistry of quaking aspen (*Populus tremuloides* Michx.) clones. *Biochemical Systematics and Ecology*, **28**, 197–208.

Osier, T.L. & Lindroth, R.L. (2001) Effects of genotype, nutrient availability, and defoliation on aspen phytochemistry and insect performance. *Journal of Chemical Ecology*, **27**, 1289–1313.

Otieno, D.O., Schmidt, M.W.T., Adiku, S. & Tenhunen, J. (2005) Physiological and morphological responses to water stress in two *Acacia* species from contrasting habitats. *Tree Physiology*, **25**, 361–371.

Oyama, K., Pérez-Pérez, M.A., Cuevas-Reyes, P. & Luna-Reyes, R. (2003) Regional and local species richness of gall-inducing insects in two tropical rain forests in Mexico. *Journal of Tropical Ecology*, **19**, 595–598.

Palik, B. & Engstrom, R.T. (1999) Species composition. In *Maintaining biodiversity in forest ecosystems* (ed. by Hunter, M.J.). Cambridge University Press, Cambridge, UK, pp. 65–94.

Parker, G.G. (1995) Structure and microclimate of forest canopies. In *Forest canopies: a review of research on a biological frontier* (ed. by Lowman, M.D. & Nadkarni, N.M.). Academic Press, San Diego, USA, pp. 73–106.

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.

Peeters, P.J., Read, J. & Sanson, G.D. (2001) Variation in the guild composition of herbivorous insect assemblages among co-occurring plant species. *Austral Ecology*, **26**, 385–399.

Peeters, P.J., Sanson, G. & Read, J. (2007) Leaf biomechanical properties and the densities of herbivorous insect guilds. *Functional Ecology*, **21**, 246–255.

Peoples, M.B. & Dalling, M.J. (1988) The interplay between proteolysis and amino acid metabolism during senescence and nitrogen reallocation. In *Senescence and aging in plants* (ed. by Noodén, L.D. & Leopold, A.C.). Academic Press, San Diego, USA, pp. 181–217.

Perkins, M.C., Woods, H.A., Harrison, J.F. & Elser, J.J. (2004) Dietary phosphorus affects the growth of larval *Manduca sexta*. *Archives of Insect Biochemistry and Physiology*, **55**, 153–168.

Pimm, S.L. & Raven, P. (2000) Biodiversity: extinction by numbers. *Nature*, **403**, 843–845.

Piotto, D. (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and Management*, **255**, 781–786.

Pitkin, B., Ellis, W.N., Plant, C. & Edmunds, R. (2017) The leaf and stem mines of British flies and other insects [WWW Document]. URL http://www.ukflymines.co.uk/ [accessed on 2017].

Poethig, R.S. (1990) Phase change and the regulation of shoot morphogenesis in plants. *Science (New York, N.Y.)*, **250**, 923–930.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.

Powell, W. (1986) Enhancing parasitoid activity in crops. In *Insect parasitoids* (ed. by Waage, J. & Greathead, D.). Academic Press, London, UK, pp. 319–340.

Price, P.W. (2002) Resource-driven terrestrial interaction webs. *Ecological Research*, **17**, 241–247.

Price, P.W., Fernandes, G.W., Lara, A.C.F., Brawn, J., Barrios, H., Wright, M.G., *et al.* (1998) Global patterns in local number of insect galling species. *Journal of Biogeography*, **25**, 581–591.

Pritchard, I.M. & James, R. (1984) Leaf mines: their effect on leaf longevity. *Oecologia*, **64**, 132–139.

R Development Core Team. (2017) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 13730–13734.

Rennwald, E. & Rodeland, J. (2017) Lepiforum: Bestimmung von Schmetterlingen (Lepidoptera) und ihren Präimaginalstadien [WWW Document]. URL http://www.lepiforum.de/ [accessed on 2017].

Reynolds, B.C. & Crossley, D.A. (1997) Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. *Environmental Entomology*, **26**, 1232–1239.

Ribeiro, S.P. & Basset, Y. (2007) Gall-Forming and Free-Feeding Herbivory along Vertical Gradients in a Lowland Tropical Rainforest: The Importance of Leaf Sclerophylly. *Ecography*, **30**, 663–672.

Ribeiro, S.P., Basset, Y. & Kitching, R. (2014) Density of Insect Galls in the Forest Understorey and Canopy: Neotropical, Gondwana or Global Patterns? In *Neotropical Insect Galls* (ed. by Fernandes, G.W. & Santos, J.C.). Springer, Dordrecht, The Netherlands, pp. 129–141.

Rijkers, T., Pons, T.L. & Bongers, F. (2000) The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Functional Ecology*, **14**, 77–86.

Rinker, H.B. & Lowman, M.D. (2004) Insect herbivory in tropical forests. In *Forest canopies* (ed. by Lowman, M.D. & Rinker, H.B.). Academic Press, San Diego, pp. 359–386.

Risch, S.J. (1981) Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology*, **62**, 1325–1340.

Roberts, M.R. & Paul, N.D. (2006) Seduced by the dark side: integrating molecular and ecological perspectives on the influence of light on plant defence against pests and pathogens. *The New Phytologist*, **170**, 677–699.

Robinson, S.K. & Holmes, R.T. (1984) Effects of plant species and foliage structure on the foraging behavior of forest birds. *The Auk*, **101**, 672–684.

Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica Oleracea*). *Ecological Monographs*, **43**, 95–124.

Rosenthal, G.A. & Berenbaum, M.R. (Eds.). (2012) *Herbivores: their interactions with secondary plant metabolites*. 2nd edn. Academic Press, San Diego, USA.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.

Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C. & Warzée, N. (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science*, **63**, 613–624.

Rowe, W.J. & Potter, D.A. (1996) Vertical stratification of feeding by Japanese beetles within linden tree canopies: selective foraging or height per se? *Oecologia*, **108**, 459–466.

Ruhnke, H., Schädler, M., Klotz, S., Matthies, D. & Brandl, R. (2009) Variability in leaf traits, insect herbivory and herbivore performance within and among individuals of four broad-leaved tree species. *Basic and Applied Ecology*, **10**, 726–736.

Russell, E.P. (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology*, **18**, 590–599.

Sala, O.E., Chapin, F.S., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Sanson, G., Read, J., Aranwela, N., Clissold, F. & Peeters, P. (2001) Measurement of leaf biomechanical properties in studies of herbivory: opportunities, problems and procedures. *Austral Ecology*, **26**, 535–546.

Schädler, M., Jung, G., Auge, H. & Brandl, R. (2003) Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. *Oikos*, **103**, 121–132.

Schmitz, O.J. (2008) Herbivory from individuals to ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 133–152.

Schowalter, T.D. (1995) Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management*, **78**, 115–125.

Schowalter, T.D. (Ed.). (2011) *Insect ecology: an ecosystem approach*. 3rd edn. Academic Press, San Diego, USA.

Schowalter, T.D., Hargrove, W.W. & Crossley, D.A. (1986) Herbivory in forested ecosystems. *Annual Review of Entomology*, **31**, 177–196.

Sellin, A., Tullus, A., Niglas, A., Õunapuu-Pikas, E., Meitern, A. & Lõhmus, K. (2013) Humidity-driven changes in growth rate, photosynthetic capacity, hydraulic properties and other functional traits in silver birch (*Betula pendula*). *Ecological Research*, **28**, 523–535.

Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**, 2057–2070.

Simonet, D.E., Clement, S.L., Rubink, W.L. & Rings, R.W. (1981) Temperature requirements for development and oviposition of *Peridroma saucia* (Lepidoptera: Noctuidae). *The Canadian Entomologist*, **113**, 891–897.

Singh, J.S. (2002) The biodiversity crisis: a multifaceted review. *Current Science*, **82**, 638–647.

Sipe, T.W. & Bazzaz, F.A. (1994) Gap partitioning among maples (*Acer*) in Central New England: shoot architecture and photosynthesis. *Ecology*, **75**, 2318–2332.

Smith, C.M.S., Bowie, M.H., Hahner, J.L., Boyer, S., Kim, Y.-N., Zhong, H.-T., *et al.* (2016) Punakaiki coastal restoration project: a case study for a consultative and multidisciplinary approach in selecting indicators of restoration success for a sand mining closure site, West Coast, New Zealand. *CATENA*, **136**, 91–103.

Sobek, S., Gossner, M.M., Scherber, C., Steffan-Dewenter, I. & Tscharntke, T. (2009a) Tree diversity drives abundance and spatiotemporal β-diversity of true bugs (Heteroptera). *Ecological Entomology*, **34**, 772–782.

Sobek, S., Scherber, C., Steffan-Dewenter, I. & Tscharntke, T. (2009b) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia*, **160**, 279–288.

Sobek, S., Steffan-Dewenter, I., Scherber, C. & Tscharntke, T. (2009c) Spatiotemporal changes of beetle communities across a tree diversity gradient. *Diversity and Distributions*, **15**, 660–670.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1986) Leaf palatability, life expectancy and herbivore damage. *Oecologia*, **70**, 544–548.

Southwood, T.R.E., Moran, V.C. & Kennedy, C.E.J. (1982) The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology*, **51**, 635–649.

Stamp, N. (2003) Out of the quagmire of plant defense hypotheses. *The Quarterly Review of Biology*, **78**, 23–55.

Stamp, N.E. & Bowers, M.D. (1988) Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). *Oecologia*, **75**, 619–624.

Steinbauer, M.J., Wallis, I.R., Davies, N.W. & Watson, S.J. (2015) Foliar quality of co-occurring mallee eucalypts: balance of primary and secondary metabolites reflects past growing conditions. *Chemoecology*, **25**, 179–191.

Stiling, P. & Moon, D.C. (2005) Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia*, **142**, 413–420.

Stork, N.E. (1988) Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society*, **35**, 321–337.

Stork, N.E., Hammond, P.M., Russell, B.L. & Hadwen, W.L. (2001) The spatial distribution of beetles within the canopies of oak trees in Richmond Park, U.K. *Ecological Entomology*, **26**, 302–311.

Strathdee, A.T., Bale, J.S., Block, W.C., Coulson, S.J., Hodkinson, I.D. & Webb, N.R. (1993) Effects of temperature elevation on a field population of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. *Oecologia*, **96**, 457–465.

Summers, C.B. & Felton, G.W. (1994) Prooxidant effects of phenolic acids on the generalist herbivore *Helicoverpa zea* (Lepidoptera: Noctuidae): potential mode of action for phenolic compounds in plant anti-herbivore chemistry. *Insect Biochemistry and Molecular Biology*, **24**, 943–953.

Tal, O., Freiberg, M. & Morawetz, W. (2008) Micro-climatic variability in the canopy of a temperate forest. In *Canopy arthropod research in Europe* (ed. by Floren, A. & Schmidl, J.). Bioform Entomology, Nürnberg, Germany, pp. 49–59.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., *et al.* (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.

Thacker, J.I., Thieme, T. & Dixon, A.F.G. (1997) Forecasting of periodic fluctuations in annual abundance of the bean aphid: the role of density dependence and weather. *Journal of Applied Entomology*, **121**, 137–145.

Thomas, S., Sztaba, A.J. & Smith, S. (2010) Herbivory patterns in mature sugar maple: variation with vertical canopy strata and tree ontogeny. *Ecological Entomology*, **35**, 1–8.

Thomas, S.C. (2010) Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. *Tree Physiology*, **30**, 555–573.

Thomas, S.C. & Winner, W.E. (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiology*, **22**, 117–127.

Tilman, D. (1986) A consumer-resource approach to community structure. *American Zoologist*, **26**, 5–22.

Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, **77**, 350–363.

Tjoelker, M.G., Reich, P.B. & Oleksyn, J. (1999) Changes in leaf nitrogen and carbohydrates underlie temperature and CO_2 acclimation of dark respiration in five boreal tree species. *Plant, Cell & Environment*, **22**, 767–778.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Tylianakis, J.M., Klein, A.-M. & Tscharntke, T. (2005) Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology*, **86**, 3296–3302.

Ulyshen, M.D. (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, **261**, 1479–1489.

Van Bael, S.A., Brawn, J.D. & Robinson, S.K. (2003) Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences*, **100**, 8304–8307.

Vanbergen, A.J., Woodcock, B.A., Heard, M.S. & Chapman, D.S. (2017) Network size, structure and mutualism dependence affect the propensity for plant-pollinator extinction cascades. *Functional Ecology*, **31**, 1285–1293.

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.

Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D. & Tscharntke, T. (2011) Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 111–119.

Wagner, D., DeFoliart, L., Doak, P. & Schneiderheinze, J. (2008) Impact of epidermal leaf mining by the aspen leaf miner (*Phyllocnistis populiella*) on the growth, physiology, and leaf longevity of quaking aspen. *Oecologia*, **157**, 259–267.

Watts, T., Woods, H.A., Hargand, S., Elser, J.J. & Markow, T.A. (2006) Biological stoichiometry of growth in *Drosophila melanogaster*. *Journal of Insect Physiology*, **52**, 187–193.

Webber, B.L. & Woodrow, I.E. (2009) Chemical and physical plant defence across multiple ontogenetic stages in a tropical rain forest understorey tree. *Journal of Ecology*, **97**, 761–771.

Weiner, J. (2004) Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 207–215.

Weisser, W.W. & Siemann, E. (Eds.). (2008) *Insects and ecosystem function*. Ecological Studies. 1st edn. Springer, Berlin-Heidelberg, Germany.

Whelan, C.J. (2001) Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology*, **82**, 219–231.

Whittaker, J.B. & Tribe, N.P. (1998) Predicting numbers of an insect (*Neophilaenus lineatus*: Homoptera) in a changing climate. *Journal of Animal Ecology*, **67**, 987–991.

Wiktelius, S. (1981) Diurnal flight periodicities and temperature thresholds for flight for different migrant forms of *Rhopalosiphum padi* L. (Hom., Aphididae). *Journal of Applied Entomology*, **92**, 449–457.

Willmer, P.G. (1982) Microclimate and the environmental physiology of insects. In *Advances in insect physiology* (ed. by Berridge, M.J., Treherne, J.E. & Wigglesworth, V.B.). Academic Press, London, UK, pp. 1–57.

Wilmers, F. & Ellenberg, H. (1986) Das Mikroklima in den untersuchten Beständen. In *Ökosystemforschung. Ergebnisse des Sollingprojekts: 1966-1986* (ed. by Ellenberg, H., Mayer, R. & Schauermann, J.). Ulmer, Stuttgart, Germany, pp. 67–76.

Wilson, E.O. (1987) The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology*, **1**, 344–346.

Witkowski, E.T.F. & Lamont, B.B. (1991) Leaf specific mass confounds leaf density and thickness. *Oecologia*, **88**, 486–493.

Wittstock, U. & Gershenzon, J. (2002) Constitutive plant toxins and their role in defense against herbivores and pathogens. *Current Opinion in Plant Biology*, **5**, 300–307.

Wraight, S.P., Carruthers, R.I., Jaronski, S.T., Bradley, C.A., Garza, C.J. & Galaini-Wraight, S. (2000) Evaluation of the entomopathogenic fungi *Beauveria bassiana* and *Paecilomyces fumosoroseus* for microbial control of the silverleaf whitefly, *Bemisia argentifolii*. *Biological Control*, **17**, 203–217.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Wright, I.J. & Westoby, M. (2002) Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist*, **155**, 403–416.

Wright, M.G. & Samways, M.J. (1996) Gall-insect species richness in African fynbos and karoo vegetation: the importance of plant species richness. *Biodiversity Letters*, **3**, 151–155.

Wright, M.G. & Samways, M.J. (1998) Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape Floristic Region, South Africa. *Oecologia*, **115**, 427–433.

Wuytack, T., Wuyts, K., Van Dongen, S., Baeten, L., Kardel, F., Verheyen, K., *et al.* (2011) The effect of air pollution and other environmental stressors on leaf fluctuating asymmetry and specific leaf area of *Salix alba* L. *Environmental Pollution (Barking, Essex: 1987)*, **159**, 2405–2411.

Xu, Z.Z. & Zhou, G.S. (2006) Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. *Planta*, **224**, 1080–1090.

Yamamura, K. (2002) Biodiversity and stability of herbivore populations: influences of the spatial sparseness of food plants. *Population Ecology*, **44**, 33–40.

Yamasaki, M. & Kikuzawa, K. (2003) Temporal and spatial variations in leaf herbivory within a canopy of *Fagus crenata*. *Oecologia*, **137**, 226–232.

Young, J., Watt, A., Nowicki, P., Alard, D., Clitherow, J., Henle, K., *et al.* (2005) Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe. *Biodiversity & Conservation*, **14**, 1641–1661.

Yun, J.I. & Taylor, S.E. (1986) Adaptive implications of leaf thickness for sun- and shade-grown *Abutilon theophrasti*. *Ecology*, **67**, 1314–1318.

Zehnder, C.B., Stodola, K.W., Joyce, B.L., Egetter, D., Cooper, R.J. & Hunter, M.D. (2009) Elevational and seasonal variation in the foliar quality and arthropod community of *Acer pensylvanicum*. *Environmental Entomology*, **38**, 1161–1167.

Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology*, **100**, 742–749.

Żmuda, M., Karolewski, P., Giertych, M.J., Zytkowiak, R., Bakowski, M., Grzebyta, J., *et al.* (2008) The effect of light conditions on leaf injury in underbrush shrubs caused by leaf-eating insects. *Acta Scientiarum Polonorum. Silvarum Colendarum Ratio et Industria Lignaria*, **7**, 47–57.

Zvereva, E.L., Lanta, V. & Kozlov, M.V. (2010) Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies. *Oecologia*, **163**, 949–960.

Zwölfer, H. (2010) Insekten und Pflanzen. In *Lehrbuch der Entomologie* (ed. by Dettner, K. & Peters, W.). Springer Spektrum, Heidelberg, Germany, pp. 499–519.

APPENDICES

Appendix A

Table 1A: Identified arthropod herbivore species of feeding traces on leaves of **(a)** *Fagus sylvatica*, **(b)** *Acer pseudoplatanus*, and **(c)** *Carpinus betulus*.

Species	Order	Family	Feeding guild	Development stage	Feeding location	Food type[1]
(a) *Fagus sylvatica*						
Diurnea fagella (Denis & Schiffermüller, 1775)	Lepidoptera	Chimabachidae	chewing	larva	external	polyphag
Orchestes fagi (Linnaeus, 1758)	Coleoptera	Curculionidae	chewing	adult	external	polyphag
Phyllobius argentatus (Linnaeus, 1758)	Coleoptera	Curculionidae	chewing	adult	external	polyphag
Fagocyba cruenta (Herrich-Schäffer, 1838)	Hemiptera	Cicadellidae	sap-sucking	adult+larva	external	polyphag
Phyllaphis fagi (Linnaeus, 1767)	Hemiptera	Callaphididae	sap-sucking	adult+larva	external	monophag
Orchestes fagi (Linnaeus, 1758)	Coleoptera	Curculionidae	mining	larva	internal	monophag
Phyllonorycter maestingella (Müller, 1764)	Lepidoptera	Gracillariidae	mining	larva	internal	monophag
Phyllonorycter messaniella (Zeller, 1846)	Lepidoptera	Gracillariidae	mining	larva	internal	polyphag
Stigmella hemargyrella (Kollar, 1832)	Lepidoptera	Nepticulidae	mining	larva	internal	monophag
Stigmella tityrella (Stainton, 1854)	Lepidoptera	Nepticulidae	mining	larva	internal	monophag
Acalitus stenaspis (Nalepa, 1891)	Acarina	Eriophyidae	gall-inducing	larva	internal	monophag
Aceria nervisequa (Canestrini, 1891)	Acarina	Eriophyidae	gall-inducing	larva	internal	monophag
Aceria nervisequa faginea (Nalepa, n.d.)	Acarina	Eriophyidae	gall-inducing	larva	internal	monophag
Contarinia fagi (Rübsaamen, 1921)	Diptera	Cecidomyiidae	gall-inducing	larva	internal	monophag
Hartigiola annulipes (Hartig, 1839)	Diptera	Cecidomyiidae	gall-inducing	larva	internal	monophag
Mikiola fagi (Hartig, 1839)	Diptera	Cecidomyiidae	gall-inducing	larva	internal	monophag
(b) *Acer pseudoplatanus*						
Phyllobius argentatus (Linnaeus, 1758)	Coleoptera	Curculionidae	chewing	adult	external	polyphag
Fagocyba cruenta (Herrich-Schäffer, 1838)	Hemiptera	Cicadellidae	sap-sucking	adult+larva	external	polyphag
Aceria macrorhyncha (Nalepa, 1889)	Acarina	Eriophyidae	gall-inducing	larva	internal	monophag
Eriophyes psilomerus (Nalepa, 1922)	Acarina	Eriophyidae	gall-inducing	larva	internal	monophag

Table 1A: Continued.

Species	Order	Family	Feeding guild	Development stage	Feeding location	Food type[1]
(c) *Carpinus betulus*						
Aceria tenella (Nalepa, 1892)	Acarina	Eriophyidae	gall-inducing	larva	internal	monophag

[1] Based on databases (Dmitriev, 2017; Ellis, 2017; Hochschule Weihenstephan-Triesdorf, 2017; Kimber, 2017; Rennwald & Rodeland, 2017).

Appendix B

Table 2A: Overview of the study sites with elevational and climatic information.

#	Site	Coordinates	Altitude (m.a.s.l.)	Meteorological station	**Precipitation** (mm yr^{-1})				**Temperature** (mean yr^{-1})			
					1961-1990	1971-2000	2001-2012	2012	1961-1990	1971-2000	2001-2012	2012
1	Winkelberg	10°24' 51°31'	365	Herzberg	874	870	669	767	n.a.	n.a.	n.a.	8.9
2	Tiefentals Ebene	09°26' 51°39'	271	Wahlsburg	783	811	806	734	8.7	8.7	9.4	9.3
3	Klingenberg/Vaaker Berg	09°38' 51°32'	187	Wahlsburg	783	811	806	734	8.7	8.7	9.4	9.3
4	Schieferstein	10°04' 51°07'	444	Sontra	743	747	698	685	7.4	n.a.	8.8	8.7
5	Heiligenberg	10°01' 51°16'	311	Eschwege	676	659	603	560	8.6	8.9	9.6	9.5
6	Bocksbühl	09°58' 51°25'	368	Göttingen	645	628	637	624	8.7	9.0	9.3	9.4
7	Hubenberg	10°28' 51°26'	376	Friedrichsthal	631	642	637	637	n.a.	n.a.	n.a.	n.a.
8	Feuerkuppe	10°45' 51°23'	309	Sondershausen	542	531	642	n.a.	n.a.	n.a.	9,3	n.a.
9	Heidelberg	10°57' 51°19'	257	Günserode	534	530	535	535	n.a.	n.a.	n.a.	n.a.
10	Eichleite	11°19' 51°16'	143	Artern	474	461	501	462	8.5	8.9	9.6	9.6

Appendix C

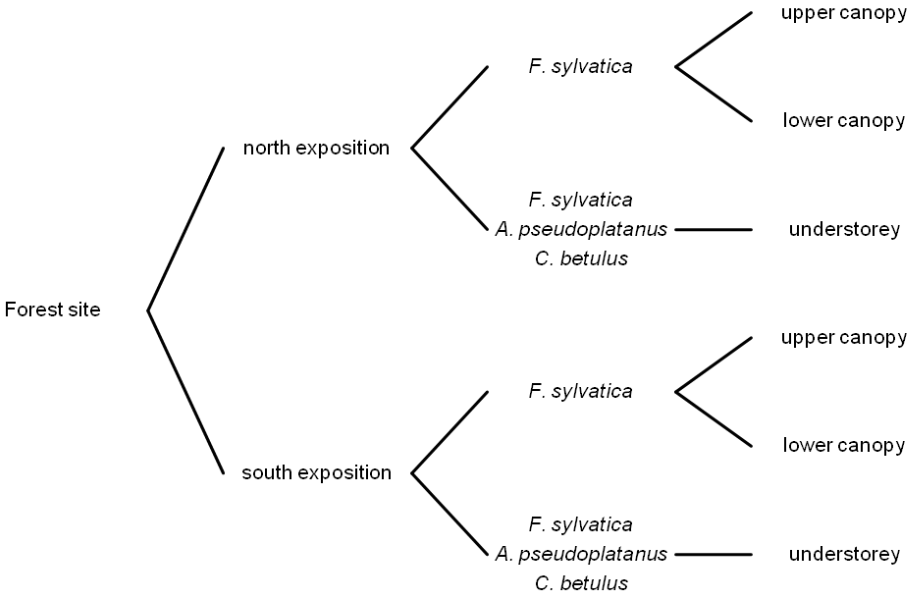

Figure 1A: Sampling trees of adult and juvenile *Fagus sylvatica*, *Acer pseudoplatanus*, and *Carpinus betulus* individuals with different potential spots in the understorey and forest canopy.

Table 3A: Results of Spearman's correlation test for all variables. Leaf trait parameters are based on data from *Fagus sylvatica*. Presented rho-values are given with significances (***: *p*>0.001; **: *p*>0.01; *: *p*>0.05). Humid = relative air humidity; temp = air temperature; Ctotal = leaf C content; Ntotal = leaf N content; SLA = specific leaf area; chloro = chlorophyll content.

Variable	humid	temp	Ctotal	Ntotal	C/N ratio	SLA	chloro
humid	-	-0.867***	-0.653***	0.447***	-0.496***	0.888***	-0.035
temp	-0.867***	-	0.590***	-0.335*	0.383**	-0.776***	-0.110
Ctotal	-0.653***	0.590***	-	-0,302*	0.387**	-0.696***	0.128
Ntotal	0.447***	-0.335*	-0,302*	-	-0.992***	0.548***	0.262*
C/N ratio	-0.496***	0.383**	0.387**	-0.992***	-	-0.605***	-0.232
SLA	0.888***	-0.776***	-0.696***	0.548***	-0.605***	-	-0.019
chloro	-0.035	-0.110	0.128	0.262*	-0.232	-0.019	-

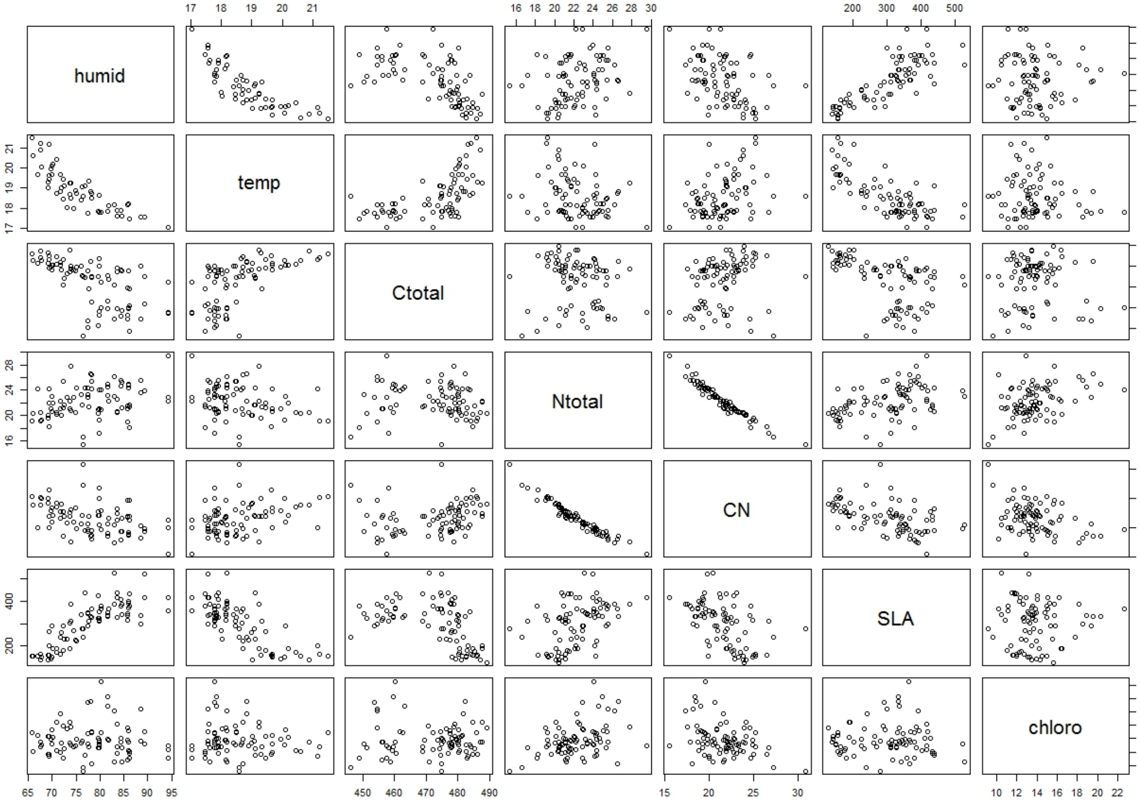

Figure 2A: Pair plot of all variables (humid: n = 57; temp: n = 57; Ctotal: n = 60; Ntotal: n = 60; CN: n = 60; SLA: n = 60; chloro: n = 60) along the vertical forest gradient. Leaf trait parameters are based on data from *Fagus sylvatica*. Humid = relative air humidity; temp = air temperature; Ctotal = leaf C content; Ntotal = leaf N content; CN = C/N ratio; SLA = specific leaf area; chloro = chlorophyll content.

Table 4A: Model selection table for model comparison[1] of microclimatic, leaf trait, and forest layer effects on herbivory (leaf area loss) of *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	Chlorophyll	C/N ratio	Ctotal	Humid	Layer	Ntotal	Temp	df	logLik	BIC	Delta	Weight
65	0.518900							-0.0199200	4	90.472	-164.8	0.00	0.130
9	-0.083760				2.984e-03				4	90.094	-164.0	0.76	0.089
10	-0.196300	0.008358			2.968e-03				5	92.114	-164.0	0.76	0.089
66	0.405800	0.006705						-0.0187600	5	91.914	-163.6	1.16	0.073
17	0.167700					+			5	91.908	-163.6	1.17	0.072
18	0.072070	0.007142				+			6	93.422	-162.6	2.19	0.043
12	-0.354700	0.010100	0.0041340		3.549e-03				6	92.955	-161.7	3.12	0.027
73	0.308600				1.155e-03			-0.0134300	5	90.644	-161.1	3.70	0.020
67	0.511000		0.0014750				0.0245200	-0.0212200	5	90.587	-161.0	3.81	0.019
44	-1.435000	0.010150	0.0274400		3.880e-03				7	94.575	-160.8	3.92	0.018
69	0.390200			3.024e-04				-0.0207600	5	90.486	-160.8	4.02	0.017
97	0.528100						-0.0002537	-0.0201100	5	90.476	-160.7	4.04	0.017
42	-0.175600	0.009478			3.299e-03		-0.0027500		6	92.468	-160.7	4.10	0.017
68	0.369300	0.007798	0.0032640					-0.0214000	6	92.437	-160.6	4.16	0.016
21	-0.792800			2.023e-03		+			6	92.421	-160.6	4.19	0.016
74	0.063730		0.007669		1.816e-03			-0.0086360	6	92.376	-160.5	4.28	0.015
11	-0.135000		0.0015630		3.207e-03				5	90.224	-160.2	4.54	0.013
14	0.002634		0.008418	-3.914e-04	2.804e-03				6	92.137	-160.0	4.76	0.012
41	-0.079230				3.027e-03		-0.0003526		5	90.100	-160.0	4.79	0.012
13	-0.083800			7.938e-08	2.984e-03				5	90.094	-160.0	4.80	0.012

[1] R code: fullmod <- lmer(sqrt(herbivory) ~ layer + temp + humid + Ctotal + Ntotal + chlorophyll + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): '1 | site'. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Layer = forest layer; Ntotal = leaf N content; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 5A: Model selection table for model comparison[1] of tree species and leaf trait effects on herbivory (leaf area loss) of *Fagus sylvatica*, *Acer pseudoplatanus*, and *Carpinus betulus* in the understorey. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	Chlorophyll	C/N ratio	Ctotal	Humid	Ntotal	SLA	Species	Temp	df	logLik	BIC	Delta	Weight
65	0.1677							+		5	69.194	-119.5	0.00	0.114
5	1.0520			-0.0018						4	66.636	-118.1	1.33	0.059
66	0.1095	0.0043						+		6	70.234	-117.8	1.70	0.049
69	-1.0500			0.0026				+		6	70.207	-117.7	1.76	0.048
193	-0.2376							+	0.0226	6	69.842	-117.0	2.49	0.033
6	0.9367	0.0046		-0.0017						5	67.843	-116.8	2.70	0.030
1	0.1931									3	63.994	-116.6	2.83	0.028
197	-2.0040			0.0034				+	0.0314	7	71.513	-116.5	2.93	0.026
73	0.3019				-1.62E-03			+		6	69.536	-116.4	3.10	0.024
81	0.1268					1.83E-03		+		6	69.402	-116.1	3.37	0.021
194	-0.3883	0.0050						+	0.0273	7	71.273	-116.1	3.41	0.021
97	0.1349						8.45E-05	+		6	69.322	-115.9	3.53	0.020
67	0.1864		-8.65E-04					+		6	69.24	-115.8	3.69	0.018
2	0.1201	0.0052								4	65.411	-115.7	3.78	0.017
77	-1.1030			0.0031	-2.26E-03			+		7	70.916	-115.3	4.12	0.015
21	1.0130			-0.0019		2.83E-03				5	67.086	-115.3	4.22	0.014
70	-0.8149	0.0034		0.0020				+		7	70.792	-115.1	4.37	0.013
83	-0.8657		2.28E-02			2.42E-02		+		7	70.778	-115.1	4.40	0.013
74	0.2508	0.0045			-1.72E-03			+		7	70.698	-114.9	4.56	0.012
7	1.0810		-2.15E-03	-0.0018						5	66.901	-114.9	4.58	0.012

[1] R code: fullmod <- lmer(sqrt(herbivory) ~ species + temp + humid + Ctotal + Ntotal + chlorophyll + C/N ratio + SLA + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): ‘1 | site’. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Species = tree species; Ntotal = leaf N content; SLA = specific leaf area; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Appendix D

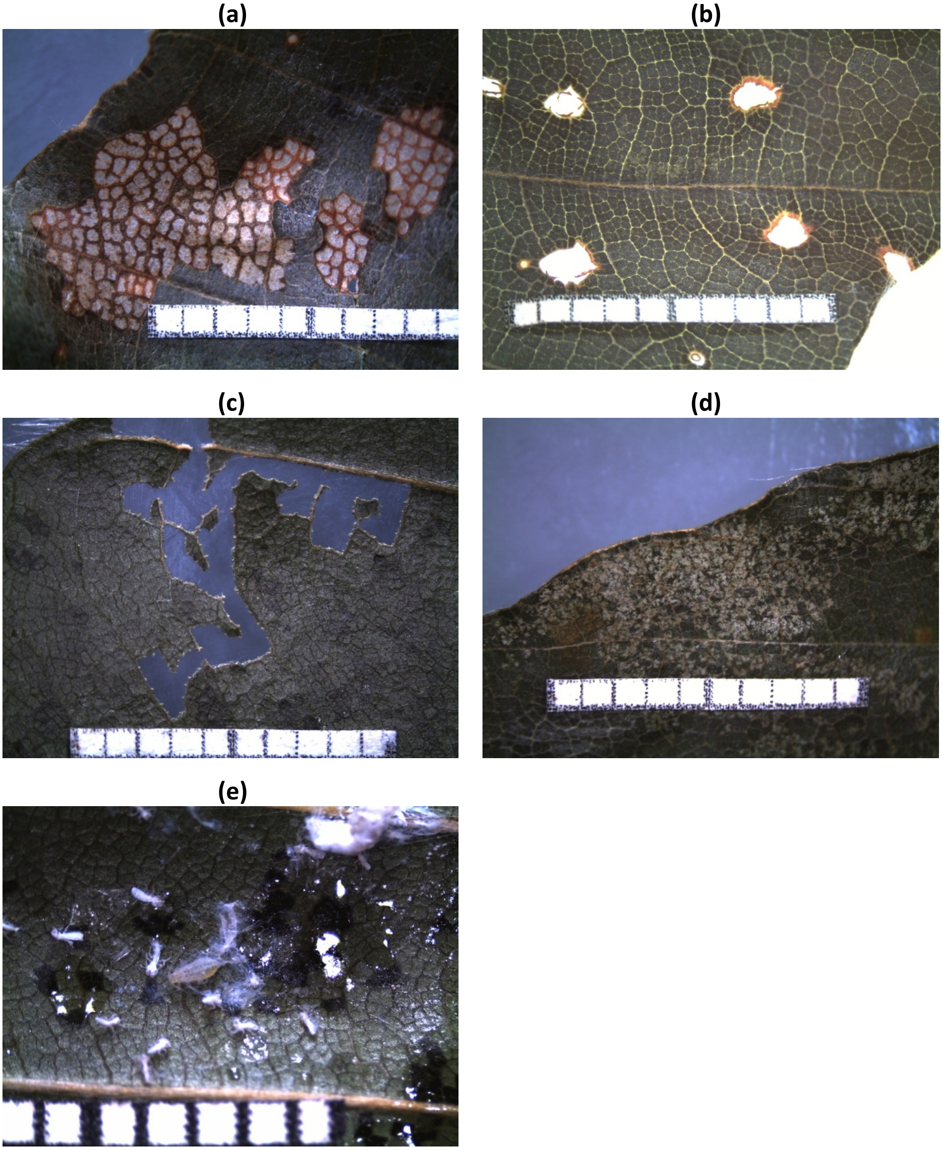

Figure 3A: Feeding traces of leaf-chewers and sap-suckers (exophagous feeding guilds) on *Fagus sylvatica* leaves. **(a)** Windows (probably *Diurnea flagella*, ADS), **(b)** small circles (probably *Orchestes fagi*, ADS), **(c)** labyrinth (probably *Phyllobius argentatus*, ADS), **(d)** whitish spots (probably *Fagocyba cruenta,* ADS), **(e)** wax wool (probably *Phyllaphis fagi*, ABS). Images were taken with an integrated digital camera of a stereo microscope (LEICA EZ4 D, Wetzlar, Germany). Little square equals 1x1 mm. ADS = adaxial side, ABS = abaxial side.

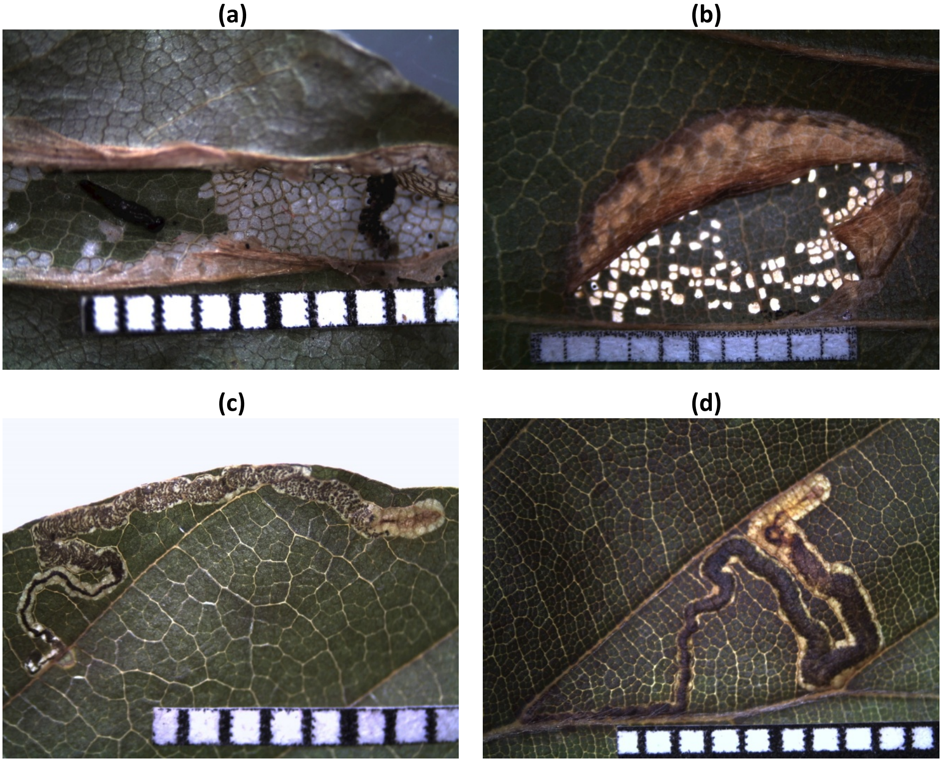

Figure 4A: Feeding traces of miners (endophagous feeding guild) on *Fagus sylvatica* leaves. **(a)** Tubular mine (probably *Phyllonorycter maestingella*, ABS), **(b)** oval mine (probably *Phyllonorycter messaniella*, ABS), **(c)** line crossing lateral veins (probably *Stigmella hemargyrella*, ADS), **(d)** line between lateral veins *(*probably *Stigmella tityrella*, ADS). Images were taken with an integrated digital camera of a stereo microscope (LEICA EZ4 D, Wetzlar, Germany). Little square equals 1x1 mm, ADS = adaxial side, ABS = abaxial side.

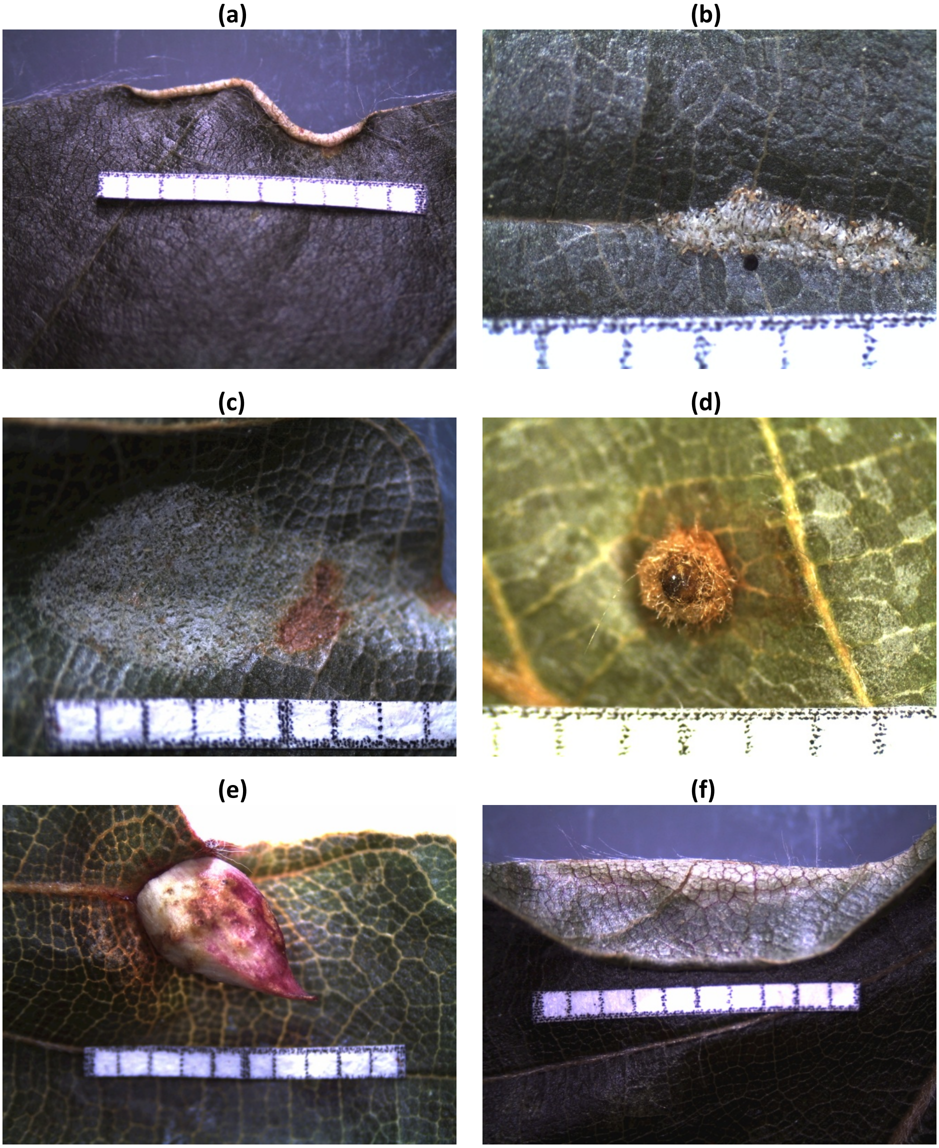

Figure 5A: Feeding traces of gall-inducers (endophagous feeding guild) on *Fagus sylvatica* leaves. **(a)** Rolled-up leaf edge (probably *Acalitus stenaspis*, ADS), **(b)** haired gall on leaf veins (probably *Aceria nervisequa*, ADS), **(c)** pannose spot between veins (probably *Aceria nervisequa faginea*, ABS), **(d)** haired brownish gall (probably *Hartigiola annulipes*, ADS), **(e)** ovate, acuminated gall (probably *Mikiola fagi*, ADS), **(f)** pleated gall (probably *Phegomyia fagicola*, ADS). Images were taken with an integrated digital camera of a stereo microscope (LEICA EZ4 D, Wetzlar, Germany). Little square equals 1x1 mm, ADS = adaxial side, ABS = abaxial side.

Table 6A: Presence (+) and absence of feeding traces on leaves of juvenile and adult *Fagus sylvatica* (European beech) individuals at all sample sites in the understorey and canopies, respectively.

Site	**Beech individual**	**Feeding guild**							
		leaf-chewing		sap-sucking	leaf-mining	gall-inducing			
		small circles	labyrinth	whitish spots	tubular mine	leaf edge gall	haired vein gall	pannose spot	ovate gall
WB-N	juvenile (US)	+	+	+	+			+	+
	adult (LC)	+		+		+	+	+	+
	adult (UC)	+		+		+	+	+	+
WB-S	juvenile (US)	+	+	+	+		+	+	+
	adult (LC)	+		+	+	+	+	+	+
	adult (UC)	+		+		+	+	+	+
TE-N	juvenile (US)	+	+	+	+	+	+	+	+
	adult (LC)	+	+	+		+	+	+	+
	adult (UC)	+	+	+	+	+	+	+	+
TE-S	juvenile (US)	+	+	+	+	+	+	+	+
	adult (LC)	+	+	+	+	+	+	+	+
	adult (UC)	+		+		+	+	+	+
KBVB-N	juvenile (US)	+		+	+	+	+	+	+
	adult (LC)	+		+	+	+	+	+	+
	adult (UC)	+		+		+	+	+	+
KBVB-S	juvenile (US)	+	+	+	+	+	+	+	+
	adult (LC)	+		+		+	+	+	+
	adult (UC)	+		+		+	+	+	+
SS-N	juvenile (US)	+	+	+	+	+	+	+	+
	adult (LC)	+		+		+	+	+	
	adult (UC)	+		+	+	+	+	+	+
SS-S	juvenile (US)	+		+	+	+	+	+	+
	adult (LC)	+		+		+	+	+	+
	adult (UC)	+		+		+	+	+	+

Table 6A: Continued.

Site	Beech individual	Feeding guild							
		leaf-chewing		sap-sucking	leaf-mining	gall-inducing			
		small circles	labyrinth	whitish spots	tubular mine	leaf edge gall	haired vein gall	pannose spot	ovate gall
HGB-N	juvenile (US)	+		+	+		+	+	+
	adult (LC)	+		+			+	+	+
	adult (UC)	+		+			+	+	+
HGB-S	juvenile (US)	+	+	+	+	+	+	+	+
	adult (LC)	+		+	+	+	+	+	+
	adult (UC)	+		+			+		+
BB-N	juvenile (US)	+	+	+	+			+	+
	adult (LC)	+		+		+	+	+	+
	adult (UC)	+		+		+	+	+	+
BB-S	juvenile (US)	+	+	+	+	+	+	+	+
	adult (LC)	+	+	+		+	+	+	+
	adult (UC)	+	+	+		+	+	+	+
HB-N	juvenile (US)	+	+	+	+		+	+	+
	adult (LC)	+	+	+		+	+	+	+
	adult (UC)	+	+	+		+	+	+	+
HB-S	juvenile (US)	+		+		+	+	+	+
	adult (LC)	+		+	+	+	+	+	
	adult (UC)	+		+		+	+	+	+
FK-N	juvenile (US)	+	+	+	+		+	+	
	adult (LC)	+	+	+		+	+	+	
	adult (UC)	+	+	+		+	+	+	

Table 6A: Continued.

Site	Beech individual	Feeding guild							
		leaf-chewing		sap-sucking	leaf-mining	gall-inducing			
		small circles	labyrinth	whitish spots	tubular mine	leaf edge gall	haired vein gall	pannose spot	ovate gall
FK-S	juvenile (US)	+	+	+		+	+	+	
	adult (LC)	+	+	+		+	+	+	
	adult (UC)	+	+	+		+	+	+	+
HDB-N	juvenile (US)	+	+	+	+	+	+	+	
	adult (LC)	+		+		+	+	+	
	adult (UC)	+		+	+	+	+	+	+
HDB-S	juvenile (US)	+		+	+	+	+	+	
	adult (LC)	+		+	+	+	+	+	
	adult (UC)	+		+		+	+		
EL-N	juvenile (US)	+	+	+	+			+	+
	adult (LC)	+	+	+			+	+	+
	adult (UC)	+	+	+		+	+	+	+
EL-S	juvenile (US)	+		+	+	+	+	+	+
	adult (LC)	+	+	+	+	+	+	+	+
	adult (UC)	+	+	+		+	+	+	+

Presence is indicated by pluses. Data are based on feeding traces identified on collected leaf samples. Forest sites: WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite; N = north exposition; S = south exposition. Forest layers: US = understorey; LC = lower canopy; UC = upper canopy.

Table 7A: (a) Microclimate and **(b)** leaf trait parameters of juvenile and adult *Fagus sylvatica* individuals along the vertical forest gradient. Microclimatic conditions for understorey (US; n = 20), lower (LC; n = 20) and upper canopy (UC; n = 17) are represented by temperature and relative air humidity. Leaf trait parameters of *F. sylvatica* (US: n = 20; LC: n = 20; UC: n = 20) are represented by specific leaf area (SLA), leaf size, total leaf carbon content (C), total leaf nitrogen content (N), C/N ratio, and chlorophyll content. Presented are the median and the interquartile range (IQR = first quartile, third quartile).

Parameter[1]	**Beech individuals**		
	juvenile (US)	adult (LC)	adult (UC)
(a) Microclimate			
temperature (°C)*	17.9 (17.6,18.2)^{a}	18.8 (18.6,19.1)^{b}	19.9 (19.6,20.6)^{c}
relative air humidity (%)°	83 (80,86)^{a}	74 (72,76)^{b}	69 (68,70)^{c}
(b) Leaf trait			
SLA ($m^2\ kg^{-1}$)°	38 (35,42)^{a}	28 (24,33)^{b}	16 (15,18)^{c}
leaf size (cm^2)°	23 (21,24)^{a}	30 (23,34)^{b}	20 (19,23)^{a}
N ($mg\ g^{-1}$)*	22 (21,24)^{a}	23 (22,24)^{a}	21 (20,22)^{b}
C ($mg\ g^{-1}$)*	475 (472,748)^{a}	478 (476,480)^{b}	483 (481,486)^{c}
C/N ratio ($g\ g^{-1}$)°	21.3 (19.8,22.1)^{a}	21.0 (19.7,22.2)^{a}	23.4 (22.5,24.4)^{b}
chlorophyll (CCI)*	13.8 (12.6,14.3)^{a}	13.5 (13.1,15.6)^{a}	13.2 (12.0,14.2)^{a}

[1] Lowercase letters indicate significant differences of parameters between the forest layers using (*) ANOVA and Tukey's HSD ($p \leq 0.05$; df = 2) or (°) Kruskal-Wallis and post-hoc test ($p \leq 0.05$; df = 2).

Table 8A: Selection of significant parameters for the ordination of sample sites and arthropod herbivore attack levels in a biplot with non-metric multidimensional scaling (NMDS). Significant environmental and leaf trait parameters are fitted all onto the ordination as *post-hoc* correlations.

Parameter[1]	**NMDS1**	**NMDS2**	R^2	p
temperature	0.99872	-0.05053	0.2489	0.001***
relative air humidity	-0.99926	0.03837	0.4612	0.001***
SLA	-0.97297	-0.23095	0.4257	0.001***
Ctotal	0.99002	-0.14094	0.1665	0.006**
Ntotal	-0.63438	-0.77302	0.1605	0.008**
C/N ratio	0.65518	0.75547	0.1729	0.007**
chlorophyll	-0.87043	-0.49229	0.0544	0.234

[1] SLA = specific leaf area; Ctotal = leaf carbon content; Ntotal = leaf nitrogen content. Significant parameters: ***: $p>0.001$; **: $p>0.01$.

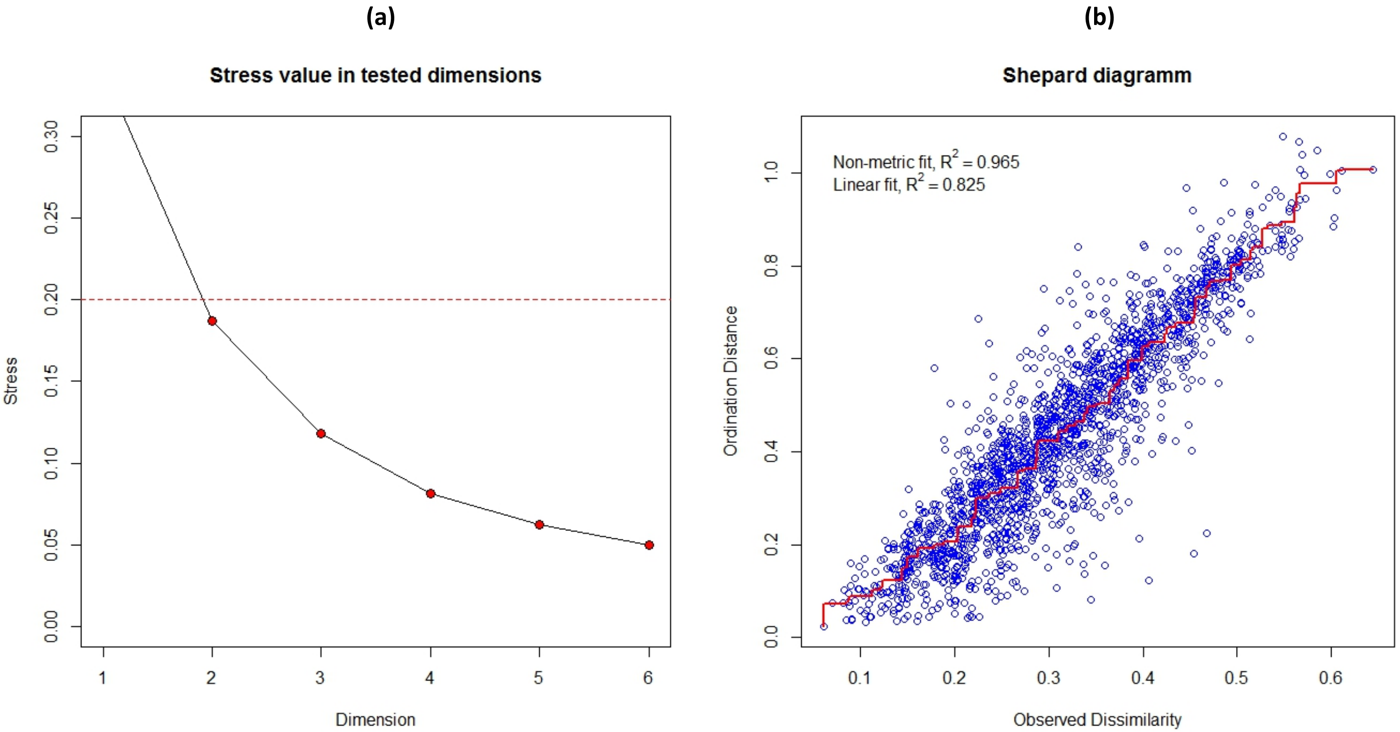

Figure 6A: Constructing the ordination of sample sites and arthropod herbivore attack levels in a biplot with **(a)** the diagnostic stress plot indicating 2 dimensions (first point under the dotted line) as the best dimensionality for non-metric multidimensional scaling (NMDS), and with **(b)** the Shepard diagram, showing the original pairwise distances (based on the Bray-Curtis dissimilarity) and the new distances of the ordination (based on ranks). Calculations were done with R packages *vegan* (Oksanen *et al.*, 2017) and *goeveg* (Friedmann & Schellenberg, 2017). The stress value 0.187 for the NMDS is determined with the category "usable" (stress value < 0.20) following the guidelines for acceptable stress values (Clarke, 1993).

Table 9A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by small circles on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
1	0.6582								3	30.371	-48.6	0.00	0.193
9	0.4226				0.0107				4	31.407	-46.6	1.97	0.072
21	1.3090			-0.0112		6.86E-04			5	33.135	-46.1	2.56	0.054
2	0.8377	-0.0082							4	31.027	-45.9	2.73	0.049
33	0.6688						+		4	30.799	-45.4	3.19	0.039
5	0.8167			-0.0021					4	30.738	-45.3	3.31	0.037
3	-0.4435		2.30E-03						4	30.590	-45.0	3.61	0.032
13	0.6222			-0.0039	0.0150				5	32.578	-44.9	3.67	0.031
17	0.6430					5.29E-05			4	30.425	-44.7	3.94	0.027
65	0.6460							0.0006	4	30.372	-44.6	4.04	0.026
69	2.8070			-0.0115				-0.0674	5	32.362	-44.5	4.10	0.025
6	1.2320	-0.0128		-0.0039					5	32.122	-44.0	4.58	0.019
10	-1.2740	0.0382			0.0494				5	32.119	-44.0	4.59	0.019
49	0.5765					3.95E-04	+		5	32.106	-44.0	4.62	0.019
41	0.4198				0.0113		+		5	31.986	-43.8	4.86	0.017
29	1.0680			-0.0105	0.0104	5.37E-04			6	33.951	-43.6	4.97	0.016
11	-1.3100		3.54E-03		0.0123				5	31.923	-43.6	4.98	0.016
23	-1.6930		6.11E-03	-0.0109		8.76E-04			6	33.903	-43.5	5.07	0.015
77	2.3600			-0.0118	0.0132			-0.0581	6	33.833	-43.4	5.21	0.014
85	2.4600			-0.0153		5.50E-04		-0.0423	6	33.717	-43.2	5.44	0.013

[1] R code: fullmod <- lmer(sqrt(small_circles) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): '1 | site'. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 10A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by labyrinths on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
33	0.0213						+		4	80.887	-145.6	0.00	0.215
17	-0.0307					2.46E-04			4	80.217	-144.3	1.34	0.110
5	-0.2410			3.71E-03					4	80.172	-144.2	1.43	0.105
49	-0.0058					1.16E-04	+		5	81.422	-142.6	2.97	0.049
34	0.0890	-3.06E-03					+		5	81.315	-142.4	3.19	0.044
41	-0.0439				2.96E-03		+		5	81.261	-142.3	3.29	0.041
37	-0.0778			1.38E-03			+		5	81.117	-142.0	3.58	0.036
35	0.3264		-6.35E-04				+		5	80.935	-141.7	3.95	0.030
97	0.0783						+	-0.0029	5	80.929	-141.6	3.96	0.030
21	-0.1448			1.92E-03		1.36E-04			5	80.576	-140.9	4.66	0.021
65	0.3996							-0.0190	4	78.439	-140.7	4.90	0.019
25	0.0018				-1.69E-03	2.63E-04			5	80.314	-140.4	5.19	0.016
18	-0.0623	1.26E-03				2.60E-04			5	80.273	-140.3	5.27	0.015
69	-0.4463			4.67E-03				0.0070	5	80.272	-140.3	5.27	0.015
81	-0.0962					2.73E-04		0.0031	5	80.240	-140.3	5.34	0.015
7	0.1066		-6.80E-04	3.41E-03					5	80.223	-140.2	5.37	0.015
19	0.0333		-1.31E-04			2.42E-04			5	80.219	-140.2	5.38	0.015
6	-0.2366	-1.37E-04		3.69E-03					5	80.172	-140.1	5.47	0.014
13	-0.2404			3.71E-03	-4.44E-05				5	80.172	-140.1	5.47	0.014
3	1.8160		-3.71E-03						4	77.653	-139.1	6.47	0.008

[1] R code: fullmod <- lmer(sqrt(labyrinth) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): '1 | site'. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 11A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by whitish spots on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
33	0.5761						+		4	37.746	-59.3	0.00	0.095
53	-0.1668			0.0128		-7.64E-04	+		6	41.535	-58.8	0.51	0.074
6	-1.2900	0.0256		0.0182					5	39.219	-58.2	1.10	0.055
38	-0.5741	0.0191		0.0101			+		6	41.060	-57.9	1.46	0.046
34	0.3489	0.0103					+		5	38.915	-57.6	1.71	0.040
35	-2.3950		0.0062				+		5	38.909	-57.6	1.72	0.040
113	1.8300					-7.12E-04	+	-5.61E-02	6	40.803	-57.3	1.97	0.035
41	0.7922				-0.0098		+		5	38.737	-57.3	2.06	0.034
49	0.6491					-3.14E-04	+		5	38.716	-57.2	2.10	0.033
54	-0.6414	0.0129		0.0148		-5.65E-04	+		7	42.736	-57.2	2.15	0.032
13	-0.1323			0.0176	-0.0248				5	38.565	-56.9	2.41	0.029
45	0.3077			0.0092	-0.0179		+		6	40.559	-56.9	2.46	0.028
40	-3.9400	0.0173	0.0068	0.0118			+		7	42.467	-56.6	2.69	0.025
47	-3.6440		0.0078	0.0117	-0.0173		+		7	42.418	-56.5	2.79	0.024
61	-0.0671			0.0143	-0.0110	-5.95E-04	+		7	42.370	-56.4	2.88	0.023
37	0.3258			0.0035			+		5	38.089	-56.0	3.36	0.018
55	-2.4440		0.0047	0.0129		-6.42E-04	+		7	42.093	-55.9	3.44	0.017
8	-3.9500	0.0249	0.0052	0.0205					6	40.006	-55.8	3.57	0.016
39	-3.8020		0.0082	0.0063			+		6	39.953	-55.6	3.67	0.015
98	0.8787	0.0151					+	-3.28E-02	6	39.923	-55.6	3.73	0.015

[1] R code: fullmod <- lmer(sqrt(whitish_spots) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): ‘1 | site’. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 12A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by tubular mines on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
33	0.0029						+		4	147.572	-279.0	0.00	0.161
34	0.0426	-1.80E-03					+		5	149.079	-277.9	1.03	0.096
37	-0.0743			0.0011			+		5	149.039	-277.9	1.11	0.093
41	-0.0334				1.65E-03		+		5	148.721	-277.2	1.75	0.067
5	-0.1554			0.0022					4	146.514	-276.9	2.12	0.056
49	-0.0066					4.10E-05	+		5	148.291	-276.4	2.61	0.044
36	-0.3730	-2.29E-03	8.88E-04				+		6	149.955	-275.7	3.32	0.031
101	-0.2316			0.0018			+	0.0054	6	149.851	-275.4	3.53	0.028
39	-0.4901		8.28E-04	0.0013			+		6	149.844	-275.4	3.54	0.027
35	-0.1922		4.06E-04				+		5	147.774	-275.3	3.64	0.026
97	0.0248						+	-0.0011	5	147.632	-275.0	3.92	0.023
38	-0.0208	-1.22E-03		0.0007			+		6	149.569	-274.9	4.09	0.021
42	0.2352	-6.01E-03			-4.51E-03		+		6	149.466	-274.7	4.30	0.019
51	-0.5151		1.05E-03			6.71E-05	+		6	149.377	-274.5	4.48	0.017
45	-0.0765			0.0008	9.94E-04		+		6	149.366	-274.5	4.50	0.017
69	-0.3135			0.0030				0.0055	5	147.328	-274.4	4.53	0.017
43	-0.3865		7.20E-04		1.98E-03		+		6	149.313	-274.4	4.60	0.016
98	0.0192	-1.98E-03					+	0.0014	6	149.167	-274.1	4.90	0.014
50	0.0363	-1.62E-03				1.02E-05	+		6	149.109	-274.0	5.01	0.013
53	-0.0714			0.0010		4.38E-06	+		6	149.044	-273.8	5.14	0.012

[1] R code: fullmod <- lmer(log(tubular_mine) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): ‘1 | site’. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 13A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by leaf edge galls on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	CN	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
41	0.6165				-0.0205		+		5	56.005	-91.8	0.00	0.175
34	-0.2598	0.0192					+		5	55.525	-90.8	0.96	0.108
105	1.1890				-0.0241		+	-0.0254	6	57.129	-90.0	1.79	0.071
121	1.5830				-0.0180	-0.0005	+	-0.0470	7	59.044	-89.8	2.01	0.064
114	0.8493	0.0169				-0.0005	+	-0.0486	7	58.777	-89.3	2.54	0.049
98	0.1710	0.0230					+	-0.0265	6	56.706	-89.2	2.64	0.047
57	0.5867				-0.0175	-0.0002	+		6	56.280	-88.3	3.49	0.031
45	0.5317			0.0016	-0.0219		+		6	56.100	-87.9	3.85	0.026
43	0.1273		1.00E-03		-0.0202		+		6	56.059	-87.9	3.94	0.024
42	0.7651	-0.0033			-0.0239		+		6	56.015	-87.8	4.02	0.023
17	0.3164					-0.0007			4	51.918	-87.7	4.13	0.022
50	-0.1478	0.0159				-0.0002	+		6	55.859	-87.5	4.33	0.020
85	2.6190			-0.0104		-0.0008		-0.0786	6	55.773	-87.3	4.51	0.018
38	-0.4207	0.0207		0.0018			+		6	55.633	-87.0	4.79	0.016
107	-0.2063		3.16E-03		-0.0239		+	-0.0320	7	57.610	-86.9	4.88	0.015
109	1.8500			-0.0052	-0.0221		+	-0.0426	7	57.586	-86.9	4.92	0.015
36	-0.2621	0.0192	4.77E-06				+		6	55.525	-86.8	5.00	0.014
93	2.9470			-0.0115	-0.0105	-0.0006		-0.0815	7	57.518	-86.7	5.06	0.014
81	1.0790					-0.0010		-0.0359	5	53.361	-86.5	5.29	0.012
86	2.4910	0.0097		-0.0113		-0.0007		-0.0817	7	57.345	-86.4	5.41	0.012

[1] R code: fullmod <- lmer(log(leaf_edge_gall) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): ‘1 | site’. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 14A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by haired vein galls on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
105	1.0020				-0.0146		+	-0.0288	6	74.344	-124.4	0.00	0.200
41	0.3601				-0.0108		+		5	71.767	-123.3	1.11	0.115
98	0.3880	0.0133					+	-0.0288	6	73.615	-123.0	1.46	0.096
34	-0.0855	0.0094					+		5	71.148	-122.1	2.35	0.062
45	0.1144			4.80E-03	-0.0153		+		6	73.140	-122.0	2.41	0.060
57	0.4084				-0.0156	2.46E-04	+		6	73.002	-121.7	2.68	0.052
106	1.4090	-0.0097			-0.0242		+	-0.0277	7	74.493	-120.7	3.74	0.031
121	0.9361				-0.0159	9.19E-05	+	-0.0250	7	74.479	-120.7	3.77	0.030
107	0.4507		1.24E-03		-0.0144		+	-0.0311	7	74.469	-120.6	3.79	0.030
33	0.1234						+		4	68.366	-120.6	3.87	0.029
38	-0.5169	0.0138		4.66E-03			+		6	72.372	-120.5	3.94	0.028
109	0.9410			5.05E-04	-0.0148		+	-0.0272	7	74.351	-120.4	4.03	0.027
42	1.0660	-0.0159			-0.0268		+		6	72.146	-120.0	4.40	0.022
50	-0.2293	0.0136				2.21E-04	+		6	72.105	-120.0	4.48	0.021
43	0.7325		-7.62E-04		-0.0110		+		6	71.818	-119.4	5.05	0.016
114	0.3036	0.0142				6.39E-05	+	-0.0262	7	73.679	-119.1	5.37	0.014
100	0.1661	0.0132	5.02E-04				+	-0.0297	7	73.634	-119.0	5.46	0.013
102	0.3430	0.0135		3.17E-04			+	-0.0279	7	73.617	-118.9	5.50	0.013
61	0.2223			3.26E-03	-0.0167	1.51E-04	+		7	73.480	-118.7	5.77	0.011
46	0.6163	-0.0109		4.49E-03	-0.0261		+		7	73.315	-118.3	6.10	0.009

[1] R code: fullmod <- lmer(log(haired_vein_gall) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): '1 | site'. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 15A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by pannose spots on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
41	0.5488				-0.0132		+		5	48.134	-76.1	0.0	0.173
33	0.2581						+		4	45.755	-75.3	0.7	0.121
34	0.0063	0.0114					+		5	47.636	-75.1	1.0	0.105
105	1.1650				-0.0170		+	-0.0275	6	49.116	-74.0	2.1	0.061
98	0.4427	0.0151					+	-0.0267	6	48.530	-72.8	3.3	0.034
42	1.5940	-0.0235			-0.0370		+		6	48.521	-72.8	3.3	0.034
37	0.5635			-0.0042			+		5	46.422	-72.6	3.4	0.031
57	0.5814				-0.0167	1.89E-04	+		6	48.424	-72.6	3.5	0.031
101	2.3460			-0.0133			+	-0.0583	6	48.370	-72.5	3.6	0.029
109	2.3870			-0.0093	-0.0133		+	-0.0601	7	50.317	-72.3	3.7	0.027
43	1.4860		-1.92E-03		-0.0140		+		6	48.279	-72.3	3.8	0.026
45	0.5554			-0.0001	-0.0131		+		6	48.135	-72.0	4.0	0.023
49	0.2936					-1.52E-04	+		5	46.041	-71.9	4.2	0.021
69	3.1780			-0.0217				-0.0706	5	45.951	-71.7	4.4	0.019
36	1.1770	0.0127	-2.50E-03				+		6	47.866	-71.5	4.6	0.018
97	0.3664						+	-0.0056	5	45.801	-71.4	4.7	0.017
50	-0.0852	0.0140				1.45E-04	+		6	47.803	-71.3	4.7	0.016
35	0.3217		-1.32E-04				+		5	45.756	-71.3	4.8	0.016
102	1.8730	0.0112		-0.0097			+	-0.0601	7	49.796	-71.3	4.8	0.016
38	0.0562	0.0109		-0.0005			+		6	47.644	-71.0	5.0	0.014

[1] R code: fullmod <- lmer(log(pannose_spot) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): ‘1 | site’. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Table 16A: Model selection table for model comparison[1] of microclimatic, leaf trait, and plant ontogenetic effects on herbivory caused by ovate galls on *Fagus sylvatica* along the vertical forest gradient. Displayed are the twenty best models according to the Bayesian Information Criterion (BIC). Calculations were done using the R libraries *lme4* (Bates *et al.*, 2017) and *MuMIn* (Bartoń, 2016).

#	Intercept	C/N ratio	Ctotal	Humid	Ntotal	SLA	Stage	Temp	df	logLik	BIC	Delta	Weight
1	0.0873								3	61.469	-110.8	0.00	0.202
33	0.0756						+		4	62.954	-109.7	1.07	0.118
5	-0.0718			2.10E-03					4	62.513	-108.9	1.95	0.076
21	-0.3006			6.32E-03		-3.17E-04			5	63.953	-107.7	3.12	0.043
49	0.1219					-1.99E-04	+		5	63.928	-107.6	3.17	0.042
69	-1.1250			7.08E-03				0.0358	5	63.879	-107.5	3.27	0.040
65	0.1972							-0.0058	4	61.656	-107.1	3.67	0.032
3	0.6303		-1.14E-03						4	61.614	-107.1	3.75	0.031
17	0.0750					4.28E-05			4	61.569	-107.0	3.84	0.030
9	0.1112				-1.08E-03				4	61.498	-106.8	3.99	0.028
2	0.0759	0.0005							4	61.476	-106.8	4.03	0.027
97	-0.1479						+	0.0115	5	63.340	-106.5	4.34	0.023
35	-0.6416		1.49E-03				+		5	63.127	-106.0	4.77	0.019
41	0.1159				-1.84E-03		+		5	63.041	-105.9	4.94	0.017
34	0.0416	0.0015					+		5	63.020	-105.8	4.99	0.017
37	0.0758			-2.82E-06			+		5	62.954	-105.7	5.12	0.016
13	-0.0189			2.57E-03	-4.01E-03				5	62.873	-105.5	5.28	0.014
6	-0.1915	0.0037		2.60E-03					5	62.832	-105.4	5.36	0.014
53	-0.1377			4.08E-03		-3.44E-04	+		6	64.670	-105.1	5.73	0.012
7	-0.7927		1.41E-03	2.73E-03					5	62.647	-105.1	5.73	0.012

[1] R code: fullmod <- lmer(log(ovate_gall) ~ stage + temp + humid + Ctotal + Ntotal + SLA + C/N ratio + (1|site), REML = FALSE); mod1 <- dredge(update(fullmod), rank="BIC"). Random terms (all models): '1 | site'. Different models have similar strength of evidence for ΔBIC = 0–2 and positive strength of evidence for ΔBIC = 2–6 against the model with the lowest BIC value (Kass & Raftery, 1995). The lowest BIC value implied either fewer explanatory variables, better fit, or both combined. Models are ordered with lowest BIC on top (specified by rank). Positive and negative values for the model variables indicate positive and negative effects on herbivory, respectively. For categorical variables, plus indicates significant effects. Ctotal = leaf C content; Humid = relative air humidity; Ntotal = leaf N content; SLA = specific leaf area; Stage = plant ontogenetic stage; Temp = air temperature; logLik = log-likelihood; Delta = delta-BIC; Weight = *Akaike weight*.

Appendix E

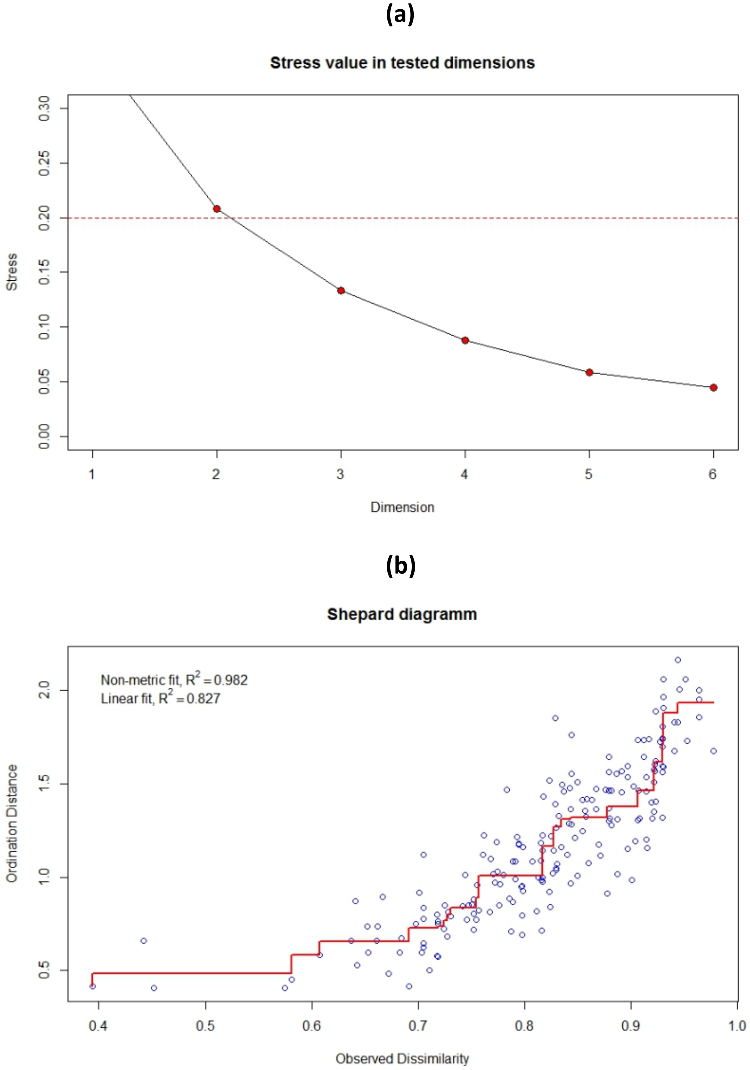

Figure 7A: Constructing the ordination of sample sites and phytodiversity (based on plant species abundances in the ground layer) in a biplot with **(a)** the diagnostic stress plot indicating 3 dimensions (first point under the dotted line) as the best dimensionality for non-metric multidimensional scaling (NMDS), and with **(b)** the Shepard diagram, showing the original pairwise distances (based on the Bray-Curtis dissimilarity) and the new distances of the ordination (based on ranks). Calculations were done with R packages *vegan* (Oksanen *et al.*, 2017) and *goeveg* (Friedmann & Schellenberg, 2017). The stress value 0.133 for the NMDS is determined with the category “usable” (stress value < 0.20) following the guidelines for acceptable stress values (Clarke, 1993).

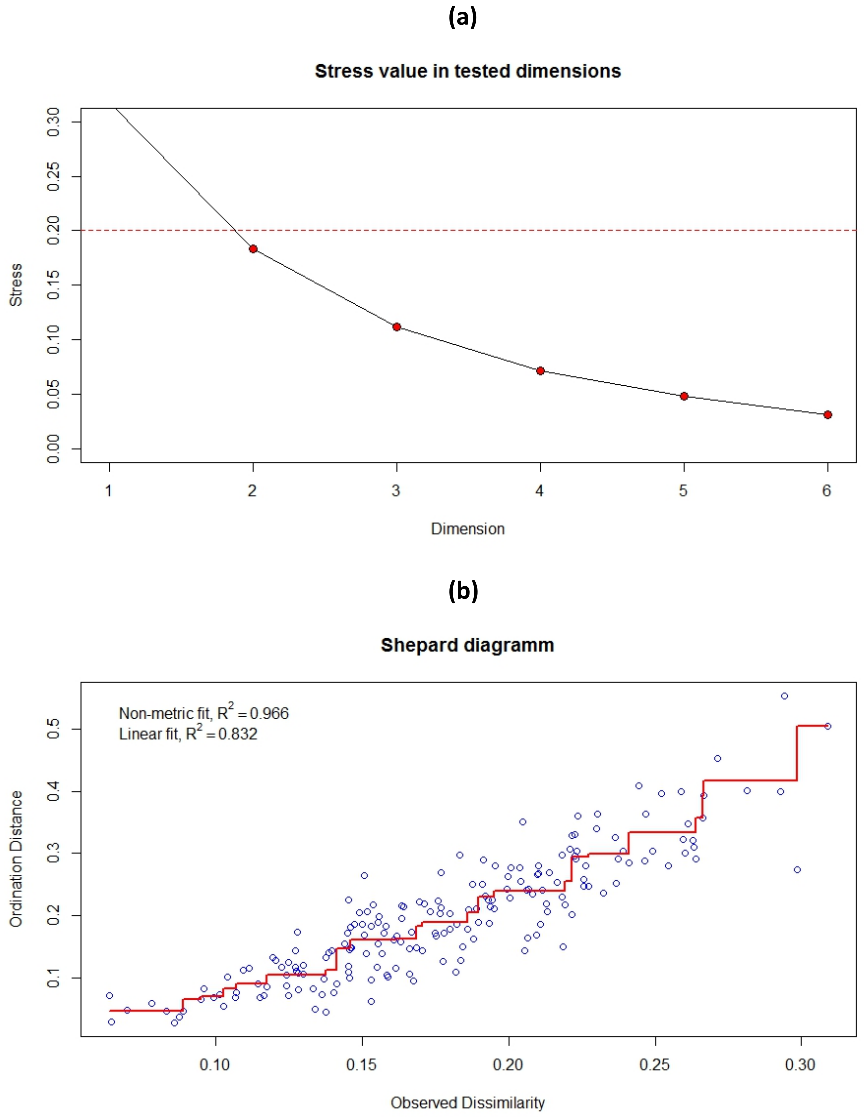

Figure 8A: Constructing the ordination of sample sites and insect diversity (based on individual abundances of insect orders) in a biplot with **(a)** the diagnostic stress plot indicating 2 dimensions (first point under the dotted line) as the best dimensionality for non-metric multidimensional scaling (NMDS), and with **(b)** the Shepard diagram, showing the original pairwise distances (based on the Bray-Curtis dissimilarity) and the new distances of the ordination (based on ranks). Calculations were done with R packages *vegan* (Oksanen *et al.*, 2017) and *goeveg* (Friedmann & Schellenberg, 2017). The stress value 0.184 for the NMDS is determined with the category “usable” (stress value < 0.20) following the guidelines for acceptable stress values (Clarke, 1993).

Table 17A: Parameters for the ordination of sample sites and **(a)** phytodiversity or **(b)** insect diversity in a biplot with non-metric multidimensional scaling (NMDS). Only significant environmental would be fitted onto the ordination as *post-hoc* correlations.

Parameter[1]	NMDS1	NMDS2	R^2	p
(a) Phytodiversity				
precipitation	0.90064	0.43456	0.1449	0.262
temperature (US)	0.09442	-0.99553	0.0767	0.518
relative air humidity (US)	0.63232	0.77470	0.1748	0.203
exposition	-0.0155	0.1294	0.0306	0.551
(b) Insect diversity				
precipitation	0.02133	0.99977	0.0598	0.577
temperature (LC)	0.30683	-0.95176	0.1580	0.223
relative air humidity (LC)	0.38396	0.92335	0.2744	0.057
exposition	0.0508	0.0014	0.1123	0.122

[1] US = understorey; LC = lower canopy.

Table 18A: The occurrence and abundance of plant species in the tree layer of all samples sites based on vegetation surveys (10x10 m plots).

Species	WB	WB	TE	TE	KBVB	KBVB	SS	SS	HGB	HGB	BB	BB	HB	HB	FK	FK	HDB	HDB	EL	EL
	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Acer platanoides								4												
A. pseudoplatanus	7						4	4						7				4	4	
Carpinus betulus					27			12										2		
Fagus sylvatica	82	52	67	67	47	72	77	67	57	47	57	57	62	57	77	57	47	47	77	62
Fraxinus excelsior	4					7	12							27					4	
Picea abies				4						7										
Pinus sylvestris					4	4														
Quercus robur		4						7										37		4

WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite; N = north exposition; S = south exposition.

Table 19A: The occurrence and abundance of plant species in the shrub layer of all samples sites based on vegetation surveys (10x10 m plots).

Species	WB	WB	TE	TE	KBVB	KBVB	SS	SS	HGB	HGB	BB	BB	HB	HB	FK	FK	HDB	HDB	EL	EL
	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Acer platanoides											R	1			1					
A. pseudoplatanus	7					57				7	27	7	7	7	1	1	4		4	R
Carpinus betulus	1	1								1							R		R	
Crataegus spec.								4												
Fagus sylvatica	67	17	52	17	17	4	12		52	77	47	77	47	32	37	7	12	7	47	57
Fraxinus excelsior											1	5				1			R	
Rubus spec.		4																		
Ulmus spec.															R					

WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite; N = north exposition; S = south exposition.

Table 20A: The occurrence and abundance of plant species in the ground layer of all samples sites based on vegetation surveys (10x10 m plots).

Species	WB N	WB S	TE N	TE S	KBVB N	KBVB S	SS N	SS S	HGB N	HGB S	BB N	BB S	HB N	HB S	FK N	FK S	HDB N	HDB S	EL N	EL S
Acer campestre								1		R							1			
A. platanoides								7	R		1				1	R	1	R	4	
A. pseudoplatanus	4			1		4	1	R	1	1	4			4	1	1	1		4	4
Aconitum spec.																	R			
Alliaria petiolata	1																			
Allium ursinum	7								1								1			
Anemone nemorosa									1	1	4						R	1		
Arctium lappa															R					
Asarum europaeum																	1	4		
Atropa belladonna	1																			
Bromus spec.												1							R	
Cardamine bulbífera														2						
C. hirsuta			1	1																
Carex distans																			4	2
C. remota													R							
C. sylvatica	4								4	7	1	1	2	2		R	R		4	
Carpinus betulus					2			12		1			R				R		4	
Circaea lutetiana	7						1				1		4							
Convallaria majalis									1							32	1	1		
Cornus sanguinea									R											
Crataegus spec.								4	R											
Digitalis purpurea		R																		
Euphorphia spec.													R			1				
Fagus sylvatica	4	4	4	4	4	4	17	17	37	7	17	7	4	7	7	7	7	7	4	4
Fragaria vesca								1	1				2			1	1			
Fraxinus excelsior	1					1	2	2	R	1	7	2		4		1	1	R	4	
Galium odoratum	22	17							1		27	4	12	37						

Table 20A: Continued.

Species	WB	WB	TE	TE	KBVB	KBVB	SS	SS	HGB	HGB	BB	BB	HB	HB	FK	FK	HDB	HDB	EL	EL
	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Galium sylvaticum	1								1				2		1	1	1			
Geranium robertianum	1																			
G. sylvaticum													2	2			R			
Glechoma hederacea												1								
Hedera helix								4	R	4						1				
Hepatica nobilis																R	1			
Hieracium spec.																R				
Hordelymus europaeus							2			R			2	2						
Hypericum perforatum													R			R			R	
Impatiens parviflora	7		1	R	1								4				7		62	
Lamiastrum galeobdolon									1		1		4	4				1		
Lathyrus vernus									R							R	R			
Lilium martagon									R	R							R			
Lonicera xylosteum								2	R											
Luzula luzuluides		1	2	4									2						2	R
Melica uniflora								2							1	7				
Mercurialis perennis	37						77	2	17	1	1						4	12		
Milium effusum									1											
Oxalis acetosella	1		2	2	1							1	7					R	4	
Phyteuma spicatum																	R			
Picea abies			R																	
Poa nemoralis	1	1											2		1		1		R	
Polygonatum multiflorum															R	R		R		
P. verticillatum																	R			
Primula elatior									R							R	1			
Quercus robur										1										
Ranunculus spec.	1																			
Rosa spec.																R				

Table 20A: Continued.

Species	WB N	WB S	TE N	TE S	KBVB N	KBVB S	SS N	SS S	HGB N	HGB S	BB N	BB S	HB N	HB S	FK N	FK S	HDB N	HDB S	EL N	EL S
Rubus spec.		10		1	1							4	R	2						
Scrophularia nodosa	1												R							
Sorbus aucuparia											R									
Stachys sylvatica	7								1		4		4	7			4		R	
Stellaria media			R																	
Tilia cordata																	R	R		
Urtica diocia																			7	
Veronica officinalis	1																			
Vicia spec.								R				1								
Vinetoxicum officinale										R										
Viola spec.								1					2							

WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite; N = north exposition; S = south exposition.

Table 21A: Abundances (percentage of individuals) of insect orders in lower canopies of all sample sites. Insect individuals were sampled with window traps.

Insects Orders	WB N	WB S	TE N	TE S	KBVB N	KBVB S	SS N	SS S	HGB N	HGB S	BB N	BB S	HB N	HB S	FK N	FK S	HDB N	HDB S	EL N	EL S
Coleoptera	13,3	13,8	10,5	12,3	27,0	25,9	17,5	18,2	14,2	9,0	18,2	8,5	11,3	13,6	14,1	40,9	32,3	39,9	12,6	18,6
Collembola	0,4	0,3	0,3	1,3	2,1	1,9	0,2	0,3	1,0	0,1	0,1	0,1	0,2	0,4	0,4	9,4	0,4	0,5	0,1	0,4
Dermaptera	0,8	1,1	0,9	2,0	1,8	6,6	0,8	0,2	0,0	0,5	0,3	0,1	1,6	0,8	1,0	3,5	2,1	0,7	0,1	1,3
Diptera	64,9	53,3	59,5	48,9	53,5	39,4	57,4	52,0	62,1	65,6	52,6	67,6	64,3	66,0	65,6	26,7	27,4	31,9	72,6	48,3
Ensifera	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2
Ephemeroptera	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,1	0,0	0,0	0,0	0,0	0,0
Hemiptera	3,9	6,8	6,8	3,1	2,9	7,1	7,4	7,8	3,2	5,2	7,2	6,5	5,5	4,2	4,1	5,1	12,9	7,4	4,9	10,2
Hymenoptera	4,1	11,9	3,5	3,1	2,8	3,5	5,6	4,9	4,1	4,3	3,0	2,6	4,0	2,7	3,4	4,3	6,6	8,0	3,5	4,2
Lepidoptera	2,5	2,6	2,8	3,7	2,0	0,9	3,0	3,4	2,8	3,0	2,8	1,8	2,9	2,3	2,3	2,7	2,1	1,6	1,0	2,5
Mecoptera	0,2	0,0	0,0	0,4	0,0	0,0	1,0	0,3	0,2	0,2	0,8	0,0	1,4	0,0	0,0	0,0	0,2	0,0	0,3	0,0
Planipennia	1,3	3,4	2,4	2,4	0,5	1,7	1,3	6,5	1,2	1,0	1,4	2,0	1,1	0,9	2,3	1,3	0,9	1,1	0,6	1,7
Psocoptera	7,0	4,5	10,7	21,6	4,9	11,8	4,6	5,5	9,7	10,0	10,8	9,7	6,6	7,5	4,3	5,1	13,9	7,1	3,5	10,3
Thysanoptera	1,6	2,2	2,5	1,1	2,5	1,2	1,2	0,9	1,6	1,0	2,8	1,1	0,9	1,6	2,6	1,1	1,3	1,8	0,8	2,3
# Traps	7	9	8	6	9	9	9	9	9	9	9	8	8	9	9	6	9	9	8	8
# Individuals (total)	828	730	746	454	854	424	929	650	507	807	879	1372	883	1132	1240	374	533	761	2121	994
# Individuals (average)	118	81	93	76	95	47	103	72	56	90	98	172	110	126	138	62	59	85	265	124

WB = Winkelberg; TE = Tiefentals Ebene; KBVB = Klingenberg/Vaaker Berg; SS = Schieferstein; HGB = Heiligenberg; BB = Bocksbühl; HB = Hubenberg; FK = Feuerkuppe; HDB = Heidelberg; EL = Eichleite; N = north exposition; S = south exposition.

Appendix F

Table 22A: Studies on herbivory caused by arthropod species on sun and shade leaves of trees and shrubs in forest ecosystems.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Basset 1991	subtropical	field	sun and shade leaves	leaf area loss, number of galls and mines	*Argyrodendron actinophyllum*	Coleoptera, Hymenoptera, Lepidoptera	leaf-chewing, leaf-mining, gall-inducing	Leaf area loss and leaf-mining are higher in sun and shade, respectively; galled leaves were distributed non-randomly.
Basset 2001	tropical	field	canopy	abundance and species richness of insect herbivores	*Pourouma bicolor*	Coleoptera, Hemiptera, Lepidoptera, Thysanoptera	leaf-chewing, sap-sucking	Species richness and abundance are higher on mature trees than on saplings.
Basset *et al.* 1992	tropical	field	shrub layer and canopy	leaf area loss, species richness	NA	NA	NA	Species-richness and density are higher in canopy; leaf damage is higher within the shrub layer.
Charles & Basset 2005	tropical	field	canopy	beetle abundance	various species	Coleoptera	leaf-chewing	Mature trees supported more and different chrysomelid species than saplings.
Coley & Barone 1996	tropical	review	understorey	NA	NA	NA	NA	Herbivory damage is greater in the understorey than in the canopy.
Dudt & Shure 1994	temperate	field (experimental design)	shade leaves	leaf area loss	*Liriodendron tulipifera*, *Cornus florida*	NA	exophag	Slow-growing, shade-tolerant species tend to have higher levels of phenolics and experience lower levels of herbivory than fast growing, shade-intolerant species; sun leaves of slow-growing species are less nutritional (more defence compounds).

Table 22A: Continued.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Forkner *et al.* 2004	temperate	field	canopy and understorey	abundance and species richness	*Quercus alba, Qercus velutina*	Lepidoptera, Hymenoptera, Phasmatoptera, Orthoptera	leaf-chewing	Herbivore densities are correlated with condensed tannins in the understorey and canopy and depend on the insect species.
Fortin & Mauffette 2002	temperate	laboratory (feeding experiment)	sun leaves	performance of insects	*Acer saccharum*	Lepidoptera	exophag	Herbivore leaf damage is more dependent on nutritional value, which is higher in sun leaves, than defense compounds.
Futuyama & Saks 1981	NA	laboratory	sun leaves	pupal weight and time to pupation	*Prunus serotina*	Lepidoptera	exophag	The difference in foliage has a pronounced effect on pupal weight and time to pupation, but no difference are evident between the species in their response to the variation in foliage.
Gossner *et al.* 2014	temperate	field	sun leaves	number of leaves with damage	*Fagus sylvatica*	NA	leaf-chewing, sap-sucking, leaf-mining, gall-inducing	Damage was generally greater in the canopy than in the understorey, in particular for chewing and scraping damage, and the occurrence of mines.
Hirao *et al.* 2009	temperate	field	sun and shade leaves	abundance by trapping	*Acer mono, Tilia japonica, and Quercus crispula*	Coleoptera, Lepidoptera	leaf-chewing	Lepidoptera and Coleoptera were more abundant in understorey and canopy, respectively.
Kamplicher & Teschner 2002	temperate	field	sun leaves and indifferent	number of galls on leaves	*Fagus sylvatica, Quercus robur, Quercus petraea*	Diptera, Hymenoptera	gall-inducing	Mikiola fagi shows a distinct vertical zonation with highest abundance in the upper canopy, while Neuroterus quercusbaccarum exhibits no vertical zonation.

Table 22A: Continued.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Karolewski *et al.* 2013	temperate	field	shade and sun leaves	leaf area loss	*Cornus sanguinea, Corylus avellana, Frangula alnus, Prunus padus, Prunus serotina, Sambucus nigra*	NA	exophag	Leaves of shrub species growing in full sun are less injured than those in the shade, except for Corylus avellana. The reason might be due to higher concentrations of defense metabolites and lower concentrations of nitrogen.
Larsson *et al.* 1986	temperate	laboratory (growth chamber)	shade leaves	leaf area loss (counting units of feeding marks)	*Salix dasyclados*	Coleoptera	leaf-chewing	The relative availability of carbohydrates for carbon-based defensive compounds might explain the different susceptibility of willow leaves when grown under the specified environments. Beetles consumed highest amount of leaf tissue on plants under low light conditions (high nitrogen and low carbon content).
Le Corff & Marquis 1999	temperate	field	sun and shade leaves, indifferent	abundance and density of herbivores	*Quercus alba, Qercus velutina*	NA	exophag, leaf-chewing	Species richness is greater in the understorey than in the canopy, and relative abundance of the main families, different feeding guilds, and most common species differed between the understorey and canopy.
Łukowski *et al.* 2015	temperate	field, laboratory (feeding experiment)	sun leaves	beetle mass, larval development	*Corylus avellana*	Coleoptera	leaf-chewing	Beetle mass is greater in beetles occupying sunlit leaves. Under laboratory conditions, larvae, pupae and beetles that were fed full-light leaves are heavier than those fed with shaded leaves, and duration of larval development is also reduced.

Table 22A: Continued.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Mairoana 1981	NA	theorie	shade	NA	*NA*	NA	NA	Hypotheses of the theory: sun plants have the energy to be more toxic and shade is a shelter for herbivores.
Medianero *et al.* 2003	tropical	field	canopy	species richness of gallers and miners	*50 species*	Coleoptera, Diptera, Hemiptera, Lepidoptera	leaf-mining, gall-inducing	The canopy of tropical forest supports a higher species richness of insect gallers and leaf miners than the understorey.
Mooney *et al.* 2009	temperate	field (experimental treatments)	sun leaves, indifferent	consumed leaf biomass, larval weight	*Lindera benzoin*	Lepidoptera	leaf-chewing	Leaves from shade plants have more protein and lower C/N ratios than from sun plants (all treatment). In control plants, larvae consumed more leaf biomass and achieved greater final weights in the sun than in the shade.
Murakami & Wada 1997	temperate	field, laboratory (feeding experiment)	sun and shade leaves	number of individuals, larvae performance	*Quercus crispula*	Lepitoptera	leaf-chewing	Seasonal change of leaf quality forces the larvae to migrate from the canopy to the forest floor. The feeding experiment shows that moth larvae do not grow up to the mature instar feeding on canopy leaves, but chaning the food material to seedling leaves after the fourth instar, larvae can survive through the fifth instar.
Muth *et al.* 2008	temperate	field	shade leaves	leaf area loss	*Lindera benzoin*	Lepidoptera	leaf-chewing	Greater natural, field herbivory is observed in shade habitats relative to high light habitats, despite similar herbivore abundances.
Neves *et al.* 2014	tropical	field	canopy	leaf area loss, number of galls and mines, species richness and abundance	*various species*	various	leaf-chewing, sap-sucking, leaf-mining	Higher leaf damage was found in the canopy, which also harbored a greater richness and abundance of chewing herbivores compared to the understory (except for leaf-miners).

Table 22A: Continued.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Nichols-Orians 1991	tropical	field	sun leaves	leaf area loss	*Inga oerstediana*	Hymenoptera	exophag	Despite higher concentrations of condensed tannins in sun foliage, leaf-cutter ants find these leaves more acceptable. The preference for sun leaves is consistent with higher concentrations of foliar nutrients.
Nielsen & Ejlersen 1977	temperate	field	sun and shade leaves	density of feeding traces	*Fagus sylvatica*	Coleoptera, Lepidoptera	leaf-chewing, leaf-mining	The leaf-chweing and leaf-mining is higher the understorey compared to the canopy. Mines of Orchestes fagi occur mainly the top of the overstorey canopy.
Niesenbaum 1992	temperate	field	shade leaves	leaf area loss, herbivore abundance	*Lindera benzoin*	NA	leaf-chewing	Herbivory was greater in shade habitats than in sun habitat but herbivore abundance did not differ across habitat types.
Niesenbaum & Kluger 2006	temperate	field, laboratory (feeding experiment)	shade and sun leaves	leaf area loss	*Lindera benzoin*	Lepidoptera	leaf-chewing	In the field, herbivores tend to remove less leaf material from plants in warm sunlit habitats. Larvae feeding at warmer temperatures consume more leaf material than in cooler conditions in the laboratory. Sun leaves seem to be more nutritious than shade leaves.
Oishi et al. 2006	temperate	laboratory (feeding experiment)	shade leaves	feeding preference, consumption and performance	*Quercus acutissima*	Lepidoptera	leaf-chewing	Larvae ingest a greater amount of lower canopy leaves to compensate for lower nitrogen contents of the foliage, resulting in having an excess of water because of the higher water content of the foliage.
Ribeiro & Basset 2007	tropical	field	sun and shade leaves	leaf area loss, number of galls	*73 tree and liana species*	various	leaf-chewing, gall-inducing	Free-feeding herbivory decreases with sampling height, while the number of living galls inversely increases, and the patterns are connected to leaf sclerophylly.

Table 22A: Continued.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Ribeiro *et al.* 2014	tropical	field	sun leaves	leaf area loss, number of galls	*NA*	NA	leaf-chewing, gall-inducing	Free-feeding herbivory decreases with sampling height, and the distribution of galls between understorey and canopy varied between study sites.
Rinker & Lowman 2004	tropical	review	NA	various	*various species*	various	various	Insects are the little things that run forests from top to bottom.
Roberts & Paul 2006	NA	review	sun leaves	various	*various species*	various	various	Interactions between the light environment and plant defence are multifaceted.
Ruhnke *et al.* 2009	temperate	field, laboratory (feeding experiment)	sun and shade leaves	leaf area loss, larval performance	*Acer pseudoplatanus, Fraxinus excelsior, Tilia cordata, Quercus robur*	Lepidoptera	leaf-chewing	Within host individuals, differences in herbivory between the upper and lower crown layer varied in direction and magnitude depending on tree species. In feeding experiments, herbivore performance also varied among and within tree individuals.
Thomas *et al.* 2010	temperate	field	sun and shade leaves	leaf area loss, leaf damage, number of galls	*Acer saccharum*	Acarina, Diptera, Hemiptera, Lepidoptera	leaf-rolling, leaf-skeletonizing, leaf-chewing, sap-sucking, gall-inducing	Damage types attributable to herbivores active on leaf surfaces, including leaf-skeletonizers, leaf-chewers, and sap-suckers show decreases with tree size, and with increasing height in the canopy. In contrast, leaf damage from the gall-forming arthropod increases markedly with tree size.

Table 22A: Continued.

Paper/ book chapter	Climate	Study type	Higher herbivory	Herbivory measurement	Host plant	Arthropod order	Herbivore feeding guild	Main result
Yamasaki & Kikuzawa 2003	temperate	field	shade leaves	leaf area loss	*Fagus crenata*	NA	leaf-chewing	Leaf mass per area, carbon concentration, C/N ratio, concentration of total phenolics, and condensed tannin concentration are higher in leaves under high light intensity compared to leaves under low light. The nitrogen concentration of leaves decreases as light availability increases. Within-tree variation in light availability affects the consumption of leaves by insect herbivores through temporal changes in leaf characteristics.
Żmuda *et al.* 2008	temperate	field	shade and sun leaves	leaf area loss	*Cornus sanguinea, Corylus avellana, Frangula alnus, Prunus padus, P. serotina, Sambucus nigra*	NA	leaf-chewing	Except for C. avellana, leaves of plants exposed to full sun were less affected by leaf-chewing insects than leaves from plants grown in low light.

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