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ARTICLE

Reduction of invertebrate herbivory by land use is only partly explained by changes in plant and insect characteristics

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Abstract

Invertebrate herbivory is a crucial process contributing to the cycling of nutrients and energy in terrestrial ecosystems. While the function of herbivory can decrease with land-use intensification, the underlying mechanisms remain unclear. We hypothesize that land-use intensification impacts invertebrate leaf herbivory rates mainly through changes in characteristics of plants and insect herbivores. We investigated herbivory rates (i.e., damaged leaf area) on the most abundant plant species in forests and grasslands and along land-use intensity gradients on 297 plots in three regions of Germany. To evaluate the contribution of shifts in plant community composition, we quantified herbivory rates at plant species level and aggregated at plant community level. We analyzed pathways linking land-use intensity, plant and insect herbivore characteristics, and herbivory rates. Herbivory rates at plant species and community level decreased with increasing land-use intensity in forests and grasslands. Path analysis revealed strong direct links between land-use intensity and herbivory rates. Particularly at the plant community level, differences in plant and herbivore composition also contributed to changes in herbivory rates along land-use intensity gradients. In forests, high land-use intensity was characterized by a larger proportion of coniferous trees, which was linked to reduced herbivory rates. In grasslands, changes in the proportion of grasses, plant fiber content, as well as the taxonomic composition of herbivore assemblages contributed to reduced herbivory rates. Our study highlights the potential of land-use intensification to impair ecosystem functioning across ecosystems via shifts in plant and herbivore characteristics. De-intensifying land use in grasslands and reducing the share of coniferous trees in temperate forests can help to restore ecosystem functionality in these systems.

KEYWORDS
abundance, composition, diversity, functional traits, herbivorous insects, invertebrate herbivory, land-use intensity, managed grasslands, structural equation modeling, temperate forests

INTRODUCTION

Invertebrate herbivory is a crucial process in terrestrial ecosystems. It stands at the base of most food webs, ensuring the cycling of energy and nutrients from producers to higher levels of consumers and back to producers (Belovsky & Slade, 2000; Price, 2002). Thus, ecosystems that show high herbivory levels are generally considered functioning ecosystems, with the exception being outbreak situations in which herbivory may reduce the functionality of a system, particularly from the perspective of provisioning services (e.g., Schowalter, 2012). Herbivory rates, which are normally quantified with measures related to the proportion of primary production that is consumed by herbivores (e.g., percentage of leaf area consumed), are known to vary greatly among ecosystems (Schowalter, 2011) and are affected by different abiotic (e.g., temperature) and biotic factors (e.g., plant species richness and composition) (Jactel & Brockerhoff, 2007; Lemoine et al., 2014). Biotic factors include complex interactions between host plants and herbivores, such that herbivory rates might ultimately depend on the composition, abundance, and diversity of both plants and herbivores.

Different pathways may link characteristics of plants, plant communities, herbivore assemblages, and herbivory rates. At foremost, different plant traits have been recognized that determine nutritional quality or palatability to herbivores. These include the content of nutrients essential to insect herbivores such as nitrogen (Loranger et al., 2012) and a variety of chemical plant defense components (Bennett & Wallsgrove, 1994). Furthermore, structural characteristics such as leaf dry matter or silica contents (Castagneyrol et al., 2019; Hartley & DeGabriel, 2016) are part of the plant's defense strategies against herbivores. Besides these characteristics, which link the herbivory of a plant population or species to its inherent characteristics, herbivory of focal plants can be decreased or increased by characteristics of neighboring plants as described by the concepts of associational resistance and associational susceptibility (Barbosa et al., 2009; Hambäck et al., 2014). These effects are often mechanistically mediated by changes in herbivore assemblages. For example, Root (1973) proposed that the load of specialist herbivores on a certain plant species increases with its abundance, resulting in higher herbivory rates on this plant species (resource concentration hypothesis) (e.g., Unsicker et al., 2006). In general, the evidence for associational resistance or associational susceptibility from a variety of systems points to the high context-specificity of the relationships among plants, herbivores, and herbivory rates (e.g., Haase et al., 2015; Sobek et al., 2009). These may be determined by changes in the composition and abundance of certain plants, as well as by changes in plant diversity. Similarly, changes in the composition, abundance, and diversity of herbivore assemblages may be related to herbivory rates (e.g., Baskett & Schemske, 2018; Deraison et al., 2015). Given the crucial role of plants in driving herbivory rates, directly or indirectly through changes in the herbivore assemblage, characteristics of focal plants and the plant community are expected to be central in determining the rate of invertebrate herbivory.

Plant communities and insect herbivore assemblages are generally affected by human land use, with potential consequences for ecosystem functions such as nutrient cycling (Soliveres et al., 2016). For example, land-use intensification in grasslands can result in a decrease of plant diversity as well as insect herbivore abundance and diversity (Allan et al., 2014; Chisté et al., 2016; Di Giulio et al., 2001; Mangels et al., 2017), but how it can in turn impact herbivory rates remains unclear. Most studies showed negative effects of intensive land use on invertebrate herbivory in a variety of ecosystems (Ambarlı et al., 2021; Gossner, Weisser, & Meyer, 2014; Mangels et al., 2015; Njovu et al., 2019; Potapov et al., 2019), but others found no or even positive effects (Gossner, Pašalić, et al., 2014; Leidinger et al., 2017; Morante-Filho et al., 2016). There are several potential reasons for these inconsistencies. First, different land-use modes in different ecosystems (e.g., grazing vs. mowing in grasslands) might affect herbivory differently. Second, studies investigating herbivory rates at the community level might provide very different results compared to those investigating herbivory rates of single plant species (Haase et al., 2015). Because herbivore assemblages and herbivory rates differ greatly among plant lineages and species (Turcotte et al., 2014), differences in the composition of the plant community (e.g., proportion of grasses) along land-use intensity gradients may explain differences in herbivory rates (Ambarlı et al., 2021; Gossner, Weisser, & Meyer, 2014; Leidinger et al., 2017; Morante-Filho et al., 2016; Njovu et al., 2019). Such land-use effects would not be reflected in herbivory rates at the level of single plant species. Finally, there are several additional pathways, through which herbivory might be affected by land use (Figure 1). Composition, abundance, and diversity of both plants and herbivores can change along land-use intensity gradients (Chisté et al., 2016; Di Giulio et al., 2001; Mangels et al., 2017; Pfestorf et al., 2013; Socher et al., 2012), and changes in plant characteristics can further act on herbivore assemblages (Borer et al., 2012; Haddad et al., 2001, 2009; Knops et al., 1999; Knuff, Staab, et al., 2019; Schaffers et al., 2008; Scherber et al., 2010; Siemann, 1998; Simons et al., 2014), which in turn will all potentially affect herbivory rates. At the same time, land-use intensity can alter top-down forces that act on herbivore assemblages by changing the abundance and composition of predators and parasites or the abiotic conditions that affect predation or parasitism rates (Meyer et al., 2019). These changes in top-down control might result in changes in the herbivore assemblages, consequently altering herbivory rates along land-use intensity gradients. Besides these indirect pathways through plant and herbivore characteristics, intensive land use may alter abiotic conditions such as microclimate, for example temperature through changes of structural characteristics of the plant community such as more open canopies in managed forests (Thom et al., 2020), which in turn may affect herbivory rates more directly (Ambarlı et al., 2021; Lemoine et al., 2014; Valdés-Correcher et al., 2021; Zvereva & Kozlov, 2006). A comprehensive assessment of herbivory covering different ecosystems and aggregation levels (plant community or species level) and including an evaluation of the role of changes in plant and herbivore characteristics is necessary to understand how and why herbivory rates change along land-use intensity gradients.

Quantifications of plant and herbivore composition, abundance, and diversity solely based on taxonomic indices may limit the conclusions about the relationships between the interacting trophic levels and herbivory rates. Quantifications involving functional traits of either plants or herbivores, which are related to herbivory, are expected to provide more mechanistic insights. For example, leaf traits related to leaf palatability such as specific leaf area (SLA, also see glossary in Appendix S1: Table S1) or leaf dry matter content (LDMC) have repeatedly been linked to herbivory rates (Castagneyrol et al., 2019; Descombes et al., 2017; Poorter et al., 2004). Also, plant biomass has been proposed to be more important in determining herbivory rates compared to plant densities based on the number of individuals (Barbosa et al., 2009). Similarly, herbivore biomass could be a better determinant of herbivory rates than herbivore abundance expressed in numbers of individuals, because metabolic rate scales with body mass (Brown et al., 2004). Furthermore, functional traits can determine species responses to environmental perturbations such as filtering imposed by land use (Lavorel & Garnier, 2002). High grassland land-use intensity for instance has repeatedly been shown to filter for smaller insects (Neff et al., 2019; Rader et al., 2014), but larger, fast-growing plants (Busch et al., 2019; Garnier et al., 2018). Thus, causal pathways relating land-use intensity and herbivory rates should not only account for differences in taxonomic characteristics of plants and herbivores, but particularly for differences in functional characteristics at both trophic levels (Reiss et al., 2009).

Here, we studied invertebrate herbivory rates of the most abundant plants on 297 plots in two important

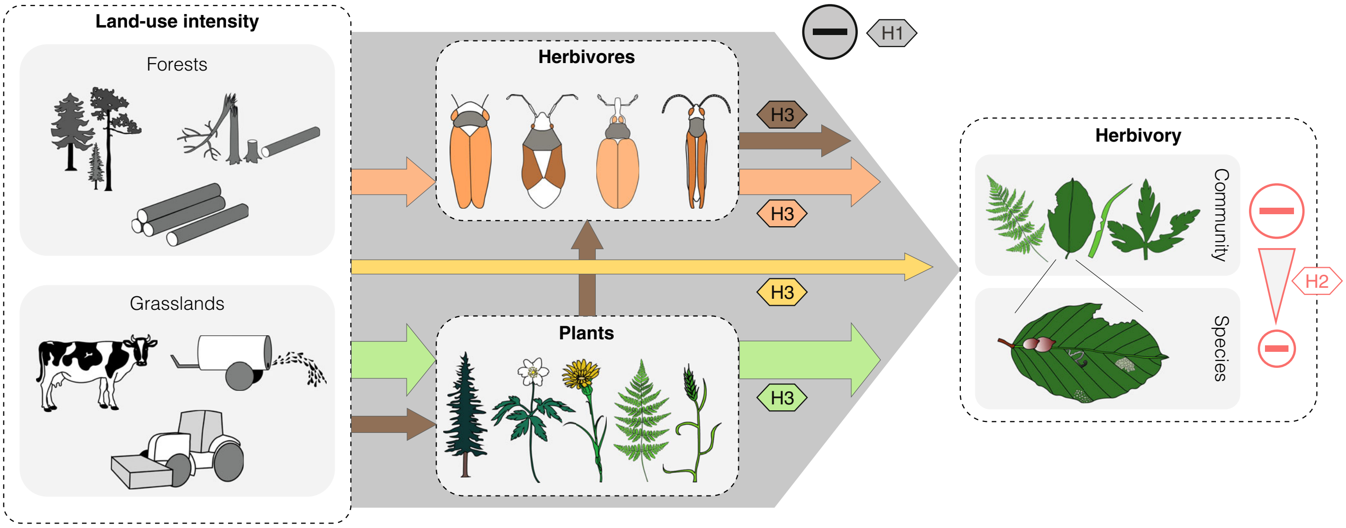

FIGURE 1 Schematic illustration of the study system and the hypotheses (hexagons). Land-use intensity in the two study systems is determined by different land-use components. Forests: proportion of tree species that are not part of the natural community, that is, conifers (*Inonat*), proportion of harvested wood volume (*Iharv*), and proportion of deadwood with saw cuts (*Idwcut*); Grasslands: grazing, mowing, and fertilization intensities. Herbivory rates were recorded on the most abundant plant species of each plot, representing different plant functional groups (trees, geophytes, forbs, ferns, grasses) and analyzed at the level of plant communities as well as at level of plant species. Our hypotheses were: (H1) Increasing land-use intensity reduces herbivory rates (without considering underlying mechanisms). (H2) The reduction in herbivory rates with increasing land-use intensity at the species level is less pronounced than at the community level. This is because plant community composition contributes disproportionally to lower community-level herbivory rates. (H3) When including plant and herbivore characteristics in the analyses, which allowed us to analyze pathways relating land-use intensity and herbivory either directly or indirectly, indirect pathways through plant characteristics will be the strongest (indicated by arrow widths). Indirect pathways involving herbivore characteristics may be next strongest. Indirect pathways may involve only plant characteristics (composition, abundance, diversity; green arrows), only insect herbivore characteristics (composition, abundance, diversity; orange arrows) or both through bottom-up control of herbivore assemblages by plants (brown arrows). Indirect pathways may be stronger than direct pathways (yellow arrows). Illustrations by Felix Neff.

temperate terrestrial ecosystems (forests, permanent grasslands). Study plots covered gradients of land-use intensities, which were made up by different land-use components. In grasslands, these included the intensities of grazing, mowing and fertilization, whereas in forests, land-use intensity was described in terms of tree species composition, amount of harvested timber and deadwood origin (natural or anthropogenic). We compared differences in land-use effects on herbivory rates aggregated at the plant community level and at the plant species level. We distinguished damage types in herbivory assessments, as different herbivore groups, that vary in degree of specialization, cause different types of damage. For example, gall inducers are generally highly specialized, whereas generalist feeders are common among herbivores causing chewing damage (Forister et al., 2015). Thus, we conducted separate analyses for the different damage types to evaluate the generality of our results. In addition, we comprehensively sampled plants and insect herbivores to quantify their taxonomic and functional composition, abundance, and diversity, which may link land-use intensity and herbivory rates through indirect pathways (Figure 1). We addressed the following hypotheses (Figure 1):

> **Hypothesis 1 (H1).** Invertebrate herbivory rates across different damage types decrease with increasing land-use intensity in both forests and grasslands, as would be in line with the majority of findings from previous studies.
>
> **Hypothesis 2 (H2).** Relationships between land-use intensity and herbivory rates are less pronounced at the level of plant species compared to the level of aggregated plant communities due to the important role of changes in plant community composition along land-use intensity gradients.
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> **Hypothesis 3 (H3).** Given the prevailing evidence for associational resistance and susceptibility, indirect pathways involving taxonomic and functional characteristics of plant composition, abundance, and diversity explain most of

the relationships between land-use intensity and herbivory rates, seconded by indirect pathways involving the taxonomic and functional characteristics of insect herbivore composition, abundance, and diversity.

METHODS

Study system and land-use intensity

This study was performed within the Biodiversity Exploratories framework (Fischer et al., 2010), comprising field sites in three regions of Germany. The UNESCO Biosphere Reserve Schwäbische Alb (*ALB*, also see glossary in Appendix S1: Table S1) is a calcareous mountain range in south-western Germany of medium elevation (48°20′28″–48°32′02″ N, 9°10′49″–09°35′54″ E; 462–858 m above sea level [asl]). The Hainich-Dün region (*HAI*), comprising the Hainich National Park and its surroundings, is an undulating landscape located in central Germany (50°56′14″–51°22′43″ N, 10°10′24″–10°46′45″ E; 285–550 m asl). The UNESCO Biosphere Reserve Schorfheide-Chorin (*SCH*) is a post-glacial moraine landscape including many wetlands in the lowlands of northern Germany (52°47′25″–53°13′26″ N, 13°23′27″–14°08′53″ E; 10–140 m asl). In each region, 50 plots in both forests (100 m × 100 m) and permanent grasslands (50 m × 50 m) were selected from an original set of 500 grid plots each, based on information on land-use intensity, vegetation, and soil characteristics, using stratified random sampling to ensure that study plots covered the full gradient of occurring land-use intensities (see Fischer et al., 2010 for details). Plots were established within larger management units. Because 2 grassland plots and 1 forest plot had to be excluded from all analyses due to missing data, a total of 297 plots were included in this study.

Forests included privately as well as publicly owned forests, which were managed for different purposes including wood production or biodiversity promotion and conservation. Thus, they covered a gradient that ranged from unmanaged forests with European beech (*Fagus sylvatica*) as main tree species over beech and oak (*Quercus* sp., only *SCH*) forests managed at different intensities to intensively managed coniferous forest. The main conifer species was Norway spruce (*Picea abies*) in *ALB* and *HAI* and Scots pine (*Pinus sylvestris*) in *SCH*. Land-use intensity in forests was quantified based on a plot-based inventory of living trees carried out between 2015 and 2016 and on an inventory of stumps and deadwood carried out in 2017–2018. From those, three basic metrics were compiled: Proportion of harvested tree volume (*Iharv*), volume proportion of tree species that were not part of the natural forest community (*Inonat*, i.e., largely represents the share of the main conifer species [*P. abies*, *P. sylvestris*] in the tree community), and proportion of deadwood volume with saw cuts as an indicator for deadwood of anthropogenic origin (*Idwcut*). Each metric ranges between 0 and 1, from no apparent management to high management intensity. *Iharv* was correlated with *Idwcut* ($r = 0.62$, $p = 4.18\text{e}{-17}$), while *Idwcut* was weakly correlated with *Inonat* ($r = 0.19$, $p = 0.023$). Combined forest land-use intensity (*ForMI*) was defined as the sum of the three component metrics. Details on methods and metrics are given in Kahl and Bauhus (2014).

The studied grasslands were all permanent grasslands under management by local farmers. They included meadows (regularly mown for hay or silage production), pastures (regularly grazed by livestock), and mown pastures (regularly mown and grazed to varying degrees). Land-use intensity was quantified in terms of mowing frequency, fertilization intensity, and grazing duration and intensity, which were recorded annually for each plot with standardized questionnaires for farmers (Fischer et al., 2010; Vogt et al., 2019). In these grasslands, pesticides are if ever extremely rarely applied, which is why pesticide application was not included in the quantification of land-use intensity. Land-use intensity values from the year of the herbivory assessment and from the previous year were used for analyses. For each component, values were averaged across years and standardized relative to their overall means. Different management components could occur concurrently. Mowing frequency was positively correlated with fertilization intensity ($r = 0.56$, $p = 6.45\text{e}{-14}$) and negatively correlated with grazing intensity ($r = -0.37$, $p = 3.05\text{e}{-06}$), while grazing intensity was slightly negatively correlated with fertilization intensity ($r = -0.17$, $p = 0.039$). Combined grassland land-use intensity (*LUI*) was defined as the square-root transformed sum of the three management components (Blüthgen et al., 2012).

Herbivory assessment

Based on plant survey data from the year prior to the sampling campaigns, the 10 most abundant plant species of each plot (hereafter "focal plant species") based on percent cover were selected (8 for *SCH* forests due to lower average plant species richness). Percent cover was estimated on a subplot of 4 m × 4 m in grasslands and 20 m × 20 m in forests (Boch et al., 2013; Socher et al., 2012 for details). In grasslands, eight individuals of each focal plant species were collected along the outer borders of the 50 m × 50 m plots to cover (spatial) variation in herbivory rates within plots. Here and in forests, collection within plot borders was avoided to not disturb ongoing surveys from other projects in the same plots. Because herbivores were also sampled along transects at the plot boundaries (grasslands) or in the outer corners of the plots (forests), these two ecosystem components could be better brought together. In forests, leaves of herb layer plants and of tree seedlings and saplings in the shrub layer were collected from a random set of individuals along the outer borders of the 100 m × 100 m plots. Leaves from the tree layer were collected using elongated lopping shears (maximum height: 6 m) to cut branches from, whenever possible, at least three trees per species. When individuals of tree species were present in the shrub and the tree layer, leaves were collected from both layers in amounts approximately representing the relative distribution of the species among the layers in terms of cover. For stand-forming pine trees in *SCH*, the lower branches could not be reached using the elongated lopping shears on several plots. Thus, branches were collected using shooting or climbing for those specific plots. When a species could not be found along the plot borders, this species was replaced by the next most abundant species on the species list. Field sampling took place before the first mowing and major grazing event in grasslands (May 2017 in *ALB*, May 2018 in *HAI*, and *SCH*). In forests, a spring sampling campaign (April 2017 in *ALB*, but April 2018 in *HAI* and *SCH* for logistic reasons) covered the early sprouting understory species that might not be available later in the season due to their phenology, and a summer campaign (June–August 2017 in all three regions) covered the remaining focal plant species. All plant material was collected in plastic bags containing a moist cloth to prevent the leaves from drying out and transferred to a fridge until further processing.

Most leaves (~95%) were processed within 7 days after sampling. Twelve to 200 randomly picked leaves were processed from each of the 10 (8 in *SCH*) focal plant species per forest plot (fewer leaves for species with large and/or composite leaves to optimize effort; Appendix S1: Table S2 for details). In grasslands, 3–10 randomly picked leaves per individual were processed, resulting in a total of 24 to 80 leaves per focal plant species and plot (depending on plant species, Appendix S1: Table S3 for details). The area of each leaf was measured with a LI-COR area meter (LI-3000C, Lincoln [NE], USA). For coniferous trees (*Abies alba*, *P. abies*, *P. sylvestris*), sets of 10 needles were measured together and average values were taken for single leaf area. For narrow-leaved grass species (*Deschampsia flexuosa*, *Festuca ovina* agg., *Festuca rubra* agg.), the area meter was unreliable and leaf length was measured using a ruler. Additionally, leaf width was determined for a subset of leaves for each species and region. Following Kemp (1960), leaf area A was then estimated for these leaves with $A = 0.905 \times L \times \overline{W}$, where L is measured leaf length and $\overline{W}$ is the mean leaf width for a species and region. Following Gossner, Weisser, and Meyer (2014), herbivory was assessed visually using a series of circular and square templates ranging in size from 1 to 500 mm^2. The following damage types were distinguished: Chewing, scraping (scraping with epidermis left, scraping without epidermis left), sucking, mines, galls (including tuft-building and leaf-rolling gall mites), and leaf rolling. Herbivory rate per leaf was calculated as the proportion of herbivory-affected leaf area compared to the corrected total area of the leaf. The latter comprised the sum of measured leaf area and estimated area lost to the damage types chewing, scraping without epidermis left, and leafroller. From those leaf-level herbivory rates, we calculated species-level herbivory as the mean herbivory rates per focal plant species and plot. To determine community-level herbivory rates per plot, we used plant cover values from the vegetation surveys of the sampling years and from tree inventories (forests) (see section on *Plant metrics*). Species-level herbivory rates were weighted by the focal species' relative contribution to the total cover of all focal plants to calculate community-level herbivory rates per plot.

Composition, abundance, and diversity metrics

To analyze effect pathways linking land-use intensity, plants, insect herbivores, and herbivory rates, a set of metrics was used to describe plant and herbivore composition, abundance, and diversity. These involved taxonomic metrics (i.e., solely based on taxon identities) as well as functional metrics (i.e., involving functional traits). Different aggregation levels were used for all metrics. To analyze community-level herbivory rates, metrics were determined at plot level. For species-level herbivory rates, metrics were determined for each focal plant species and plot. An overview of all plant and herbivore metrics is given below and in Appendix S1: Tables S4–S7.

The calculation of the metrics and the statistical analyses were performed in R v. 3.5.2 (R Core Team, 2018).

Plant metrics

For the characterization of plant composition, abundance, and diversity, we used data from vegetation surveys in both systems and from tree inventories in forests. In forests, the cover of vascular plants up to 5 m height was estimated in subplots within each plot (20 m × 20 m) in spring and summer 2017 (Boch et al., 2013 for details).

Because tree species composition was poorly covered by surveys on these subplots, we used additional data from a tree inventory on large trees, which was carried out between 2014 and 2018 on the whole plot (100 m × 100 m) (Schall et al., 2018), and from an inventory of tree regeneration, which was carried out in 25 circles of 1 m radius (trees smaller than 1.3 m) and 2.5 m radius (trees higher than 1.3 m) between 2014 and 2016. Cover of trees higher than 5 m was determined from crown projection area, which was estimated from the recorded diameter at breast height through allometric equations (Schmitz et al., 2008). Cover for all trees was standardized to a sum of 100% at the plot level and then corrected for canopy cover (estimated from airborne laser scan data [LiDAR]). Vegetation survey and tree inventory data were eventually combined for each plot and plant species by taking the maximum observed cover value across the different layers. In grasslands, the cover of all vascular plants was estimated on a subplot (4 m × 4 m) in the year of the respective herbivory assessment (Socher et al., 2012). Subplot size in each system was chosen to cover small-scale variabilities in plant communities.

From plant cover data, different metrics were calculated to characterize plant composition, abundance, and diversity taxonomically (Appendix S1: Tables S4 and S6):

1. Community-level composition was described by the first three axes from principal coordinate analysis (PCoA), which was conducted on Bray–Curtis dissimilarities obtained from complete communities through the package “ecodist” (Goslee & Urban, 2019) (metrics Com_{Tax} *axis1*, Com_{Tax} *axis2*, Com_{Tax} *axis3*). No species-level taxonomic metric was included in the models (except for species identity as a random variable).
2. To quantify community-level abundance, we used total cover of all recorded plants (Abu_{Tax} *cover*). Species-level abundance was described by the relative cover value of the focal species (Abu_{Tax} *cover*).
3. Community-level diversity was described with Hill numbers of orders 0, 1, and 2, which are increasingly sensitive to species abundances in determining diversity (Chao et al., 2014), through the package “hillR” (Li, 2018) ($Div_{Tax}\ q = 0$, $Div_{Tax}\ q = 1$, $Div_{Tax}\ q = 2$). In species-level analyses, dominance of the focal plant species, which determines associational resistance or susceptibility, was represented by abundance metrics (cover, biomass). Thus, diversity metrics were not included in species-level analyses.

Additional data on functional traits were used to characterize plant composition, abundance, and diversity functionally. Two leaf traits that are linked to leaf palatability and have repeatedly been shown to be associated with herbivory rates are SLA and LDMC (Castagneyrol et al., 2019). Along with the herbivory assessment, these functional traits were determined for each focal plant species and plot from measurement replicated at the level of individuals (grasslands) or of bundles of randomly assembled three to five leaves (forests, see Appendix S1: Table S2 for details). We measured total leaf area (see section on *Herbivory assessment*), fresh weight as well as dry weight after leaves had been dried at 80°C for at least 48 h. These were used to determine SLA (total area divided by dry weight) and LDMC (dry weight divided by fresh weight). Furthermore, tissue contents of various elements (e.g., nitrogen) or organic structures (e.g., lignin) have been related to herbivory rates (Loranger et al., 2012). Thus, we included average concentrations of N, P, Ca, Mg, lignin, and primary fiber (cellulose and hemicellulose; Loranger et al., 2012), which were measured from bulk plant biomass from the grassland plots in the year of the herbivory assessment (Kleinebecker et al., 2011 for details). These data were only included in the grassland community-level analyses.

The following metrics were used to characterize plant composition, abundance, and diversity functionally (Appendix S1: Tables S4 and S6):

1. Firstly, community composition in terms of plant functional groups (grasses, forbs, legumes [only grasslands], trees, geophytes, ferns [all three only forests]) was used. We used the cover-weighted relative share of different plant functional groups and the plant functional group of the focal species (two-level factor) for the species-level composition (Com_{Fun} *grass*; Com_{Fun} *legume* [only grasslands]; Com_{Fun} *forb*, Com_{Fun} *tree*, Com_{Fun} *geophyte* [all three only forests]). Because most plant functional traits were only available for the focal plant species per plot, relative shares of functional groups were also calculated for the subset of focal plant species to increase comparability. Secondly, measured functional traits were used to describe plant functional composition. Based on mean SLA and LDMC measurements and plant cover values per focal plant species and plot, community-weighted means among the focal plant species were determined for both functional traits using the package “FD” (Laliberté et al., 2014), which were then included as metrics for functional community-level composition (Com_{Fun} *LDMC*, Com_{Fun} *SLA*). In grasslands, we additionally included average nutrient concentrations of bulk biomass to describe functional community-level composition (Com_{Fun} *N*, Com_{Fun} *P*, Com_{Fun} *Ca*, Com_{Fun} *Mg*, Com_{Fun} *lignin*, Com_{Fun} *prim. fiber*).

Functional species-level composition was described by mean SLA and LDMC per focal plant species and plot (*Com_{Fun} LDMC*, *Com_{Fun} SLA*).

2. Functional abundance was described through biomass (*Abu_{Fun} biomass*), which was estimated using a set of different methods. In grasslands, community-level *Abu_{Fun} biomass* was measured from dried aboveground biomass, which was collected on eight fenced subplots (50 cm × 50 cm each) from all plots in spring 2018, and species-level *Abu_{Fun} biomass* was estimated from recorded cover and literature-based height (Jäger et al., 2017) for each focal plant species and plot by multiplying those two measures. In forests, biomass of each plant species was estimated from vegetation survey, forest inventory, and tree regeneration data described above. For trees higher than 1.3 m, foliage biomass was estimated from diameter at breast height using a set of allometric equations (Forrester et al., 2017). For non-tree understory plants and trees smaller than 1.3 m, biomass was estimated from recorded cover and height using another set of allometric equations (Bolte, 2006; Bolte et al., 2009). Height of non-tree understory plants was estimated from mean literature values (Jäger et al., 2017). Community-level *Abu_{Fun} biomass* was determined with total biomass, whereas species-level *Abu_{Fun} biomass* was defined with the biomass estimates of each focal plant species. Additionally, in forests, community-level functional abundance was described with the leaf area index (*Abu_{Fun} LAI*), which might be more directly related to leaf-area-based herbivory rate estimates. *Abu_{Fun} LAI* was estimated from airborne LiDAR scanning conducted in 2008–2010 on all plots by using the methods described in Getzin et al. (2017).
3. Functional community-level diversity was determined using the attribute-diversity approach, which is an adaptation of Hill numbers for functional diversity (Chao et al., 2019). Functional dissimilarity between all focal plant species and plot combinations, based on which attribute diversity of each plot was calculated, was determined from Euclidean distances between mean values of SLA and LDMC of all focal plant species in each plot. Functional diversity of orders 0, 1, and 2 was included (*Div_{Fun}* $q = 0$, *Div_{Fun}* $q = 1$, *Div_{Fun}* $q = 2$).

Herbivore metrics

For the characterization of the composition, abundance, and diversity of insect herbivore assemblages, we used data from insect sampling carried out in 2017 or 2018 (depending on year of herbivory assessment) on all plots except for the seven oak forest plots in *SCH* and one beech forest plot in *ALB*, which had to be excluded from pathway analyses ($n = 289$). Different methods were chosen to representatively cover the vegetation-associated insect assemblage within the two systems. In forests, flight-interception traps were installed 1.5 m above ground in three randomly selected corners of the plots from March until July. The traps consisted of a pair of transparent plastic shields (60 cm × 40 cm), which were framed by funnels that opened into sampling jars at the top and at the bottom of the traps (Gossner & Ammer, 2006; Knuff, Winiger, et al., 2019). The sampling jars, which were filled with a solution of 3% $CuSO_4$ and a drop of detergent used to reduce surface tension, were emptied monthly. Two of the three traps in each plot and emptying round were randomly selected for further processing. In grasslands, two rounds of sweep netting (in June and August) were used to sample the insect assemblages. In each sampling round, 60 double sweeps were conducted along three plot border transects (150 m in total) with a net of 30 cm diameter. All insect samples were stored in 70% ethanol until further processing. Samples were then sorted to higher taxonomic levels. Sorting data were used to describe total herbivore abundance. For further analyses, specimens were identified to species level by taxonomic experts (cf. *Acknowledgments*) for four main herbivorous insect groups: Coleoptera, Hemiptera: Auchenorrhyncha, Hemiptera: Heteroptera, and Orthoptera (only grasslands). Together, they account for 53.5% of all groups containing species that contribute visibly to leaf herbivory that were systematically sampled on the Biodiversity Exploratories forest plots across several years (Coleoptera part. 48.65%, Heteroptera 2.89%, Auchenorrhyncha 1.95%), and for 93.0% of all groups sampled on the Biodiversity Exploratories grassland plots (Auchenorrhyncha 40.81%, Heteroptera 38.11%, Coleoptera part. 10.87%, Orthoptera 3.20%). The other groups were either rare, difficult to identify to species level without knowing the host plants or inadequately recorded with the chosen sampling approach (holometabolic larva 43.13% in forests/5.11% in grasslands, adult Lepidoptera 3.06%/1.02%, Orthoptera 0.04% in forests, adult Symphyta 0.04%/0.18%). Species identifications were done for adults only and all specimens that could not be identified to at least genus level were excluded. Because species identification was not possible for female specimens in several genera (particularly Auchenorrhyncha), genus-resolution specimens were assigned to species based on relative abundances of congeneric species on plots or in regions whenever possible. Only herbivorous species that feed on leaves during at least one stage of their life cycle were considered. Thus, species only recorded to feed on, for example, seeds were excluded from species-resolution data as well.

For herbivore metrics at plant species level, the herbivore assemblage per focal plant species was restricted to species potentially feeding on this plant species. To this end, we determined potential interactions based on relevant literature sources for the analyzed herbivore groups (Appendix S1: Table S8). For polyphagous herbivore species for which data on specific host plants were not available, all plant species within broad categories such as trees were considered as potential host plants. Herbivore metrics at plant community level included all recorded herbivores. The following metrics were used to characterize insect herbivore assemblage composition, abundance, and diversity taxonomically (Appendix S1: Tables S5 and S7):

1. For both community- and species-level composition, we used the first three axes of a PCoA on species-resolution records (Com_{Tax} *axis1*, Com_{Tax} *axis2*, Com_{Tax} *axis3*). For some focal plant species at some plots, all herbivores were excluded based on literature records, resulting in empty herbivore assemblages. In these cases, all compositional metrics describing assemblages were set to zero. To account for this introduced bias, an additional two-level factor variable was included, denoting whether composition was set to zero ($Com = 0$).
2. Community-level abundance was determined from both sorting data (also including juveniles; Abu_{Tax} *all*) as well as species-resolution data (Abu_{Tax} *id.*), through the total sum of all records. Sorting data were restricted to invertebrate groups dominated by species that cause visible leaf herbivory. Species-level abundance was only described with Abu_{Tax} *id.*
3. Community- and species-level diversity was, as for plants, described by Hill numbers of orders 0, 1 and 2 ($Div_{Tax}\ q = 0$, $Div_{Tax}\ q = 1$, $Div_{Tax}\ q = 2$) based on species-resolution data.

To describe herbivore assemblages functionally, traits that are potentially related to species occurrences at different land-use intensities (response traits) or to species effects on the process of herbivory (effect traits) were used (Lavorel & Garnier, 2002). A set of five traits collected from different literature sources was included (Gossner et al., 2015 for details): Body length (numeric), dispersal ability (ordinal), feeding mode (nominal), feeding specialization (ordinal) and stratum use (nominal). These traits were available at the level of individual herbivore species, so only species-resolution data were used to calculate functional herbivore metrics. The following metrics were used to describe herbivore composition, abundance, and diversity functionally (Appendix S1: Tables S5 and S7):

1. To combine these different traits into few continuous metrics of functional composition, functional dissimilarities between assemblages of all plots (community level) or between assemblages of all samples of focal plant species (species level) were calculated using the trait probability density (TPD) framework (Carmona et al., 2016) through its implementation in the R package "TPD" (Carmona, 2018). The first three axes of a PCoA conducted on functional dissimilarities were used as composition metrics (Com_{Fun} *axis1*, Com_{Fun} *axis2*, Com_{Fun} *axis3*) for both community- and species-level metrics. Because the TPD framework was developed for a maximum of four trait dimensions, the five traits were reduced to four multivariate axes using ordination for mixed quantitative variables and factors implemented in the "ade4" package (Dray et al., 2018). Intraspecific trait variation, which is included in the TPD framework, was estimated to 0.5 after scaling all trait axes to SD of 1 (Lamanna et al., 2014).
2. Functional community- and species-level abundance was described by total metabolic rate estimated based on body length (Abu_{Fun} *met.*). Metabolic rate is a suitable proxy to describe intake of leaf material per species (Brown et al., 2004). For each species, we determined total metabolic rate R following Kleiber (1932) with

$$R = N \times w^{\frac{3}{4}} \tag{1}$$

   where N is the total abundance recorded and w is the average weight. W was estimated from body length using a set of taxon-specific allometric equations (Sohlström et al., 2018a, 2018b).
3. Functional community- and species-level diversity were determined using the attribute-diversity approach (Chao et al., 2019), which was also used for plant functional diversity. Functional dissimilarity between species was determined with Gower's dissimilarity measure (Gower, 1971) calculated based on the five functional traits. Again, functional diversity of orders 0, 1, and 2 was included ($Div_{Fun}\ q = 0$, $Div_{Fun}\ q = 1$, $Div_{Fun}\ q = 2$).

Statistical analyses

Herbivory rates were transformed prior to analyses to meet distributional assumptions (normal response distribution). Given the relatively small proportion values that were observed (Appendix S1: Table S9), the log-transformation proved adequate for the data. If a herbivory data set contained zero, 0.1% was added to all herbivory rate values in that data set prior to transformation. All continuous predictor variables were scaled to mean 0 and SD 0.5 at the level of recording to make estimates of model coefficients comparable, also between continuous and nominal variables (Gelman & Hill, 2007).

Land-use intensity models

To analyze the effects of land-use intensity on herbivory, three different sets of models were used. First, community-level herbivory rates were analyzed for both systems (forests, grasslands) using linear models, once with combined land-use intensity (*ForMI*, *LUI*) and once with the three respective separate land-use intensity components as predictor variables. Additionally, region (*ALB*, *HAI*, *SCH*) was included as a factor variable in all models to correct for regional differences in herbivory rates. Second, herbivory rates at species level were analyzed, that is, with herbivory rates for each focal plant species and plot as response variables. Herbivory rates were analyzed for both systems using linear mixed effects models. The fixed effects included either the combined land-use intensity metric or the separate land-use components, plus the region. Each model included two random effects, one for the plot and one for the plant species to account for inherent differences in herbivory rates among plots and plant species. These models were run with the package "glmmTMB" (Magnusson et al., 2020). Third, to check whether land-use effects can also be observed within single plant species, linear models were used to analyze herbivory rates on frequently sampled plant species. To this end, plant species were selected that were sampled on at least 10 plots within a system (forests, grasslands), and only if sampled plots covered at least two thirds of the observed gradient of combined land-use intensity. Separate linear models were then run for each of these species. If samples covered more than one region, the models also included region as an additional predictor to account for regional differences. Because eight forest plots including all oak forests had to be excluded from pathway analyses due to missing insect samples, we repeated community- and species-level analysis for forests on the subset of plots not including these eight plots. Results matched those for the complete data set (Appendix S1: Figure S1); thus, only results based on data from all plots are presented in the main text.

To check whether herbivory rates were differently affected by land use depending on damage type, herbivory rates per damage type were analyzed using the same models as for the overall herbivory rates (community and species level). To test for spatial autocorrelation of model residuals among study plots, semi-variograms were created for all models analyzing overall community- or species-level herbivory rates using the package "gstat" (Pebesma & Graeler, 2020) (Appendix S1: Figures S2–S9). Additionally, spatial autocorrelation of random effects for plots used in species-level models was tested by plotting effect estimates along plot coordinates (Appendix S1: Figures S10–S13). As spatial autocorrelation was not significant, it was not further accounted for in any of the analyses.

Pathways

To analyze potential pathways through which land-use intensity is affecting herbivory rates, an exploratory structural equation modeling (SEM) approach was used. Plant as well as herbivore metrics described above were included, which involved 34 metrics for community-level analyses in forests, 36 metrics for community-level analyses in grasslands, 23 metrics for species-level analyses in forests, and 20 metrics for species-level analyses in grasslands. To reduce the number of variables, a model selection procedure was used for both aggregation levels. Stepwise backward model selection was used starting from a global model with herbivory rate as response variable, all plant and herbivore metrics, land-use metrics (i.e., combined land-use indices or separate land-use components) and region as explanatory variables and—for species-level data—random variables for plot and plant species. Land-use metrics and region as well as the random structure were not subjected to the selection procedure. All other metrics were subjected to the selection procedure, so it was possible that no metric of a particular trophic level (plant, herbivore), metric category (composition, abundance, diversity), and metric type (taxonomic, functional) was included in the final model. Each model selection step included the possibility to exclude either one or two predictor variables at a time. Thus, the selection procedure was suitable to also exclude pairs of highly collinear predictor variables. Selection was done by minimizing the model AIC value. Because this model selection procedure still resulted in models containing some highly collinear metrics, the final model was checked for metrics of the same metric category in terms of trophic level (plant, herbivore), metric category (composition, abundance, diversity), and metric type (taxonomic, functional). All abundance and diversity metrics as well as some plant functional composition metrics (SLA and LDMC) within one metric category and metric type were quantifying very similar plant or herbivore characteristics, which was apparent from high correlations (Appendix S1: Figures S14–S17), which is why sets of several of these metrics per metric category and metric type were eventually reduced to one metric based on AIC values.

Based on the final model for herbivory rate, a set of models was created to be used for piecewise SEM. Besides the selected model for herbivory, linear models (community level) or linear mixed effects models including plot and species as random factors (species level) with land-use intensity metrics and region as predictor variables were used for each of the selected metrics. For binary response variables (species-level plant Com_{Fun} metrics and herbivore $Com = 0$), we used generalized linear mixed effects models with a binomial distribution and logit link. For plant Com_{Fun} metrics at species level, the random effect for species was not included because these metrics were perfectly explained by plant species. Then, piecewise SEM was used on these sets of models to identify missing pathways (Lefcheck, 2016a). Next, significant missing pathways ($p \leq 0.05$) were added to the models following a set of rules (illustrated in Figure 2):

1. We assumed bottom-up control of herbivores by plants. This is in line with variety of studies showing effects of plant abundance (productivity), composition, and/or diversity on arthropod abundance, composition, and/or diversity (Borer et al., 2012; Haddad et al., 2001, 2009; Knops et al., 1999; Knuff, Staab, et al., 2019; Schaffers et al., 2008; Scherber et al., 2010; Siemann, 1998), some of which could also be shown in the studied grasslands (Simons et al., 2014).
2. Within trophic levels, we chose effect pathways to be directed from composition over abundance to diversity. Composition was chosen to be the causal starting point because it is, at least for the plant side, directly influenced by our sampling design, where we selected the most abundant plant species. Furthermore, at least in forests, plant species composition is directly influenced by management decisions. While other directions of causality could be imagined, effects of composition on abundance and diversity are manifold. For example, the functional composition of a herbivore (assemblage) will influence its abundance, as, for example, body size is often linked to abundance (White et al., 2007). Similarly for plants, the presence of certain species can have large effects on abundance (biomass) (Huston, 1997). Diversity and abundance (biomass) are often correlated, but causal pathways in both directions are possible (Grace et al., 2016). In our study system, abundance (biomass) is closely related to management, for example, fertilization in grasslands and harvest intensity in forests. Thus, we decided to only include effects of abundance on diversity and not vice-versa.

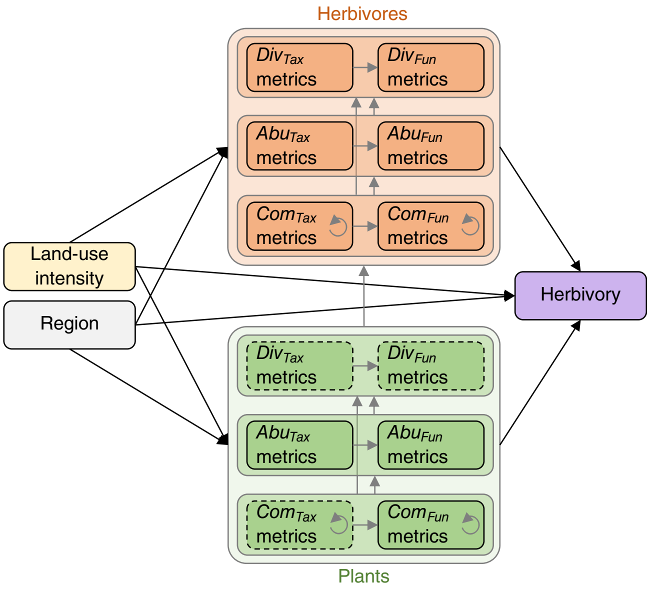

FIGURE 2 Illustration of how the structural equation models were constructed. Original predictor variables included land-use intensity metrics, the region and metrics describing plant and herbivore characteristics (see Appendix S1: Tables S4–S7). Metrics describe the composition (*Com*), abundance (*Abu*), or diversity (*Div*) and can be classified as taxonomic (*Tax*) or functional (*Fun*). Taxonomic plant composition metrics and plant diversity metrics were only included in community-level analyses, but not in species-level analyses (indicated with dashed lines). Based on that original set of metrics, model selection was performed on a full model including all predictor variables and herbivory rate as response variable. Land-use intensity metrics and region were defined to be set and were not excluded during model selection. Based on the final set of predictor variables, from which highly collinear variables were excluded as well, structural equations were defined in a stepwise procedure. First, land-use intensity metrics and region were included as predictor variables of all other metrics and all variables were included as predictor variables of the herbivory rate (black arrows). Second, connections were complemented based on significant *d*-separation claims until no significant *d*-separation claims were left (gray arrows). The directionality of how these connections were implemented is indicated in the figure. Plant metrics were always predictors of herbivore metrics, composition metrics were always predictors of abundance and diversity metrics, abundance metrics were always predictors of diversity metrics, taxonomic metrics were always predictors of functional metrics. If there were significant *d*-separation claims between metrics belonging to the same category (only compositional metrics), these were generally implemented reciprocally (indicated by the circle arrows).

3. Depending on the degree of functional redundancy between species, taxonomic and functional indices might be more weakly or strongly correlated (Naeem, 2002). Because we did not account for intraspecific functional variability, we chose to direct the causal pathways from taxonomic to functional indices

within a metric category (composition, abundance, or diversity).

4. For most compositional metrics, it was possible that several metrics of the same category in terms of trophic level (plant, herbivore) and metric type (taxonomic, functional) were present in the final model. If this were the case, reciprocal pathways going in both directions were used if indicated by the missing pathways analysis, except for plant functional composition, where we did not allow functional-group based composition metrics to be affected by functional-trait based composition metrics, as we expected functional-trait based composition to be influenced by functional-group based composition but not vice versa.

This step of adding missing pathways was repeated until no significant missing pathways were left, resulting in a final set of models. To address the study hypothesis, pathways of the final SEM were summarized into different groups (e.g., through plant metrics). To this end, pathways coefficients for binomial response variables were adjusted to properly reflect their relative contributions (see Appendix S1: Section S1). All SEM analysis was implemented in the package "piecewiseSEM" (Lefcheck, 2016b). It should be noted that while we state a set of potential causal relationships, SEM analysis is based on correlations between indices and will not allow to prove causal pathways, particularly given the exploratory approach chosen to create the SEMs in this study.

RESULTS

A total of 161,644 leaves belonging to 229 plant species were measured. Mean species-level invertebrate herbivory rate was 2.89% (0.17%–8.81% [5% and 95% quantiles]) in forests and 1.84% (0.02%–6.78%) in grasslands (Appendix S1: Table S9 for details). Chewing damage contributed the highest share of total herbivory, followed by scraping and mining damage (Appendix S1: Figure S18 for details). Leaf rolling damage in both systems and galls in grasslands were extremely rare and thus not included in damage-specific analyses. Community-level herbivory rates in forests were disproportionally based on herbivory rates on trees due to high relative cover values, followed by the contributions of forbs and geophytes, whereas grasses contributed the highest share to community-level herbivory rates in grasslands (Appendix S1: Figures S18 and S19).

Community-level herbivory

Increasing land-use intensity was associated with a decrease in community-level herbivory rates in both forests (Figure 3a, Appendix S1: Table S10) and grasslands (Figure 3b, Appendix S1: Table S10). In forests, this decrease was strongly driven by the share of conifers in the tree community (*Inonat*, also see glossary in Appendix S1: Table S1). The observed pattern was found for all damage types (Appendix S1: Figure S20). In grasslands, the amount of fertilizer applied most strongly drove the observed pattern. A negative association between herbivory rates and *LUI* was found for all regularly reported damage types (chewing, scraping, sucking) except for mining damage, whereas the contribution of land-use components differed marginally between damage types (Appendix S1: Figure S20).

Species-level herbivory

Increasing land-use intensity was associated with a decrease in species-level herbivory rates in both forests (Figure 3c, Appendix S1: Table S11) and grasslands (Figure 3d, Appendix S1: Table S11). In forests, this decrease was strongly driven by the share of conifers (*Inonat*), in accordance with the relationships found at community level, although model coefficients were smaller. The relative variance estimate for the random effect of plant species was larger than for the plot and particularly large for forests (Appendix S1: Table S11). When analyzing damage types separately, the observed patterns were only confirmed for chewing damage. In grasslands, significant associations were found for all three land-use components, with associations being strongest for grazing and mowing. This was confirmed for all damage types (Appendix S1: Figure S21).

Herbivory of single common plant species was also negatively affected by land-use intensity. In forests, 23 out of 29 analyzed plant species showed a negative association between land-use intensity (*ForMI*) and species-level herbivory rates (Appendix S1: Figure S22). Statistically significant relationships were found for plant species of different plant functional groups such as for *Rubus fruticosus corylifolius* agg. and *F. sylvatica*. The negative associations between herbivory rates and land-use intensity were mainly driven by the share of conifers (*Inonat*) (Appendix S1: Figure S23). In grasslands, all 21 separately analyzed plant species showed a negative association between *LUI* and species-level herbivory rates (Appendix S1: Figure S24). Significant relationships were found for grasses (e.g., *Dactylis glomerata*) and forbs (e.g., *Plantago lanceolata*). There was no single land-use component driving species-level responses in grasslands, but significant effects were found for all three components depending on plant species (Appendix S1: Figure S25).

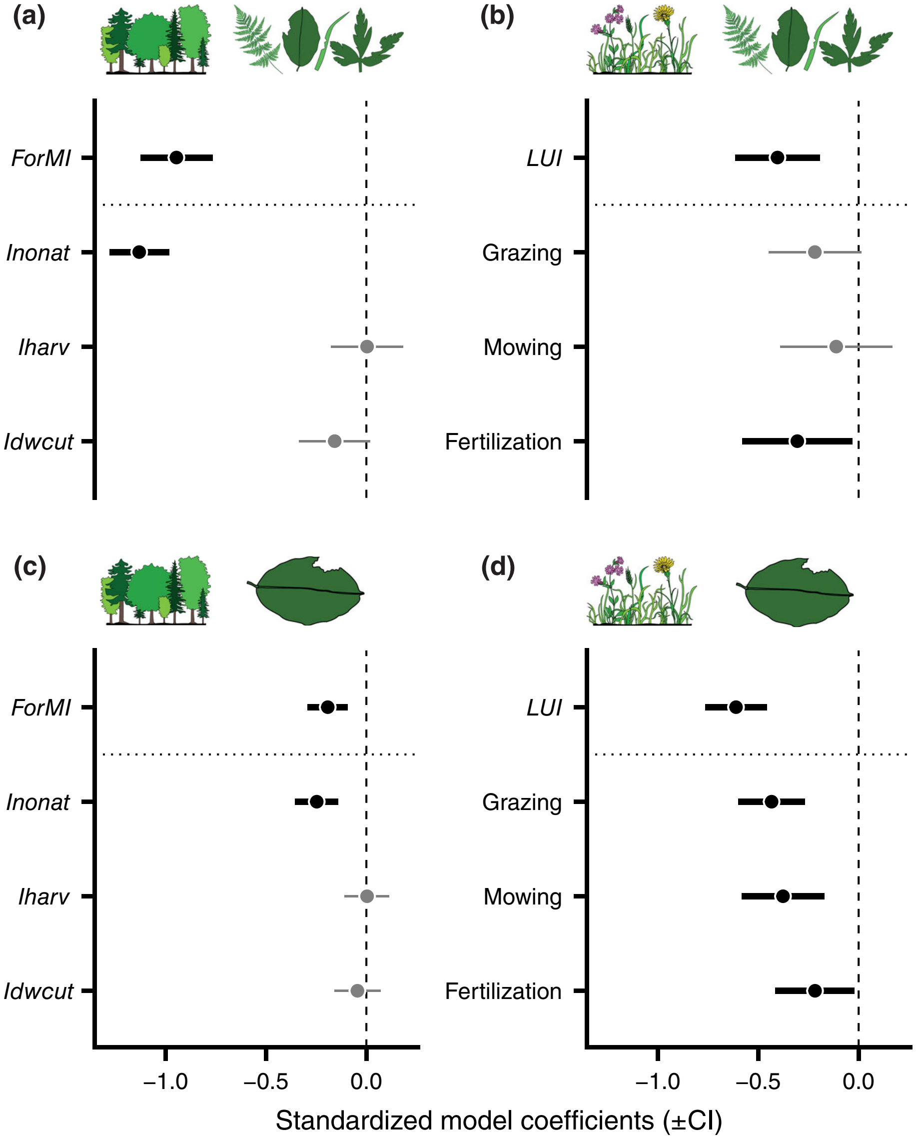

FIGURE 3 Standardized coefficients (±95% confidence intervals) from models analyzing the association between land-use intensity and herbivory rates. (a) Community-level analysis in forests, (b) community-level analysis in grasslands, (c) species-level analysis in forests, (d) species-level analysis in grasslands. For each system, a model was run for the combined land-use intensity index (*ForMI* in forests, *LUI* in grasslands) and for the separate land-use components (*Inonat*: proportion of tree species that are not part of the natural community, i.e., conifers; *Iharv*: proportion of harvested wood volume; *Idwcut*: proportion of deadwood with saw cuts). All models contained an additional covariate for region, for which results are not shown. Species-level models additionally contained random effects for plot and plant species (Appendix S1: Tables S10 and S11 for detailed results). Significant effects are shown in bold. $N = 149$ (forest community level)/$n = 147$ (grassland community level)/$n = 1325$ (forest species level)/$n = 1480$ (grassland species level). Illustrations by Felix Neff.

Direct versus indirect effects of land use

In forests, community-level piecewise structural equation modeling (SEM) analysis indicated that both direct pathways and indirect pathways via plant metrics link higher land-use intensity to lower herbivory rates at similar extents (Figure 4a). The associations were mainly driven by the share of conifers (*Inonat*). The main indirect pathway was through the community-weighted mean of SLA (*Com*$_{Fun}$ *SLA*) (Figure 5a, Appendix S1: Figure S26a), which was negatively associated with the share of conifers (*Inonat*) but positively associated with herbivory rates (Appendix S1: Figures S27 and S28), resulting in a net negative effect. This was driven by much higher SLA values in *F. sylvatica* compared to the stand-forming conifer species (*P. abies*, *P. sylvestris*) that dominated at high shares of conifers (high *Inonat* and *ForMI*). Particularly in the SEM including the combined land-use intensity metric (*ForMI*), another important indirect pathway lead through the proportion of forbs in the plant community

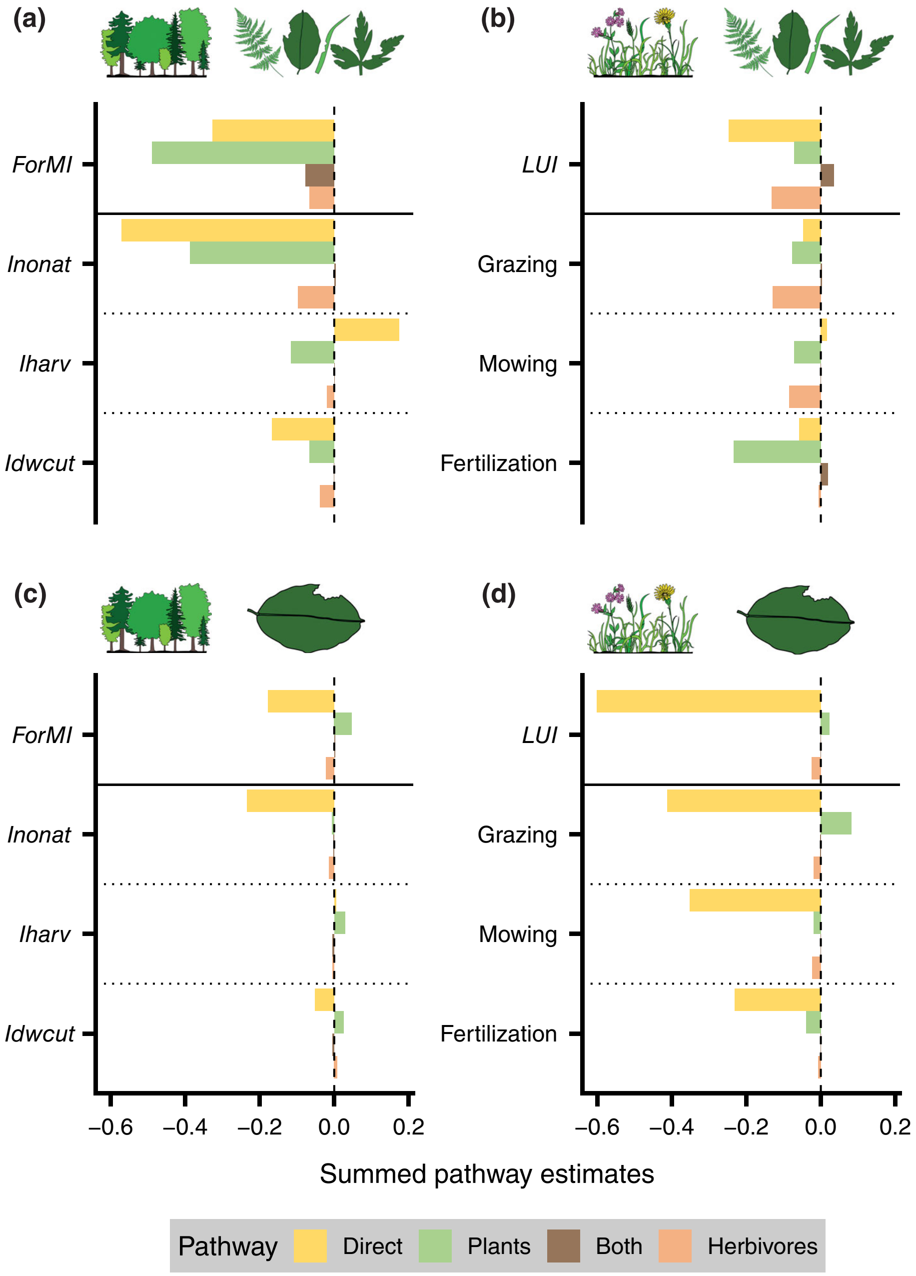

FIGURE 4 Summarized pathways from piecewise structural equation modeling to identify pathways linking land-use intensity, plant metrics (composition, abundance, diversity), insect herbivore metrics (composition, abundance, diversity) and herbivory rates. (a) Community-level analysis in forests, (b) community-level analysis in grasslands, (c) species-level analysis in forests, (d) species-level analysis in grasslands. Separate structural equation modeling procedures were run for combined land-use intensity indices (*ForMI*, *LUI*) and separate land-use components (*Inonat*: proportion of tree species that are not part of the natural community, i.e., conifers; *Iharv*: proportion of harvested wood volume; *Idwcut*: proportion of deadwood with saw cuts). For each land-use metric, the estimates of the direct pathways (yellow) and the summed estimates of all indirect pathways are shown. Indirect pathways are distinguished into pathways only including plant metrics (green), pathways only including herbivore metrics (orange), and pathways including both plant and herbivore metrics (brown). Details on metrics included in the indirect pathways are given in Figure 5 and Appendix S1: Figure S26. Detailed results for all structural equation models are given in Appendix S1: Figures S27–S30 and S32–S35. Illustrations by Felix Neff.

(Com_{Fun} *forb*) (Appendix S1: Figure S26a). With increasing land-use intensity (*ForMI*), the proportion of forbs increased (mainly driven by share of conifers, *Inonat*), which resulted in a net negative effect on herbivory rates. While plant taxonomic diversity of order 0 (Div_{Tax} $q = 0$) was negatively related to herbivory in analyses for separate land-use components (net negative pathway for share of conifers, *Inonat*), plant taxonomic diversity of order 2 (Div_{Tax} $q = 2$) was positively related to herbivory for combined land-use intensity (*ForMI*) analyses (net

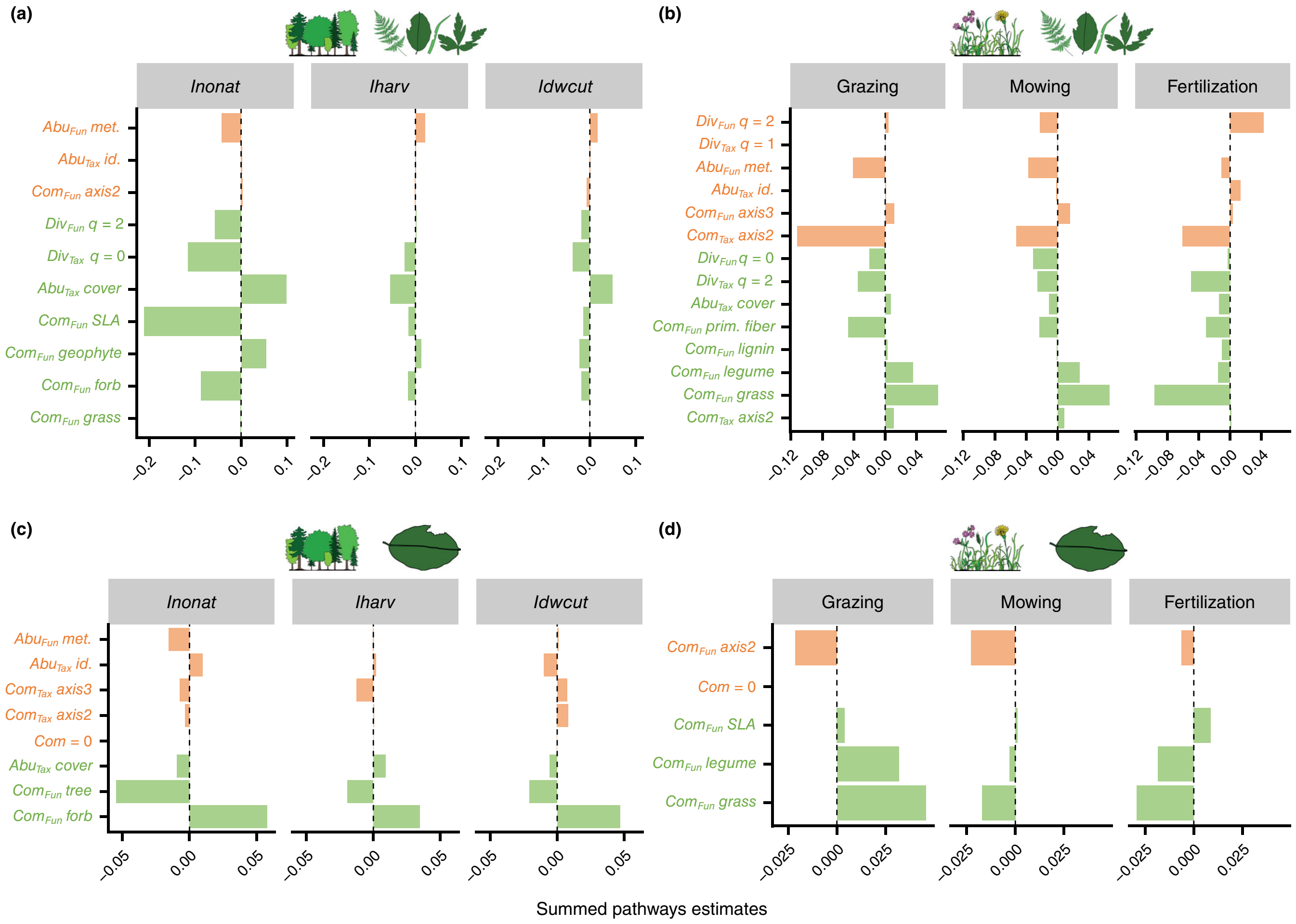

FIGURE 5 Summary of indirect path coefficients from structural equation models linking land-use components, plant metrics (composition, abundance, diversity), insect herbivore metrics (composition, abundance, diversity), and herbivory rates (*Inonat*: proportion of tree species that are not part of the natural community, i.e., conifers; *Iharv*: proportion of harvested wood volume; *Idwcut*: proportion of deadwood with saw cuts). (a) Community-level analysis in forests, (b) community-level analysis in grasslands, (c) species-level analysis in forests, (d) species-level analysis in grasslands. For each plant and herbivore metric that was included in the respective structural equation models, the sum of all estimates of pathways that connect the respective land-use component and herbivory rate through the focal metric is shown. Indirect pathways can link several metrics, which is why the same pathways might be included in sums of several metrics. Plant (green) and herbivore (orange) metrics describe the composition (*Com*), abundance (*Abu*), or diversity (*Div*) and can either be classified as taxonomic (*Tax*) or functional (*Fun*) metrics. $Com = 0$: no herbivores recorded for that focal plant species and plot; id., identified; met., metabolic rate; prim. fiber, primary fiber (cellulose and hemicellulose); q, order of Hill series; SLA, specific leaf area. A detailed description of all metrics is given in Appendix S1: Tables S4–S7. Detailed results for the structural equation models are given in Appendix S1: Figures S28, S33, S30 and S35. Illustrations by Felix Neff.

positive pathway). Pathways through insect herbivore metrics were generally weak (Figure 4a).

Community-level SEM in grasslands revealed that the negative associations between land-use intensity and herbivory rates for the combined *LUI* as well as for all separate land-use components were driven by both direct and indirect effects (Figure 4b, Appendix S1: Figures S29 and S30). A direct negative association was particularly evident for combined *LUI* and to a lesser degree for grazing and fertilization intensities. Negative indirect pathways via plant metrics were evident for combined *LUI* as well as for all three separate land-use components and were particularly strong for fertilization intensity. Negative indirect pathways via herbivore metrics were evident for combined *LUI* as well as for grazing and mowing intensity, whereas positive and negative associations leveled out for fertilization intensity. Main drivers of indirect pathways were the proportion of grasses and of legumes (Com_{Fun} *grass*, Com_{Fun} *legume*), primary fiber concentration (Com_{Fun} *prim. fiber*), and plant richness ($Div_{Tax}\ q = 0$ and $Div_{Tax}\ q = 2$) for pathways via plant metrics and herbivore taxonomic composition (Com_{Tax} *axis2*) and total metabolic rate (Abu_{Fun} *met.*) for pathways via herbivore metrics (Figure 5b, Appendix S1:

Figure S26b). The proportion of grasses decreased with increasing grazing and mowing, but increased with fertilization, whereas the opposite was true for legumes. Because the proportion of grasses was negatively associated with herbivory rates, whereas the opposite was true for the proportion of legumes, this resulted in net positive pathways for grazing and mowing, but net negative pathways for fertilization. Primary fiber concentration was negatively related to all three land-use components but positively related to herbivory rates, resulting in net negative pathways for all land-use components. Taxonomic plant diversity showed different patterns for the models including either combined or separate land-use metrics. In combined land-use intensity analyses, diversity of order 0 ($Div_{Tax}\ q = 0$) was negatively related to herbivory rates (net positive pathway). In the separate land-use components analyses, diversity of order 2 ($Div_{Tax}\ q = 2$) was positively related to herbivory rates (net negative pathway for all three components). Herbivore taxonomic composition (Com_{Tax} *axis2*) was directly negatively related to all land-use metrics, but positively related to herbivory rates, resulting in a net negative pathway. High Com_{Tax} *axis2* values were associated to higher numbers of mirid bugs, cicadellid leafhoppers, and several beetle families (Apionidae, Chrysomelidae, Curculionidae, Elateridae), as well as lower numbers of acridid grasshoppers (Appendix S1: Figure S31). Herbivore total metabolic rate (Abu_{Fun} *met.*) was particularly low in intensively grazed or mown plots, but was positively related to herbivory, resulting in net negative pathways for grazing and mowing intensity.

Species-level SEM in forests revealed weaker negative direct associations between land-use intensity (*ForMI*, *Inonat*) and herbivory rates compared to community-level analysis (Figure 4c, Appendix S1: Figures S32 and S33). The direct negative association between the share of conifers (*Inonat*) and herbivory rates was most striking and was also driving the negative association for combined land-use intensity (*ForMI*). Additionally, there was a weak positive indirect pathway through plant metrics for all land-use components and for combined land-use intensity. This was driven by the probability of the focal plant species being a forb (Com_{Fun} *forb*) (Figure 5c, Appendix S1: Figure S26c), which was positively associated with all land-use metrics. Herbivory rates on forbs were significantly higher compared to other plant functional groups, but not trees (Appendix S1: Figures S32 and S33). The pathway through Com_{Fun} *forb* was counteracted by a negative indirect pathway through Com_{Fun} *tree*, that is, the probability of the focal plant being a tree, which was lower in plots with high land-use intensity. Pathways involving insect herbivore metrics were generally weak (Figure 4c).

Species-level SEM in grasslands revealed strong negative direct associations between all land-use metrics and herbivory rates (Figure 4d, Appendix S1: Figures S34 and S35). Indirect pathways were comparably weak and partly opposing for the three land-use components. They were strongly driven by the probability of the focal plant species being a grass (Com_{Fun} *grass*) or a legume (Com_{Fun} *legume*) and by the functional composition of herbivore assemblages (Com_{Fun} *axis2*) (Figure 5d, Appendix S1: Figure S26d). Herbivory rates were clearly lower on grasses but higher on legumes compared to forbs (Appendix S1: Figures S34 and S35). At the same time, focal plant species in grazed plots were more likely to be legumes but less likely to be grasses, whereas the opposite was true for mown and fertilized plots. This resulted in net negative indirect pathways for fertilization and mowing intensity, but a net positive indirect pathway for grazing intensity. The functional composition of herbivore assemblages (Com_{Fun} *axis2*) was positively related to herbivory rates and was particularly reduced at high grazing and mowing intensities, resulting in net negative pathways. Assemblages with high Com_{Fun} *axis2* values were characterized by species with larger bodies and lower dispersal ability that tended to feed monophagously or oligophagously as chewers (Appendix S1: Figure S36).

DISCUSSION

Land-use intensity is expected to impact invertebrate herbivory rates in ecosystems of the temperate zone (forests, grasslands). Here, we show negative associations between land-use intensity and herbivory rates in both systems and for both aggregation levels (plant community, plant species). While associations on community level were stronger compared to species level in forests, the opposite was true in grasslands. In forests, the share of conifers in the tree community had the strongest negative relationships with herbivory rates. The change in tree species composition affected herbivory rates strongly through a shift in the functional composition of leaf traits related to palatability (broadleaf versus needle). In grasslands, all three land-use components (grazing, mowing, fertilization) had negative associations with herbivory rates. Pathway analyses in both systems revealed several indirect effects of land-use intensity on herbivory, mainly through changes in plant composition (mainly functional composition) and herbivore composition. Direct effects of land-use intensity on herbivory were strong in both systems, particularly at species level, indicating effects mediated by unmeasured variables.

Herbivory along land-use intensity gradients

Herbivory rates decreased along land-use intensity gradients in both forests and grasslands, in line with our first hypothesis (H1). This finding supports previous findings from various ecosystems (Ambarlı et al., 2021; Gossner, Weisser, & Meyer, 2014; Mangels et al., 2015; Njovu et al., 2019; Potapov et al., 2019). The fact that these patterns were consistent for most damage types suggests that generalist and specialist herbivores are equally affected by land-use intensity, as some damage types (e.g., mining) tend to be caused by more specialized species, while other damage types (e.g., chewing) tend to be associated with less specialized species (Forister et al., 2015). In grasslands, herbivory rates were negatively associated with fertilization intensity at community level (largely driven by higher proportions of less palatable grasses, see section on *Direct versus indirect effects of land use*) and negatively associated with all three land-use components at species level. The patterns were observed from three distinct regions and are stable over time (Ambarlı et al., 2021; Gossner, Weisser, & Meyer, 2014), indicating that a negative relationship of herbivory and land-use intensity is typical for Central European grasslands. It might however not hold for other grassland systems differing in various conditions such as climate and land-use mode (Leidinger et al., 2017). In forests, we found that the negative response of herbivory rates to land-use intensity was mainly related to the share of conifers in the tree community (*Inonat*). So far, studies on land-use intensity effects from temperate forests were to our knowledge confined to two studies on beech herbivory conducted in the same system. One study found that herbivory rates decrease with increasing land-use intensity mainly due to changes in tree species composition (Mangels et al., 2015), which is in line with our findings. Another study did not find conclusive land-use effects (Gossner, Pašalić, et al., 2014), but did not consider coniferous forests, which were the main driving factor of the observed effects in our study. Other forest management components such as harvest intensity were not associated with herbivory rates at either aggregation level. Thus, our study further indicates that differences in land-use intensity within beech forests are less important in affecting the ecosystem process of herbivory, at least if clear-cuts are not considered.

A complete analysis of herbivory rates along land-use intensity gradients including not only trees, but also understory plants was missing so far. Because herbivory rate on understory plants might react differently to land-use intensification, a community-wide approach is however essential. For example, studies from rain forests show positive associations of understory herbivory rates and land-use intensity in the form of forest loss (Dodonov et al., 2016; Morante-Filho et al., 2016). For temperate forests, we show that such an increase in understory herbivory, which is indicated in pathways analyses (see section on *Direct versus indirect effects of land use*), cannot compensate for reduction in other layers, resulting in clear reductions of herbivory rates at community level. In sum, our results support the negative relationship between land-use intensity and herbivory in Central European grasslands and show for the first time that herbivory across whole plant communities is also negatively affected by land-use intensity in temperate forests, driven by the share of coniferous trees.

Community- versus species-level herbivory

In forests, the association of land-use intensity with community-level herbivory rates was much stronger than with species-level herbivory rates, supporting the important role of shifts in plant community composition postulated in our second hypothesis (H2). Stand-forming tree species contribute disproportionally to community-level herbivory in forests (66% of total cover, see Appendix S1: Figure S19 for details) and tree species composition (share of conifers, *Inonat*) was the main driver of the negative association of land-use intensity and herbivory rates. This shows that the difference in herbivory rates between broadleaf and coniferous trees is crucial for determining community-level herbivory rates, probably because herbivory rates on coniferous trees are generally lower due to lower leaf palatability compared to broadleaf trees (Turcotte et al., 2014). This could mean that during non-outbreak situations, less biomass is lost to herbivory in coniferous compared to broadleaf forests, which would imply that nutrient cycling is impaired in these systems. Impaired nutrient cycling would be evident, for example, in slower cycling of nitrogen and consequently lower plant productivity (Belovsky & Slade, 2000). Because the leaf area per forest area (i.e., leaf area index) is generally higher in coniferous forests compared to broadleaf forests, the reduced biomass transfer per leaf area might, however, be partly compensated in coniferous forests (Appendix S1: Figure S37).

In grasslands, most associations between land-use components and herbivory rates were larger in species-level analyses compared to community-level analyses, in contrast to hypothesis H2. Previous studies from grasslands hypothesized that changes in herbivory rates along land-use gradients might mainly be due to changes in the proportion of grasses in the community (Gossner, Weisser, & Meyer, 2014; Leidinger et al., 2017). This would imply weaker species-level associations, which were not found in this study. In fact, herbivory rates even decreased with increasing land-use intensity for many species analyzed individually including also grass species, supporting findings from another study in the same system that found negative relations of land-use intensity and herbivory on grasses (Ambarlı et al., 2021). Accordingly, other mechanisms such as changes in leaf palatability at plant population level or of specific herbivore characteristics, discussed in detail in the section on *Direct versus indirect effects of land use*, might better explain the observed decline in herbivory rates with increasing land-use intensity in grasslands. In sum, while the stand-forming tree species explain much of the negative effect of land-use intensity on herbivory in forests, plant composition in grasslands plays a less important role.

Direct versus indirect effects of land use

In contrast to our third hypothesis (H3), indirect effects through changes in plant and herbivore characteristics were not stronger than direct effects except for community-level grassland analyses. Still, in line with hypothesis H3, we found clear indirect pathways through plant metrics in both systems, mainly involving compositional metrics. In forests, these indirect pathways were particularly important in community-level analyses, where we found a strong pathway through functional plant composition, that is, community-weighted mean of SLA. Higher SLA is associated with higher leaf palatability, which results in higher herbivory rates (Castagneyrol et al., 2019). The differences in community-weighted mean SLA in this study mainly relied on interspecific differences in SLA between stand-forming tree species (broadleaf or coniferous), with considerably lower SLA in coniferous trees, explaining the lower herbivory rates in coniferous stands. This finding thus supports the above indicated role of changes in leaf palatability of the stand-forming trees in explaining the forest land-use intensity effects. Other indirect pathways through plant metrics in forests involved the differences between plant functional groups, which were evident from both community- and species-level analyses. Herbivory rates on forbs and broadleaf trees were generally higher than on other plant functional groups such as grasses, again indicating differences in leaf palatability (Turcotte et al., 2014). Changes in their relative proportion (community level) or sampling probabilities (species level) therefore indirectly affected herbivory rates. At higher land-use intensities (particularly driven by higher shares of conifers, but also harvest intensity and deadwood origin), the share of trees was decreased, whereas the share of understory forbs increased. This resulted in net negative indirect pathways through tree sampling probabilities in species-level analysis, but net positive indirect pathways through forb sampling probabilities. For community-level analysis, the pathway through the proportion of forbs was negative, thus opposing species-level analysis. However, the proportion of trees was not included in this analysis, thus this pathway indicates the net effect of partly replacing trees (with highest herbivory rates) by forbs (with slightly lower herbivory rates) in community-level herbivory rates. The general increase of understory forb cover and diversity at high land-use intensity, which should improve food supply for herbivores at the forest floor, can be explained by better light conditions at the forest floor due to regular disturbances and because conifer stands allow more light to be transmitted than dense beech stands (Boch et al., 2013). Thus, while community-level herbivory rates were negatively affected by high shares of coniferous trees with less palatable leaves, understory herbivory rates might still be enhanced in these stands due to higher supply of food plants.

In grasslands, several indirect pathways through plant metrics linked land use and herbivory rates. In line with previous findings (Gossner, Weisser, & Meyer, 2014; Loranger et al., 2014), a high proportion of grasses as well as a low proportion of legumes were both negatively associated with herbivory rates, because herbivory rates were lowest on grass species, but highest on legumes. Grasses were repeatedly shown to experience lower rates of invertebrate herbivory (Fischer et al., 2012; Loranger et al., 2013; Turcotte et al., 2014). Functionally, they differ from other herbaceous plants by their significant content of silica bodies (phytoliths) with a particularly high protective effect against leaf chewers (Hartley & DeGabriel, 2016; Massey et al., 2006). Legumes, however, have high nitrogen contents, which makes them more attractive for herbivores in general (Loranger et al., 2012), thus increasing their herbivory level. While fertilization intensity was positively linked to the proportion of grasses, but negatively to the proportion of legumes, the opposite was true for grazing intensity (Socher et al., 2012). This resulted in negative indirect relationships to overall herbivory rates for fertilization, but positive effects for grazing (note that this does not include herbivory by livestock grazing, which was not included in this study). Other strong pathways via plant metrics had equal signs for all three land-use components and resulted in net negative relationships to herbivory rates for all three components. At foremost, these negative relationships were mediated by primary fiber concentrations (cellulose and hemicellulose), which were reduced by intensive land use, but were positively linked to herbivory rates. The positive link to herbivory rates is surprising at first, as high fiber contents normally mean lower nutritional quality of these plants for herbivores, as is also indicated by the negative correlation between concentrations of primary fiber and several nutrients (N, P, Mg, Ca) (Appendix S1: Figure S15). Such a positive link between primary fiber concentration and herbivory has, however, previously been found (Loranger et al., 2013) and might indicate that the lower nutritional quality of these plants results in higher consumption rates to meet nutrient demands (Simpson & Simpson, 1990). The higher primary fiber concentrations in low-intensity grasslands might reflect lower nutrient concentrations generally encountered in such conditions opposed to, for example, fertilized sites (e.g., Klaus et al., 2011), resulting in the negative indirect relationship between land-use intensity and herbivory rates. The remaining direct negative relations between fertilization intensity and herbivory rates support such a more ambivalent role of nutritional quality for herbivory rates in grasslands, which is contrary to common expectations that fertilization would increase herbivory (Throop & Lerdau, 2004).

Across systems, we found consistent but opposing relations of plant diversity of different orders (Hill numbers) to herbivory rates. While diversity of order 0 ($Div_{Tax}\ q = 0$) was negatively related to herbivory, diversity of order 2 ($Div_{Tax}\ q = 2$) was positively related. Lower herbivory rates with increasing plant species richness (diversity of order 0) indicate associational resistance. Following the resource concentration hypothesis (Root, 1973), higher plant species richness would mean that resources for specialist herbivores are diluted, resulting in lower (specialist) herbivore loads and thus lower herbivory rates. Unlike diversity of order 0, high diversity of order 2 indicates a higher evenness within the plant community. Thus, high values of $Div_{Tax}\ q = 2$ not necessarily result in resource dilution for specialist herbivores, but might rather allow for more complementing specialist herbivores to persist, resulting in higher mean herbivory rates, which would again be in line with the resource concentration hypothesis (Root, 1973). These opposing diversity results underline the complexity of diversity-herbivory relationships due to various underlying mechanisms.

While pathways involving herbivore metrics were weaker compared to pathways involving plant metrics in forests, which is in line with our expectations, they were equally strong or even stronger than those involving plant metrics in grasslands. Interestingly, they were particularly strong for grazing and mowing intensity, the two land-use components accounting for many changes in herbivore assemblages (Neff et al., 2019). In community-level analyses, the strongest effects were found for the compositional metric Com_{Tax} *axis2*. This suggests that not primarily the abundance of herbivores determines herbivory rates, but that their composition may be of equal importance. Here, herbivore assemblages in high-intensity grasslands tended to have lower numbers of several groups of specialized grassland species (e.g., mirid bugs, cicadellid leafhoppers), which might contribute significantly to community-level herbivory in functionally less impaired low-intensity grasslands, as is indicated by the resulting lower herbivory rates with shifting herbivore composition. Still, reductions in herbivore abundance explained some of the reductions, as was evident by the negative pathway between land-use intensity and community-level herbivory via total metabolic rate (Abu_{Fun} *met.*). Similarly, the negative pathways through herbivore functional composition (Com_{Fun} *axis2*) for species-level herbivory might reflect reduced herbivore pressures. In line with previous studies (Neff et al., 2019; Rader et al., 2014), herbivore assemblages in high-intensity grasslands were composed of smaller species, which might have lower metabolic demands (Brown et al., 2004), resulting in lower biomass consumption (Moretti et al., 2013). In species-level analyses, these herbivore-mediated indirect pathways were, however, weak compared to direct pathways linking land-use intensity and herbivory.

The mechanisms behind the unexpectedly strong direct pathways between land-use components and herbivory rates remain unclear and must involve factors that were not quantified in this study. There are several possibilities for such factors. First, plant metrics that were chosen might be incomplete. For example, we did not quantify differences between plant communities or samples in nitrogen content (Tylianakis et al., 2008) (except for community-level analyses in grasslands), sodium content (Welti & Kaspari, 2021), chemical diversity (Schuman et al., 2016), or other metrics explaining more specific attributes of leaf palatability (Loranger et al., 2012) that could potentially be affected by land use (Klaus et al., 2011; Schaffers, 2002). Second, herbivore metrics might not reflect herbivore assemblages sufficiently. On the one hand, functional traits directly related to feeding activities or feeding behavior might provide important links. For example, in a few previous studies mandibular traits were associated with herbivory rates (Deraison et al., 2015; Ibanez et al., 2013). Also, directly quantifying differences in ingestion rates between herbivore groups or species rather than indirectly through proxies such as body size might be promising (Peters et al., 1996). On the other hand, changes in herbivore feeding behavior might explain differences in herbivory rates (Hahn & Orrock, 2015). Third, we did not include the complete herbivore insect assemblage—for example, Lepidoptera and Symphyta were, although important, not considered except for rough abundance estimates. Fourth, we did not consider higher trophic levels, that is, the role of top-down forces, in our study. Although most studies indicate bottom-up forces to be more important than top-down effects in controlling herbivore assemblages, we cannot rule out that predation and parasitism influenced the observed relationships. Previous studies have shown that land use has complex effects on predation rates with different land-use components affecting predation rate in opposite directions (Meyer et al., 2019) and supported the potential for top-down control of herbivory rates in some systems (Dekeukeleire et al., 2019), particularly in high-nutrient environments such as fertilized grasslands (Welti et al., 2020). Finally, our study did not assess changes in abiotic conditions such as in microclimate due to land-use intensity changes. For example, differences in temperatures (Ambarlı et al., 2021; Lemoine et al., 2014; Valdés-Correcher et al., 2021; Zvereva & Kozlov, 2006) might be important drivers of herbivory rates, for example, by directly increasing herbivore activity. Light conditions have also been regularly related to herbivory rates. Several studies have found that herbivore rates are lower under sunny than under shady conditions due to changes in plant characteristics, such as nutritional quality (e.g., Muth et al., 2008; Uyi, 2020). These indirect effect of changed light conditions could explain some of the observed direct negative effects of forest land-use intensity, as high-intensity forests had more light at the forest floor (Boch et al., 2013). In summary, a variety of factors involving biotic (plant and herbivore characteristics), abiotic conditions, as well as combinations of both could explain the strong direct pathways linking land-use intensity and herbivory rates.

Limitations

The current study relies on leaf area-based estimations of herbivory rates, which poses several limitations that should be considered when interpreting the results. First, the content of energy and nutrients per leaf area might vary substantially between plant populations (Siefert et al., 2015). This might partly explain the negative effect of community-weighted mean SLA in forests on herbivory, as herbivores need to consume less area to obtain the same amount of biomass. Second, particularly for sucking insects, area-related herbivory rates might only partly reflect the real damage imposed on plants, as only, if at all, the punctures are visible. This is particularly important because many herbivores specialized on grasses belong to the sucking insects, which might partly explain why higher proportions of grasses lead to lower herbivory rates. Additionally, the area-based measure of herbivory misses cases in which whole leaves or even plant individuals are lost to herbivores, as can for example be the case for grass blades being completely consumed by orthopterans or needles being removed by caterpillars, and might thus also underestimate chewing damage. Experimental studies will need to show how well plant area loss is connected to loss and transfer of energy and nutrients. Third, herbivores are often not restricted to leaves, but will also feed on other plant parts. This was partly accounted for by only considering species potentially feeding on plant leaves, but there might still be considerable differences in preferences for plant parts for feeding. Fourth, the presence of particular herbivore species or groups either not captured in our samplings (e.g., gastropods; Peters, 2007) or not well described by the chosen metrics might explain missing links between land use and herbivory. However, our results are generally confirmed across different damage types, indicating that different herbivore groups respond similarly to land use. Finally, while we show consistent effects of land use on herbivory rates in two important temperate terrestrial ecosystems, we neglect important ecosystems that have also experienced land-use intensification, with pressures being substantially different from those covered by the systems studied. For example, crop fields are abundant ecosystems of the temperate zone that are exposed to high inputs of pesticides. While some of these substances are used specifically to reduce herbivory rates (i.e., insecticides), the effects of different substances on the multi-trophic system and herbivory rates could be more nuanced (e.g., Gutiérrez et al., 2020). Another example is urban ecosystems, which include gradients of urbanization where other processes such as light pollution or large microclimatic differences are also likely to alter plant and herbivory characteristics as well as herbivory rates (Miles et al., 2019). Thus, while we find consistent effects of land-use intensity on herbivory rates in temperate forests and grasslands, further work needs to show how other ecosystems respond to land-use intensification. The present study sets the ground by providing various new insights into the mechanisms underlying land-use intensity effects on invertebrate herbivory across ecosystems.

CONCLUSIONS

This study provides new evidence for detrimental effects of intensive land use on the ecosystem process of invertebrate herbivory across different ecosystems. Shifts in plant composition (e.g., proportion of coniferous trees in forests and grasses in grasslands) explain part of these negative associations, particularly for community-level herbivory. Shifts in the characteristics of herbivore assemblages contributed less (forests) or equally (grasslands) to the observed negative relationships. Still, there were strong direct effects of land-use intensity on herbivory rates, particularly for species-level herbivory, which indicate that additional mechanisms play important roles in controlling responses of herbivory rates to land-use intensification. These potentially involve changes in non-measured variables, such as other leaf traits related to palatability (e.g., nutrient contents, as indicated by community-level analyses in grasslands), herbivore traits and behavior directly affecting feeding rates, top-down control by predators and parasites, as well as abiotic conditions (e.g., light conditions), which should be further addressed in future studies. Consequences of the observed lowered herbivory rates at higher land-use intensities are manifold. Most importantly, they underpin the potential of land-use intensification (tree species selection in forests; mowing, grazing and fertilization in grasslands) to impair ecosystem functioning. As such, lowered herbivory rates mean changes in the flow of energy and nutrients in the food webs, potentially affecting various ecosystem components, such as higher trophic levels or soil organisms, which might further contribute to ongoing biodiversity loss.

AUTHOR CONTRIBUTIONS

Felix Neff, Loïc Pellissier, and Martin M. Gossner developed the ideas for the manuscript and defined the analyses; Felix Neff, Arturo Knecht, Daniel Prati, and Martin M. Gossner designed and conducted the herbivory assessment; Felix Neff, Daniel Prati, Rafael Achury, Didem Ambarlı, Ralph Bolliger, Martin Brändle, Martin Freitag, Norbert Hölzel, Till Kleinebecker, Arturo Knecht, Deborah Schäfer, Peter Schall, Sebastian Seibold, Michael Staab, Wolfgang W. Weisser, and Martin M. Gossner provided data; Felix Neff analyzed the data, wrote the first draft, and finalized it together with Martin M. Gossner; all authors contributed to the revisions of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All relevant R code used for data preparation and analyses (Neff et al., 2022) is available in Zenodo at https://doi.org/10.5281/zenodo.7469081. Data to repeat analyses are available in the BEXIS repository in Neff (2023a) at https://doi.org/10.25829/BEXIS.31412-13 and Neff (2023b) at https://doi.org/10.25829/BEXIS.31413-13.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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