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LETTER

From bottom-up to top-down control of invertebrate herbivores in a retrogressive chronosequence

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Abstract

In the long-term absence of disturbance, ecosystems often enter a decline or retrogressive phase which leads to reductions in primary productivity, plant biomass, nutrient cycling and foliar quality. However, the consequences of ecosystem retrogression for higher trophic levels such as herbivores and predators, are less clear. Using a post-fire forested island-chronosequence across which retrogression occurs, we provide evidence that nutrient availability strongly controls invertebrate herbivore biomass when predators are few, but that there is a switch from bottom-up to top-down control when predators are common. This trophic flip in herbivore control probably arises because invertebrate predators respond to alternative energy channels from the adjacent aquatic matrix, which were independent of terrestrial plant biomass. Our results suggest that effects of nutrient limitation resulting from ecosystem retrogression on trophic cascades are modified by nutrient-independent variation in predator abundance, and this calls for a more holistic approach to trophic ecology to better understand herbivore effects on plant communities.

KEYWORDS

apparent competition, bottom-up control, cross-ecosystem flows, ecosystem retrogression, exploitation ecosystem hypothesis, plant–herbivore interactions, soil fertility gradient, top-down control

INTRODUCTION

Nutrient availability and limitation shape ecosystems and food webs in fundamental ways (Vitousek, 2004). Following major disturbances, increases in nutrients initially lead to a build-up in plant biomass and productivity (Peltzer et al., 2010; Wardle et al., 2004). However, in the long-term absence of major disturbances (often over millennia), nutrient limitation increases (Peltzer et al., 2010; Vitousek, 2004), frequently leading to 'ecosystem retrogression' characterised by decreases in plant biomass and primary productivity, and in rates of decomposition and nutrient cycling (Laliberté et al., 2013; Wardle et al., 2004). While the build-up phase and its consequences for higher trophic levels, such as herbivores and their predators, are relatively well understood (e.g. Brown, 1985; Fagan & Bishop, 2000; Neves et al., 2014; Siemann et al., 1999), the consequences of ecosystem retrogression for higher trophic levels are less clear (Crutsinger et al., 2008; Gruner, 2007). Long-term chronosequences that include retrogressive states can improve our general understanding of how herbivore and predator communities are affected by nutrient limitation, as they occur over longer time scales and are less impacted by short-term processes typical for the build-up phase such as high plant species turnover (Peltzer et al., 2010). Thus, retrogressive chronosequences are excellent model systems to develop general principles about the factors regulating higher trophic levels and their impact on plants.

As retrogression proceeds, plant species composition shifts from species or genotypes with resource-acquisitive traits towards those with more conservative traits (Coley et al., 1985; Reich, 2014). Thus, nutrient concentrations in plant tissues often decrease and plant defences increase (Hättenschwiler et al., 2003; Vitousek, 2004; Wardle et al., 1997). This may influence herbivore preference and performance, and hence herbivore identity, abundance and impact (Feeny, 1976; Kempel et al., 2011; Root, 1973). Shifts towards more conservative plant species and reduced plant productivity that accompany declining soil fertility are expected to reduce herbivore biomass (Chase et al., 2000; McNaughton et al., 1989), which has frequently been shown in managed grasslands and grassland experiments (Borer et al., 2012; Ebeling et al., 2022; Simons et al., 2014; Welti et al., 2020). However, few studies have assessed the relationship between nutrient availability and invertebrate herbivores along natural nutrient gradients (Cuevas-Reyes et al., 2004), and the few studies that have been performed across long gradients such as those provided by retrogressive chronosequences have produced mixed results (Crutsinger et al., 2008; Gruner, 2007).

In addition to bottom-up forces, top-down regulation by predators can strongly affect herbivore biomass and their impact on plants (Barnes et al., 2020; Hairston et al., 1960). Recent findings suggest that the strength of bottom-up control depends on predator abundance (Barnes et al., 2020; Letnic & Ripple, 2017; Welti et al., 2020). Similarly, the 'exploitation ecosystems hypothesis' (EEH) predicts that bottom-up and top-down forces operate simultaneously, but their relative importance within communities changes with ecosystem productivity (Fretwell, 1987; Oksanen et al., 1981). In unproductive systems, predators are predicted to be absent and herbivore biomass therefore increases strongly as plant biomass increases. In more productive systems, herbivore biomass is predicted to show only weak responses to increasing plant biomass as predators control herbivores. This theory was originally formulated for vertebrates, and the 'trophic flip' (from bottom-up to top-down) has been shown for vertebrate food webs (Aunapuu et al., 2008; Crête, 1999; Letnic & Ripple, 2017). For invertebrates, there is some support for the EEH from a study showing that grassland plant biomass only increased grasshopper and Auchenorrhyncha (Hemiptera) biomass when spider biomass was low, but the theory was not fully supported because spider biomass was unrelated to plant biomass (Welti et al., 2020). Furthermore, invertebrate predators may not respond strongly to plant biomass if they also feed on detritivores, pollinators or prey from interconnected aquatic systems (Gounand et al., 2018), which are not necessarily linked to plant biomass (Clough et al., 2014). Hence, whether the trophic flip predicted by the EEH can be found in forested ecosystems, and holds for entire invertebrate communities, remains unexplored.

While few studies have assessed the relationship between herbivore and plant biomass along productivity gradients, our understanding of how the *impact* of herbivores, that is, their effect on plant biomass or other community components, changes across these gradients is even less clear (Barnes et al., 2020; Coupe & Cahill, 2003; Schädler et al., 2003; Stein et al., 2010). The resource availability hypothesis (Coley et al., 1985) predicts that impact should be higher in resource rich environments, which select for fast-growing, poorly defended plants. However, fast-growing plants typically tolerate herbivores better, as they can compensate for lost biomass (Gianoli & Salgado-Luarte, 2017). Conversely, the plant stress hypothesis (White, 1969) posits that impact should be higher in more stressful, low-resource environments. Considering that top-down forces increase in parallel with productivity, the EEH states that herbivore impact should show a hump-shaped relationship with productivity (Fraser & Grime, 1997; Schädler et al., 2003). Several studies use herbivore *damage* to infer *impact* (e.g. Crutsinger et al., 2008; Denno et al., 2002; Ebeling et al., 2022; Endara & Coley, 2011). However, damage is not necessarily related to impact because some plants might be more tolerant to enemies than others (Gianoli & Salgado-Luarte, 2017), and the actual *impact* might be lower than expected based on damage alone (Schädler et al., 2003). Moreover, damage caused by sap-suckers is difficult to quantify and impact could be greater than expected. To test for variation in impact, herbivore exclusion studies along soil fertility gradients are necessary, but have rarely been performed (but see Stein et al., 2010 for grasslands).

We use a well-studied system of 30 forested lake islands in the boreal zone of northern Sweden, for which fire from lightning strikes is the main agent of disturbance. Large islands have burned more frequently than smaller ones, resulting in a 5000-year post-fire retrogressive chronosequence (Wardle et al., 1997, 2003, 2012). As island size declines, and time since fire increases, nutrient availability declines, and there is a shift to domination by plants with resource-conservative traits and reduced plant biomass (Table S1, Figure S1, Wardle et al., 2012). On each island, we sampled invertebrates and quantified the biomass of chewing and sucking herbivores, and of predators. Additionally, we assessed herbivore damage and impact using herbivore exclusion experiments on phytometers. We assessed biomass of chewing and sucking herbivores separately, as these different guilds may respond differently to variation in plant quality and quantity (Gely et al., 2020). Through structural equation modelling (SEM), we aimed to disentangle the direct and indirect drivers of invertebrate herbivore biomass, damage and impact.

We tested three main hypotheses: (1) Invertebrate herbivore biomass tracks plant biomass, that is, herbivore biomass declines with decreasing island size as time since fire increases and nutrients become more limiting. (2) Invertebrate predator biomass is low on small and unproductive islands, thus plant biomass is the dominant control of herbivore biomass, while on large, productive islands predator biomass is higher and suppresses herbivores, resulting in a trophic flip from top-down to bottom-up control of herbivores with decreasing island size and increasing nutrient limitation. (3) Herbivore damage decreases with decreasing plant and herbivore biomass as island size decreases (resource availability hypothesis), but herbivore impact does not change because plant tolerance and predator abundance are lower in less fertile environments. Additionally, we test a range of other hypotheses, see Table 1 for all 14 hypotheses that we test.

METHODS

Island system

We conducted our study on 30 forested islands varying in size from 0.03 to 15 ha in two adjacent freshwater lakes in northern Sweden, Lake Hornavan and Lake Uddjaure. All islands were formed following the retreat of land ice 9000 years ago. The major extrinsic factor that varies among islands is the frequency of fires, which occur as a result of lightning strikes: larger islands are struck more often and have, on average, burned more recently (Wardle et al., 1997, 2012), which has been demonstrated by tree fire scar data, as well as ^{14}C analysis of charcoal collected from each island (Wardle et al., 1997, 2003). With increasing time since fire, nutrients become increasingly limiting (Gundale et al., 2012; Lagerström et al., 2009), which causes a strong decline in plant standing biomass, ecosystem productivity, decomposition rates and nutrient fluxes (Wardle et al., 2012, see legend in Table S1). The lack of disturbance by fire on smaller islands has led to ecosystem retrogression, as a consequence of strongly increasing nutrient limitation in the prolonged absence of disturbance (see Figure S1).

There are large changes across the island gradient in vegetation composition (Wardle et al., 2012). Larger, regularly burned islands are dominated by relatively fast-growing plant species with resource-acquisitive traits, such as the tree *Pinus sylvestris* and the dwarf shrub *Vaccinium myrtillus* (hereafter *Pinus*, *V. myrtillus*). Smaller, infrequently burned islands are dominated by slow-growing resource-conservative species, such as the tree *Picea abies* and dwarf shrub *Empetrum hermaphroditum* (hereafter *Picea*, *Empetrum*). Mid-sized islands are dominated by the tree *Betula pubescens* and dwarf shrub *Vaccinium vitis-idaea* (hereafter *Betula* and *V. vitis-idaea*) which show intermediate growth strategies (Figure S1). Although the relative abundance of the species varies across the island gradient, all species occur on all 30 islands, except for *Pinus* and *Picea* which are absent from five small and three large islands respectively. The decline in soil nutrient availability across the chronosequence, and associated decline in plant biomass and primary productivity are ideal for exploring plant–herbivore–predator interactions along a natural soil fertility gradient.

Plant standing biomass and plant functional composition

For each island we obtained data on plant standing biomass per square metre from a previous study which assessed biomass of the six dominant plant species (i.e. *Pinus*, *Betula*, *Picea*, *V. myrtillus*, *V. vitis-idaea* and *Empetrum*) using allometric equations (Wardle et al., 2003, 2012). To obtain a relative estimate of plant functional composition per island we ran a principal component analysis (PCA, Figure S2) across the 30 islands with net primary production (NPP) for these six species which collectively account for >98% of total NPP, using data from Wardle et al. (2003). The first PCA axis (PC1) explained 66% of the total variation in the data, and we used PC1 values as an indicator of plant functional composition. High scores of PC1 indicate the plant community is mostly composed of resource-conservative plant species such as *Picea*, low values indicate the community is dominated by more resource-acquisitive species such as *Pinus*. Plant standing biomass and plant functional composition were negatively correlated ($r = -0.57$).

Invertebrate herbivore and predator biomass

We sampled invertebrates on each of the six dominant plant species on each island over a 10-day period in July 2016 (when plant productivity peaks, Kempel et al., 2022). For each tree species on each island, we randomly selected five trees, and sampled one branch per tree. We

TABLE 1 Hypothesised mechanisms affecting herbivore and predator biomass, and herbivore damage and impact, used to underpin the full SEM model that we tested (Figure 1).

Path	Hypothesised mechanism	References
1	(+) Large islands have been burned more frequently which increases soil fertility and consequently plant standing biomass	Wardle et al. (2003, 2012)
2	(−) Small islands are dominated by resource-conservative plant species like *Picea*, which are associated with negative values at the first PCA axis (see Figure S1)	Wardle et al. (2003, 2012)
3	(?) Island biogeography theory predicts that large islands harbour a higher herbivore diversity but does not make prediction about herbivore biomass	MacArthur and Wilson (1967)
4	(+) The resource availability hypothesis predicts that herbivore biomass increases with plant biomass. Several studies support this for grasslands	Borer et al. (2012); Coley et al. (1985); Lind et al. (2017)
5	(−) More acquisitive plant species should invest less in defence than slower growing species. Hence, they may support a larger biomass of herbivores. Since resource-acquisitive species are associated with negative first PCA axis scores in Figure S2 we expect a negative relationship	Coley et al. (1985); Kempel et al. (2011)
6	(±) Predator biomass could be bottom-up regulated and hence herbivore biomass may increase predator biomass. However, herbivores may also be top-down regulated by predators, and predator biomass may therefore reduce herbivores	e.g. Hunter and Price (1992)
7	(+) A high standing biomass may positively affect predators as biomass is usually correlated with a high structural complexity offering hiding and nesting sites	Lawton (1983); Root (1973)
8	(?) Plant composition may directly affect predator biomass as certain plant species may be particularly beneficial to predators, offering shelter and structural complexity	
9	(−) From previous studies we know that spiders (the most abundant group of predators in our study) benefit from the larger perimeter to area ratios on small islands and thus lake-derived subsidies (i.e. insects that spend their larval and nymph stages in the lake water surrounding the islands but whose adult stage is on shore and serve as prey)	Jonsson et al. (2009); Jonsson and Wardle (2009)
10	The exploitation ecosystem hypothesis predicts that predator abundance is low in unproductive habitats, and hence plant biomass is the dominant control of herbivores, while in productive habitats predators are abundant and suppress herbivores. Hence, we expect that predators may change the relationship between plant biomass and herbivore biomass, resulting in a trophic flip in herbivore control from bottom-up to top-down with increasing nutrient availability	Oksanen et al. (1981); Welti et al. (2020)
11	(+) A higher herbivore biomass should translate into higher herbivore damage. Whether it also results in a higher impact may depend on a plant's ability to compensate for tissue loss and to tolerate herbivore attack	Coley et al. (1985); Fraser and Grime (1997)
12	(?) There might also be a direct effect of plant standing biomass on herbivore damage and impact (and not only indirectly via increasing herbivore biomass), which likely indicates changes in the functional composition or size structure of the herbivore community which we have not assessed. In addition, a direct effect on impact might also indicate a potential impact of belowground insect plant enemies, which we have not assessed with our sampling approach	Brown et al. (2004); Barnes et al. (2018)
13	(+/−) A high invertebrate predator abundance may control herbivores and reduce damage and impact on plants. This effect might not only be driven via effect on herbivore biomass (via paths 6), but also because predators might change the herbivore community composition or their behaviour	Hairston et al. (1960); Schmitz et al. (2004)
14	(?) The resource availability hypothesis predicts that plant species growing in more productive environments are usually faster growing and less defended. Hence, we expect higher herbivore damage in plant communities which are dominated by resource-acquisitive plant species. Whether the impact of herbivores is also higher in such communities is less clear, because faster growing species might be better able to compensate for tissue loss and are more tolerant to herbivore attack. Additionally, top-down effects on herbivores from predators might reduce impact in very productive environments	Coley et al. (1985)

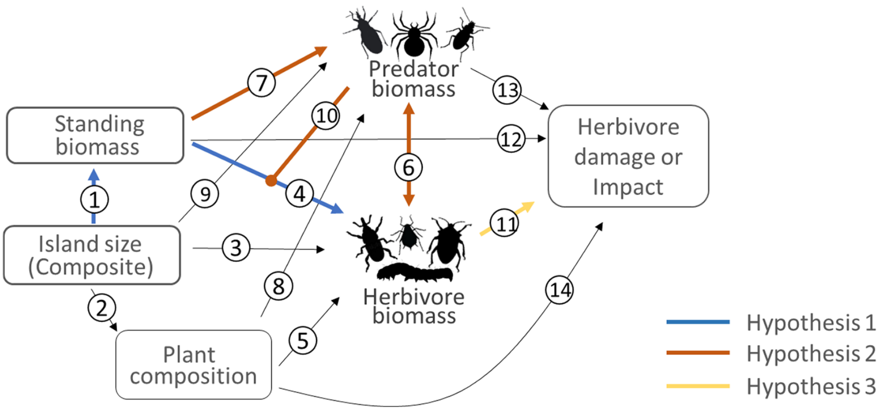

FIGURE 1 Schematic figure of the full SEM that was used to test the drivers of herbivore and predator biomass and herbivore damage. The path with the dot at one end (path 10) indicates a potential interactive effect of standing biomass and predator biomass on herbivore biomass. We tested all paths. The numbered paths and the hypotheses behind are explained in Table 1. Coloured paths in red, blue and yellow, respectively, correspond to the main hypotheses 1–3 that were tested.

collected insects from each branch using a beating sheet, which was placed below the branch and beaten with a stick (SM1, Figure S3). The samples were pooled within each tree species on each island.

For each of the three shrub species on each island, we sampled invertebrates with a leaf blower set to suction mode (Stihl SH86), on two randomly selected shrub patches (50 cm × 50 cm). We selected patches with at least 80% cover by the target species. The sampling area was covered with a frame 45 cm high to prevent arthropods escaping and was immediately vacuumed for 100 s at full power. Arthropods were intercepted in a gauze bag within the nozzle of the suction sampler and were transferred to jars (Figure S4). Samples were pooled by shrub species and island. One-time surveys might not fully characterise the invertebrate community. However, growing season in northern Sweden is short (<3 months) and by measuring at the peak of this short growing season we suggest that our data should provide a reasonable estimate enabling unbiased comparisons among islands.

Invertebrates from each sample were sorted to order or suborder level. Individuals of the sub-orders Auchenorrhyncha and Heteroptera, and the orders Coleoptera and Diptera, were identified to species by experts, as some of these groups can contain both herbivorous and predatory species. We classified invertebrates to the trophic levels 'herbivores' and 'predators', and divided herbivores into those with chewing versus sucking mouthparts (Table S2). Although ants can also be predators, we did not consider them as predators as they get most of their food from aphid honeydew in this system (Domisch et al., 2009; Rosengren & Sundström, 1987). We also classified invertebrates to the group 'aquatic insects', which are species that have aquatic larval and terrestrial adult stages, for an additional analysis.

To obtain an estimate of herbivore, predator and aquatic insect biomass on each plant species on each island, we measured body length of all individuals using a digital microscope (LEICA-DVM6), and length–mass regressions from Sohlström et al. (2018) to estimate individual fresh body mass (Table S3). For each plant species on each island, we separately summed up the biomass of all individuals classified as predators, chewing and sucking herbivores and aquatic insects.

To obtain a measure of total herbivore, predator and aquatic insect biomass, per island, for each plant species we calculated the invertebrate biomass per g aboveground standing plant biomass (dry mass). We used existing allometric equations for both trees and shrubs to convert our sampling unit (five branches for trees, 0.5 m^2 ground cover for shrubs) to plant biomass (see SM2). We then multiplied the invertebrate biomass per g plant biomass by estimates of the standing biomass (g/m^2, quantified in Wardle et al., 2003, 2012) for each of the tree and shrub species on that island. Finally, we summed up the values across all plant species per island, to get one estimate of invertebrate biomass for each island. We estimated total herbivore biomass, predator biomass, chewing herbivore biomass, sucking herbivore biomass and aquatic insect biomass per m^2 for each island in this way.

Herbivore damage and impact on phytometer tree saplings

We assessed herbivore damage and herbivore impact on the growth of planted saplings of each of three tree species which we used as phytometers. We planted phytometers on each island and grew them with and without an insecticide treatment (for details see SM3). The use of phytometers has the advantage that the genetic material is homogenous across the study, and any variation in phytometer damage and performance reflects variation in the local herbivore community (Gibson, 2015).

In August 2018 we visually assessed mean herbivore damage on each sapling by inspecting all leaves per sapling and estimating the percentage leaf area removed by chewing herbivores. To get one value of herbivore damage per island, we only considered tree saplings that had not been sprayed with insecticide. We averaged the percentage herbivore damage of those unsprayed saplings per species and island, and calculated the mean percentage herbivore damage across all three species.

To assess herbivore impact on plant biomass we harvested all phytometer saplings and assessed their aboveground dry weight. We calculated a log-response ratio comparing biomass of saplings with insecticide (reduced herbivory) to those without insecticide (ambient herbivory) as LRR = log(Biomass with insecticide)/log(Biomass without insecticide, details see SM3). A LRR of 0 would indicate that herbivores have no impact on sapling biomass, a LRR >0 would indicate that herbivores have a negative impact. To get one value of impact per island, we averaged the LRR per species on that island, and calculated the mean LRR over all species.

Statistical analysis

We used structural equation models to estimate the direct and indirect drivers of herbivore and predator biomass, as well as herbivore damage and impact. Our main question was whether invertebrate biomass depended on island size, and whether this effect was direct (path 3 in Figure 1 and Table 1) or indirectly mediated by plant standing biomass (path 4) or plant functional composition (path 5). Predictions about direct effects of island size on invertebrate biomass are less clear, as theory about how island size might affect higher trophic levels is instead focused on the diversity of organisms (MacArthur & Wilson, 1967); however, we included the direct path as well. We did not include nutrient availability as a variable in our model, because this is reflected by several different variables which show partly contrasting responses to retrogression and if would therefore be difficult to select a single variable that is fully indicative of nutrient availability in soil and foliage. We included plant standing biomass, as this responds strongly to nutrient availability in our system (Wardle et al., 2012) and is the variable most relevant to the performance of herbivores. Additionally, we tested whether effects of island size and plant biomass on herbivore biomass cascade up to predator biomass (path 6). We then tested models in which herbivore biomass is affected by predator biomass (top-down influence) and in which predator biomass is affected by herbivore biomass (bottom-up influence). These models were equivalent (same AICs), but as herbivore biomass was positively related to predator biomass, we consider the bottom-up model to be more ecologically plausible. We included an interaction term between predator biomass × standing plant biomass, to test whether the relationship between plant and herbivore biomass is stronger when predator biomass is low, and weaker when predator biomass is high (path 10 in Figure 1 and Table 1), as predicted by the EEH hypothesis. Thus, our model contained a feedback, whereby herbivore biomass affects predator biomass and at the same time predator biomass affects herbivore biomass in interaction with plant biomass (for discussion and details, see SM4). Finally, we investigated the drivers of herbivore damage and impact on phytometer biomass (paths 11–14). We tested whether damage and impact are driven by herbivore biomass, but we also included a direct path from plant standing biomass and plant functional composition, as these variables might affect the functional composition of the herbivore community (which we did not measure) and might alter damage and impact independent of their effects on herbivore biomass. We included a direct path from predator biomass to damage and impact for the same reason.

We log-transformed island area, and the biomass of invertebrates. All variables were standardised to comparable scales (Grace, 2006). To account for nonlinear relationships between island size and the other variables, we modelled the island size effect using a composite of the first- and second-order terms of log-transformed island size. We ran different SEMs: one in which we included total herbivore biomass, one with only chewing and one with only sucking herbivore biomass, to test whether the drivers of herbivore biomass differ between the different feeding guilds. To test whether the drivers of herbivore damage and impact are similar, we ran the model with total herbivore biomass, once with herbivore damage and once with impact. We also ran an additional SEM to test whether aquatic insects affect predators.

We removed non-significant paths from the model and tested whether their exclusion affected the overall model fit (i.e. whether it increased AIC). We also investigated the possible effects of spatial autocorrelation, island isolation and the possible impact of the islands being located in two separate (although close) lakes (SM4). All analyses were performed using R (R Core Team, 2017), and with the LAVAAN and lme4 package (Bates et al., 2015; Rosseel, 2012). We explain how we modelled the feedback as well as other structural equation modelling procedures in detail in the Supporting information (SM4).

RESULTS

We collected 18,979 invertebrate individuals, with a total biomass of 57,450 mg fresh weight. Of those, 3232 individuals (13,009 mg fresh weight) were herbivores (chewing herbivores: 546 individuals and 9737 mg; sucking herbivores: 2686 individuals and 3272 mg), and 10,537 individuals (31,261 mg) were predators (Tables S4 and S5). The remaining invertebrates were detritivores, fungivores or aquatic insects hatching from the lake.

In our SEM, island size appears to strongly affect plant standing biomass, with larger islands having higher plant standing biomass (Figures 2 and 3a, Tables S6 and S7). Island size also explains plant composition as it is negatively related to PC1 (Figures 2 and 3b), meaning that larger islands were dominated by the most resource-acquisitive species, *Pinus* and *V. myrtillus* and smaller islands by the most resource conservative species, *Picea* (Figure S1; Figure S2).

Model results suggest herbivore biomass was strongly affected by bottom-up forces and increases with plant standing biomass (Figures 2a and 4). The observed strength of this relationship depended on invertebrate predator biomass—when predator biomass was higher, the relationship between herbivore biomass and plant standing biomass was weaker (shown by the interactive effect of invertebrate predator biomass and plant standing biomass on herbivore biomass, Figures 2 and 4). This agrees with the trophic flip predicted by the EEH. Herbivore biomass was also related to plant species composition, and was found to be higher in plant communities dominated by more resource conservative species (Figures 2 and 3c).

Invertebrate predator biomass was higher on islands with a higher herbivore biomass (Figures 2 and 3d). This effect was mainly driven by chewing herbivores (Figure 5, Table S8, Figures S5–S7). Invertebrate predator biomass was also higher on smaller islands (Figures 2 and 3e, Table S6). When we included a path from aquatic insects to predator biomass, we found that a higher biomass of aquatic insects increased invertebrate predator biomass (Figure S8, Table S10), and the effect of island size on predator biomass then disappeared.

The insecticide treatment was effective in reducing herbivore damage on the three phytometer species across all islands (SM3, Table S11). The damage on the unsprayed

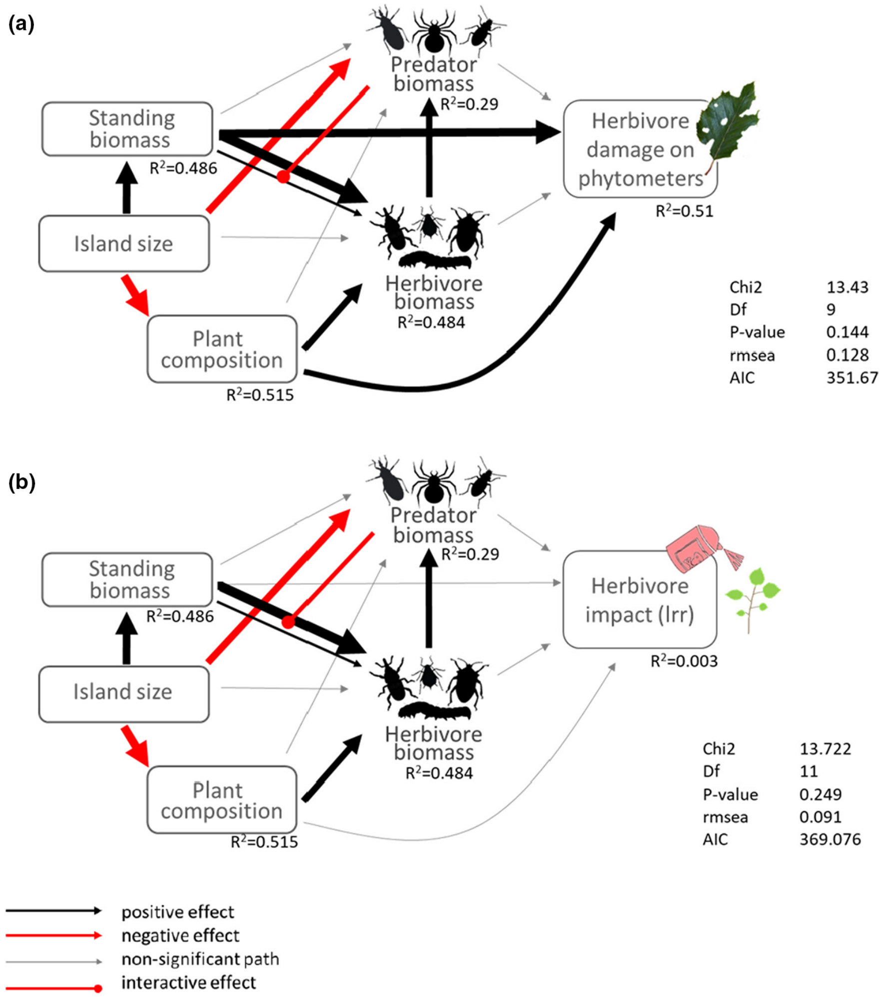

FIGURE 2 Results of structural equation models on the drivers and consequences of herbivore and predator biomass. (a) Investigates the drivers of herbivore damage on the phytometer tree saplings, (b) investigates the drivers of herbivore impact, which is the biomass of insecticide treated phytometer trees relative to the biomass of untreated phytometer trees (i.e. $\text{LRR}_{(\text{herbivore impact})}$). Black lines: Significant positive effects at $p = 0.05$. Red lines: Significant negative effects at $p = 0.05$. Grey lines: Non-significant paths. The red line with the dot at the end indicates the interactive effect of standing biomass and predator biomass on herbivore biomass. Arrow width: Relative strength of the path, see Tables S6 and S7.

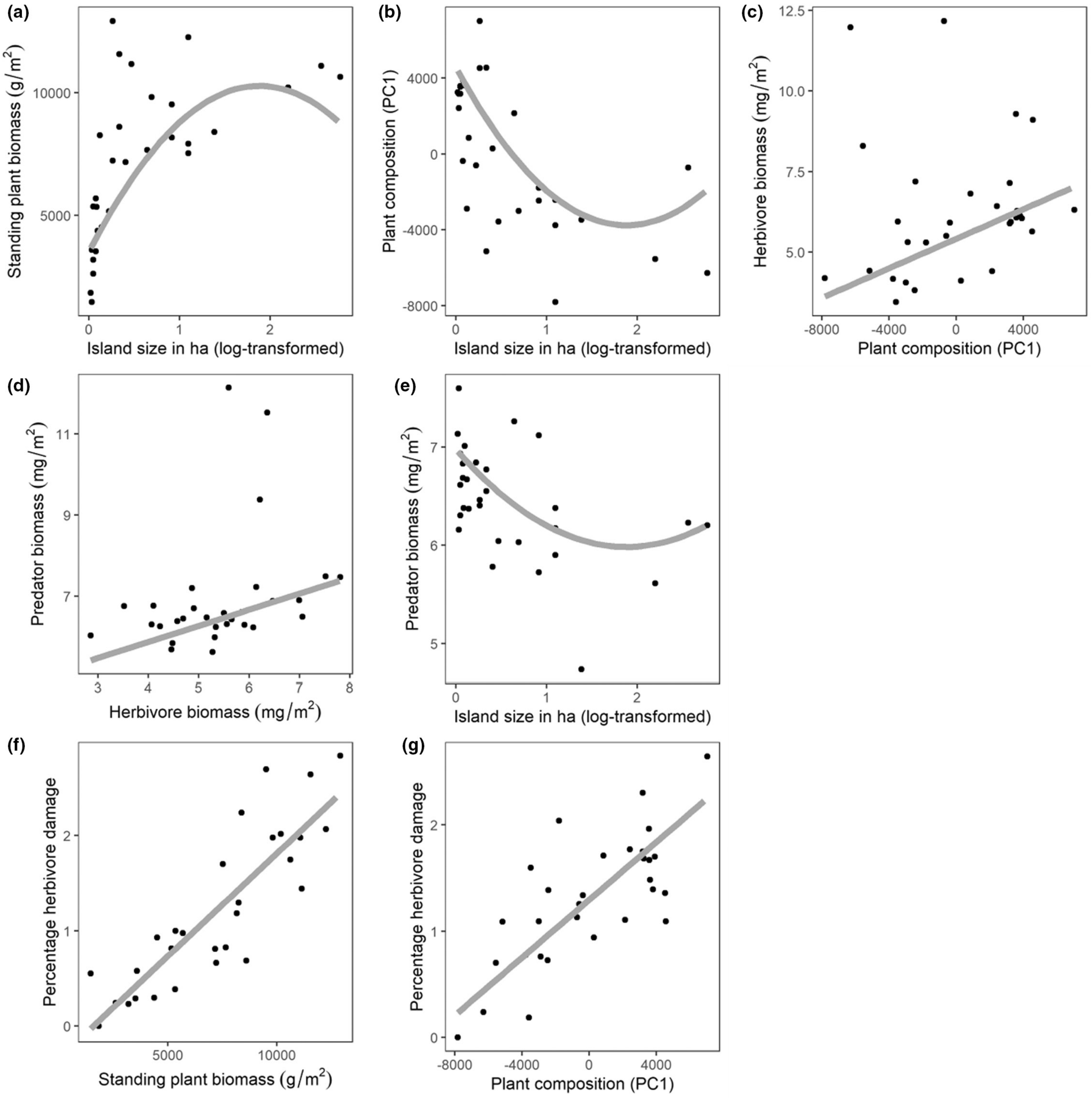

FIGURE 3 Partial plots of the SEM in Figure 2a. Impact of significant predictor variables on standing plant biomass (a), plant composition (b), herbivore biomass (log-transformed) (c), predator biomass (log-transformed) (d, e) and percentage herbivore damage on the phytometer saplings (f, g), after removing all effects of all the other variables which are not plotted. Lines are predicted calculated using the coefficients of the SEM.

phytometer tree saplings was highest on islands with higher standing plant biomass (Figures 2a and 3g). This effect could not be explained by herbivore biomass (Figure 2a). Plant composition also had strong direct effects on herbivore damage to the phytometer plants; phytometers on islands where resource conservative plant species dominated had the highest damage (Figure 3j). In contrast, herbivore *impact* on phytometer biomass (comparing biomass of control and insecticide treated tree saplings) was not affected by any of the tested drivers (Figure 2b, Table S7).

DISCUSSION

Our study across a retrogressive forested chronosequence shows that nutrient availability strongly controls invertebrate herbivore biomass when invertebrate predators are rare, but that there is a switch from bottom-up to top-down control of herbivores when invertebrate predators are common. This trophic flip is likely to contribute to the large variation we observe across herbivore impact studies (Coupe & Cahill, 2003; Jia et al., 2018; Schädler

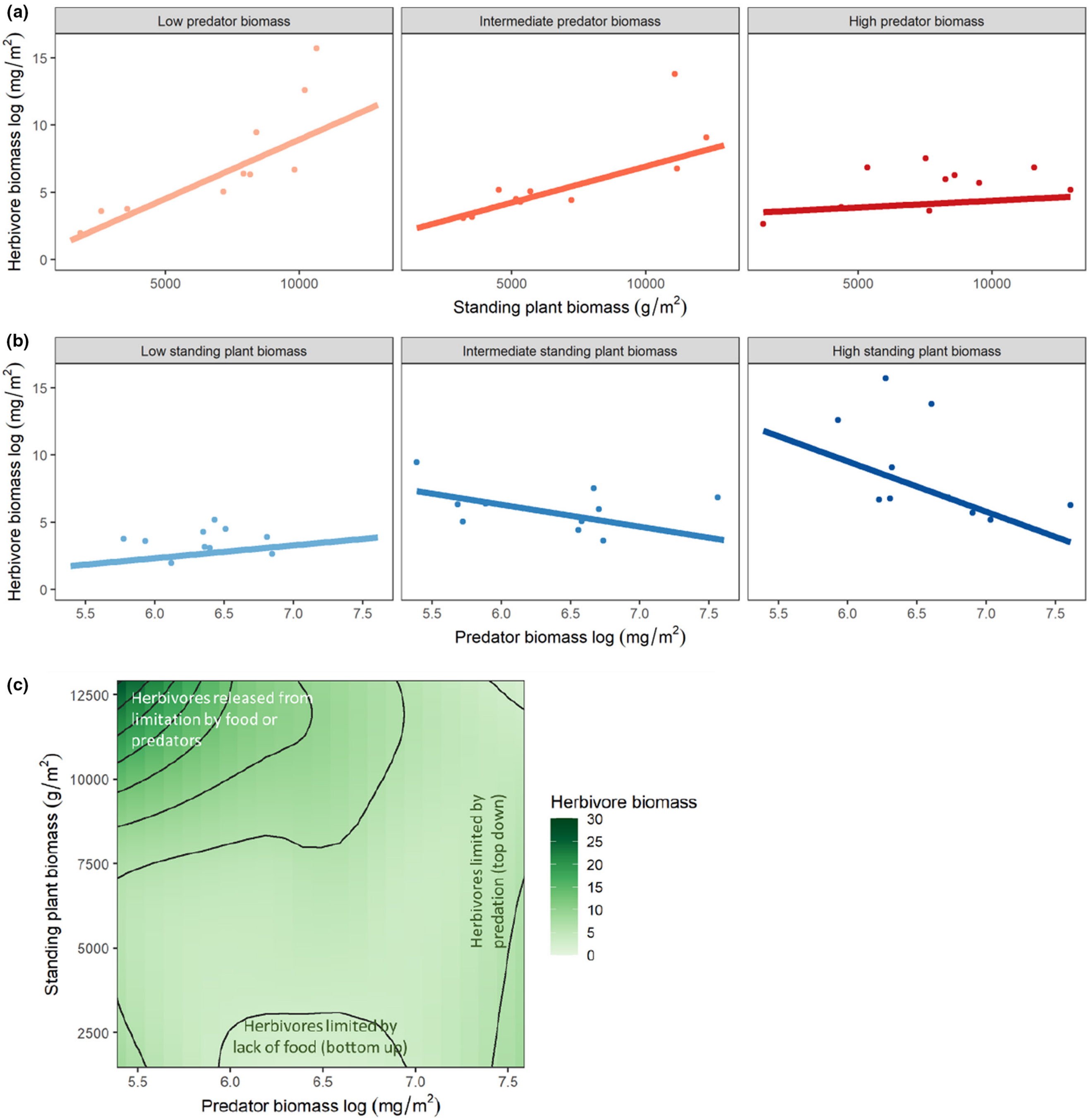

FIGURE 4 Partial plots of the SEM in Figure 2a, showing the interactive effect of standing plant biomass and predator biomass on herbivore biomass, after removing all effects of all the other variables which are not plotted. (a) Herbivore biomass increases strongly with plant standing biomass for lower predator biomass, but less strongly for higher predator biomass. (b) Herbivore biomass is unresponsive to predator biomass for low standing plant biomass, but decreases for high plant biomass. For easier graphical visualisation, predator biomass (a) and plant standing biomass (b) have been binned into equal sized groups (low, intermediate and high), each group containing 10 islands (predator biomass: Low [5.39–6.3], intermediate [6.3–6.63], high [6.63–7.61]; standing biomass: Low [1460–5340], medium [5340–8460], high [8460–12,900]). Lines are predicted calculated using the coefficients from the SEM. We show relationships for low, intermediate and high values of predator biomass or standing plant biomass (low values = 5% quantile, intermediate = median and high values = 95% quantile. (c) Shows the interactive effect of standing plant biomass and predator biomass on herbivore biomass in a contour plot, where dark colours indicate a high herbivore biomass. Herbivore biomass can only increase if herbivores are neither limited by food nor by predators (upper left corner).

et al., 2003), and may arise because invertebrate predators can respond to alternative energy channels independent of plant biomass. Our results further suggest that herbivore impact cannot necessarily be inferred from damage. We discuss these findings in the context of each of our three hypotheses to better understand the factors that regulates herbivore communities and their impacts on plants.

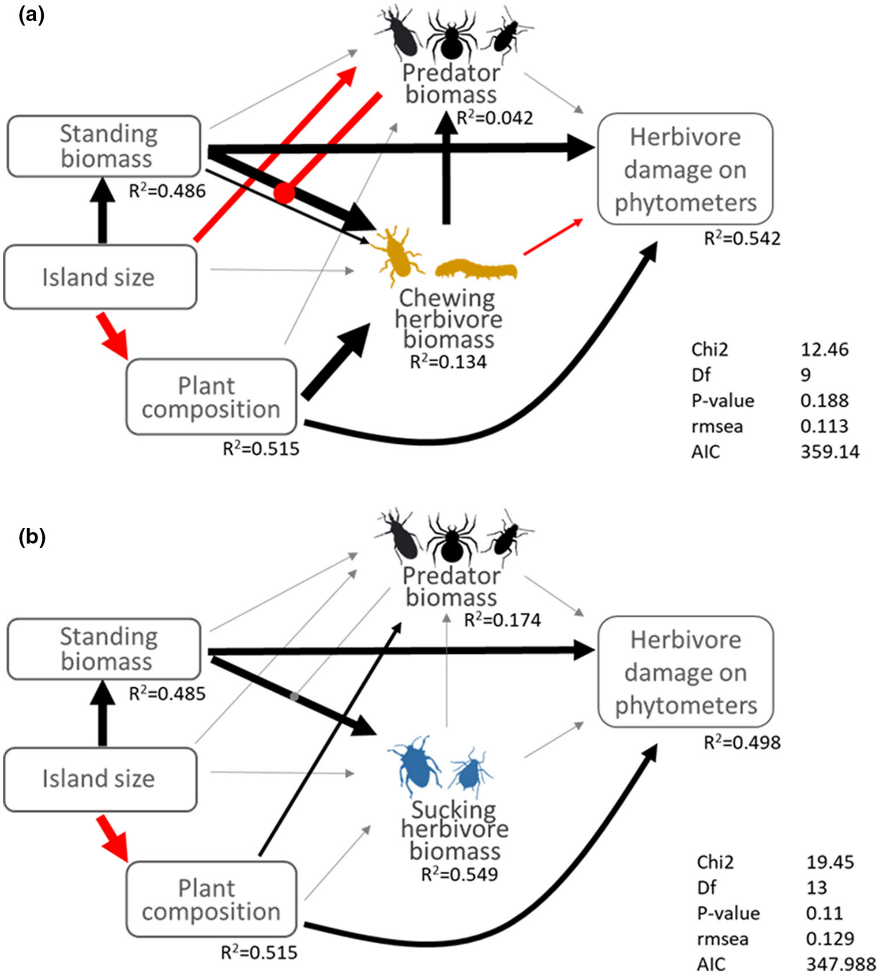

FIGURE 5 Structural equation models on the drivers and consequences of the biomass of (a) chewing herbivores and (b) sucking herbivores. Black lines: Significant positive effects at $p = 0.05$. Red lines: Significant negative effects at $p = 0.05$. The red line with the large dot at one end in panel a indicates the interactive effect of standing biomass and predator biomass on herbivore biomass. Grey lines: Non-significant paths. The dashed red line in panel (b) indicates a marginally significant effect at $p = 0.092$. Thickness of line indicates strength of the path or correlation, see Tables S8 and S9.

Bottom-up versus top-down control of invertebrate herbivores

We found evidence that plant biomass controls invertebrate herbivore biomass: both plant and herbivore biomass declined with decreasing island size as nutrients become more limiting and plant biomass and productivity declines, which supports hypothesis 1. The cascading bottom-up effect of changes in plant biomass on higher trophic levels that we found is in line with empirical studies using anthropogenic fertility gradients and experiments in grasslands (e.g. Borer et al., 2012; Simons et al., 2014; Welti et al., 2020), as well as theory (Coley et al., 1985; McNaughton et al., 1989; Power, 1992). However, few studies have explored invertebrate trophic responses to lengthy natural gradients of nutrient availability associated with ecosystem retrogression, and our results align with one previous study on total herbivore abundance in Hawaii (Gruner, 2007), but not with another on a specialist weevil in our study system (Crutsinger et al., 2008). Specialist herbivores may respond differently to resource availability than generalists, or the entire herbivore community, because they often use secondary compounds as cues to find their host plants or sequester chemicals for their own defence (Ali & Agrawal, 2012), which could explain the discrepancy between our results and those of Crutsinger et al. (2008). Altogether, our results indicate that changes in plant biomass along natural soil fertility gradients involving retrogressive states strongly cascade up to affect higher trophic levels.

Despite the bottom-up effects of plant biomass on herbivore biomass, we also found evidence of top-down control of invertebrate herbivores by invertebrate predators. The strength of top-down control was not highest on the most productive islands as predicted by the EEH, but instead appeared to depend on invertebrate predator biomass. This involved a switch from bottom-up control of herbivores when invertebrate predators were few to top-down control when invertebrate predators were common, in line with previous studies on vertebrates (Letnic & Ripple, 2017) and two arthropod groups in grasslands (Welti et al., 2020). Thus, consistent with hypothesis 2, herbivore control flipped from bottom-up to top-down with increasing invertebrate predator biomass. However, although plant standing biomass indirectly promoted invertebrate predator biomass via the biomass of chewing herbivores, parts of hypothesis 2 were not confirmed as invertebrate predators did not peak in abundance on islands with the highest plant biomass. Instead, invertebrate predators were affected directly by island size, and their biomass was highest on the smallest (most nutrient limited) islands (Tables S4 and S5). This may be because the predators in our system do not depend entirely on herbivores, and also use insects hatching from the surrounding lake water as prey (Jonsson et al., 2009). Small islands have a larger perimeter-to-area ratio, and thus on average a larger per-unit-area aquatic insect abundance than larger islands (Polis et al., 1997), supporting greater predator populations (Twining et al., 2016). The addition of aquatic insect biomass to our SEMs indeed confirms the idea that predators not only prey on terrestrial herbivores, but are additionally supported by the availability of aquatic insect prey (Figure S8, Table S10).

The partial independence of invertebrate predator biomass from plant and herbivore biomass that we found contrasts with the strong relationship between plant and predator biomass found for vertebrate communities (e.g. Crête, 1999; Letnic & Ripple, 2017; Oksanen et al., 2020). However, it might apply more generally to invertebrate predators. For instance, many invertebrate predators also feed on pollinators which show contrasting responses to soil fertility compared to herbivores (Allan et al., 2014; Carvalheiro et al., 2020; Clough et al., 2014), or can benefit from cross-ecosystem flows of organisms such as between interconnected aquatic and terrestrial habitats (Gounand et al., 2018). Thus, the prediction of the EEH and hypothesis 2, that predator biomass is highest and herbivore impact reduced in productive systems, may not hold for invertebrates. However, the other prediction of the EEH, the trophic flip in herbivore control from bottom-up when predators are few to top-down when they are common, seems to be important in our system and partly confirms hypothesis 2 (Figure 4c). Our results suggest that switches between top-down and bottom-up control may indeed occur for invertebrate food webs but that these may be mediated more by changes in predator biomass than by cascading effects of changes in plant productivity.

Herbivore damage is not equal to herbivore impact

Herbivore leaf damage of phytometers was highest on islands with the highest plant standing biomass, supporting the resource availability hypothesis, and hypothesis 3. Surprisingly, however, phytometer leaf damage was not driven by total herbivore or chewing herbivore biomass, but was directly promoted by standing plant biomass and dominance by resource conservative plant species (see SEM in Figures 2a and 5a). A direct effect of island plant biomass or composition on phytometer damage is unlikely, as increased plant biomass could not result in more damage without altering some aspect of the herbivore community. Instead, it is more plausible that variation in plant biomass and composition affected phytometer damage by altering the island's herbivore community composition, which we did not measure. Moreover, damage was lower on phytometers growing on islands dominated by resource-acquisitive species (*Pinus*). Large islands, with higher plant biomass are dominated by resource-acquisitive species, however, this result shows that after correcting for island size and plant biomass, phytometers on islands with a high abundance of *Pinus* actually suffered less damage. This may have occurred because our phytometers were all broad-leaved species which might have suffered less attack by the herbivore community associated with *Pinus*.

Although herbivore leaf damage on phytometers peaked on fertile islands, herbivore impact, that is, the effect of herbivores on phytometer biomass, was unrelated to any predictor variables, or to leaf damage, in line with hypothesis 3. This brings into question the use of damage as an indicator of herbivore impact (Galmán et al., 2018; Moles et al., 2011). The lack of a relationship between damage and impact may have arisen because plants on more fertile islands are more tolerant of herbivore attack (Cronin et al., 2010). In addition, sap-sucking insects can strongly affect plant biomass, but their impact is hard to quantify visually. While some studies have suggested that the impact of herbivores on primary production varies as a function of productivity (Fraser & Grime, 1997), the results of meta-analyses of insect exclusion studies in grasslands have been inconclusive (Coupe & Cahill, 2003; Jia et al., 2018; Schädler et al., 2003). Thus, our results for tree sapling phytometers agree with findings from studies in grasslands that herbivore impact is not clearly linked to resource availability. However, our phytometer approach might not perfectly reflect herbivore impact on the islands, as we used only broad-leaved tree saplings and no conifers or ericaceous shrubs (the other dominant plant group present in the island system) as phytometers (see SM3). Moreover, exclusion experiments remain rare, and more replicated exclusion experiments across contrasting ecosystems, like the one we performed here, or like those proposed by global research networks (e.g. the Bug-Network, bug-net.org) are key to further understanding context dependency of herbivore impact on plant communities.

CONCLUSION

We found a trophic flip in herbivore control, from bottom-up, when invertebrate predators were few, to top-down when invertebrate predators were common, which likely arose because predators were not affected by cascading effects of plant productivity but used additional energy channels. Our findings have several implications. First, they highlight that classic theories of community regulation (e.g. Hairston et al., 1960; Oksanen et al., 1981), based on in-situ productivity, can be incomplete when organisms forage across ecosystem boundaries (Leroux & Loreau, 2012). Such cross-ecosystem energy flow can lead to apparent competition between organisms from different systems, because increased resources in one system can increase predators, and hence top-down pressure on consumers, in the other system (Guichard & Marleau, 2021; Loreau et al., 2003). Second, our study calls for a better understanding of the drivers of herbivore impact. Herbivore community biomass may be a poor proxy of herbivore energy demand and impact (Barnes et al., 2018; Ehnes et al., 2011), and future studies that combine classical exclusion experiments with herbivore impact assessments based on energy fluxes (Barnes et al., 2020) could help bring clarity to these relationships. Third, our study highlights that retrogressive chronosequences can be useful model systems to study trophic relationships along *natural* soil fertility gradients. Given the large contribution of invertebrate herbivores to ecosystem functioning (Soliveres et al., 2016), and the ongoing changes in insect biomass currently occurring in terrestrial systems (van Klink et al., 2020), the need to improve our understanding of the drivers regulating insect biomass and impact is taking on a new importance.

AUTHOR CONTRIBUTIONS

Anne Kempel and David A. Wardle designed the study and obtained the necessary funding. Anne Kempel collected the data, analysed the data with substantial input from Eric Allan and James B. Grace and wrote the manuscript with substantial input from Eric Allan, David A. Wardle, Martin M. Gossner, James B. Grace and Malte Jochum. Anne Kempel, Malte Jochum and Martin M. Gossner coordinated the length measurements of the invertebrates. Malte Jochum calculated invertebrate biomass.

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DATA AVAILABILITY STATEMENT

Data and R-code are available in the public repository Dryad (Kempel et al., 2022; https://doi.org/10.5061/dryad.mw6m90610). The method section and Supporting Information files provide all necessary information about the dataset.

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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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