

Spatially Heterogeneous Perturbations Homogenize the Regulation of Insect Herbivores

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ABSTRACT: Anthropogenic influences on resources and consumers can affect food web regulation, with impacts on trophic structure and ecosystem processes. Identifying how these impacts unfold is challenging because alterations to one or both resources and consumers can similarly transform community structure, especially for intermediate consumers. To date, empirical testing of perturbations on trophic regulation has been limited by the difficulty in separating the direct effect of perturbations on species composition and diversity from those unfolding indirectly via altered feeding pathways. Moreover, disentangling the independent and interactive impacts of co-varying stressors that characterize human-altered systems has been an ongoing analytical challenge. We used a large-scale metacommunity experiment in grasslands to test how resource inputs, stand perturbation, and spatial factors affect regulation of insect herbivores in tritrophic grassland food webs. Using path-model comparisons, we observed significant simplification of food web regulation on insect herbivores, shifting from mixed predator-resource regulation in unaltered mainland areas to strictly resource-based regulation with landscape perturbation and fragmentation. Most changes were attributed to homogenization of plant community caused by landscape fragmentation and the deterministic influence of eutrophication that reduced among-patch beta diversity. This led to a simplified food web dominated by fewer but more abundant herbivore taxa. Our work implies that anthropogenic perturbation relating to resources and spatial isolation can transform the regulation of food web diversity, structure, and function.

Keywords: global change, trophic consumer regulation, metacommunity, habitat fragmentation, eutrophication, plant-insect interactions.

Introduction

Anthropogenic changes are affecting the abundance, richness, and spatial distribution of consumers, often leading to regime shifts and the degradation of ecosystem processes

(Silliman et al. 2013). These effects are especially acute for insect herbivores, which influence numerous ecological and evolutionary processes, including functional attributes relating to plant production and pollination (Crawley 1989; Branson et al. 2006; Schmitz 2010; Agrawal et al. 2012; Silliman et al. 2013; Borer et al. 2014). There is widespread evidence for anthropogenic-based changes to insect herbivore communities, with signals including reduced species richness, invasion, outbreaks, and selection toward generalist feeding strategies (Tscharntke and Brandl 2004; Branson et al. 2006; Clavel et al. 2010; Martinson and Fagan 2014). What remains unclear are the main drivers of these changes, given that human disturbances (e.g., habitat loss, stand perturbation) may directly affect herbivore diversity and composition but also do so indirectly via trophically mediated effects on plants and predators (Halpern et al. 2005; Shurin et al. 2012; Rzanny et al. 2013).

Theoretical models for the regulation of insect herbivores, as for most consumers, generally emphasize interactions between resource-based bottom-up and predatory top-down processes (Strong et al. 1984; Crawley 1989; Schmitz 2008; Price et al. 2011). Both processes can be affected by human activity, but the consequences for herbivore diversity and composition can be unclear (Silliman et al. 2013). Eutrophication, for example, can elevate the production of insect herbivores by increasing plant productivity (Polis et al. 1997) but can simultaneously select against herbivore richness, especially specialist feeders, because nutrient-rich plant communities tend to be species poor (Stevens et al. 2004; Hautier et al. 2014) and support fewer feeding guilds (Haddad et al. 2000, 2009; Borer et al. 2012).

Loss of apex arthropod predators (Hendrickx et al. 2007; Shochat et al. 2008), however, can have similar effects, with reduced predation increasing herbivore abundance but also lowering richness if one or a few herbivores dominate (Holt 1977; Oliver et al. 2009). There may also be strong interactions between human-induced changes to resources and predators: nutrient enrichment may drive consumer birth

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rates that far exceed predator-driven herbivore mortality or may cause system instability by creating top-heavy feeding webs (Polis et al. 1997; McCann 2011; Shurin et al. 2012; Tunney et al. 2012).

Uncertainties concerning top-down and bottom-up influences on insect herbivores can be compounded by the transformation of spatial processes in anthropogenic landscapes, through factors such as habitat loss and patch isolation (Kruess and Tschamtk 1994; Polis et al. 1997; Valladares et al. 2006). This can directly affect the spatial turnover of herbivore species by dispersal constraints but can also affect it indirectly by limiting their resources and predators. Habitat loss, for example, can maximize either stochastic influences on plant community assembly (i.e., different plant communities on different islands due to random dispersal) or deterministic ones by favoring the same subsets of species with traits for long-distance colonization (Arroyo-Rodríguez et al. 2013; Harvey and MacDougall 2014). Habitat loss can also modify predation pressure by concentrating predators in smaller remnant areas, creating predation-free patches via dispersal limitation (Kruess and Tschamtk 1994; Hein and Gillooly 2011), or reducing predator diversity on smaller patches because of food limitation (Holt 1997; Gravel et al. 2011). The end result of all of these potential changes to insect herbivores, both direct and indirect, is that the outcomes of anthropogenic change on insect-based food webs can be difficult to predict.

One way to address the uncertainty is to combine multi-factorial and large-scale experimental approaches that capture direct and indirect human impacts with integrative statistical modeling that can account for these variable influences (Weiher et al. 2004; Grace 2006; Grace et al. 2012; Hooten and Hobbs 2015). Such an integrative approach, which is the focus of this study, avoids the limitations of global change experiments emphasizing mostly univariate processes (Rösch et al. 2013; Shurin et al. 2012; Hautier et al. 2014; Thébault et al. 2014) while analytically accounting for many of the interactive and indirect mechanisms that can determine outcomes to global change (Grace et al. 2012). Here we test how multiple stressors on consumers and resources affect insect herbivore diversity, composition, spatial turnover, and trophic regulation in continuous grassland versus fragmented grassland. We use a large-scale (25-ha) mainland island experiment, factorially manipulating a range of co-occurring changes associated with anthropogenic impacts (eutrophication, stand perturbation, and habitat fragmentation). Our main objective is to test whether these typical anthropogenic-based impacts associated with human activity affect insect herbivores mainly via direct effects or indirectly by their effects on plant or predator composition and diversity. We do this with three complementary steps: (i) testing for the main effects of habitat size, spatial constraints, eutrophication, and defoliation on

herbivore diversity, composition, and among-island spatial turnover; (ii) using a path model comparison approach to test whether these effects on herbivores occur through direct or food web-mediated effects; and (iii) contrasting how these changes compare to herbivore dynamics in unperturbed and continuous mainland habitat. This approach allows us to separate the direct effects of perturbation on herbivores versus those mediated indirectly by how perturbations affect plants, predators, and spatial constraints.

Material and Methods

Experimental Design

We worked in a 25-ha study area at the rare research reserve (<http://www.raresites.org/>) near Cambridge, Ontario, Canada (43.4°N, -80.4°W). The study area had two sections: a 13-ha array of prairie islands constructed in fall 2011 in a field that previously had been farmed intensively for 50+ years and a 12-ha adjacent mainland oldfield. The islands were of three sizes (25, 100, and 400 m²) randomly located on an isolation gradient from the nearest edge of the mainland (see fig. A1; figs. A1, A2 available online). The mainland was dominated by plant species ubiquitous to oldfields of eastern North America (grasses: *Festuca rubra*, *Poa pratensis*; forbs: *Solidago* spp., *Daucus carota*, *Cirsium* spp.) and served as the main source of insect colonization to the islands (Harvey and MacDougall 2014). The south and east boundaries of our study area were agricultural fields (corn, soy, and wheat); a line of scattered trees borders the area between the prairie islands and the crop fields (fig. A1).

At the beginning of the experiment, the 13-ha island area was bare ground. Plant colonization of the islands likely came from two main sources: wind dispersal and the seed bank (i.e., seeds deposited prior to island establishment). The matrix between the islands was mowed to ~10-cm height throughout the growing season to maintain isolation. To monitor the effectiveness of mowing for island isolation, we sampled the matrix for arthropods along three north-south transects (see appendix, “Experimental Design and Sampling Location”; appendix available online).

Starting in 2012, one of four perturbation treatments was applied to each island: nitrogen addition in the spring, defoliation by mowing in the fall, nitrogen and defoliation combined, and control. The treatments were replicated three times per island size (4 treatments × 3 sizes × 3 replicates = 36 islands). Enriched islands had 10 g N m⁻² of urea pellets (46-0-0) applied once per year in early June. Patches were mowed to ground level annually at the end of the growing season (November), with all biomass raked and removed. The main purpose of the mowing treatment was to remove structural habitat for arthropods and to increase ground-level light availability for plants in the following spring.

Arthropod and Plant Sampling

Plants and arthropods were sampled at peak plant biomass at the end of July 2013. For insects, we sweep netted 4-m² quadrats randomly located on each island. There were two quadrats on the 25-m² islands, three on the 100-m² islands, and five on the 400-m² islands, for a total of 120 quadrats. In the mainland, we complemented the information collected on the islands by sampling insect and plant diversity and abundance in nine randomly located 4-m² quadrats. All insect specimens were stored on ice before being frozen in the lab the same day. Sampled insects were first sorted by morphotypes to separate predators from herbivores (especially important for large taxonomic groups containing both predators and herbivores, e.g., Miridae) and then identified to the family level, following Marshall (2007). For heterometabola groups (Hemipteran and Orthoptera families) that are not going through complete metamorphosis or ontogenetic diet shifts, we included nymphs with adults, as they fill the same functional role for the purpose of this study. Overall, the most abundant herbivores were Cercopoidea (spittlebugs), Chrysomelidae (leaf beetles), Cicadellidae (leafhoppers), Gryllidae (crickets), and Miridae (plant bugs); the most abundant predators were Dictynidae (sac spiders), Salticidae (jumping spiders), and Thomisidae (crab spiders).

In all 4-m² quadrats, we measured the composition, richness, and relative abundance (percent cover to 1%) of all plants. The final data set, including the mainland, contained 74 plant species and 4,848 arthropod individuals from 24 primary consumer families and 23 predator families (see tables A1, A2 for a description of sampled plant and insect taxa in mainland and island areas; tables A1, A2 available online).

Statistical Analyses

Our analysis had three complementary steps. We first tested the individual and interactive effects of the treatments (island size, spatial constraints, fertilization, defoliation) on insect herbivore richness, abundance, evenness, and among-island spatial turnover in composition. Then we used a model comparison approach to evaluate whether the detected effects of the stressors on insect herbivores were mainly mediated by changes in plants, predators, or both. Finally, we contrasted our findings with plant, herbivore, and predator diversity and composition data from adjacent untreated mainland grassland.

Treatment Effects. To determine the individual and interactive effects of the treatments on insect herbivores, we used three-way ANOVA testing the effects of island size, fertilization, and defoliation with spatial constraints as a covariate (principal coordinates of neighborhood matrix [PCNM] axes; see below). We tested for changes in herbi-

vore taxa richness, abundance, and evenness, given that not all community metrics will be as sensitive to each of the treatments. To integrate spatial autocorrelation patterns related to distance between islands and isolation, we performed a PCNM analysis on the geographical coordinates of each sampling quadrat (Borcard and Legendre 2002). For the structural equation models (see below) and the ANOVA analyses, we selected the minimum number of PCNM axes to maximize both parsimony and explanatory power. Based on a forward selection procedure (Legendre and Legendre 2012), we determined that two PCNM axes (total $R^2 = 25\%$) explained most of the among-island spatial effects on plant and arthropod diversity and composition (i.e., adding more axes had no qualitative effects on the results).

To test for treatment effects on herbivore among-island spatial turnover in composition, we used PERMANOVA-post hoc multivariate homogeneity of group dispersions (PERMDISP) analyses on square-root-transformed Bray-Curtis abundance matrices (Anderson 2001). PERMANOVA analyses are more robust than other similar tests (e.g., Mantel) but still tend to confound differences in species composition across treatments (location) versus within-treatment (dispersion) differences in community dissimilarity (Warton et al. 2012). In order to separate these two effects, for each significant term from the PERMANOVA, we used a PERMDISP analysis to test for a change in within-treatment variance (Anderson 2001; Anderson and Walsh 2013). To preserve between-object distance accurately (Legendre and Legendre 2012), we illustrated the results using nonmetric multidimensional scaling (NMDS).

Mediated Effects. To evaluate the relative importance of direct effects versus trophically mediated effects of the treatments on herbivores, we built four different candidate SEMs (or path models) that we compared using Akaike's information criterion (AIC; following Burnham and Anderson 2002). Each model described different possible outcomes covering current hypotheses on the regulation of consumer diversity (see appendix, "Candidate Models Description," for more details on each candidate model). The first and second models represented the treatment effects on herbivores by a direct effect on either plants (bottom-up model) or predators (top-down model). The third model represented interactive top-down/bottom-up effects, with the treatments affecting herbivores via effects on both plants and predators (mixed model). The fourth model represented the direct effects of the treatments on herbivores without mediated effects by plants or predators (set to zero; nontrophic model).

For each candidate SEM we included the effect of richness, abundance, evenness, and composition at each trophic level (i.e., producers, herbivores, and predators). To integrate changes in community composition at each tro-

phic level, we reduced the number of variables using principal coordinate analyses (PCoA) on Bray-Curtis dissimilarity matrices. For each trophic level, we selected the number of axes necessary to explain at least 70% of the variation (five for plants, two for herbivores, and six for predators) and included them within each SEM as composite variables (plant composition, herbivore composition, and predator composition).

Within-trophic-level community metrics (richness, abundance, evenness, PCoA axes) that were strongly correlated (correlation coefficient higher than 80%, e.g., predator richness and abundance) and thus generated covariance matrix issues and model instability were removed to keep only one of the two, since they are considered redundant (Grace 2006). Indeed, the remaining within-trophic-level community metrics are nonetheless expected to covary to a certain degree. Because this source of variation was not of interest for the purpose of our analyses, we controlled for it by including in each SEM the residual covariance among-trophic-level community metrics until this covariation represented less than two units of variation in maximum likelihood (based on modification indexes; Rosseel 2012). To facilitate comparison between selected models, we present standardized path coefficients where the effect of any endogenous (dependent) variable i on another potentially covarying endogenous variable j is noted β_{ji} and the effect of any exogenous (explanatory) variable k on an endogenous variable j is noted γ_{jk} (following Grace 2006).

Mainland Islands. To test how the among-island dynamics differed from the unperturbed, continuous mainland, we used the same model selection approach but with all the treatment effects set to zero (i.e., because this area was not treated with nitrogen or perturbations). We also used one-way ANOVA to test the effect of fragmentation (i.e., transition from the mainland to the islands) on plant, herbivore, and predator richness, abundance, and evenness. To test for the effects of fragmentation on changes in spatial turnover in composition, we used PERMANOVA-PERMDISP analyses (see above).

One issue that could bias our analysis is the imbalances in sampling effort across different island sizes. The issue derived from the necessary sampling differences in plot number by island size, with smaller islands being relatively oversampled and larger ones undersampled (as described above). For both plants and insects, the sampling covered 32%, 12%, and 5% of total island area, from small to large islands, respectively. This sampling protocol represented a trade-off between the need to increase the sampling coverage of the larger islands versus the difficulty in matching the sampling intensity of the smaller islands (only 5 m × 5 m) in the larger patches (20 m × 20 m). To account for this issue and evaluate our capacity to correctly assess

the effects of island size, we used a resampling method akin to rarefaction curves (for details on the method and all linear modeling result tables, see appendix, “Linear Modeling of Treatment Effects at Each Trophic Level”).

All analyses were conducted with R 3.1.2 (R Development Core Team 2014), using the vegan package (Oksanen et al. 2014) for the PERMANOVA and PERMDISP and the lavaan package (Rosseel 2012) for the structural equation analyses. We provide in a zip file, available online, the entire R code to see the structure and to reproduce each SEM model.¹ The data used for this study are available from the Dryad Digital Repository (Harvey and MacDougall 2015).

Results

Treatment Effects

Fertilization was the strongest driver of insect herbivore abundance and diversity among the experimental treatments (see appendix, “Linear Modeling of Treatment Effects at Each Trophic Level,” for complete treatment effect tables). It increased herbivore abundance in fertilized islands compared to unfertilized islands (fig. 1a; $F_{1,23} = 40.4$, $P < 0.001$), reduced evenness (fig. 1b; $F_{1,23} = 17.2$, $P < 0.001$), and reduced among-island spatial turnover in composition ($R^2 = 0.22$; fig. 1c). Most herbivore taxa present in fertilized islands were also present in the unfertilized ones (see nested pattern in fig. 1c). Therefore, the homogenization effect of fertilization on among-island insect herbivore composition unfolded because of a filtering effect where fewer and less spatially variable but more abundant herbivorous taxa persisted in and dominated fertilized islands. Defoliation by mowing did not have detectable individual or interactive effects on herbivore richness, evenness, or abundance. However, mowing did significantly affect among-island herbivore taxa composition (i.e., spatial turnover among islands) by supporting taxa that were otherwise mostly absent in unmowed islands and excluding taxa that were otherwise present in unmowed islands ($R^2 = 0.07$; fig. 1d). Interestingly, neither island size nor spatial constraints had any significant direct impact on insect herbivores.

Mediated Effects

The path model comparison analysis showed that the observed effects of fertilization and defoliation on insect herbivores were mainly explained by changes in plant composition (bottom-up model Akaike information criterion

1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

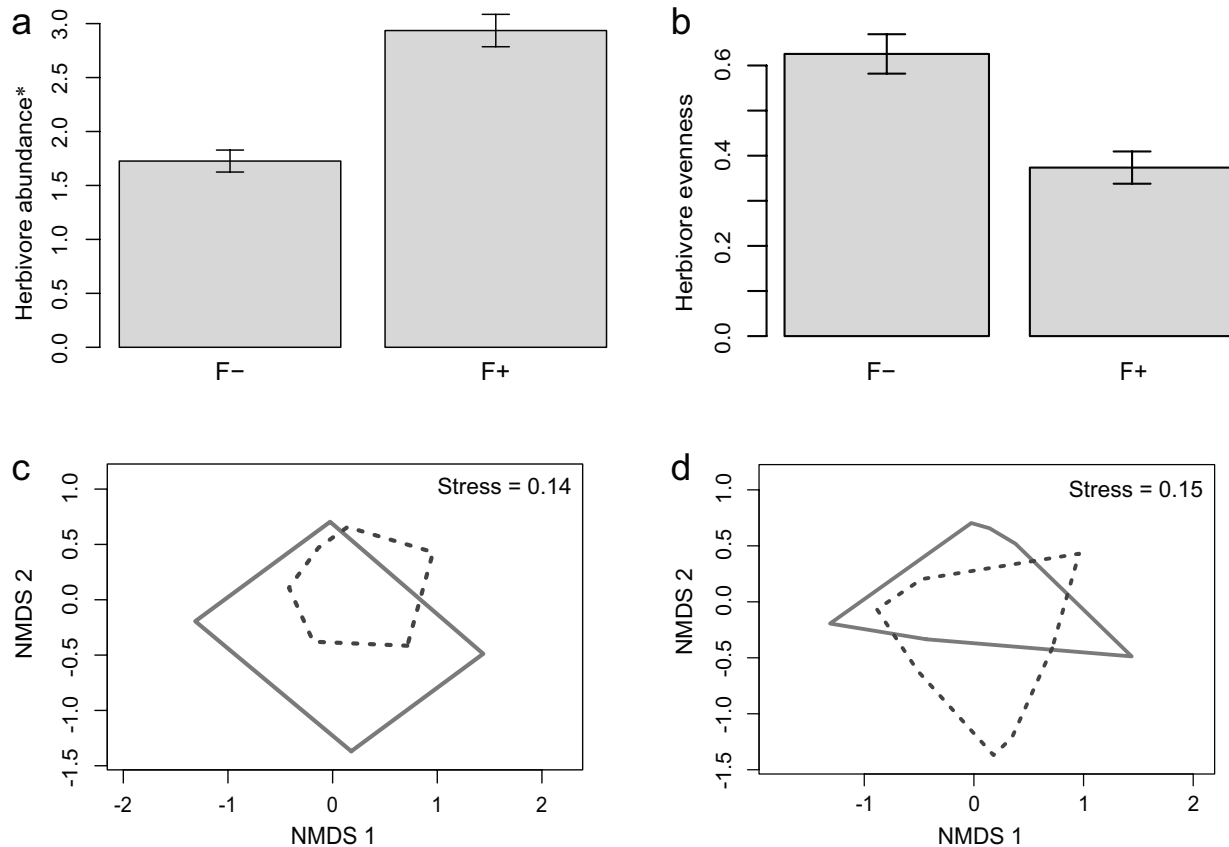


Figure 1: Main drivers of among-island insect herbivore communities. *a*, Effect of fertilization on herbivore abundance (per 4 m²). *b*, Effect of fertilization on herbivore evenness (per 4 m²). *c*, Nonmetric multidimensional scaling (NDMS) representation of herbivore community composition Bray-Curtis dissimilarity between fertilized (dashed line) and unfertilized (solid line) islands. *d*, NDMS representation of herbivore community composition Bray-Curtis dissimilarity between defoliated (dashed line) and not defoliated (solid line) islands. An asterisk indicates log-transformed axes. Error bars indicate \pm SE. Averages are based on 18 independent observations per treatment. Only significant results at $P < 0.05$ are shown (see appendix, “Linear Modeling of Treatment Effects at Each Trophic Level,” for full linear modeling tables).

[AIC] = 8,251.8; see table 1), with predator-mediated effects negligible on the islands ($\Delta AIC_{\text{bottom-up vs. top-down}} = 186.4$; table 1). The selected bottom-up path model showed that the observed homogenization effect of fertilization on insect herbivores unfolded because nitrogen addition reduced plant richness ($\gamma_{Rr:N} = -0.240$, where Rr is resource richness; fig. 2) and altered among-island plant composition ($\gamma_{PCoA1:N} = -0.648$ and $\gamma_{PCoA3:N} = -0.340$; fig. 2) by supporting fewer specific forb species (mainly *Chenopodium* spp.). Fewer forb species, in turn, favored higher abundance and dominance of specific herbivore groups (mainly Miridae and Cicadellidae) on fertilized islands. The changes in insect herbivore composition associated with defoliation unfolded because it affected among-island plant composition ($\gamma_{PCoA2:mowing} = -0.162$ and $\gamma_{PCoA2:mowing} = -0.221$; fig. 2), which in turn favored higher abundance of Aphidoidea and Scarabidae herbivores on mowed islands.

Mainland Islands

In contrast to the islands, insect herbivores in the untreated and continuous mainland were associated with a mixture of top-down effects from predators and bottom-up effects from the plants (table 1). Similar to what was found on the islands, plant composition was the most important driver of herbivore composition ($\beta_{Hc:Rc} = 0.648$, where Hc is herbivore composition and Rc is resource composition), richness ($\beta_{Hr:Rc} = 0.455$, where Hr is herbivore richness), and abundance ($\beta_{Ha:Rc} = 0.849$, where Ha is herbivore abundance). However, we also found evidence for top-down effects from predators on herbivores, with predator richness negatively associated with herbivore richness ($\beta_{Hr:Pr} = -0.349$, where Pr is predator richness) and abundance ($\beta_{Ha:Pr} = -0.846$). This negative effect of predators suggested a transition from a mixed top-down/bottom-up regulation of herbivores in

Table 1: Summary of the Akaike information criterion (AIC) model selection procedure

Candidate models	df	AIC	Δ AIC	χ^2	Difference support
Islands:					
Bottom-up	123	8,251.8		156.9	
Bottom-up and top-down	123	8,252.6	.8	157.8	None
Nontrophic	124	8,402.8	150.2	311.0	Strong
Top-down	135	8,438.2	35.4	367.4	Strong
Mainland:					
Bottom-up	2	25.3		4.7	
Bottom-up and top-down	2	25.4	.1	4.8	None
Top-down	2	30.1	4.7	9.5	Substantial
Nontrophic	8	33.0	2.9	24.5	None

Note: Each candidate model represents different scenarios of plant-mediated effects versus predator-mediated effects of the treatments (island size, spatial constraints, fertilization, and defoliation) on insect herbivore local richness, evenness, and among-island spatial turnover in abundance and composition (see “Material and Methods” for more details). Shown are degrees of freedom (df) in each model and χ^2 estimates of each model based on maximum likelihood estimations. Critical values for model difference support are none: Δ AIC < 2; substantial: $4 < \Delta$ AIC < 7; and strong: Δ AIC > 10 (after Burnham and Anderson 2002).

the mainland to a solely bottom-up regulation of herbivores in the fragmented and perturbed islands. This latter effect on the islands was associated with the homogenization of the plant community (fig. 3*d*), a decline in herbivorous taxa richness and top predator abundance (fig. 3*a–3b*), and a change in herbivore composition (fig. 3*c*).

Overall, these results illustrated that despite the potential for interactive effects of multiple stressors on each trophic level, plant-mediated processes mostly predicted the responses of herbivore abundance and composition ($R^2 = 0.69$; fig. 2) to fertilization and defoliation. The transition from the continuous unperturbed mainland to the fragmented islands was characterized by a simultaneous homogenization of plant composition and a shift toward species-poor herbivore communities dominated by fewer herbivore species with larger population sizes compared to unmanipulated islands.

Discussion

Despite the potential for interactive effects of multiple stressors at each trophic level, plant-mediated processes mostly predicted herbivore abundance and composition responses to multiple anthropogenic-based perturbations in the fragmented islands. For instance, the strongest driver, fertilization, reduced plant richness and increased dominance by a specific set of plants, which in turn increased the abundance of a few dominant herbivore taxa and reduced the among-island spatial turnover of herbivores. These among-island perturbation effects generated an important spatial homogenization of the plant community compared to the untreated continuous mainland by causing a decline in herbivore richness in the fragmented island compared to the mainland. This study suggests that resource dependencies may play a fundamental role in the

regulation of insect herbivore communities in response to the interactive effects of landscape fragmentation and perturbations (here, fertilization and defoliation).

Top predators can be especially sensitive to anthropogenic perturbations, mainly because of their large habitat range requirement, high metabolic demand (McKinney 1997; Purvis et al. 2000), and stronger trophic dependencies (Gravel et al. 2011; Harvey and MacDougall 2014). This study did find evidence for a reduction in top predator abundance from the continuous mainland to the fragmented islands habitat. However, this decline was not associated with any density or diversity-based responses from the herbivore community that would be indicative of a disruptive effect on top-down control. Despite clear experimental evidence of the impact of top predators on grassland insect herbivores (for a review see Schmitz 2010), empirical findings generally emphasize bottom-up control from plants (Haddad et al. 2009; Borer et al. 2012; Rzanny et al. 2013). Our results confirm the well-documented sensitivity of top predators to landscape alteration (Purvis et al. 2000; Martinson and Fagan 2014) but suggest that for grassland insect communities, the decline of top predators does not necessarily lead to predator-mediated effects on herbivore communities. However, recent studies have shown that the regulatory effect of top predators on insects can be context dependent as a function of seasonality (Gratton and Denno 2003), wind speed (Barton 2014), and especially temperature (Hoekman 2010; Shurin et al. 2012; Barton and Ives 2014). In the current context of global change, caution is therefore required when predicting the relative importance of predator-mediated processes versus plant-mediated processes, as it is likely to change as a function of the focal stressors.

This study illustrates that habitat fragmentation interacts with other stressors associated with global change (eutrophication, perturbation) to simplify the trophic-mediated

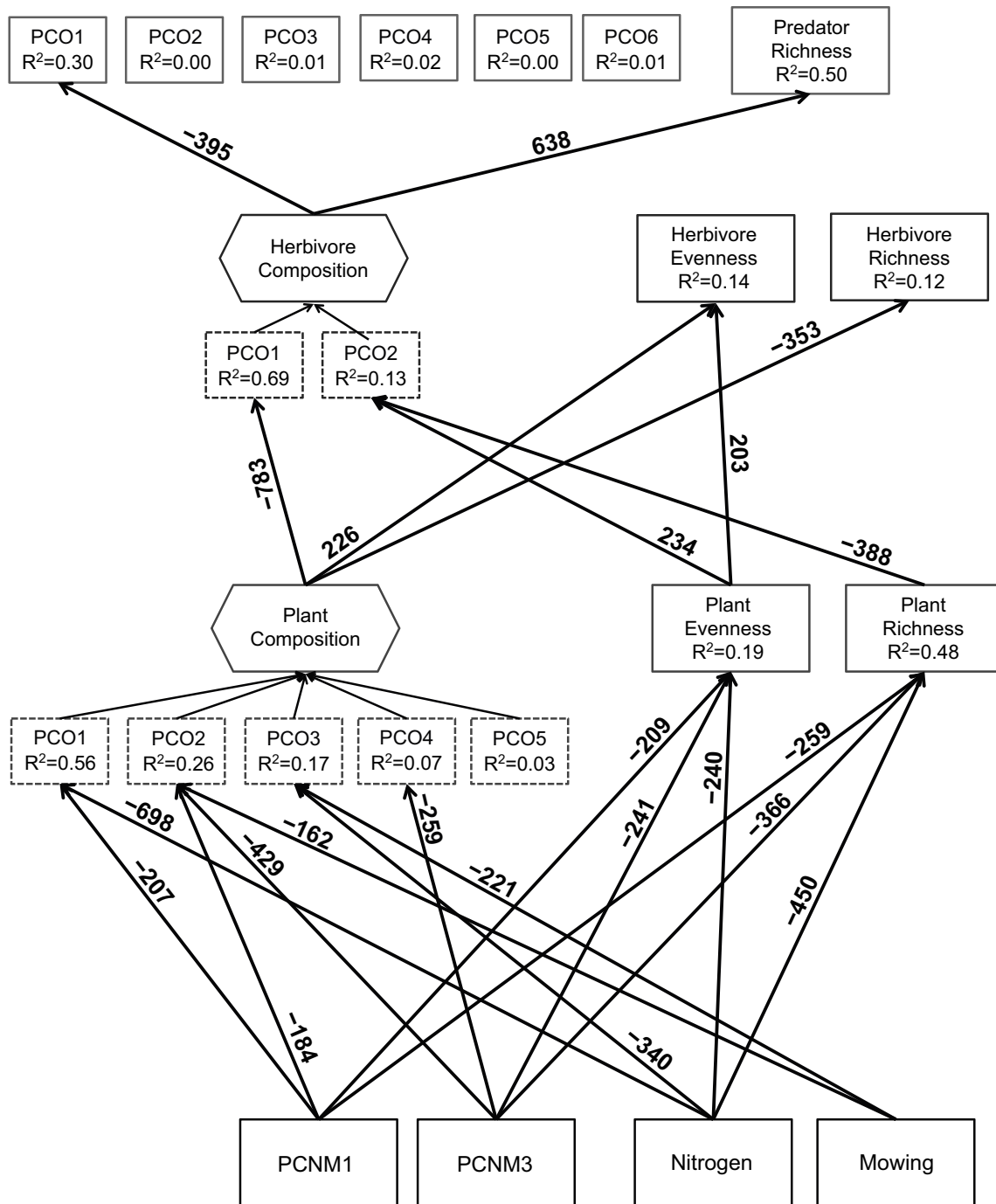


Figure 2: Bottom-up trophic path model in which perturbations affect insect herbivores via plant-mediated effects. Pentagons represent composite variables (plant composition, herbivore composition) and rectangles with dashed lines their respective descriptors (i.e., principal coordinate axes). Each arrow indicates a hypothesized cause-and-effect relationship, and each value represents the estimate path coefficient for each link. Only significant path coefficients at $P < 0.05$ are represented.

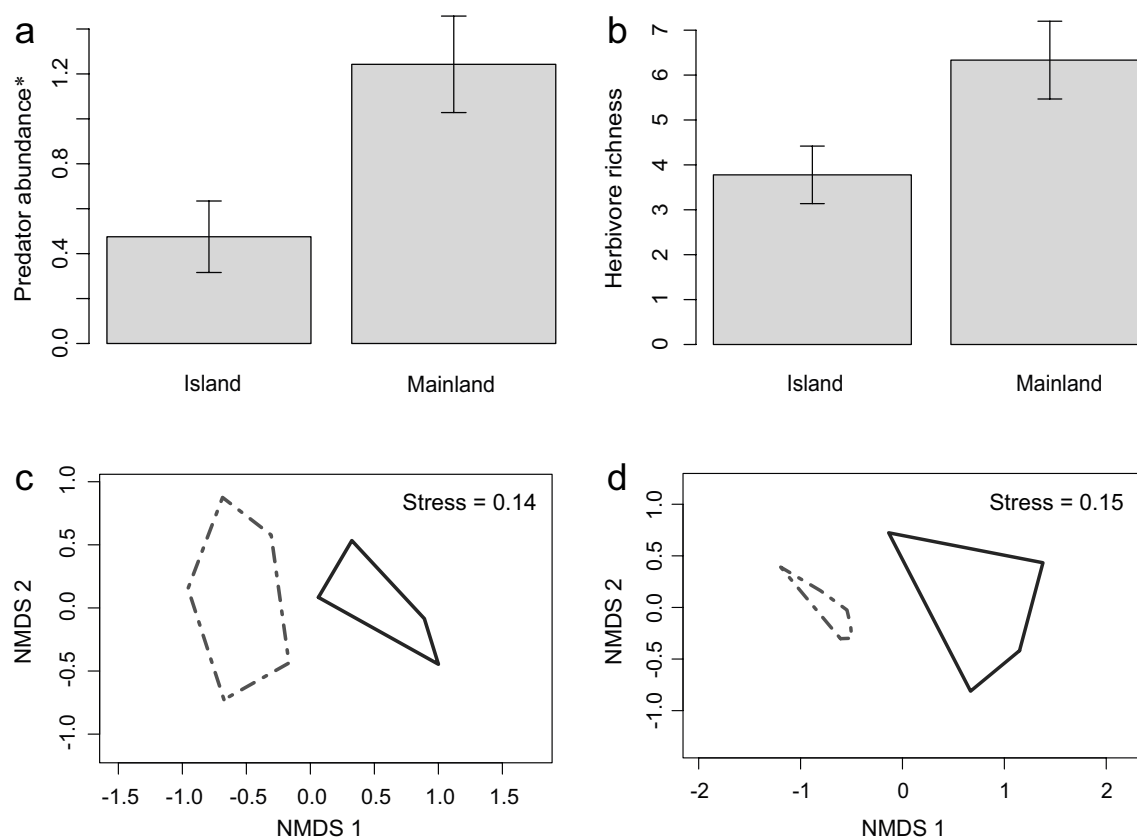


Figure 3: Differences in insect community along the transition from continuous mainland to fragmented island habitats. *a*, Difference in predator abundance (per 4 m²) between the mainland and the islands. *b*, Difference in herbivore richness (per 4 m²) between the mainland and the islands. *c*, Nonmetric multidimensional scaling (NDMS) representation of herbivore community composition Bray-Curtis dissimilarity between the islands (dash-dotted line) and the mainland (solid line) quadrats. *d*, NDMS representation of plant community composition Bray-Curtis dissimilarity between the islands (dash-dotted line) and the mainland (solid line) quadrats. An asterisk indicates log-transformed axes. Error bars indicate \pm SE. Averages are based on nine independent observations per treatment. Only significant results at $P < 0.05$ are shown (see appendix, “Linear Modeling of Treatment Effects at Each Trophic Level,” for full linear modeling tables).

control of insect primary consumers, from mixed predator resource to unidirectional resource regulation. Past work had made the connection between habitat fragmentation and the potential disruption of trophic control (Nelson et al. 2013; Martinson and Fagan 2014). However, mechanistic linkages with multiple stressors have been needed to accurately describe potential effects of global change, which are typically multivariate in nature (i.e., simultaneous alterations to resource, consumers, and spatial dynamics). Most studies have focused on alterations either to spatial dynamics (Tscharrntke et al. 2012; Rösch et al. 2013; Damschen et al. 2014) or to resource and consumers via resource-based processes such as eutrophication (Haddad et al. 2000; Borer et al. 2014) and/or climate-based processes such as increased temperature (Shurin et al. 2012; Sentis et al. 2014). However, landscape fragmentation is likely to occur in already altered habitats, with the potential for synergetic ef-

fects among these multiple stressors (Brook et al. 2008). For instance, habitat fragmentation can lead to both higher and lower (Arroyo Rodriguez et al. 2013) regional species diversity, depending on the spatial distribution of local perturbations and how the species dispersal dynamics and trophically mediated assembly constraints are affected by these perturbations. Here, we showed that the among-island influences of nutrient enrichment, defoliation, and habitat size interacted to generate lower among-island spatial variability in plant composition compared to continuous habitat. These plant-mediated effects reinforced trophic dependencies (*sensu* Holt 1997), leading to dominance by fewer but more abundant and less spatially variable herbivorous taxa.

By clearly quantifying the direct and indirect effects of each perturbation, we were able to empirically demonstrate how human alterations can homogenize the regula-

tion of insect herbivores in food webs. These modifications in community structure have longer-term implications for system stability. Given that generalist feeders are often favored by landscape simplification (Rand and Tscharntke 2007; Bommarco et al. 2010; Filippi-Codaccioni et al. 2010), our results suggest that regional outbreaks of generalist insect herbivores could occur more frequently with increased spatial homogenization of plant diversity associated with landscape alteration and nutrient pollution (Tilman and Lehmann 2001; Bobbink et al. 2010; Barbosa et al. 2012; Hautier et al. 2014) and that, concurrently, specialist consumers might be at risk of population collapse because of increased difficulty in finding sufficient resources (Bommarco et al. 2010; Clavel et al. 2010; Filippi-Codaccioni et al. 2010). It is even possible that monophagous insect consumers might also be favored with regional homogenization, because these taxa can potentially outcompete other consumers for a single resource across landscapes (Pillai et al. 2011). These predictions remain to be tested, with important implications for conservation and pest management efforts.

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Prairie islands of different size and isolation distances, surrounded by a mowed matrix. Each island was sampled to follow insect colonization and food web assembly following a combination of interacting local perturbations. Photograph by Eric Harvey.