Research Letter

"Brown" World Invertebrates Contradict "Green" World Biodiversity Theory

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Biodiversity-productivity theory predicts that ecosystems with increased productivity due to excessive limiting-nutrient loading will have decreased taxonomic diversity. In this 4-year study, we elevated productivity by adding NPK fertilizer to 20 m diameter plots in an old-field grassland to test the effects of anthropogenically mediated nutrient loading on plant and epigeal arthropod communities. While plants responded as predicted by the biodiversity-productivity theory, the epigeal arthropod community had highest species richness within the fertilized high-productivity treatments. We conclude that the contradictory response of the largely detrital-based epigeal community should alter conventional biodiversity-productivity theory and could affect terrestrial biodiversity conservation strategies.

1. INTRODUCTION

The biodiversity-productivity theory stating that local richness declines from mesotrophic to eutrophic systems has received considerable empirical and theoretical support [1–5]. Although most empirical studies examined plant communities, studies of invertebrates have also shown that reduced plant diversity caused by high productivity corresponds to reduced diversity in the primary-producer-based (or "green" world) herbivore community as well as higher trophic levels [5, 6]. Hutchinson [7] referred to this as the diversity-trophic structure hypothesis, where a reduced diversity and concomitant architectural structure within the plant community will correspond with a reduced diversity in the herbivore community and upper trophic levels.

The relationship between biodiversity, productivity, and trophic interactions is understudied [3], especially considering that humans have significantly altered the global nitrogen (N) pool causing nutrient loading into ecosystems and degradation of biodiversity in a variety of habitats [2, 4]. Especially little attention has been given to the detritus-based (or "brown" world) component of the invertebrate community [3, 5, 6], but see [8–10], despite the fact that detritivores can alter nutrient cycling and trophic interactions [3, 8]. Ungrazed or unmown temperate grasslands can produce an abundance of plant litter [11], which provides an opportunity for controlled manipulative experiments to test the effects of litter on the epigeal community.

Here we report results of a large-scale 4-year study in which plant litter and nutrient loading were manipulated with NPK fertilizer to elucidate the response of the plant and epigeal invertebrate communities in a temperate old-field grassland [12]. Our goal was to test the biodiversity-productivity theory with respect to the epigeal invertebrate community. Our hypothesis was that invertebrate species richness would be reduced by fertilization and by plant litter.

2. MATERIALS AND METHODS

A complete description of the field site and the plant sampling are described elsewhere [12], though a brief description of the general experimental design and invertebrate sampling procedure are given below.

In August 2001, twenty-four 20 m diameter circular plots ($314\,m^2$) were established. These experimental plots were separated by at least 20 m and were at least 30 m away

from any other habitat (e.g., roads, forest). Treatments were applied in a 2×2 factorial design of fertilizer ($+$F = fertilizer added, $-$F = no fertilizer) and plant litter ($-$L = litter removed, $+$L = litter left in situ after yearly mowing) with the control plots characterized as no fertilization and plant litter left in situ ($+$L/$-$F), resulting in six replicates per treatment. In April 2002 and continuing each April through 2005, Scotts brand Osmocote 8-9 month slow release fertilizer 19-6-12 (NPK; Scotts, Marysville, Ohio, USA) was applied at $20 \, \mathrm{g \, N \, m^{-2}}$ in fertilized plots. Within two days of annual mowing of the whole site with a large tractor and brush hog mower (autumn 2001–2004), litter was removed from litter removal treatments using a small 23 hp lawn tractor with a pull-behind 8 hp Agri-Fab Mow-N-Vac trailer attachment (Agri-Fab, Sullivan, Ill, USA). After litter removal, loads of removed litter were left standing for at least 10 minutes to allow inadvertently vacuumed arthropods to return to the site.

Beginning in 2002, invertebrates were collected using four pitfall traps in each plot ($n = 96$ total pitfall traps). Within each plot, a single trap was placed 5 m from the center of the plot at each of four magnetic compass directions (northeast, northwest, southeast, and southwest). Each trap consisted of a 10 cm diameter, 18 cm tall PVC sleeve into which a 710-mL plastic cup was inserted and filled to approximately 4 cm with a 50/50 water/propylene glycol mixture. To deter trap raiders (e.g., microtine mammals), to prevent captured invertebrates from climbing out of the trap, and to prevent precipitation from directly flooding the trap, an 8 cm powder funnel with a base enlarged to approximately 3 cm was inserted into the trap and covered by a 15 cm $\times$ 15 cm board, leaving approximately 3 cm clearance. Starting in May and continuing through August, traps were alternately left open for two weeks and closed for two weeks. When closed, the plastic cups were removed, the contents collected and preserved in 70% EtOH, and the PVC sleeve was tightly capped. This resulted in 3 sampling periods each year from 2002 to 2005, with no overlap between sampling, mowing, and vacuuming. We only report on our final 2005 harvest because the trends were similar in earlier years and 2005 results had the greatest treatment effects.

Invertebrates were identified to species when possible, otherwise to the lowest possible taxonomic level, and the numbers within each taxonomic identification unit (TIU) in each trap were recorded. Each TIU within a trap was dried at 70°C for 72 hours, then TIU biomass to the nearest 0.0001 g was determined. Because some extremely small TIUs did not register a biomass at 0.0001 g, their biomass was recorded as "0.0000 g," unless caught in number sufficient to register a mass.

3. RESULTS AND DISCUSSION

While the plant community largely responded to our treatments as predicted by the biodiversity-productivity theory (Figure 1(a)) [12], the epigeal invertebrate community did not. Invertebrate species richness increased with invertebrate biomass (Figure 1(b)). Moreover, invertebrate species richness also increased as plant biomass increased

(Figure 1(c)) and was inversely related to plant species richness (Figure 1(d)). These results are contrary to previous research [5, 6] and predictions [4, 7], and instead support the idea of a bottom-up control of diversity in the epigeal invertebrate community [8–10]. Our results suggest that the present biodiversity-productivity theory does not adequately describe the dynamics of the predominately "brown" portion of terrestrial ecosystems [8–10].

We acknowledge that pitfall trap sampling does not represent the entire epigeal community. Only the most active epigeal invetebrates are sampled by pitfall traps. Furthermore, pitfall trapping is not simply a representation of just the detrital-based community. Combining pitfall traps with litter extraction using Berlese funnels or D-Vac sampling would have given a more complete picture, with the inclusion of many important litter arthropods that might not have been adequately counted.

Why does epigeal invertebrate species richness increase with productivity? If we were to assume a direct causal connection between plant productivity and the species richness of the detrital community it would seem that dead plant material limits detritivore diversity. However, epigeal richness was equally high in fertilized plots where litter was removed compared to fertilized plots with litter left in situ. Perhaps the limitation to epigeal invertebrate richness was nitrogen since the fertilizer was a high-N mix. High quality, N-rich detritus, from both above-ground (even if it were minimal) and below-ground (e.g., fine root turnover) may regulate epigeal richness. If nitrogen, through fertilization, was the major factor that controlled detritivore richness, we could say that bottom-up effects were important within the epigeal food web. Another possible controlling factor is through indirect predator-prey interactions mediated by the increased flow of energy through the "green" trophic levels (primary producer to herbivore to carnivore) caused by fertilization. For example, Fraser and Grime [13, 14] reported evidence to support top-down cascading effects in highly productive plant communities (carnivores controlled herbivores, thus releasing herbivore pressure on vegetation), but little signs of herbivore activity at high productivity, which begged the question: *What are the carnivores feeding on?* One possible explanation is that the carnivores also prey on a large detritivore community, which increases carnivore abundance well above the levels that could be supported by the herbivores alone; these elevated carnivore populations in turn suppress the herbivores to extremely low levels [15, 16]. A knowledge of the detritivore population and the extent to which carnivores are generalized enough to prey on detritivores and herbivores is needed.

We suggest the causal link between productivity and biodiversity is bidirectional [3], and is also potentially complicated by trophic interactions: productivity can control diversity, but diversity can also regulate productivity. In the first case, a productivity-driven reduction in plant diversity may be positively correlated with herbivore diversity [5], but may also have the potential to indirectly affect the detritivore trophic level. In the second case, a diverse detritivore-based community may affect nutrient cycling, thereby influencing both plant and animal productivity
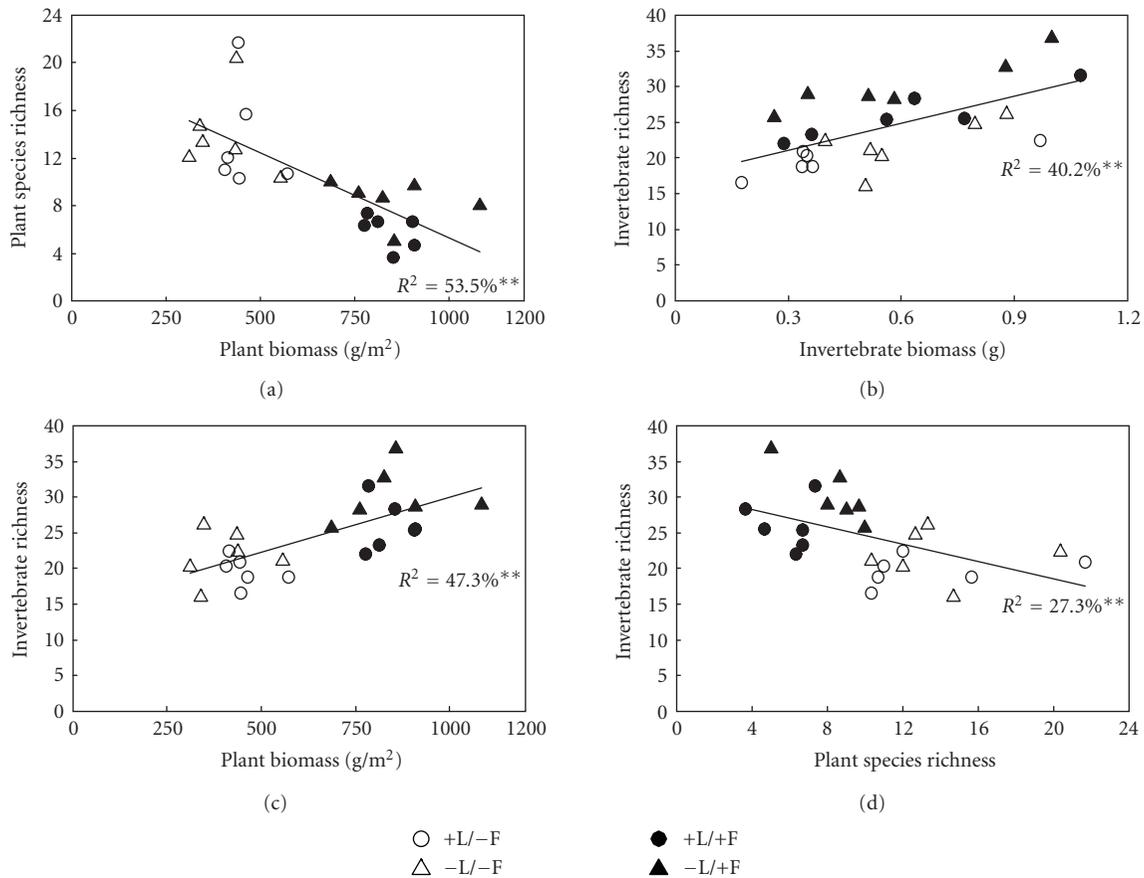
FIGURE 1: Scatter plots with linear regressions of the average of the three sampling periods in 2005 data for (a) plant species richness versus standing crop plant biomass (g/m^2), (b) invertebrate richness versus invertebrate biomass (g), (c) invertebrate richness versus plant biomass (g/m^2), and (d) invertebrate richness versus plant species richness. Invertebrate data represent three 14-day sampling periods (4032 "traps nights," or 96 traps × 14 nights open × 3 sampling periods) during which 46208 invertebrates were captured. –L and +L indicate plant litter biomass removed and plant litter biomass left in situ, respectively, and –F versus +F indicate no fertilizer and fertilized at 20 g N/m^2, respectively. ** indicates regression significant at $P < .0001$.

[8–10]. This influence of the "brown" community on the "green" community's productivity is largely ignored by current biodiversity-productivity theory, despite theoretical and empirical evidence suggesting a potentially strong feedback from the detritus-based community to the producer-based community [8–10].

Another interesting finding that emerged from our study was that our results do not support the diversity-trophic structure hypothesis posed by Hutchinson [7]. A reduction in plant species richness was inversely related to invertebrate species richness. We think this suggests that productivity and energy flow has a greater control on invertebrate richness than does plant richness. However, more work is needed to elucidate the relative affects of bottom-up and top-down control on detritivores.

The relationships highlighted by our study are of particular importance given the negative human influences on biodiversity and ecosystems. Humans are altering ecosystems and accelerating biodiversity loss at an alarming rate [3, 4, 12]. As a result, terrestrial biodiversity conservation strategies have largely focused on the primary producer

and the primary producer-based portions of biological communities. These community components are often more easily sampled and identified, and are typically more visible to the general public. Thus, producers and visible consumers lend themselves readily to the rapid biological assessments required for conservation policy, especially in ecosystems with charismatic threatened species. However our results suggest that more comprehensive studies that include the animal component of the "brown" world are needed, lest we ignore significant portions of the biological community which can substantially affect nutrient cycling and trophic dynamics.

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