Ecology Letters, (1999) **2** : 286–293

REPORT

Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity

Johannes M.H. Knops,[1,2] David Tilman,[1] Nick M. Haddad,[1,3] Shahid Naeem,[1,4] Charles E. Mitchell,[1] John Haarstad,[1] Mark E. Ritchie,[5] Katherine M. Howe,[1,4] Peter B. Reich,[6] Evan Siemann,[7] and James Groth[8]

[1]Department of Ecology, Evolution and Behaviour, University of Minnesota, St. Paul, MN 55108, U.S.A. E-mail: knops@lter.umn.edu [2]Present Address: Department of Biological Sciences, University of Nebraska, Lincoln, NE 68588, U.S.A. [3]Present Address: Department of Zoology, North Carolina State University, Raleigh, NC 27695, U.S.A. [4]Present Address: Department of Zoology, University of Washington, Seattle, WA 98195, U.S.A. [5]Department of Fisheries and Wildlife, Utah State University, Logan, UT, U.S.A. [6]Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, U.S.A [7]Department of Biology, Rice University, Houston, TX 77005, U.S.A. [8]Department of Plant Pathology, University of Minnesota, St. Paul, MN 55108, U.S.A.

Abstract

Declining biodiversity represents one of the most dramatic and irreversible aspects of anthropogenic global change, yet the ecological implications of this change are poorly understood. Recent studies have shown that biodiversity loss of basal species, such as autotrophs or plants, affects fundamental ecosystem processes such as nutrient dynamics and autotrophic production. Ecological theory predicts that changes induced by the loss of biodiversity at the base of an ecosystem should impact the entire system. Here we show that experimental reductions in grassland plant richness increase ecosystem vulnerability to invasions by plant species, enhance the spread of plant fungal diseases, and alter the richness and structure of insect communities. These results suggest that the loss of basal species may have profound effects on the integrity and functioning of ecosystems.

Keywords

Biodiversity, biological invasions, ecosystem functioning, insect abundance, insect diversity, plant diseases, plant pathogens.

Ecology Letters (1999) 2 : 286–293

INTRODUCTION

In the 1950s, Charles Elton and G. Evelyn Hutchinson, two of the leading ecologists of that era, hypothesized that the diversity of an ecosystem would impact three aspects of ecosystem functioning. First it was proposed that greater diversity would increase resistance to invasions by other species (diversity–invasibility hypothesis) (Elton 1958). Invasibility of a site should depend on the availability of the resources that limit the growth of the invading species. Because levels of limiting resources are generally lower in more diverse ecosystems within the same habitat (Tilman *et al.* 1996, 1997a), a lower portion of potential invaders should be able to become established in more diverse ecosystems. A variety of studies have supported the diversity-invasibility hypothesis (Rejmánek

1989, 1996; Case 1990; Law & Morton 1996; Tilman 1997), others have not (Knops *et al.* 1995; Robinson *et al.* 1995; Palmer & Maurer 1997). Second, it was proposed that greater diversity would decrease the severity of plant disease (diversity–disease hypothesis) (Elton 1958). A fundamental principle of epidemiology is that transmission rates are proportional to the abundance of the host (Van der Plank 1963; May & Anderson 1979; Burdon & Chilvers 1982; Antonovics *et al.* 1995). If higher plant richness leads to lower abundances of most plant species, then disease severity would decrease as richness increases. Some agricultural studies support this hypothesis, but tests in more complex ecosystems are rare (Boudreau & Mundt 1997). Third, it was hypothesized that greater diversity would increase the richness of higher trophic levels (diversity–trophic structure hypothesis) (Hutchinson 1959). Because most herbivorous insect species are specialized on one or a few host plant species, increased plant diversity should allow increased diversity of herbivorous insects, which in turn should allow increased diversity of predatory and parasitic insects. Observational studies show a positive correlation between plant and insect richness (Murdoch *et al.* 1972; Nagel 1979; Southwood *et al.* 1979), but this should be tested via experimental control of plant richness under field conditions (Tilman *et al.* 1997c).

Here we report the relationships between experimentally manipulated plant species richness and (a) plot resistance to invasion by plant species that had not been planted in a plot; (b) the severity of foliar fungal diseases; and (c) the richness and abundance of insect assemblages for the third and fourth field seasons, 1996 and 1997. This provides direct tests of the hypotheses that plant richness has effects that impact invasions and other trophic levels.

METHODS

Our work was performed in two field experiments in which plant richness and composition were directly controlled (Tilman *et al.* 1996, 1997a). These two experiments differ in their plot size. One experiment, the "small biodiversity experiment", has 147 plots, each 3 m × 3 m. The "large biodiversity experiment" has 342 plots, each 13 m × 13 m. These two experiments have different purposes. Because of its size, the small biodiversity experiment allows us to exert excellent control of species composition and diversity via frequent manual weeding. It was designed to determine the effects of diversity on primary productivity, and soil carbon and nitrogen dynamics (Tilman *et al.* 1996). Because observations during the first two years suggested that diversity might also be influencing the colonization and growth rates of species not planted in the plots, we began gathering data on abundances of nonplanted species in 1996 in the small biodiversity experiment. In contrast, because of its size (5.8 hectares), the large biodiversity experiment cannot be weeded as carefully or frequently, and thus its desired treatments are not as well imposed as in the small biodiversity experiment. However, the large plot size allows for within-plot dynamics of plant diseases and of arthropods, and thus for determination of the effects of plant species richness on disease and arthropod dynamics.

SMALL BIODIVERSITY EXPERIMENT

The 147 plots of the small experiment were planted with a randomly assigned species richness treatment of 1, 2, 4, 6, 8, 12, or 24 grassland species with 20–24 replicates (Tilman *et al.* 1996). Plots were seeded in the spring of 1994, and the total seed mass was the same for each plot. The species pool consisted of *Agropyron smithii*, *Elymus canadensis*, *Koeleria cristata*, *Poa pratensis*, *Sporobolus cryptandrus*, *Andropogon gerardii*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Achillea millefolium*, *Anemone cylindrica*, *Asclepias tuberosa*, *Aster azureus*, *Coreopsis palmata*, *Euphorbia corollata*, *Liatris aspera*, *Rudbeckia hirta, Solidago nemoralis*, *Astragalus canadensis*, *Lespedeza capitata*, *Petalostemum purpureum*, and *Vicia villosa.*

We define "invading species" as all plant species that were observed in a plot, but that were not specifically planted in the plot. This includes both native and exotic species. Our purpose is to explore how plant species richness influences the ability of other species to colonize and grow in a plot. We are not exploring an equally important issue, which is the influence of diversity on the success of invasion by exotic species. Furthermore, we define "external invaders" as plant species that were present in a plot, but that were not planted in any plots, i.e. were not part of the pool of 24 species used in the experiment.

We weeded each plot by manually removing seedlings of all invading species to maintain species composition. To prevent damage to the plots, we did all weeding from elevated walkways. We used these data to determine the total above-ground invader biomass at five time points equally spaced during the entire growing season of 1996 and at four such times in 1997. Plots were similarly weeded, but no data were collected in 1994 and 1995. We determined the invader species richness and the biomass of the external invaders by identifying, sorting to species, drying, and weighing all seedlings of invading species in one 0.5 × 1 m subplot per plot four times in 1997. Finally, we established another small experiment nested within

each plot in 1996 to determine the effects of plant species richness on invader growth by allowing two common invaders, *Crepis tectorum* (an introduced biennial forb) and *Digitaria ischaemum* (an introduced annual C_4 grass), to grow to maturity in a 0.5 m^2 subplot. Plots were not sterilized, thus part of the invaders may be from the soil seedbank.

Soil NO_3, plant above-ground community biomass, percentage cover, and light penetration were measured three times in 1996, in mid-June, July, and August and once in mid-July of 1997. To determine levels of soil mineral nitrogen, the limiting soil resource (Tilman *et al.* 1996), four 0–20 cm soil cores per plot were composited and extracted with 0.01 M KCl for NO_3, which was measured on an Alpkem RFA autoanalyser. Total plant above-ground community biomass was determined by clipping one 10 cm × 2 m strip per plot at the soil surface. Long, narrow clip strips average across plot heterogeneity. This sample was sorted to living biomass versus litter, dried, and weighed. Total plant above-ground community biomass is the biomass of all living plants. Percentage cover of each species in a plot, was visually estimated in two 0.5 × 1 m subplots per plot with the total plot cover (plants plus bare soil) being 100%. These subplots are located at opposite sides of the centre 1.5 × 1.5 m of each plot. The clipped strips were located just outside of these. No overlap occurred between any clipped strips or any of the cover subplots. Light penetration was estimated as the ratio of light (PAR) measured below the vegetation, to that above it, using a Decagon Sunfleck Septometer.

LARGE BIODIVERSITY EXPERIMENT

For the large experiment we used 163 of the 342 plots. We used those that had species composition randomly chosen from a pool of 18 grassland species and that were planted with 1, 2, 4, 8, or 16 species. These were seeded in 1994 and reseeded in 1995 (Tilman *et al.* 1997a). Because of poor germination by three of these species, other species were substituted for the original upon reseeding in 1995. Because of the large scale of the experiment, later germinating individuals of the originally planted three species were not weeded from the plots. Rather, the plots were selectively weeded, mainly to remove a few rapidly growing weedy species, especially *Crepis tectorum* and *Erigeron canadensis*. Species were *Andropogon gerardii*, *Schizachyrium scoparium*, *Agropyron smithii*, *Panicum virgatum*, *Poa pratensis*, *Sorghastrum nutans*, *Amorpha canescens*, *Elymus canadensis*, *Koeleria cristata*, *Quercus ellipsoidalis*, *Quercus macrocarpa*, *Lespedeza capitata*, *Petalostemum villosum*, *Lupinus perennis*, *Achillea millefolium*, *Asclepias tuberosa*, *Monarda fistulosa*, *Liatris aspera*, *Solidago rigida*, *Petalostemum candidum* and *Petalostemum purpureum*. Plant biomass in the large experiment was the average of that obtained by four 10 cm by 3 m clipped strips. Plant species richness is reported as the average observed in visual estimates of percentage cover in four permanently located 0.5 × 1 m subplots per plot. Both these measurements were taken in late July 1997.

Disease severity was quantified in the large experiment for the four most prevalent diseases three times in 1997. We determined disease severity by assaying individual leaves of 20 plants per plot for four target plant species (e.g. *Septoria liatridis* on *Liatris aspera, Uromyces lespedezae-procumbentis* on *Lespedeza capitata, Erysiphe cichoracearum* on *Monarda fistulosa and Colletotrichum* sp. on *Schizachyrium scoparium*) in June, July, and August in a total of 102 plots of the large experiment in 1997. All four of these diseases are plant specific, have no alternative hosts within this experiment, and are passively dispersed by wind or rain splashes. We used all of the one, two, four, and eight species plots in which the target plant species occurred, and a randomly chosen subset of the 16 plant species plots in which it occurred. Disease severity, defined as the percentage area infected for each leaf, was estimated visually on five leaves of 20 host plants per plot (e.g. the sum of five host plants in each of four cover subplots) by comparing with known infected leaf areas. Host plant density is the average number of host plant stems counted in the four permanent 0.5 by 1 m subplots.

All 163 plots in the large experiment were swept for all insects, mites, and spiders in mid-June, July, and August in 1997. A plot was swept 25 times while walking the length of the plot 3 m from the edge. While sweeping provides a biased composition of insects, this bias is consistent among plots and has provided results consistent with those obtained by other methods (Siemann *et al.* 1998). Arthropods were identified to species or morphospecies and classified as herbivores, parasites and predators, detritivores, or omnivores.

RESULTS AND DISCUSSION

In the small experiment, external invaders comprised 58% of the total biomass of all invading species. The remaining 42% was biomass from species in the 24 species pool that were not planted in a given plot. The dominant external invaders, in order of abundance, were *Digitaria ischaemum* (non-native), *Crepis tectorum* (non-native), *Ambrosia artemisiifolia* (native), *Erigeron canadensis* (native), *Berteroa incana* (non-native), *Hedeoma hispida* (native), *Euphorbia glyptosperma* (native), *Agropyron repens* (non-native), and *Polygonum tenue* (native). The number of external invaders and the biomass of invading species were all highly negatively correlated with plant species richness

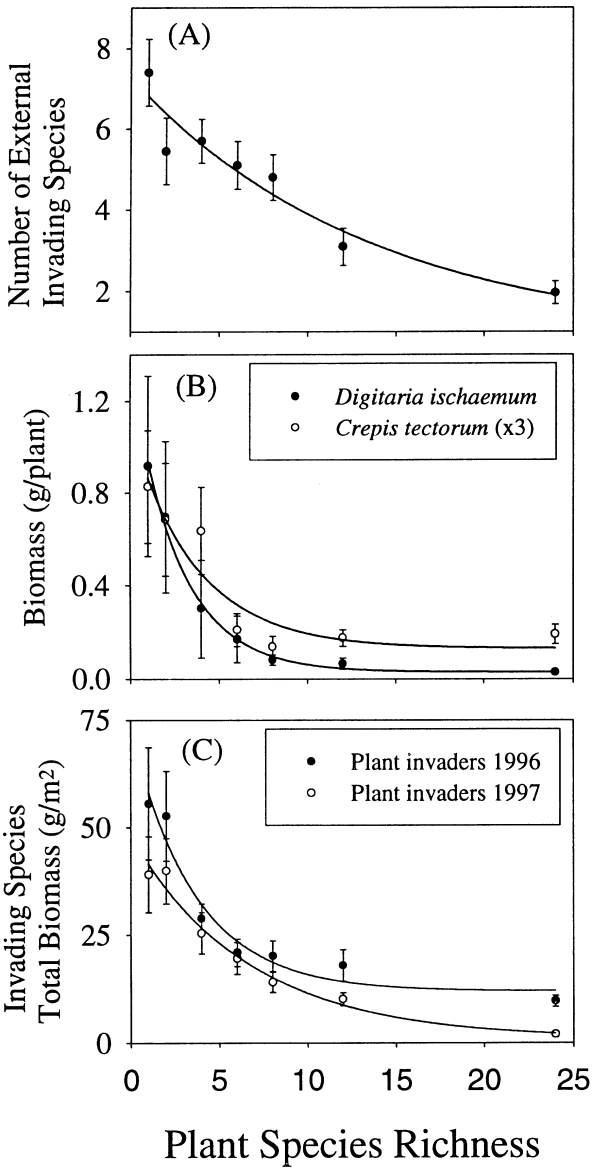

Figure 1 Plant invasions. (A) Invading external plant richness as number of invading species (excluding the 24 planted species), fitted curve is $y = 1.92 + 5.94e^{-0.105X}$, $F = 51.1$, $R^2 = 0.283$, $n = 147$, $P < 0.001$, sample size 20–24. All results plotted are means ± SEM. Note that the biomass of the smaller *Crepis* plants is multiplied by three to provide a similar scale of that of *Digitaria* for purposes of illustration. (B) *Digitaria ischaemum* and *Crepis tectorum* average above-ground plant size. Fitted curve for *Digitaria* is $y = 0.095 + 0.786e^{-0.439X}$, $F = 15.7$, $R^2 = 0.094$, $n = 137$, $P < 0.001$, sample size 18–22; and for *Crepis* is $y = -0.0136 + 0.193/(x^{0.5})$, $F = 13.4$, $R^2 = 0.112$, $n = 109$, $P < 0.001$, sample size 12–20. (C) Total invading plant biomass. Fitted curve for 1996 is $y = 11.7 + 60.8e^{-0.271X}$, $F = 41.0$, $R^2 = 0.230$, $P < 0.001$ and for 1997 is $y = 0.93 + 47.0e^{-0.150X}$, $F = 52.5$, $R^2 = 0.271$, $n = 147$, $P < 0.001$, sample size 20–24.

(Fig. 1A, C). The total biomass of external invaders significantly declined with increasing species richness (simple regression, $F = 9.7$, $R^2 = 0.063$, $P = 0.002$). In addition, the whole plant biomass for the *Digitaria* and *Crepis* that were allowed to grow to maturity in small subplots decreased highly significantly as plant species richness increased (Fig. 1B).

Total plant above-ground community biomass, percentage bare soil, and light penetration were highly correlated. Of these three variables, light intensity at the soil surface was used in the multiple regressions, because we expected it to have the largest direct influence on the growth of seedlings of invading plants. Multiple regressions showed a strong positive relationship between the total biomass of invading species and both levels of extractable soil nitrate in the rooting zone and light penetration (Table 1A). These two variables eliminated plant species richness as a significant explanatory variable in the multiple regression (Table 1A), which suggests that the effects of richness on invasibility resulted from the effects of richness on resource levels (Tilman *et al.* 1996, 1997a), with resource levels controlling invasibility. This supports the hypothesis that the increased use of limiting resources that occurs at higher levels of plant richness (Tilman *et al.* 1997b) is a mechanism inhibiting invasion by other plant species. Multiple regressions showed that the biomass per individual plant for two common external invaders, *Crepis tectorum* and *Digitaria ischaemum*, were similarly dependent on soil nitrate and light interception (Table 1A). Inclusion of these two variables eliminated plant species richness as a significant variable, similarly suggesting that the mechanism whereby diversity impacts growth of invaders is via its effect on resource levels. This hypothesis is further supported by the dependence of the species richness of external invaders on soil nitrate and light dependence, and not on plot species richness, in a multiple regression (Table 1A). In total, these analyses provide strong support for the diversity-invasibility hypothesis.

For each plant species, the level of foliar fungal disease was significantly negatively correlated with the experimentally imposed plant species richness (Fig. 2). Note that these dynamics are highly nonlinear. The high variance in the low species richness plots likely indicating the stochastic nature of disease outbreaks. Interestingly, multiple regressions that included both plant species richness and density of a host plant within a plot showed that disease severity was strongly dependent on host plant density, but not on richness (Table 1B). This suggests that disease transmission depends on richness simply because, on average, host plant species have lower densities at higher plant richness. This supports the disease–diversity hypothesis.

Table 1 Parameter estimates of a multiple regressions of the dependence on plant species richness and other variables of (A) total invader biomass 1996, 1997 ($n = 147$), *Crepis* plant size ($n = 109$) and *Digitaria* plant size ($n = 137$) and invader richness ($n = 147$); (B) disease severity on four different plant species; host plant *Liatris aspera*, disease species *Septoria liatridis*; *Lespedeza capita*, *Uromyces lespedezea-procumbentis*; *Monarda fistulosa*, *Erysiphe cichoracearum*; *Schizachyrium scoparium*, *Colletotrichum sp.*; (C) insect richness and abundance ($n = 285$)

(A)

	Invading species biomass		Invader plant size		
Variable	1996	1997	*Crepis*	*Digitaria*	External invader richness
Overall regression R^2	0.352***	0.513***	0.227***	0.345***	0.471***
Intercept	–31.1*	–25.3**	–0.171*	–0.995***	$0.871^{n.s.}$
Actual plant species richness	$-0.74^{n.s.}$	$-0.026^{n.s.}$	$-0.0003^{n.s.}$	$-0.0049^{n.s.}$	$-0.0878^{n.s.}$
Extractable soil NO_3	100.5***	195.3***	0.338***	1.37***	17.7***
% light penetration	76.4***	34.0***	0.293***	1.66***	3.53**
Invader biomass			not included		0.0599*

(B)

	Liatris	*Lespedeza*	*Monarda*	*Schizachyrium*
n	25	40	27	45
Overall regression R^2	0.568***	0.431***	0.422***	0.227***
Intercept	$-0.231^{n.s.}$	0.773*	$-0.537^{n.s.}$	$-0.086^{n.s.}$
Actual plant species richness	$0.014^{n.s.}$	$-0.024^{n.s.}$	$0.040^{n.s.}$	$-0.002^{n.s.}$
Host density	0.184***	0.029*	0.166***	0.110**

(C)

	Herbivore insects		Predator and parasite insects	
Variable	Richness	Abundance	Richness	Abundance
Overall regression R^2	0.627***	0.078**	0.661***	0.233***
Intercept	10.5***	76.7***	$1.16^{n.s.}$	9.57*
Actual plant species richness	0.769***	3.21*	0.218*	$0.698^{n.s.}$
Plant biomass	0.0138***	0.0676*	not included	
Herbivore abundance	0.0766***	not included	not included	
Predator abundance	not included		0.207***	not included
Herbivore richness	not included		0.202***	not included
Herbivore abundance	not included		not included	0.135***

$^{n.s.}P \geqslant 0.05$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Insect richness, composition, and abundance were sampled in the large biodiversity experiment in June, July, and August 1997. For 1997, both herbivore and predator richness were positively correlated with actual plant species richness (Fig. 3), as they were in 1996 (Siemann *et al.* 1998). Multiple regressions showed that herbivore richness remained significantly dependent on plant richness when controlling for changes in total plant biomass and herbivore abundance (Table 1C). Herbivore abundance was weakly correlated with both plant biomass and plant richness. Another measure of herbivore abundance, herbivore load (calculated as herbivore abundance divided by plant biomass), was negatively correlated with actual plant richness ($n = 163$, $R^2 = 0.03$, $P = 0.041$). However, herbivore load calculated as insect biovolume/plant biomass was not significantly ($P > 0.05$) related to plant species richness. This provides some support for earlier findings (Pimentel 1961; Root 1973; Andow 1991).

Predator and parasite richness was positively dependent on both herbivore richness and predator abundance, and also weakly dependent on plant richness in a multiple regression. Predator and parasite abundances were dependent on herbivore abundance, but independent of plant richness in a multiple regression (Table 1C).

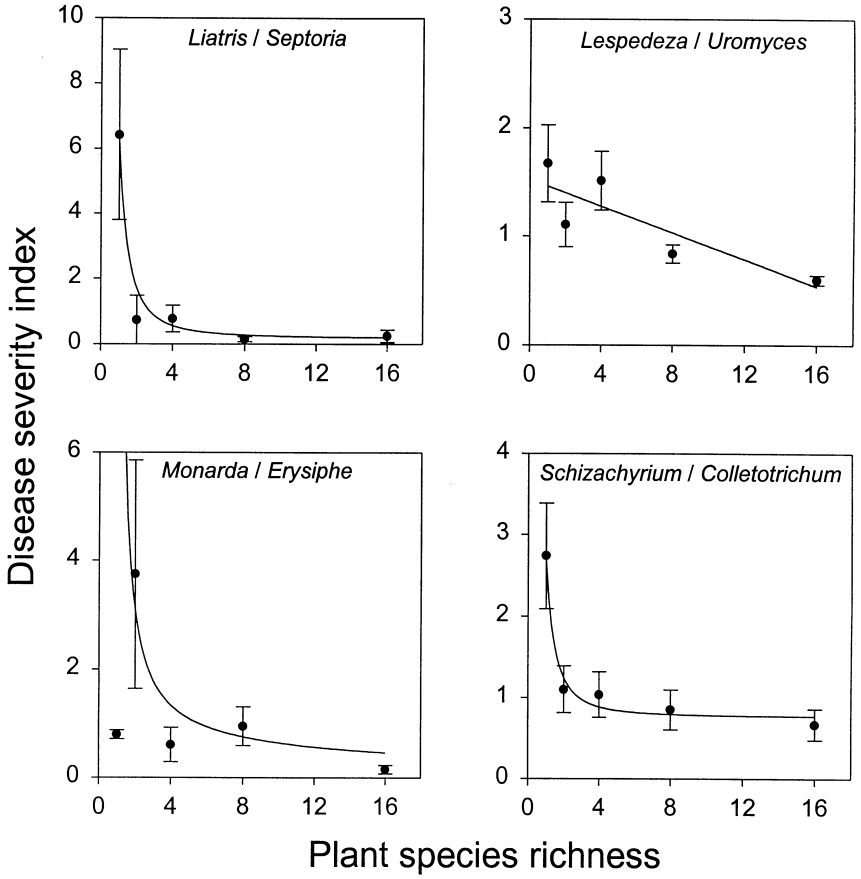

Figure 2 Disease severity index. This index was calculated from the average over all leaves for each disease in a plot standardized to a mean of one and averaged for the three sampling periods. Data shown are means ± SEM; fitted curves are (A) a leaf spot of *Liatris aspera* induced by the fungus *Septoria liatridis* ($y = 0.182 + 6.06x^{-2}$, $n = 26$, $F = 50.5$, $R^2 = 0.68$, $P < 0.01$), (B) a rust of *Lespedeza capitata* induced by *Uromyces lespedezae-procumbentis* ($y = 1.52–0.0618x$, $n = 40$, $F = 18.8$, $R^2 = 0.33$, $P < 0.01$), (C) a powdery mildew of *Monarda fistulosa* induced by *Erysiphe cichoracearum* ($y = –0.418 + 2.43/\ln(x)$, $n = 31$, $F = 10.8$, $R^2 = 0.27$, $P < 0.01$), and (D) a leaf spot of *Schizachyrium scoparium* induced by *Colletotrichum* sp. ($y = 0.764 + 1.92x^{-2}$, $n = 45$, $F = 15.4$, $R^2 = 0.26$, $P < 0.01$).

The strong positive effects of plant richness and of herbivore abundance on herbivore and predator richness strongly support the diversity–trophic structure hypothesis (Hutchinson 1959). Thus, the richness of both herbivorous and predatory insects is dependent on the richness of the trophic level below them (Hutchinson 1959; Murdoch *et al.* 1972; Root 1973; Altieri 1984; Hunter & Price 1992). This, though, does not preclude additional top-down effects of predators and parasites on herbivores richness or abundance (Siemann *et al.* 1998), nor the importance of the spatial structure of the vegetation (Root 1973; Andow 1991).

Earlier work in these plant biodiversity experiments showed that greater plant richness led to greater plant productivity, lower light levels, lower levels of unconsumed soil nutrients, and lower leaching losses of soil nutrients (Tilman *et al.* 1996, 1997a). Our new results show that plant richness, by influencing these resources, also impacts plant invasions. In addition, greater plant richness dilutes the density of disease hosts and supports a greater number of herbivorous insects, which are themselves resources for predatory and parasitic insects. Thus the effects of plant richness impact other trophic levels. In combination with other recent studies (Naeem *et al.* 1994; Tilman *et al.* 1996, 1997a; McGrady-Steed *et al.* 1997; Hooper & Vitousek 1998; Symstad *et al.* 1998), our results suggest that diversity should be added to productivity, disturbance, and composition as the variables jointly influencing the dynamics, structure, and functioning of ecosystems.

ACKNOWLEDGEMENTS

We thank Dave Andow, John Barthell, Dave Bosanko, Charles Bristow, Walt Carson, Dale Krueger, Nancy Larson, John Lawton, Clarence Lehman, Troy Mielke, Bill Schlesinger, Amy Symstad, and Dave Wedin for their comments, and the Cedar Creek interns for assistance. This research was supported by the US NSF and the Andrew Mellon Foundation.

REFERENCES

Altieri, M.A. (1984). Patterns of insect diversity in monocultures and polycultures of brussels sprouts. *Protection Ecol.*, 6, 227–232.

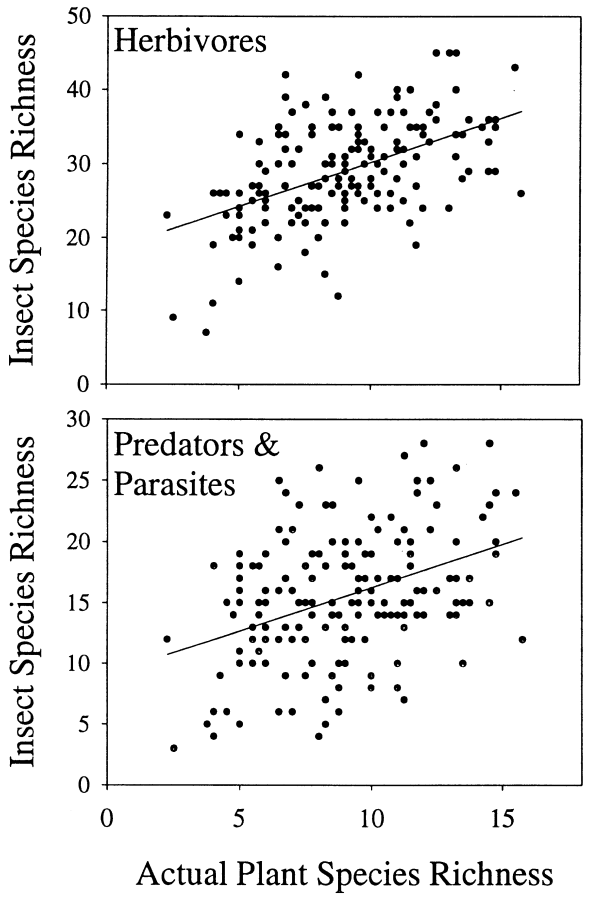

Figure 3 Herbivore and predator and parasite richness. Each point represents the total number of species or individuals collected in three samples in each experimental plot. Linear regressions are against actual plant species richness for (A) herbivore species richness ($F = 57.7$; $R^2 = 0.26$; $P = 0.001$; $n = 163$: $y = 1.20x + 18.28$), (B) predator and parasite species richness ($F = 30.07$; $R^2 = 0.16$; $P = 0.001$; $n = 163$; $y = 0.71x + 9.15$).

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

Antonovics, J., Iwasa, Y. & Hassell, M.P. (1995). A generalized model of parasitoid, venereal, and vector-based transmission processes. *Am. Naturalist*, 145, 661–665.

Boudreau, M.A. & Mundt, C.C. (1997). Ecological approaches to disease control. In *Environmental Safe Approaches to Crop Disease Control*, eds Rechcigl, N.A. & Rechcigl, J.E. Boca Raton: CRC Press, pp. 33–62.

Burdon, J.J. & Chilvers, G.A. (1982). Host density as a factor in plant disease ecology. *Annu. Rev. Phytopathology*, 20, 143–166.

Case, T.K. (1990). Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl. Acad. Sci.*, 87, 9610–9614.

Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. London: Methuen & Co.

Hooper, D.U. & Vitousek, P.M. (1998). Effects of plant composition and diversity on nutrient cycling. *Ecol. Monographs*, 68, 121–149.

Hunter, M.D. & Price, P.W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73, 724–732.

Hutchinson, G. (1959). Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Naturalist*, 93, 145–159.

Knops, J.M.H., Griffin, J.R. & Royalty, A.C. (1995). Introduced and native plants of the Hastings reservation, central coastal California, A comparison. *Biol. Conservation*, 71, 115–123.

Law, R. & Morton, R.D. (1996). Permanence and the assembly of ecological communities. *Ecology*, 77, 762–775.

May, R.M. & Anderson, R.M. (1979). Population biology of infectious diseases: Part II. *Nature*, 280, 455–461.

McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997). Biodiversity regulates ecosystem predictability. *Nature*, 390, 162–165.

Murdoch, W., Evans, F. & Peterson, C. (1972). Diversity and pattern in plants and insects. *Ecology*, 53, 819–829.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.

Nagel, H. (1979). Analysis of invertebrate diversity in a mixed prairie ecosystem. *J. Kansas Entomol. Soc.*, 52, 777–786.

Palmer, M.W. & Maurer, T.A. (1997). Does diversity beget diversity? A case study of crops and weeds. *J. Vegetation Science*, 8, 235–240.

Pimentel, D. (1961). Species diversity and insect population outbreaks. *Ann. Entomol. Soc. Am.*, 54, 76–86.

Rejmánek, M. (1989). Invasibility of plant communities. In *Biological Invasions*, eds Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., & Williamson, M. New York: John Wiley & Sons, pp. 369–388.

Rejmánek, M. (1996). Species richness and resistance to invasions. In *Biodiversity and Ecosystem Processes in Tropical Forests*, eds Orians, G.H., Dirzo, R., & Cushman J.H. Berlin: Springer, pp. 153–172.

Robinson, G.R., Quinn, J.F. & Stanton, M.L. (1995). Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology*, 76, 786–794.

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

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998). Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Naturalist*, 152, 738–750.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1979). The relationships of plant and insect diversities in succession. *Biol. J. Linnean Soc.*, 12, 327–348.

Symstad, A.J., Tilman, D., Willson, J. & Knops, J.M.H. (1998). Species loss and ecosystem functioning: effects of species identity and community composition. *Oikos*, 81, 389–397.

Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.

Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci.*, 94, 1857–1861.
Tilman, D., Naeem, S., Knops, J., Reich, P., Sieman, E., Wedin, D., Ritchie, M. & Lawton, J. (1997c). Biodiversity and ecosystem properties. *Science*, 278, 1866–1867.
Van der Plank, J.E. (1963). *Plant Diseases: Epidemics and Control.* New York: Academic Press.

BIOSKETCH

Jean Krops is an assistant professor at the School of Biological Sciences at the University of Nebraska. His research interests are in species effects on nutrient cycling, biological invasions, biodiversity and the influence of global change on these.

Editor, B. Hawkins
Manuscript received 19 March 1999
First decision made 30 April 1999
Manuscript accepted 19 May 1999