Species evenness, not richness, has a consistent relationship with productivity in old-field vegetation

R. A. Laird, J. Pither and L. W. Aarssen[1]

Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada
[1] *Corresponding author: Fax: 1 613 533-6617, E-mail: aarssenl@biology.queensu.ca*

Abstract: The relationship between productivity and species diversity was investigated at the quadrat level for three old-field plant communities that varied in time since the last major disturbance from cultivation. A positive relationship between productivity (estimated by above-ground dry biomass) and the species richness component of diversity was detected only for quadrats from the most recently disturbed community. The communities that experienced longer post-disturbance time showed no significant relationship between productivity and species richness. Quadrat productivity, however, was negatively related to the species evenness component of diversity in all three communities, i.e., regardless of time since disturbance. Furthermore, analyses of covariance using log biomass, species richness and species evenness as response variables, log soil nitrate concentration as a covariate and time since disturbance as a factor revealed that residual log biomass was significantly negatively correlated with residual species evenness, but was not significantly correlated with residual species richness. These results support the view that the productivity of plots within natural vegetation is related more predictably to the relative composition of species (reflected by evenness) than to the number of species present, especially as succession progresses.

Introduction

Several recent experiments (e.g., ECOTRON (Naeem et al. 1994) and BIODEPTH (Hector et al. 1999)) have tested the degree to which the primary productivity or biomass production of a plot depends on the diversity of species present. The interpretation of data from these and other similar studies has become one of the most contentious issues in community ecology (e.g., Aarssen 1997, 2001, Garnier et al. 1997, Grime 1997, Huston 1997, Naeem and Li 1997, 1998, Tilman 1997, Tilman et al. 1997, Chapin et al. 1998, Hector 1998, Loreau 1998a, b, 2000, Wardle 1998, 1999, 2001, Naeem et al. 1999, Schlapfer et al. 1999, van der Heijden 1999, Waide et al. 1999, Huston et al. 2000, Schwartz et al. 2000). Some empirical studies have reported a significant increase in productivity with increasing species diversity (Naeem et al. 1994, 1996, Tilman et al. 1996, Hector et al. 1999, Troumbis and Memtsas 2000, Loreau and Hector 2001a,b) while others have detected negative (Rusch and Oesterheld 1997, Wardle et al. 1997b, Grime 1998) or inconsistent relationships (Hooper and Vitousek 1997, Hooper 1998, Wardle et al. 1997a, Kenkel et al. 2000). The interpretation of positive relationships has attracted particular attention because of claims (e.g., Naeem et al. 1994, Tilman et al. 1996) that they represent evidence for higher species diversity causing higher productivity through effects of complementary resource use or facilitative interactions.

Most of the published data on the role of species diversity in affecting productivity and other ecosystem processes have come from artificial experimental plots of planted species. A complete and rigorous assessment of this relationship, however, will require a combination of experimental as well as theoretical and observational survey approaches (Tilman 2000). In the present study, we examined the productivity / diversity relationship for plots harvested from within natural vegetation. While controlled experiments allow greater potential for detection of causal relationships, correlational data from natural vegetation has greater potential to reflect the outcome of real ecological mechanisms operating under field conditions. Obviously, the benefits of these two approaches represent tradeoffs (Diamond 1986); we chose to emphasize the latter. In order to explore the robustness of the results, we base our analyses on separate surveys from three different old-field communities that varied in time since the last major disturbance (cultivation).

Materials and methods

From an old-field, 10 ha in size, at the Queen's University Biological Station (Frontenac County, Ontario, Canada, 44°30' N, 76°23' W), we harvested above-ground vegetation from each of three 30 m x 100 m regions within the field that varied in treatments representing the amount of time that had elapsed since the last major disturbance from cultivation (i.e., 'short-term', 'intermediate-term' and 'long-term' communities). The entire field was tilled in 1972 and seeded with a standard forage mixture of grasses and legumes. The long-term post-disturbance community was not tilled again in the interim, the intermediate-term community was tilled in 1997 and 1994, and the short-term community was tilled in the early spring of 1999 (before harvesting), and in each of the five previous years. The entire field has been mown for hay once every summer since 1972. Other than this mowing, however, vegetation was allowed to regenerate naturally between disturbance events with no livestock grazing, pesticide application or other disturbances permitted. A total of sixty randomly chosen 1 m^2 quadrats was harvested between June 7-9, 1999, twenty quadrats from each of the three communities. All living vascular plant vegetation from each quadrat was cut at ground level and separated by species. The total above-ground plant matter from each species was then dried for three days at 80 °C and weighed as an estimate of its contribution to the total quadrat net primary productivity.

We determined the relationships between quadrat productivity (estimated by total above-ground dry biomass per m^2, log-transformed to achieve the assumption of normality, Shapiro-Wilk test, $P > 0.05$) and the two components of quadrat diversity, species richness and species evenness for each community. We followed Smith and Wilson's (1996) recommendation of E_{var} to estimate species evenness, as it is independent of species richness and is not biased towards highly productive species, as are other indices:

$$E_{var} = 1 - \frac{2}{\pi} \arctan\left\{ \sum_{s=1}^{S} \left(\ln(x_s) - \sum_{t=1}^{S} \ln(x_t)/S \right)^2 / S \right\}$$

where x_s and x_t are the relative productivities of species s and t, respectively, and S is the total number of species in the assemblage (i.e., the quadrat species richness).

In addition to vegetation samples, soil cores (2.5 x 15 cm) were taken from three randomly chosen locations within each 1 m^2 quadrat. The three samples were mixed together thoroughly and the composite sample was analyzed by Agri-Food Laboratories (Guelph, Ontario) for pH and plant available phosphorous, potassium, magnesium and nitrogen (KCl, extractable NO_3^-). Nitrate concentration (log-transformed) was included as a covariate in three analyses of covariance, where log above-ground biomass, species richness and species evenness (respectively) were the response variables (taken separately) and time since disturbance was a factor. The residual log biomass was then correlated with residual species richness and residual species evenness (with each set of residuals taken from the corresponding ANCOVA).

Results

Mean productivity (log above-ground biomass) and mean species richness were both significantly lower in the short-term post-disturbance community than in the intermediate-term and long-term post-disturbance communities (Table 1). Mean species evenness, however, was similar among the three communities (Table 1).

Table 1. Observed mean species richness, mean species evenness and mean productivity for long-term, intermediate and short-term post-disturbance plant communities ($n = 20$ for each community). Dissimilar superscript letters within columns indicate significantly different values (ANOVA, $P < 0.05$, Tukey-Kramer post-hoc comparison).

Community (post-disturbance time interval)	Mean species richness species/m^2 (± 1 SE)	Mean evenness E_{var} (± 1 SE)	Mean productivity log_{10} dry biomass (g/m^2) (± 1 SE)
Long-term	20.6 (1.01)[a]	0.15 (0.008)[a]	2.14 (0.033)[a]
Intermediate	20.6 (0.87)[a]	0.14 (0.08)[a]	2.24 (0.23)[a]
Short-term	17.2 (0.62)[b]	0.13 (0.009)[a]	1.87 (0.07)[b]
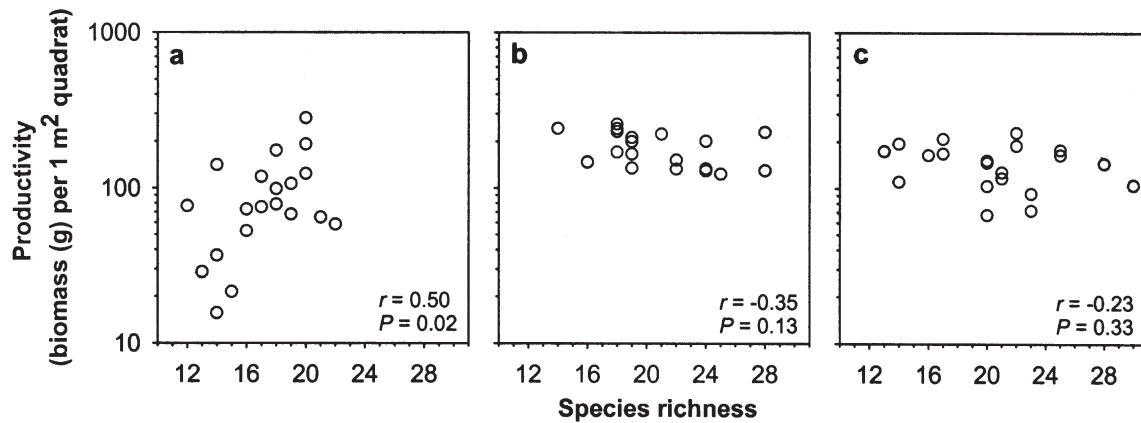
Figure 1. Relationships between plant productivity (above ground dry biomass) and species richness within 1 m² quadrats from three communites differing in post-disturbance time interval: short-term (a), intermediate (b), and long-term (c). *r*- and associated *P*-values are from product moment correlation analysis (*n* = 20 for each analysis).
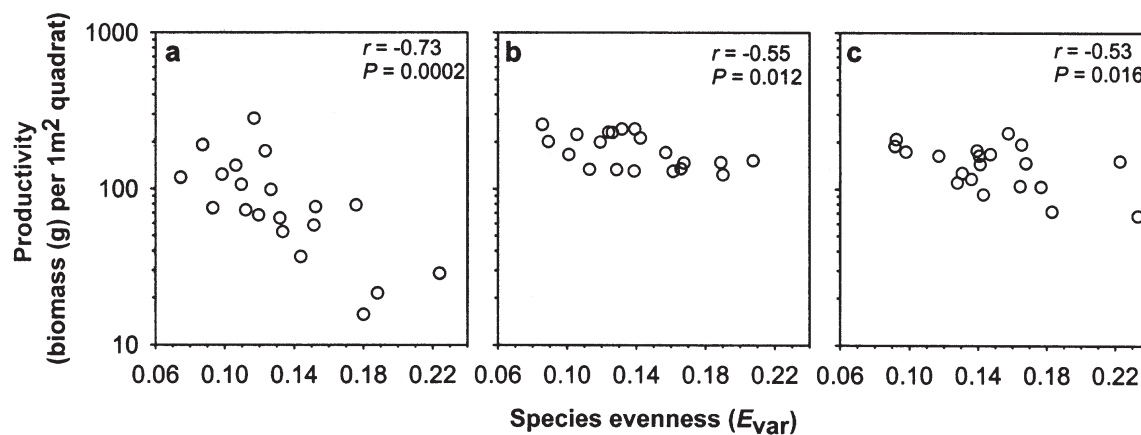
Figure 2. Relationships between plant productivity (above ground dry biomass) and species evenness (E_{var}) within 1 m² quadrats from three communites differing in post-disturbance time interval: short-term (a), intermediate (b), and long-term (c). *r*- and associated *P*-values are from product moment correlation analysis (*n* = 20 for each analysis).

A significant positive relationship between productivity and species richness was detected for quadrats from the short-term post-disturbance community (Figure 1a). For the intermediate- and long-term post-disturbance communities, however, productivity was not correlated with variation in species richness (Figure 1b, c). Quadrat productivity was significantly negatively related to species evenness in all three communities (Figure 2).

Soil nutrient levels were generally positively correlated with each other (data not shown). Hence, because nitrogen is often the limiting resource in terrestrial vegetation (Tilman 1990), soil nitrogen content alone was used as a proxy for quadrat soil fertility. For the short-term post-disturbance community, there was a significant positive correlation between quadrat productivity (log above-

ground biomass) and log soil [NO_3^-] ($r = 0.62$, $P = 0.0038$, $n = 20$). However, there was no significant correlation between productivity and log soil [NO_3^-] for the intermediate- ($r = 0.16$, $P = 0.49$, $n = 20$) and long-term post-disturbance communities ($r = 0.29$, $P = 0.21$, $n = 20$).

Analysis of covariance (ANCOVA) using log biomass as the response variable revealed significant effects of time since disturbance, log nitrate concentration (as a covariate), and the interaction between the two (Table 2a). ANCOVA using species richness as the response variable revealed a significant effect of time since disturbance only (Table 2b). The ANCOVA model using species evenness as the response variable was not significant (i.e., whole model $P > 0.05$; Table 2c). Residual log biomass and residual species richness from their respec-

Table 2. Analyses of covariance (ANCOVAs) using (a) log biomass, (b) species richness, and (c) species evenness (E_{var}) as the response variables (results of whole models in parentheses), with time since disturbance (DIST) as the factor and log soil NO_3^- concentration as the covariate.

Source of variation	df	SS	F	P
(a) log biomass (whole model: F = 13.3, P < 0.0001, df = 5, 54)				
Time since disturbance (DIST)	2	0.856	12.91	< 0.0001
log soil $[NO_3^-]$	1	0.453	13.66	0.0005
DIST x log soil $[NO_3^-]$	2	0.395	5.96	0.0046
Error	54	1.79		
(b) species richness (whole model: F = 3.20, P = 0.013, df = 5, 54)				
Time since disturbance (DIST)	2	159.4	5.69	0.0057
log soil $[NO_3^-]$	1	7.66	0.55	0.46
DIST x log soil $[NO_3^-]$	2	65.8	2.35	0.11
Error	54	756.7		
(c) species evenness (E_{var}) (whole model: F = 1.84, P = 0.12, df = 5, 54)				
Time since disturbance (DIST)	2	0.00540	2.19	0.12
log soil $[NO_3^-]$	1	0.00559	4.54	0.038
DIST x log soil $[NO_3^-]$	2	0.00413	1.68	0.20
Error	54	0.066		
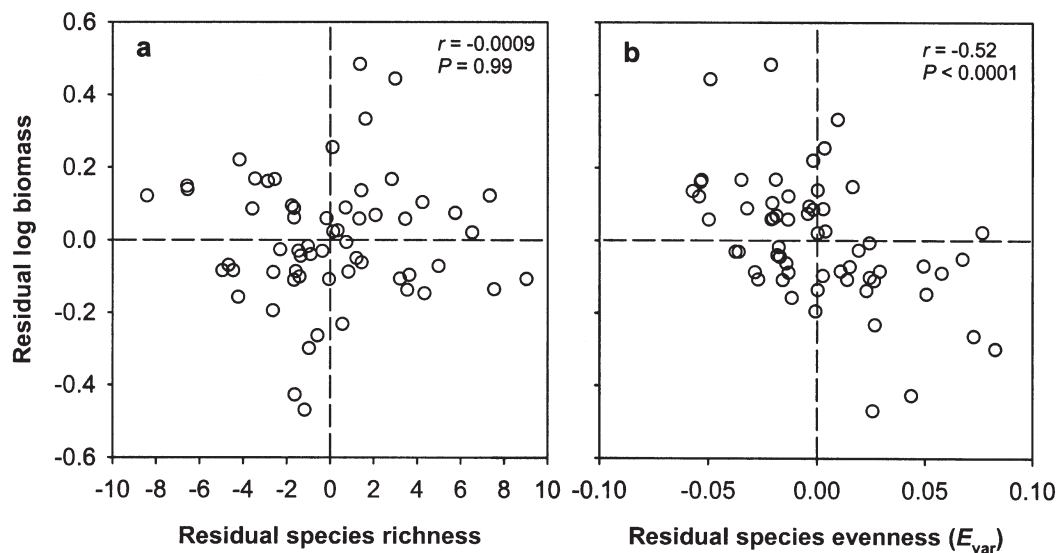
Figure 3. Relationships between residual log biomass and (a) residual species richness, and (b) residual species evenness (E_{var}) (residuals taken from three separate ANCOVA models using time since disturbance as a factor, log soil $[NO_3^-]$ as a covariate, and log biomass, species richness and species evenness (E_{var}) as the respective response variables). r- and associated P-values are from product moment correlation analysis (n = 60 for each analysis).

tive ANCOVA models were not significantly correlated (Figure 3a). However, residual log biomass was significantly negatively correlated with residual species evenness (Figure 3b).

Discussion

Of the three study communities, results from only the short-term post-disturbance community revealed a significant positive productivity / species richness relationship (Figure 1a). We consider this treatment to be analogous to some planting experiments in that insufficient time had elapsed for ecological processes to affect community structure (Wardle et al. 1997c). Indeed, the fact that average quadrat biomass was significantly less in the short-term versus intermediate- and long-term quadrats (Table 1), indicates that the short-term quadrats may have been well below carrying capacity. This is unavoidable in short-term experiments, unless the structuring forces happen to be rapid and strong (unlikely in most natural vegetation). Hence, we suggest that these short-term quadrats, being in a very early stage of succession, were largely stochastically determined, non-equilibrium assemblages of species with respect to productivity where the most productive quadrats were those that happened to include the largest, most productive species, which, according to the 'sampling effect' (Aarssen 1997, Huston 1997, Tilman et al. 1997) are more likely to occur within plots that happen also to include more species. Moreover, presumably because the high productivity of these species rich plots is due to the presence of large productive species (occurring together with smaller species), the species evenness of these plots is relatively low (Figure 2a) and species richness and evenness are negatively correlated ($r = -0.442$, $P = 0.05$, $n = 20$). Hence, we interpret the positive relationship between productivity and species richness in the short-term post-disturbance community (Fig. 1a) as only an incidental consequence of the fact that species evenness has a negative relationship with both productivity and species richness. These relationships represent signature predictions of the sampling effect (Aarssen et al. 2003).

Perhaps then, the view that the sampling effect is itself an ecological process affecting productivity (Tilman 1997, Tilman et al. 1997) can be applied to newly disturbed communities because they may satisfy the assumption that plant community assembly is largely stochastically determined and below equilibrium (Wardle 1999, Wilson 1999). Note, however, that only in the short-term post-disturbance community was productivity positively correlated not only with species richness ($r = 0.50$) but also (and even more strongly) with log soil $[NO_3^-]$ ($r =$

0.62). Hence, there may be no causative relationship between the higher biomass values and the coincidently higher species richness values in these short-term post-disturbance quadrats. Both may instead be a product of the higher soil $[NO_3^-]$ promoting not only higher total quadrat biomass, but also, in representing a more 'favourable' growing environment, promoting local establishment success for a greater number of species following disturbance. Indeed, in separate analyses of covariance with either log biomass or species richness as response variables, log soil $[NO_3^-]$ as covariate and time since disturbance as a factor, residual log biomass was not significantly correlated with residual species richness (Figure 3a).

The lack of a positive productivity / species richness relationship within the intermediate- and long-term post-disturbance communities (Figure 1b, c) suggests that if complementarity and/or facilitative species interactions were influencing productivity, their magnitudes did not increase with the number of species present, or their effects saturate at much lower levels of species richness. The lack of a positive relationship here also suggests that the sampling effect has ceased to be important in these older plots. The reason, we speculate, is because the sampling effect has a limited duration and is replaced gradually by a 'competitive dominance' effect (Aarssen et al. 2003). Hence, we suggest that the results in the intermediate- and long-term quadrats reflect an increase, over time, in the effect of competitive dominance causing deterministic structuring; i.e., the most productive of these quadrats were those dominated by the strongest (largest) competitors and, hence, because there has been time for local (quadrat-level) competitive exclusion here, these highly productive quadrats generally have more limited species richness (compared with highly productive quadrats from earlier successional stages) (see also Kenkel et al. 2001). Under this effect, the early-successional negative relationship between species richness and species evenness can be expected to disappear over time (Aarssen et al. 2003), which is indeed the case for the intermediate ($r = -0.061$, $P = 0.798$, $n = 20$) and long-term ($r = 0.201$, $P = 0.396$, $n = 20$) post-disturbance communities.

Larger data sets from future studies will be required in order to adequately explore this possible interaction of sampling effect and competitive dominance effect on the productivity / diversity relationship (Aarssen et al. 2003). We note, however, that previous studies in the same site as the present study have shown that the role of competition in affecting old-field community structure is much stronger in later stages of community development (Epp and Aarssen 1989). Further, in the present study, the

Table 3. The five most dominant taxa (indicated by the percent of total above-ground biomass) in each of the three communities differing in time since disturbance.

Short-term	Intermediate	Long-term
Apocynum cannabinum (26.7%)	*Solidago canadensis* (33.0%)	*Poa pratensis* (31.2%)
Elytrigia (*Agropyron*) *repens* (14.5%)	*Elytrigia* (*Agropyron*) *repens* (11.6%)	*Phleum pratense* (13.0%)
Phleum pratense (11.4%)	*Poa pratensis* (9.3%)	*Solidago canadensis* (10.3%)
Asclepias syriaca (11.2%)	*Phleum pratense* (7.8%)	*Carex* sp. (9.5%)
Equisetum sp. (7.6%)	*Asclepias syriaca* (6.2%)	*Fragaria virginiana* (3.8%)

dominant species in the long-term post-disturbance community (*Poa pratensis*) and intermediate-term post-disturbance community (*Solidago canadensis*) accounted for over 31% and 33% of the total above-ground biomass, respectively, and were found in all twenty quadrats. However, the dominant species in the short-term post-disturbance community (*Apocynum cannabinum*) was found in only thirteen of twenty quadrats (and accounted for only 27% of the biomass) (Table 3). Also, several small annual species (e.g., *Chenopodium album*, *Erysimum cheiranthoides*) were present in the short-term post-disturbance quadrats, but were absent in the long-term post-disturbance quadrats.

Positive relationships between productivity and diversity expressed as species richness have been interpreted from several recent factorial planting experiments (e.g., Naeem et al. 1996, Tilman et al. 1996, Hector et al. 1999). Our results for natural vegetation, however, show that productivity was negatively related to diversity expressed in terms of species evenness and this was statistically significant ($P < 0.05$) in all three of our study communities (i.e., regardless of time since the last major disturbance) (Figure 2). This negative relationship between productivity and species evenness within natural vegetation has been reported in only two other studies that we are aware of (Drobner et al. 1998, Weiher and Keddy 1999). Wilsey and Potvin (2000) found a *positive* relationship between productivity and evenness for artificially planted plots. However, this latter study used very low species richness and plant density (three species from a total pool of three, and fourteen individuals per 40 cm x 40 cm quadrat); hence, it is not comparable to our data from natural vegetation.

Our results support the view that variation in the relative composition of species (i.e., evenness) has a more significant and predictable relationship with productivity within natural vegetation than does variation in species richness (Aarssen 1997, 2001, Hooper and Vitousek 1997, Grime 1998, Hooper 1998, Wardle 1999, Špačková and Lepš 2001). This view was further supported by the analyses of covariance using log soil $[NO_3^-]$ as a covariate and time since disturbance as a factor (Table 2): residual log biomass was strongly negatively correlated with residual species evenness (but, as mentioned above, was not significantly correlated with residual species richness) (Figure 3). Given that these results were derived from a relatively natural community where (i) ecological processes were free to act, (ii) species richness was naturally determined, and (iii) natural levels of variation in species-specific productivities existed, we suggest that the methods used here are a promising extension to short-term planting experiments for investigating how species diversity relates to ecosystem functioning. If the impetus for such research is indeed to provide sound evidence to aid conservationists, then, although experiments have the potential to reveal causative effects of diversity on ecosystem functioning (Hector 1998, Loreau 1998b, Emmerson and Raffaelli 2000, Loreau and Hector 2001a,b), we suggest that they are most valuable for the analysis of ecosystems of relatively low species richness, such as the studies of experimental two-species mixtures reviewed by Jolliffe (1997), where 38 / 54 experiments demonstrated that mixtures were significantly more productive than monocultures, or other studies where monocultures are available (e.g., Loreau and Hector 2001a,b). The effects of complementarity and facilitation in contributing to a positive productivity-diversity relationship may saturate at lower levels of species richness than are likely to be observed within natural communities, as in our data set (i.e., 'redundant species' hypothesis; Walker 1992, Schwartz et al. 2000; but see Loreau and Hector 2001a, b for a counter example). However, there are obviously many additional reasons to conserve diversity that this study does not address (see Hector et al. 2001).

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