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Dynamics of plant and arthropod diversity during old field succession

Evan Siemann, John Haarstad and David Tilman

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The successional dynamics of arthropod diversity in 18 abandoned agricultural fields (age 15–54 yr) at Cedar Creek, MN, USA were determined using sweep net sampling (44833 individuals of 618 species). Total arthropod species richness and equitability (J), but not abundance, increased significantly with field successional age. Herbivore and parasite species richness, but not detritivore and predator species richness, also increased significantly with field age. All of these arthropod variables were significantly positively correlated with plant species richness in the fields. When plant species richness was included as a covariate in regressions, there were no longer any significant effects of field age. These results supported the hypothesis that increases in arthropod diversity with field age are influenced by increases in plant diversity. The additional significant positive dependence of herbivore species richness on predator species richness suggests that predator-prey interactions may also influence the successional dynamics of arthropod diversity. Nine of the ten most common arthropod species decreased in abundance with field age, two of them significantly. The abundances of these two generalist forb-feeding species, *Melanoplus femurrubrum* (Orthoptera: Acrididae) and *Scaphytopius acutus* (Homoptera: Cicadellidae), each depended significantly on amount of forbs. The average body size of arthropod species (total and herbivores) decreased significantly with field age. An efficiency vs specialization hypothesis predicts such a decrease. Because plants in later secondary succession are generally less palatable, a diversity of smaller, potentially more specialized herbivores may have an advantage over larger and more efficient herbivores in later succession.

E. Siemann (siemann@rice.edu), J. Haarstad and D. Tilman, Dept of Ecology, Evolution and Behavior, Univ. of Minnesota, St. Paul, MN 55108, USA. (Present address of E.S.: Dept of Ecology and Evolutionary Biology, Rice Univ., Houston, TX 77005, USA).

During secondary succession following a field's abandonment from agriculture, plant diversity and composition change in predictable ways (Huston and Smith 1987, Tilman 1990, Corbet 1995, Tscharntke and Greiler 1995). Less well known is how animal communities respond to these changes. Recently there have been a number of studies of arthropod succession that have begun to clarify the general patterns of arthropod succession and identify possible causes (e.g. Brown 1985, 1990, 1991, Brown and Hyman 1986, Edwards-Jones and Brown 1993, Corbet 1995, Tscharntke and Greiler 1995, Steffan-Dewenter and Tscharntke 1997) but the overall dynamics and the factors governing these dynamics are still not fully understood.

Different families or orders of arthropods increase in diversity (e.g. Southwood et al. 1979, Brown and Southwood 1983, Brown 1984, Corbet 1995, Tscharntke and Greiler 1995, Steffan-Dewenter and Tscharntke 1997), decrease in diversity (e.g. Southwood et al. 1979, Brown and Hyman 1986, Corbet 1995, Paquin and Coderre 1997) or do not change in diversity (e.g. Corbet 1995, Steffan-Dewenter and Tscharntke 1997) during particular successions. Two recent reviews (Corbet 1995, Tscharntke and Greiler 1995) have suggested that

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overall arthropod diversity also likely increases during succession because more groups seem to increase in diversity than decrease in diversity. However, because only a subset of the arthropod community has been investigated in any study, this has never been tested. Further, studies have typically examined only herbivores, so the successional dynamics of parasite and predator diversity are much less well described.

Correlative studies have generally supported the hypothesis that changes in arthropod herbivore diversity are driven by changes in vegetation (e.g. Southwood et al. 1979, Brown and Southwood 1983, Brown and Hyman 1986, Steffan-Dewenter and Tscharntke 1997). Because each plant species may represent one or more resources for herbivores, theory predicts (e.g. Hutchinson 1959, MacArthur 1972, Whittaker 1975, Tilman 1986, Rosenzweig 1995) and correlative (e.g. Murdoch et al. 1972, Prendergast et al. 1993, Niemelä et al. 1996) and experimental studies (e.g. Pimentel 1961, Root 1973, Lawton 1983, Altieri and Letourneau 1982, Siemann 1998, Siemann et al. 1998) have found that increasing plant diversity increases herbivore diversity. Herbivores may be sensitive not only to plant taxonomic diversity per se, but also to plant architectural or height diversity (Southwood et al. 1979, Lawton 1983, Brown 1991) or plant productivity (Rosenzweig and Abramsky 1993, Siemann 1998) which are all likely correlated with plant diversity (e.g. Naeem et al. 1995, Hooper and Vitousek 1997, Tilman et al. 1997) and field successional age (Inouye et al. 1987, Corbet 1995, Tscharntke and Greiler 1995). The importance of these different factors can be assessed by testing the dependence of both arthropod diversity and the abundances of individual species on different vegetation characteristics.

Similarly, predator and parasite diversity may depend on herbivore diversity. However, the hypothesis that predators and parasites control the diversity of herbivores (Paine 1966, Connell 1972), which in turn control the diversity of plants (e.g. Crawley 1983, Brown 1984, De Steven 1991a, b, Huntly 1991, Hunter and Price 1992) also predicts positive correlations between predator and herbivore diversity and between herbivore and plant diversity. Because many parasites and predators consume nectar and pollen (Clausen 1940), they may also respond directly to vegetation changes (Price et al. 1980, Powell 1986, Hagen 1987, Jervis et al. 1993).

Changes in the physical and biotic environments during succession constrain the types of species that dominate different stages of succession (Tilman 1990). Conversely, changes in the types of arthropods that characterize different stages of succession may indicate the environmental constraints and organismal tradeoffs that are important in determining arthropod successional dynamics. Because body size is correlated with many important organismal characteristics including dispersal ability (Peters 1983) and metabolic and digestive efficiencies (Peters 1983, Brown 1995) that likely influence the degree of diet specialization (Brown et al. 1993, Brown 1995), changes in the body sizes of arthropods during succession may be a powerful indicator of changing environmental constraints. The few studies of the successional dynamics of body size show no clear pattern (Brown 1982, 1984, Gathmann et al. 1994, Steffan-Dewenter and Tscharntke 1997).

To investigate arthropod successional dynamics, we sampled arthropods in 18 fields that ranged from 15 to 54 yr since abandonment from agriculture (hereafter "field age"). We sought to document the successional dynamics of arthropod diversity, abundance and body size and investigate possible causes of these patterns.

Materials and methods

Arthropods were sampled in 18 grassland fields (ages: 15 yr (3 fields), 17, 27, 31, 32, 34, 35 (2), 40, 41 (2), 42, 49 (3), 54) at Cedar Creek, Minnesota throughout the 1992 growing season using sweep nets. The same person (JH) collected all the samples which should increase comparability between samples. These grasslands are dominated by herbaceous vegetation, especially native prairie plants (Inouye et al. 1987). The productivity in these fields is lower than those at Silwood Park, England (Southwood et al. 1979, Brown and Southwood 1983). Sweep net sampling was done during midday when the vegetation was dry. Each sample contained the arthropods captured with a 38 cm diameter muslin net that was swung 100 times while walking along a 50 m transect located in the vegetation survey area (see below). Sweep net sampling was done semi-monthly from late-May to mid-September, giving 8 samples per field.

Specimens were manually sorted and identified to species when possible, or otherwise to morphospecies within known genera or families, and enumerated. Five individuals of the oldest life stage caught of each species (90% of the species in our samples were represented by only one life stage), unless fewer were caught, were measured for length, width and thickness using an optical micrometer (see Siemann et al. 1996 and in press for details). We used the average of the product of these three measurements for species body size. Each species was assigned a single average body size.

Field observations and a literature review (see Siemann 1997) were used to assign each species to one of four trophic categories. The parasite category included all species that were either parasitic in the adult stage or were parasitic as larvae regardless of adult diet (usually nectar, pollen and/or host fluids, Clausen 1940). Non-parasites were divided into three other mutually exclusive categories, a) herbivore, b) predator or

c) detritivore, based on whether the adults fed primarily on a) plants, b) animals or c) dead matter or fungi.

For all analyses, we pooled the samples from the 8 sampling dates so that we had a single data point for each field. For each of these samples, we calculated total arthropod species richness, abundance and mean body size and species richness of each of the four trophic groups. Because species richness indicates only a single aspect of diversity, we also calculated equitability ($J = H'/\ln(\text{species richness})$) for total arthropods in each sample (Southwood 1978).

In 1989 and 1994, as part of a Long Term Ecological Research project at Cedar Creek investigating plant successional dynamics (begun in 1983 by Tilman et al.), plants were sampled in each of the 18 fields according to the protocol of Inouye et al. (1987). In brief, each field has 4 parallel 40 m long transects spaced 25 m apart. For each field, percent cover of bare ground, litter and vegetation by species were estimated in each of 100 1 × 0.5 m plots located on the transects. We calculated total plant species richness in a field as the average of the total number of plant species recorded in the field in 1989 and 1994 (sampling done in late-June and early-July). We calculated total plant cover as the average of the vegetation cover (0–100%) in the field in 1989 and 1994. Analyses using plant data from 1989 or 1994 gave similar results.

Simple Ordinary Least Squares (OLS) regressions were performed to test how total arthropod species richness, abundance, and equitability (J) depended on a field age. To investigate the dependence of significant responses of arthropod species richness on plant diversity, plant composition and plant productivity, we performed multiple regressions with field age, total plant species richness, proportional diversity of forbs (forb species richness divided by total plant species richness) and total plant cover as predictors. We then used backwards elimination ($p < 0.05$) to arrive at final models. Additionally, we performed simple regressions to test the dependence of the species richness and mean sizes of each of the four trophic groups on field age. To investigate the potential causes of significant responses of the species richness of trophic groups, for each trophic group we performed multiple regressions using field age, total plant species richness, proportional diversity of forbs, total plant cover and the species richness of the other three trophic groups as predictor variables followed by backward elimination ($p < 0.05$). Because the final models determined by backwards elimination can be sensitive to correlations between predictors, for every multiple regression we also used forward selection ($p < 0.05$) with the same set of predictors to arrive at a final model. In every case, the models indicated by backwards elimination and forward selection were identical.

Simple regressions were performed to test how total and trophic groups mean sizes depended on a field's successional age. We used the method of Griffiths (1986) to test whether body size distributions were unimodal or bimodal. In brief, we first fitted a unimodal curve to categorical body size distributions, and then used Kolmogorov-Smirnov goodness of fit tests to compare the real and fitted curves. A good fit was taken as evidence for unimodal size distributions.

Results

In total, sweep net sampling caught 44833 individual arthropods of 618 species (Table 1, Appendix 1).

Total species richness of arthropods increased significantly with field age (Fig. 1A). The total abundance of arthropods was independent of field age (Fig. 1B). Total sweep net equitability (J) increased significantly with field age as ($J = 0.53 + 0.0028 \times \text{age}$, $R^2 = 0.07$, $p < 0.05$). Herbivore and parasite species richness increased significantly with field age but detritivore (note the nearly significant p-value of 0.06) and predator species richness were independent of field age (Fig. 2).

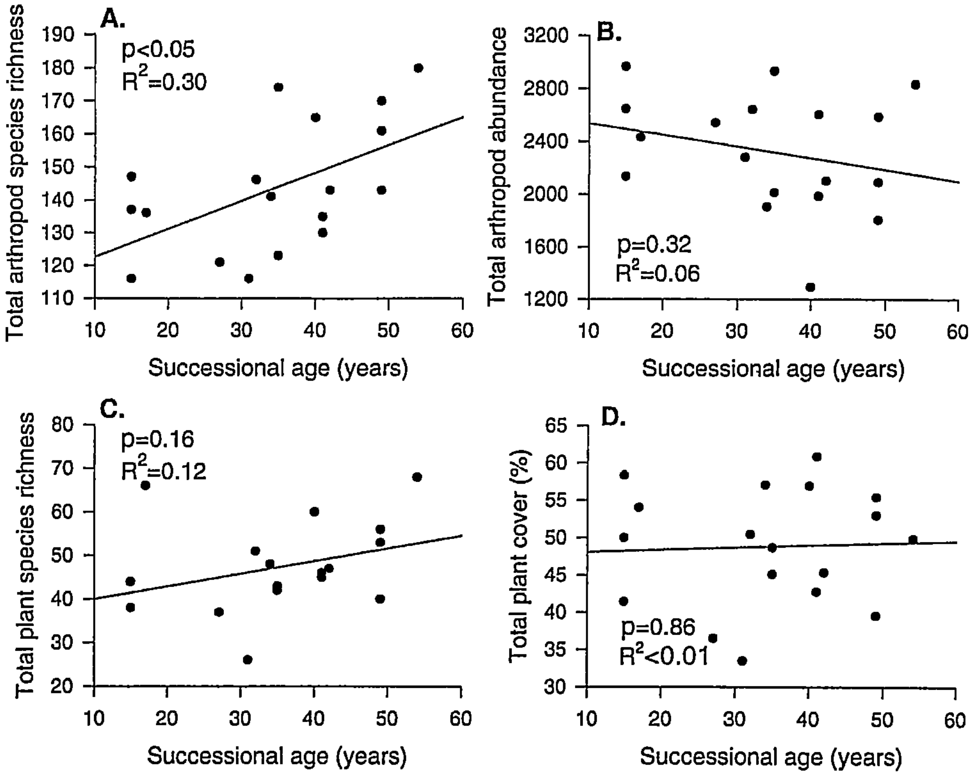
After backwards elimination or forward selection, 1) total species richness depended on plant species richness as ($\text{totsr} = 80.19 + 1.46 \times \text{plsr}$, $R^2 = 0.30$, $p < 0.05$), 2) herbivore species richness depended on plant species richness and predator species richness as ($\text{herbsr} = 1.34 + 1.25 \times \text{plsr} + 2.32 \times \text{predsr}$, $R^2 = 0.52$, $p < 0.01$) and 3) parasite species richness depended on plant species richness as ($\text{parsr} = 7.87 + 0.40 \times \text{plsr}$, $R^2 = 0.23$, $p < 0.05$). In no cases in this study was any eliminated predictor except field age ever significant in simple regressions. The pattern of simple correlations among plant and arthropod diversity are shown in Fig. 3.

Nine of the ten most abundant species (all herbivores) decreased in abundance with field age (decreased: *Doratura stylata* (Boh.) (Homoptera: Cicadellidae) $p = 0.32$, *Nysius niger* (Baker)

Table 1. Species and individuals within taxonomic and trophic groups.

Group	Species	Individuals
Araneida	29	906
Coleoptera	133	2 899
Diptera	177	2 905
Hemiptera	55	6 629
Homoptera	67	24 870
Hymenoptera	146	1 156
Lepidoptera	22	803
Orthoptera	42	4 564
Miscellaneous	8	101
TOTAL	618	44 833
Detritivore	17	177
Herbivores	361	41 214
Parasites	139	880
Predators	101	2 562
TOTAL	618	44 833

Fig. 1. The dependence of A) the total species richness ($\text{totsr} = 114 + 0.85 \times \text{age}$) of arthropods, B) abundance of arthropods on field successional age, C) total species richness of plants, and D) total cover of plants on field successional age.



(Hemiptera: Lygaeidae) $p = 0.34$, *Macrosteles fascifrons* (Stal) (Homoptera: Cicadellidae) $p = 0.38$, *Quantas sayi* (Fitch) (Homoptera: Cicadellidae) $p = 0.18$, *Ageneotettix deorum* (Scudder) (Orthoptera: Acrididae) $p = 0.07$, *Athysanus argentarius* (Metc.) (Homoptera: Cicadellidae) $p = 0.36$, *Delphacodes campestris* (Van Duzee) (Homoptera: Delphacidae) $p = 0.90$; increased: *Diplocolenus configuratus* (Uhl) (Homoptera: Cicadellidae) $p = 0.41$). For two of these species, *Melanoplus femurrubrum* (DeGeer) (Orthoptera: Acrididae) a generalist forb eating grasshopper ($N = 144 - 2.9(\text{age})$, $R^2 = 0.49$, $p < 0.001$) and *Scaphytopius acutus* (Say) (Homoptera: Cicadellidae) a generalist forb eating leafhopper ($N = 123 - 2.6(\text{age})$, $R^2 = 0.39$, $p < 0.01$), these decreases were significant. After backwards elimination (predictors: field age, plant species richness, plant cover, proportional diversity of forbs), *M. femurrubrum* abundance depended significantly on only proportional diversity of forbs ($AB = -10.0 + 200 \times \text{forb}$, $R^2 = 0.65$, $p < 0.01$) and *S. acutus* abundance depended on field age and proportional diversity of forbs ($AB = 73.8 = 131.9 \times \text{forb} - 2.2 \times \text{age}$, $R^2 = 0.65$, $p < 0.001$). The abundance of the most abundant parasite and predator species were independent of field age (parasite: *Tiphia* sp. (Hymenoptera: Tiphiidae) $p = 0.21$; predator: *Nabis americoferis* (L.) (Hemiptera: Nabidae) $p = 0.81$).

The mean size (mm^3) of arthropods decreased significantly with field age (Fig. 4). The mean size of herbivores also decreased significantly with field age ($\text{size} = 174.89 - 1.29 \times \text{age}$, $R^2 = 0.41$, $p < 0.01$). The mean sizes of parasites ($\text{mean} = 17.4$, $p = 0.11$), predators ($\text{mean} = 59.8$, $p = 0.08$) and detritivores ($\text{mean} = 21.4$, $p = 0.58$) all decreased non-significantly with field age. In multiple regressions with all combinations of the factors field age, plant species richness, plant cover and proportional diversity of forbs as predictors, only field age was ever significantly correlated with the mean size of arthropods. All body size distributions were unimodal (Kolmogorov-Smirnov statistics $= 0.03$, $0.86 = p < 0.99$).

Total plant species richness ($p = 0.13$) and total plant cover ($p = 0.33$) in a field both tended to increase with field age (Fig. 1C, D). The proportions of plant cover that were nonvascular plants ($p = 0.07$), forbs ($p = 0.004$) and legumes ($p = 0.79$) tended to decrease with field age and the proportions that were C4 grasses ($p = 0.11$), C3 grasses ($p = 0.66$), and woody plants ($p = 0.01$) tended to increase with field age.

Discussion

We found that the overall species richness (Fig. 1A) and equitability (J) of arthropods increased significantly throughout 40 yr of succession. The species richness of herbivores and parasites, but not predators and detritivores, also increased significantly with field age (Fig. 2). The independence of arthropod abundance (Fig. 1B) is

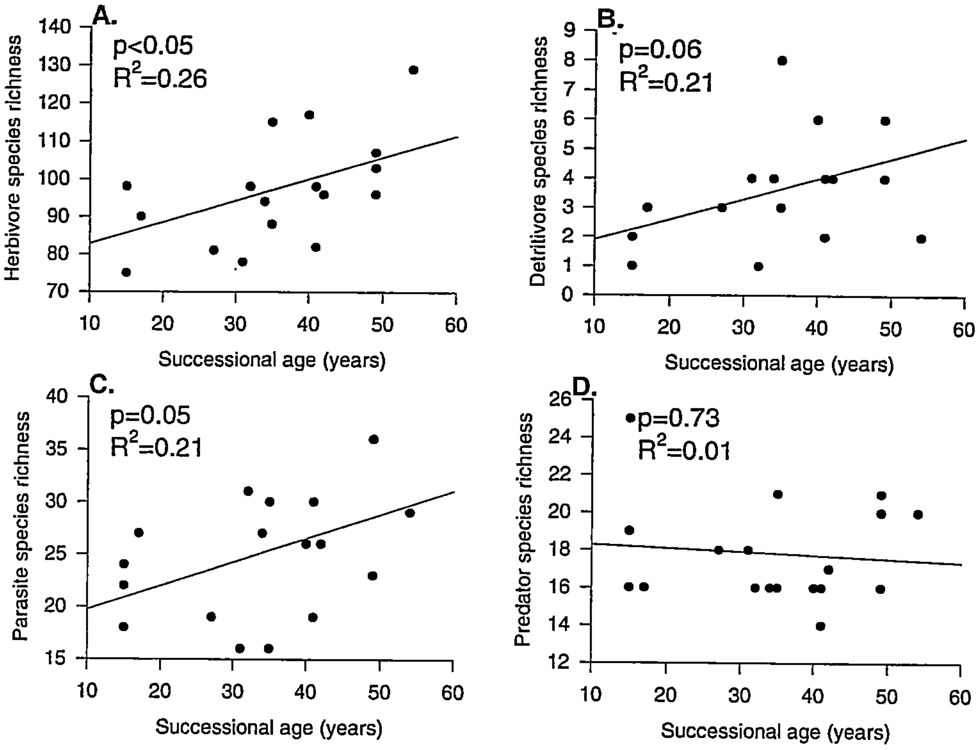


Fig. 2. The dependence of the species richness of arthropod trophic groups on field successional age ($herbsr = 77 + 0.58 \times age$; $parsr = 17 + 0.23 \times age$).

evidence that these results were not simply artifacts of differences in sampling efficiency.

Sweep net sampling is a good measure of relative abundance and relative species richness for all but the smallest vegetation-dwelling arthropods for areas with similar vegetation structure (Turnbull and Nicholls 1966, Evans et al. 1983). Our conclusions require only that measures of abundance and diversity be relative. Our study areas were all sparsely vegetated with percentage cover independent of field age (Fig. 1D). Furthermore, although the proportion of cover that was woody plants (that may interfere with sweep net sampling) increased significantly with field age, all fields had extremely low amounts of shrub and tree cover (0–4% cover) and sampling efficiencies should have been similar in the intermediate stages of succession that were the subject of this study. Our sampling effort per field (800 swings) exceeded the guidelines suggested by Southwood (1978) to give accurate estimates of density for most taxa (250–650 swings). Further evidence that the pattern of arthropod successional dynamics indicated by sweep net sampling was accurate is that multiple sampling methods have never found conflicting patterns of arthropod diversity or community structure in either descriptive (Siemann et al. 1997 – sweep nets, pitfall traps, light traps and visual surveys) or experimental studies (Siemann 1998 – sweep nets and vacuum samplers (i.e. d-vacs)) at Cedar Creek even though each of these studies had greater ranges of productivity, plant diversity and plant functional composition than this study. In the experimental study, estimates of body size from the two sampling methods were almost identical (Siemann unpubl., $p < 0.0001$, $r = 0.89$). The differences we observed here in the arthropod communities of fields of different ages are almost certainly real.

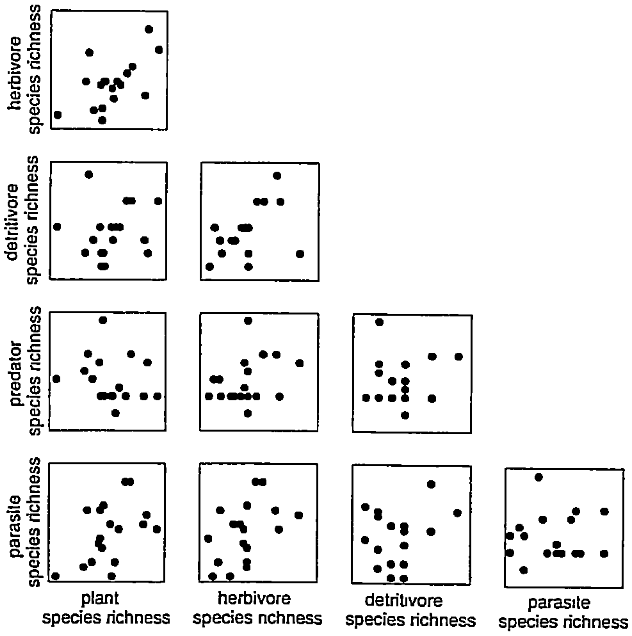


Fig. 3. The simple correlations among plant species richness and arthropod detritivore, herbivore, parasite and predator species richness.

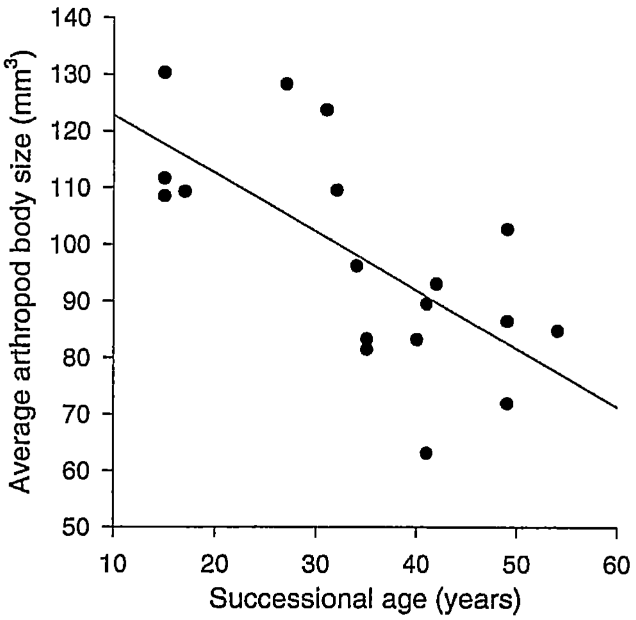


Fig. 4. The dependence of mean size of arthropod species in sweep net samples on field successional age ($size = 133.18 - 1.03 \times age$, $R^2 = 0.46$, $p < 0.01$).

The pattern of arthropod succession may have been influenced by the pattern of plant succession. Because a diversity of plants may represent a diversity of resources for herbivores (e.g. Hutchinson 1959, MacArthur 1972, Whittaker 1975, Tilman 1986, Hunter and Price 1992), increasing plant diversity may increase the diversity of herbivores. In this study, total, herbivore (Fig. 3) and parasite (Fig. 3) species richness were all significantly positively correlated with plant species richness. When plant species richness was included as a predictor in regressions, there were no longer any significant effects of field age on any arthropod diversity variables. Although this appears to be clear support for the hypothesis that plant successional dynamics drive arthropod successional dynamics (Southwood et al. 1979, Brown and Southwood 1983, Brown 1984), the interpretation is not simple. In 1989, in 1994, and for the average of the two sampling yr (Fig. 1C), plant species richness increased with successional age, but not significantly. So, a simple chain of direct effects, with field age determining plant diversity which in turn determines arthropod diversity, is not likely a complete explanation. However, prior to a drought in 1988, plant species richness increased highly significantly with field age (Inouye et al. 1987, Tilman and ElHaddi 1992). A conservative explanation is that the successional dynamics of arthropods were correlated with the successional dynamics of plants but that other factors also contributed to the significant increase in arthropod diversity through succession. In fact, periodic drought may itself be important in influencing arthropod diversity (Tilman and ElHaddi 1992, Rosenzweig 1995). The significant dependence of herbivore species richness on predator species richness (Fig. 3) suggests predator-prey interactions that can promote herbivore coexistence (Paine 1966, Connell 1972, Tilman 1986) may be another such factor.

Of course, the correlation between plant diversity and arthropod diversity does not establish causation. However, experiments at Cedar Creek in which plant diversity has been manipulated have established a causal dependence of total arthropod diversity, as well as arthropod herbivore, parasite and predator diversity, on plant diversity (Siemann et al. 1998). On the other hand, manipulations of herbivores at Cedar Creek (Tilman 1983, 1990, Inouye et al. 1994) indicate that herbivores have little impact on plant diversity or productivity and are not likely to drive plant succession. Together these studies suggest that the correlation we observed in this study between plant and arthropod herbivore diversity is more likely to reflect an effect of plant diversity on arthropod diversity than vice versa.

Nine of the ten most abundant arthropod species decreased in abundance with increasing field age, but only two of these decreasing relationships were significant. This is consistent with there being constant arthropod abundance (Fig. 1B), increasing species richness (Fig. 1A) and increasing equitability during succession. The significant dependence of the abundance of these two generalist forb feeding species, *Melanoplus femurrubrum* and *Scaphytopius acutus*, on the proportional diversity of forbs suggests that their food supply influences their abundances. This agrees with the evidence from community level analyses that plant successional dynamics strongly influence the arthropod community. Likewise, the additional significant dependence of *S. acutus* abundance on successional age is evidence that there are also non-plant factors that impact the arthropod community. These results agree with those reported for butterflies: some butterfly species are most abundant in early succession even though their host plants are most abundant in middle or late succession (Steffan-Dewenter and Tscharntke 1997). Thus, something other than food supply, perhaps predators or parasites or abiotic conditions, may influence arthropod species abundances during succession.

The significant decrease in the average size of all arthropods (Fig. 4) and of herbivorous arthropods with field age also suggests that there are changes in the environment that favor different types of species at different stages of succession. Many organismal traits correlate with an animal's body size but especially pertinent to succession are life history, dispersal ability, efficiency, and diet specialization. Odum (1969) suggested that variable nutrient supplies in later succession would favor larger animals but our data do not support this (Fig. 4). Because larger arthropods are more efficient active dispersers and smaller arthropods are more efficient passive dispersers, it has been suggested that size distributions in early succession should be bimodal

(Corbet 1995). However, such tradeoffs can cause unimodal size distributions with intermediate size organisms making the most successful compromise (Hutchinson and MacArthur 1959, Dial and Marzluff 1988, Brown et al. 1993). In the successional stages we investigated, body size distributions were all unimodal. Colonization can't be eliminated as a cause of the body size patterns we observed. However, because herbivores but not other trophic groups decreased significantly in size with field age, an explanation that involves herbivory may be more likely.

An efficiency/specialization tradeoff is another potential explanation for decreases in herbivore body size during succession. In early succession, plants are poorly defended (Reader and Southwood 1981) and have higher growth rates and lower tissue C:N (Tilman 1990). Because larger animals have 1) greater digestive efficiency due to larger guts and longer food retention times (Peters 1983, Brown 1995) and 2) greater metabolic efficiency (Hemingsen 1960, Peters 1983, West et al. 1997), larger herbivores may be able outcompete smaller herbivores in early succession. In later succession, plants are less palatable (Reader and Southwood 1981) and have lower growth rates and higher average tissue C:N (Tilman 1990). Because smaller species may perceive greater levels of heterogeneity, smaller herbivores may be better able to specialize on individual plants or parts of plants, such as growing leaf tips or phloem cells (Morse et al. 1985, May 1986, Shorrocks et al. 1991, Dixon and Kindlmann 1994). In later succession, by consuming the high quality parts of heterogeneous resources, smaller herbivores may be able to outcompete larger herbivores that must consume food of low average quality.

In fact, herbivores in later succession seem to be more specialized (Brown and Southwood 1983, Brown and Hyman 1986) which supports this hypothesis. Additionally, such specialization of arthropods on individual species of plants or parts of these plants is also consistent with the correlation between plant diversity and arthropod diversity that we observed. Because parasites increased in diversity during succession (Fig. 2C) and predators did not (Fig. 2D), this hypothesis may also explain the patterns we observed for higher trophic levels. The efficiency/specialization hypothesis may explain not only the change in body size observed in this study but also is consistent with the greater arthropod diversity in later succession.

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Appendix 1. Diversity and abundance by order and family for families represented by 3 or more species. Species richness is the total number of species in the family (or families for miscellaneous category). Abundance is the total number of individuals summed across the species in the family(ies).

Order	Family	Species richness	Abundance
Araneida	Thomisidae	11	136
	Araneidae	7	555
	Salticidae	6	126
	Misc (4 families)	5	89
Coleoptera	Chrysomelidae	33	712
	Curculionidae	28	571
	Coccinellidae	13	452
	Carabidae	10	41
	Buprestidae	6	267
	Scarabaeidae	4	143
	Elateridae	3	5
	Cerambycidae	3	8
	Meloidae	3	10
	Cicindelidae	3	13
	Anthicidae	3	51
	Mordellidae	3	139
	Cantharidae	3	321
	Misc (15 families)	18	166
Diptera	Chloropidae	13	495
	Tachinidae	12	67
	Syrphidae	12	297
	Anthomyiidae	9	846
	Sarcophagidae	8	92
	Bombyliidae	7	29
	Tephritidae	6	120
	Sciomyzidae	5	25
	Asilidae	5	43
	Chamaemyidae	4	120
	Dolichopodidae	3	153
	Misc (25 families)	33	618
Hemiptera	Lygaeidae	15	4 765
	Miridae	10	1 028
	Pentatomidae	8	70
	Rhopalidae	3	8
	Alydidae	3	14
	Cydnidae	3	15
	Scutelleridae	3	104
	Misc (7 families)	10	625
Homoptera	Cicadellidae	44	22 258
	Issidae	5	404
	Delphacidae	5	968
	Cercopidae	4	625
	Dictyopharidae	3	78
	Membracidae	3	81
	Misc (3 families)	3	456
Hymenoptera	Ichneumonidae	44	177
	Braconidae	18	172
	Colletidae	17	184
	Sphecidae	12	21
	Scelionidae	11	60
	Cynipidae	6	22
	Tiphiidae	4	64
	Megachilidae	3	5
	Bethylidae	3	23
	Misc (21 families)	28	428
Lepidoptera	Noctuidae	7	194
	Pyralidae	3	505
	Misc (6 families)	12	104
Mecoptera	Panorpidae	1	1
Neuroptera	Misc (3 families)	3	85
Orthoptera	Acrididae	28	3 961
	Tettigoniidae	8	493
	Tetrigidae	3	12
	Misc (2 families)	3	98
Psocoptera	Psocidae	1	1
Thysanoptera	Thripidae	1	13
Trichoptera	Leptoceridae	1	1