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Species Frequency Dynamics in an Old-Field Succession: Effects of Disturbance, Fertilization and Scale

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Species frequency dynamics in an old-field succession: Effects of disturbance, fertilization and scale

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Abstract
Question:
Can patterns of species frequency in an old-field be explained within the context of a metapopulation model? Are the patterns observed related to time, spatial scale, disturbance, and nutrient availability?

Location: Upland and lowland old-fields in Illinois, USA.

Method: Species richness was recorded annually for seven years following plowing of an upland and lowland old-field subject to crossed fertilizer and disturbance treatments (mowing and rototilling). Species occupancy distributions were assessed with respect to the numbers of core and satellite species.

Results: In both fields, species richness became higher in disturbed plots than in undisturbed plots over time, and decreased in fertilized plots irrespective of time. A bimodal pattern of species richness consistent with the Core-satellite species (CSS) hypothesis occurred in the initial seed bank and through the course of early succession. The identity of native and exotic core species (those present in > 90% of blocks) changed with time. Some core species from the seed bank became core species in the vegetation, albeit after several years. At the scale of individual plots, a bimodal fit consistent with the CSS hypothesis applied only in year 1 and rarely thereafter.

Conclusions: The CSS hypothesis provides a metapopulation perspective for understanding patterns of species richness but requires the assessment of spatial and temporal scaling effects. Regional processes (e.g. propagule availability) at the largest scale have the greatest impact influencing community structure during early secondary succession. Local processes (e.g., disturbance and soil nutrients) are more important at smaller scales and place constraints on species establishment and community structure of both native and exotic species. Under the highest intensity of disturbance, exotic species may be able to use resources unavailable to, or unused by, native species.

Keywords: Core-satellite species hypothesis; Exotic species; Seed bank; Species frequency distribution; Species richness; Succession.

Nomenclature: Mohlenbrock (2002).

Introduction

To understand species richness dynamics in plant communities it is important to incorporate scaling processes (Collins et al. 2002; Gering & Crist 2002). Metapopulation models of community structure and composition inform our understanding of species richness because they incorporate regional scaling processes (Gibson et al. 1999). Colonization/extinction factors allow these models to be temporally and spatially dynamic (Gotelli & Simberloff 1987). Hanski's core-satellite species (CSS) hypothesis (Hanski 1982a) is a regional metapopulation model that assesses the proportion of patches occupied by species to predict a bimodal distribution of species occupancy frequencies (occurrence of both core and satellite species Hanski & Gyllenberg 1993). Core species are widely distributed and abundant, whereas satellite species are rare and patchy. Assumptions of the CSS hypothesis include homogeneity of patch structure, semi-automatos population fates, similarity of migration and emigration patterns of all species in the assemblage, and a rescue effect (i.e. large populations decrease the extinction risk of nearby small populations).

Biological mechanisms assumed by the CSS hypothesis relate to the shape of species occupancy distributions. First, bimodality reflects colonization and dominance by a few species in homogeneous areas within the range centres of a large, regional species pool (McGeoch & Gaston 2002). The importance of the regional species pool and the effect of local filters (i.e. habitat limitation) on the occurrence of bimodal species occupancy distributions has not been rigorously tested (Bossuyt et al. 2004). Secondly, niche pre-emption models suggest that bimodality in habitats of low productivity reflects local dominance by a few species (Maurer 1990). Highly disturbed and highly productive habitats may be recruitment-limited and subject to size-asymmetric competition effects by a few locally dominant core species

(Rajaniemi 2003). The shape of the curve between species richness and habitat productivity is not linear, with a maximum at intermediate levels of productivity. There is high local dominance at low species richness/productivity and beyond a certain point as productivity increases, dominance again increases, and species richness decreases. Thus, as the balance of core and satellite species across productivity gradients changes, species occupancy distributions may change from bimodal dominated by core species to unimodal distributions dominated by satellite species back to bimodal distributions. Likewise, because of the similarity between diversity-productivity and diversity-disturbance patterns, we expect a similar shift in species occupancy distributions with increasing levels of disturbance.

Spatial scale, i.e. sample unit size (grain, Collins & Glenn 1997), can affect the shape of species occupancy distributions with a shift from unimodal to bimodal distributions as spatial scale and habitat heterogeneity decreases (McGeoch & Gaston 2002; Bossuyt et al. 2004). Temporal effects on species occupancy distributions may be as important as spatial scale but are largely unexplored (McGeoch & Gaston 2002). Most previous studies provide snapshots of assemblages from a single sample period, making investigation of temporal shifts impossible. Hanski (1982b) suggested that core and satellite species will change roles over time as species become regionally common or rare (see also Grime 1998; Gibson et al. 1999), and we expect to see such shifts in a successional setting. We only expect occupancy distributions to change if the mechanisms determining community structure change too (e.g. Guo et al. 2000).

The role of exotic species in communities is frequently attributed to that of space filling, or the opportunistic utilization of excess resources (Davis et al. 2000; Hierro et al. 2005), and would not alter species occupancy patterns if exotics were added to the species pool at random. Under these conditions, presence of exotics can reflect the incorporation of efficiently dispersed taxa into the community under a similar set of niche-constraints as the native species. Nee et al. (1991) suggested that the incorporation of species not previously considered part of the community would lead to unimodal distributions; however, this proposition has not been tested.

We monitored permanent plots over seven years in an upland and a lowland old-field allowing us to test some of the poorly understood aspects of species occupancy distributions. We assessed observed patterns of species occupancy distributions with respect to predictions of the CSS hypothesis, although the implications have relevance for other metapopulation models (Bossuyt et al. 2004). Four hypotheses were addressed: Ho_1: Species occupancy distributions will change through succession. There will be a shift from bimodal to satellite-species dominated unimodal and back to bimodal species occupancy distributions along productivity (Ho_2) and disturbance (Ho_3) gradients; and Ho_4: Exotic species inflate the number of satellite species and this inflation will lead to unimodal species occupancy distributions.

Material and Methods

Study area (see App. 1 for full details)

The experiment was conducted in two old-fields in Jackson County, IL, USA, one an upland (37°37'35" N, 89°09'13" W) and the other a frequently flooded lowland (37°42'53" N, 89°14'44" W). Each field was divided into eight (upland field site) or 16 (lowland field site) 225-m^2 square blocks in June 1996; each block consisted of nine 25-m^2 square plots assigned to all crossed combinations of three levels each of disturbance and fertilizer. The fertilizer treatment levels were: no fertilizer (control), first year only (and in year 5 at the upland site only), and annual fertilizer. The fertilizer produced a productivity gradient affecting biomass (Mathis 2001; Spyreas et al. 2001; Brandon et al. 2004). At the upland site, the disturbance treatment levels were: no disturbance, mowed in the spring annually, and mowed in the spring and autumn annually. At the lowland site, the disturbances were: no disturbance, mowed in the summer annually, and mowed and rototilled in the summer annually. The disturbances provided an extreme gradient ranging from maintenance of early successional grassland in the mowed and/or rototilled plots to conditions allowing woody species invasion in the undisturbed plots.

Data collection

Soil samples were taken for seed bank analysis one month after site preparation prior to initiation of the disturbance or fertilizer treatments. Nine soil samples of ca. 1200 g each were collected to a depth of 20 cm from the southern edge of each block. The samples were stored at 6 °C for four months in the laboratory, vegetation and roots were removed, and the nine soil samples per block were sieved and mixed thoroughly. Five replicate samples of ca. 1000 g each were placed in 26 cm × 26 cm plastic flats over 900 g of sterile vermiculite. The replicates from each block were randomly placed in five blocks in a glasshouse. Emerging seedlings were observed and identified over 12 months. A summary analysis of the samples from the lowland field are described in Mathis (2001).

Occurrence (presence/absence) of all vascular species was recorded in a 5-m^2 circular quadrat located in the centre of each plot annually from 1996 to 2002.

Data analysis

Species richness per plot was analysed by using a mixed linear model assuming a randomized complete block design, treating time periods as a repeated measure, block as a random effect, and fertilizer and disturbance treatments as the fixed effects (Proc Mixed in SAS Ver 8.0; Littell et al. 1996). In all cases, block effects were significant ($P < 0.05$). Species richness data were square-root transformed prior to analysis to meet model assumptions (normality and homogeneity). Separate analyses were conducted of the data from the upland and lowland sites, and of total, native and exotic species richness at each site. Total species richness is the sum of native and exotic species richness.

The shape of species occupancy distributions was quantified using Tokeshi's (1992) exact probability test. Class intervals were established to ca. 10% levels. Core species were those species with a maximum occurrence (occupancy) in the largest interval class (≥ 90% of samples), and satellite species were those with maximum occurrence in the smallest interval class (≤ 10% of samples) following common usage (Collins & Glenn 1990; Tokeshi 1992; Perelman et al. 2001).

The effect of spatial scale was assessed by examining the species occupancy distributions at both the block (225 m^2) and the plot (25 m^2) scales. Data from the seed bank prior to the establishment of experimental treatments were included in the assessment of distributions at the block scale. At the plot scale, species occupancy distributions were examined with respect to the disturbance and fertilizer treatments, and their interaction, for each year.

χ^2 contingency tests were used to investigate the effects of fertilizer and disturbance treatments and time period (1996-1997, 1998-1999, and 2000-2002) on the number of significantly bimodal (i.e. weakly-bimodal and bimodal) versus non-bimodal (i.e. unimodal or uniform) species occupancy distributions per plot. We pooled categories (Quinn & Keough 2002) and also combined native and exotic occupancy distributions to obtain sufficiently large expected values.

Results

General patterns of species richness

In the upland site, the total species richness declined during the second and third years of succession, subsequently oscillating thereafter (Fig. 1a). The richness of core and satellite species and of exotic species did not show a clear trend through time. In the lowland site, total species richness was low in year 1 compared to species richness in the seed bank (Fig. 1b). Total species richness increased in year 2 at the lowland site, declined by year 4 and increased thereafter. Exotic, core, and satellite species richness was also low in year 1. The richness of exotics decreased steadily from year 2 to year 7 while the number of core species steadily increased. The richness of satellite species reached its maximum number in year 3 but otherwise showed little temporal pattern.

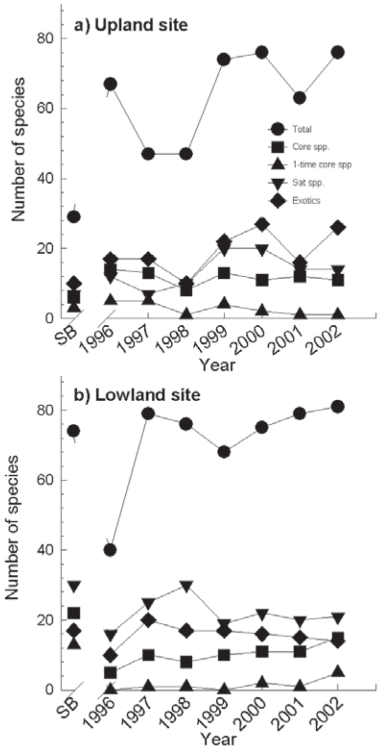

Fig. 1. Species richness (total number of species recorded across all experimental plots) in the seed bank (SB) and from 1996 – 2002 at (**a**) an upland, and (**b**) a lowland site in southern Illinois. 1-time core species are those which were core species only once from 1996-2002.

At the upland site, disturbance interacting with time affected total, native, and exotic species richness per plot (total species $F_{12,433} = 8.14$; native species $F_{12,433} = 5.58$; exotic species $F_{12,433} = 6.35$; all $P < 0.0001$). The highest levels of species richness were recorded in year 1, and then decreased in both year 2 and year 3 (Fig. 2a). In year 4, species richness increased in the mowed plots, but did not change thereafter. By contrast, species richness declined in the control plots through 1999 and remained level thereafter, but lower than in the mowed plots.

The fertilizer treatment at the upland site influenced species richness per plot as a main effect without any interaction with time or disturbance (total species $F_{2,433} = 9.53, P < 0.0001$; native species $F_{2,433} = 9.51, P < 0.0001$; exotic species $F_{2,433} = 4.04$, $P = 0.0183$). The highest

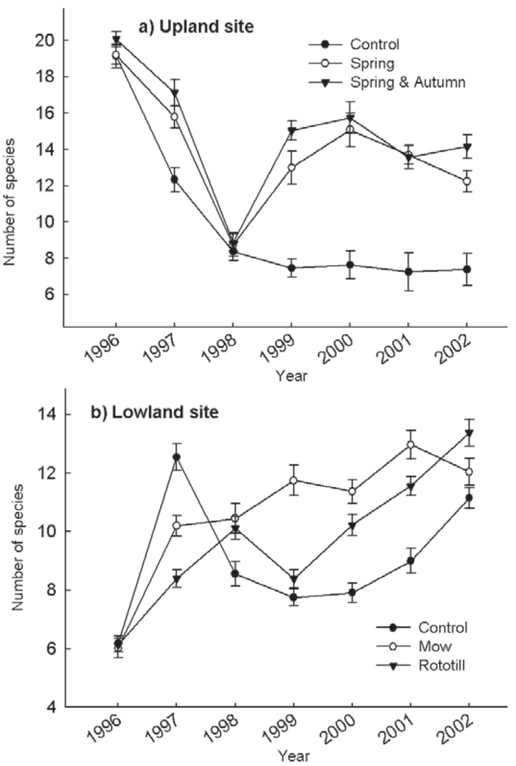

Fig. 2. Effect of disturbance on species richness (number per 9 m^2 ± 1 SE) in (**a**) mowed treatments at an upland site; (**b**) mowed and rototilled treatments at a lowland site, from 1996-2002.

levels of total species richness in response to fertilizer were in the control and years 1 and 5 only fertilized plots (13.2 ± 1 ± 0.4 and 13.5 ± 0.4 species per plot, respectively) compared with 12.1 ± 0.4 species per plot in response to annual fertilizer. Native and exotic species richness showed the same pattern in response to fertilizer (control = 8.45 ± 0.3, 4.8 ± 0.1; year 1 and 5 fertilizer = 8.9 ± 0.3, 4.6 ± 0.2; and annual = 7.8 ± 0.3, 4.3 ± 0.2; for native and exotics per plot, respectively).

At the lowland site, the species richness in plots was affected by disturbance over time (total species $F_{12,930}$ = 15.71, native species $F_{12,930}$ = 12.15, exotic species $F_{12,930}$ = 8.28, $P < 0.0001$ in all cases, Fig. 2b). The interaction between disturbance and fertilizer affected total species and native species richness ($F_{4,930}$ = 4.07, P = 0.003; $F_{4,930}$ = 3.82, P = 0.004, respectively), and fertilizer alone affected exotic species richness ($F_{2,930}$ = 10.12, P < 0.0001). The three-way interaction between disturbance, fertilizer and time on richness of native, exotic, or total species was non-significant (P > 0.05 in all cases).

In the lowland plots, the richness of all species did not differ among treatments in year 1, but rapidly diverged so that in year 2 the highest richness was in the control plots, the second highest was in the mowed plots and lowest in the rototilled plots (Fig. 2b). Thereafter, richness increased steadily in the mowed and rototilled plots, albeit with some fluctuations. By contrast, richness in the control plots decreased after year 2 before starting to increase again following year 4. The disturbance by fertilizer interaction at the lowland site was driven by the response of native species, with high levels of richness in plots mowed only once when not fertilized (8.3 ± 0.3 species per plot) or fertilized only in year 1 (8.4 ± 0.3), thus approximating a humped-backed disturbance-diversity relationship. By contrast, when annually fertilized, species richness was lowest in the undisturbed plots (6.8 ± 0.3). Exotic species richness decreased with increased application of fertilizer (2.5 ± 0.1 in unfertilized plots, 2.4 ± 0.1 in year 1 fertilizer plots, and 2.1 ± 0.1 with annual fertilizer).

Identity of core and satellite species

The identity of core and satellite species changed throughout the course of succession at both sites. Each year, one or two species became sufficiently frequent to be designated as a core species at each site (Fig. 1, App. 2); 27 species were identified as core species in the vegetation at the upland site (App. 2), of which *Ambrosia artemisiifolia* and *Oxalis stricta* were also core species in the seed bank. Three species were core species throughout the seven years of observation – *Festuca arundinacea, Lespedeza cuneata*, and *Tridens flavus* – while others were core species only early on (e.g. *Acalypha virginica*) or became core species as succession progressed (e.g. *Cardamine hirsuta*). Four species switched roles between core and satellite status (*Barbarea vulgaris, Trifolium repens, Eupatorium serotinum*, and *Rumex crispus*) while only *B. vulgaris* attained core or satellite status in more than two years.

Of 78 species 36 were identified as core species in the vegetation at the lowland site, of which 20 were represented in the seed bank (App. 3). *Gratiola neglecta* and *Krigia biflora* were core species in the seed bank but did not achieve this status in the vegetation. Two species were core species throughout (*Cyperus erythrorhizos* and *Solidago canadensis*). *Sorghum halepense* was a core species in the first two years, but declined in frequency with time, whereas *Fraxinus pennsylvanica* and *Valerianella radiata* became core species from year 4 onwards. Seven species switched core and satellite roles over the course of succession, either increasing in frequency through time (*Cerastium fontanum*, *Erigeron philadelphicus*, *Geranium carolinianum*, *Paspalum laeve*, *Plantago rugelii*), or decreasing (*Bromus secalinus*, *Ranunculus aborvitus*). Only two of these species showed a complete back and forth switch (core – satellite – core: *Cerastium fontanum* or vice versa: *Bromus secalinus*).

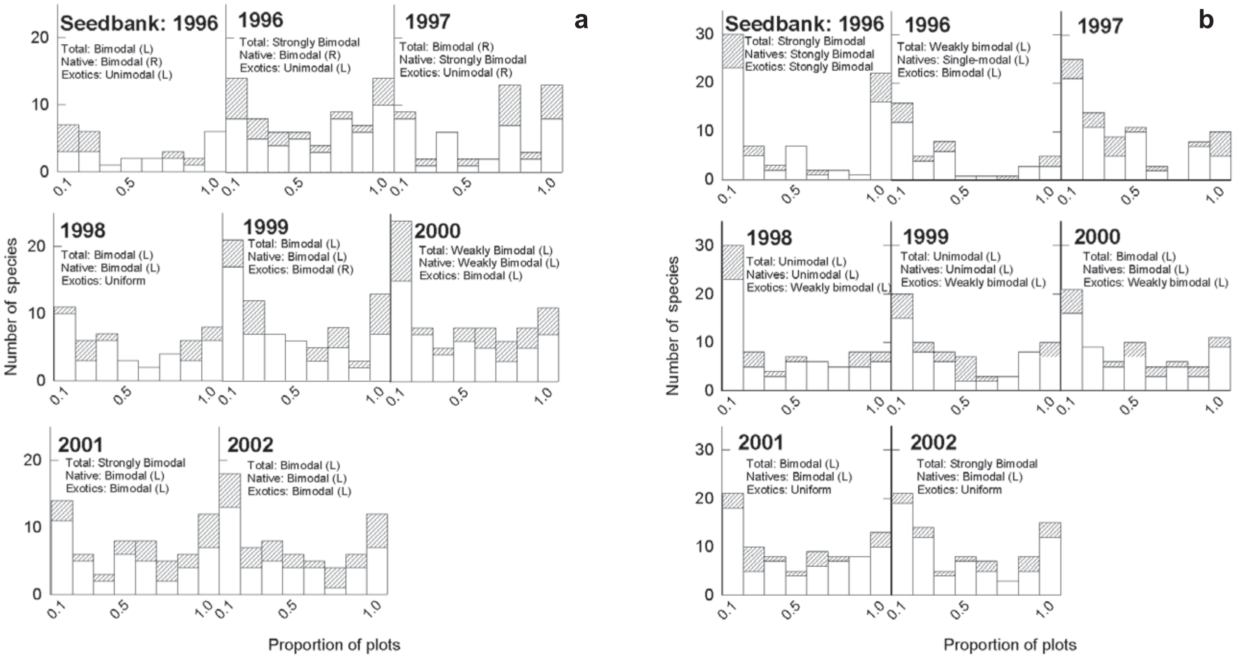

Fig. 3. Species occupancy distributions at (**a**) an upland site and (**b**) a lowland site in southern Illinois in the seed bank and from 1996-2002. Diagnosis from Tokeshi's (1992) test is shown for total (complete bar), native (lower bar), and exotic (upper bar) species. Data are expressed as number of species according to the proportion of plots sampled (based upon 8 and 16 blocks at the upland and lowland sites, respectively). (L) and (R) indicate whether bimodal distributions were left- or right-skewed, respectively.

Species occupancy distributions

At the block scale, occupancy distributions for all species at the upland site varied from weakly bimodal (in 2000) to strongly bimodal (1996 and 2001) (Fig. 3a). Distributions from all other years including the seed bank were bimodal. These distributions were largely determined by the native species which were predominantly bimodal (strongly bimodal in 1997, weakly bimodal in 2000). Exotic species distributions were initially unimodal, dominated by satellite species (seed bank, 1996) or core species (1997) but became uniform in 1998 and bimodal thereafter.

At the lowland site, the block scale species occupancy distributions for all species varied from unimodal dominated by satellite species (1998-1999) to strongly bimodal (1996 seed bank and 2002) without an obvious temporal pattern (Fig. 3b). The species occupancy distributions of native species were unimodal during the first four years (1996-1999) and became bimodal thereafter. By contrast, the species occupancy distributions of exotic species were strongly bimodal in the seed bank, then became bimodal (1996-1997), weakly bimodal (1998-2000), and uniform thereafter.

At the plot scale, species occupancy distributions were predominantly unimodal or strongly unimodal (274 of 378) (Table 1). The eight bimodal and 41 weakly bimodal distributions were not clearly related to either fertilizer or disturbance treatments (data and analyses not shown, $P > 0.05$) except in the upland field where there was a significant relationship between fertilizer level and the number of bimodal and weakly bimodal versus non-bimo-

Table 1. Species occupancy distributions in response to fertilizer by disturbance interaction from 1996-2002 in an upland and a lowland abandoned field. Values are the number of distributions significantly fitting the diagnosis according to Tokeshi's (1992) test. 27 distributions were tested in each field (3 fertilizer treatments × 3 disturbance treatments × 3 classes of plants: all species, native species, and exotic species). All unimodal distributions were left-skewed dominated by satellite species. There were no strongly bimodal distributions.

Diagnosis	Upland field								Lowland field							
	1996	1997	1998	1999	2000	2001	2002	Total	1996	1997	1998	1999	2000	2001	2001	Total
Bimodal	2	2	0	1	1	1	0	7	1	0	0	0	0	0	0	1
Weakly bimodal	11	7	1	5	1	1	0	26	4	3	2	0	0	2	4	15
Unimodal	9	9	10	18	18	12	11	82	19	14	15	17	19	15	16	115
Strongly unimodal	0	0	4	5	6	8	9	32	0	10	8	8	5	9	5	45
Uniform/Other	5	9	12	3	1	5	7	42	3	0	2	2	3	1	2	13

dal (unimodal, strongly-unimodal or uniform) distributions ($\chi^2 = 8.15$, df = 2, $P = 0.017$). The number of bimodal and weakly bimodal distributions decreased with the application of fertilizer (18 in control plots versus 7 and 8 in first year and annually fertilized plots, respectively), and the number of non-bimodal distributions was lowest in the unfertilized control plots (45) compared with the fertilized plots (56 and 55, respectively). Of the 33 bimodal and weakly bimodal distributions in the upland field, 14 were due to exotic species. Only 2 of 16 bimodal or weakly bimodal distributions were due to exotic species in the lowland field. Uniform distributions were predominantly due to exotic species (23 of 42 in the upland field, 13 of 13 in the lowland field). There was a significant effect of time period on the contrast between bimodal and weakly bimodal, unimodal and strongly unimodal, and uniform distributions in the upland field, but not in the lowland field (upland field: $\chi^2 = 38.4$, df = 4, $P < 0.001$; lowland field: $\chi^2 = 8.08$, df = 4, $P = 0.089$). In the upland field, the number of bimodal distributions decreased through time (1996-1997 = 22; 1998-1999 = 7; 2000-2002 = 4; Table 1).

Discussion

Successional patterns

The general patterns of species and diversity change over the seven years of secondary succession in the old-fields studied here are consistent with other studies in the region (Bazzaz 1968; Collins et al. 2001). Species richness generally increased over time. Short-term decreases in richness in years 2 and 3 in the upland site and in year 4 in the lowland site may have been caused by short-term weather patterns. 1996 was an exceptionally wet year (1000 mm precipitation April-October, compared with the 73-year average of 670 mm: http://www.ncdc.noaa.gov/oa/ncdc.html) which may have facilitated high levels of recruitment at the usually well drained upland site which subsequently collapsed with the return of normal conditions in the ensuing years (69 and 76 cm precipitation in 1997 and 1998, respectively). Such inter-annual extreme weather can provide colonization windows presaging temporal collapses of vegetation development and diversity (Bartha et al. 2003). By contrast, recruitment at the lowland site was comparatively low in 1996, increasing thereafter, consistent with reduced recruitment in the flooded conditions that were present at this site during the wet year of 1996.

The dynamics of species richness in our system were moderated by disturbance and fertilizer application. Disturbance can cause local extinction; an event that may be uncoupled from the system response and have little relationship to subsequent recruitment patterns (Collins et al. 1995, 2001). In both the upland and lowland systems studied here, the response to disturbance was an increase in richness. Thus, while the actual disturbance may have caused species extinctions, the decrease of species dominant before disturbance allowed other species to establish and thus richness increased. High levels of production, such as by fertilizer application, reduced native species richness when disturbance was absent or low, but increased richness when disturbance was high in the lowland site. In successional systems, high production levels enhance the competitiveness of dominant species (Foster & Gross 1998; Wilson & Tilman 2002) and limit recruitment (Stevens et al. 2004) leading to a decrease in richness. High richness under high production and disturbance may reflect colonization opportunities afforded by the specific type of disturbance (rototilling) enhanced with high resource availability from the fertilizer. Together these factors provided a relatively large assortment of microsites available for colonization by a diversity of taxa.

Regarding the core-satellite species hypothesis (CSS), our results are consistent with Ho_1 (species occupancy distributions change through time) at the lowland site, but not at the upland site. At the lowland site the increase in bimodality of native species over time suggests increasing development and integrity of the community consistent with the CSS metapopulation model. This pattern suggests a lack of recruitment limitation and increasing colonization from the regional species pool through time (Pickett et al. 1987; Foster et al. 2004). By contrast, there was not a clear temporal pattern of change in species occupancy distributions through succession at the upland site, but the observed patterns were bimodal and consistent with the CSS. Thus, at the upland site, recruitment from the regional species pool occurred throughout succession. Colonization opportunities from the regional species pool may have been moderated at the upland site by some of the highly competitive and dominant core species (e.g. *Festuca arundinacea* and *Lespedeza cuneata*) (Spyreas et al. 2001; Brandon et al. 2004).

As expected for a dynamic successional sequence we found partial support for Hanksi's proposition that core and satellite species will switch roles over time (Hanski 1982b, 1999). The identity of the most frequent species changed through time (Apps. 2 and 3). Over the course of seven years, several satellite species became core species, but only one core species became a satellite species. Moreover, five species were core species throughout the seven year sequence. Our results are consistent with models which suggest that temporal dynamics in core-satellite species are reflective of species turnover (Collins et al. 1993). Satellite species define local patches (Glenn & Collins 1990) but, due to their ephemeral nature, are more likely than core species to change in abundance. The applicability of the CSS to this successional system suggests that predictions of the CSS have applicability for understanding the dynamics of non-equilibrium systems at small scales (Bossuyt et al. 2004) as well as relatively undisturbed regional dynamics.

Scale dependency

The patterns and the underlying causes and mechanisms of succession are scale related (Pickett et al. 1987) as are species occupancy distributions. We observed scale related differences in species occupancy distributions whilst keeping sample number and extent constant and found bimodality characterizing the largest scale and unimodal satellite species dominated distributions characterizing the smallest scale of observation. This change from bimodality to unimodal distributions with a decrease in spatial scale could be artifactual due to the decreasing sample grain (Nee et al. 1991), although with a biological/ecological basis (McGeoch & Gaston 2002). Regional factors such as a widely available species pool can give rise to bimodality at large scales, while at the same time increasing heterogeneity *among* samples can also give rise to proportionally more satellite species and unimodal distributions at smaller scales (Bossuyt et al. 2004). However, in our system, while this pattern was observed, bimodality occurred at the largest, most heterogeneous scale, the blocks, each of which encompassed all nine disturbance/fertilizer combinations and thus the complete range of heterogeneity. Unimodal species occupancy distributions characterized the smaller, more homogeneous plots where single disturbance/fertilizer combinations were being compared. Unimodal distributions at all scales would have reflected a preponderance of fine-scale factors influencing species distributions (Perelman et al. 2001).

With an emphasis on local factors at the smallest scales (Gibson et al. 1993; Münzbergová 2004), we expected a shift from bimodal to unimodal back to bimodal species occupancy distributions with increasing productivity and disturbance (Ho_3 and Ho_4, respectively). In the upland field we observed a shift from bimodal to unimodal species occupancy distributions from low to high productivity plots (Ho_3), but not from low to high disturbance plots (Ho_4) where the opposite trend was observed. There was no disturbance-related pattern of species occupancy change in the lowland field. It is possible that our three-level productivity treatment was insufficient to allow the development of the expected ‘humped back’ species richness response (Collins et al. 1995), although this was observed in response to disturbance with no or infrequent fertilizer. The lack of a shift in species occupancy distributions toward a hump backed distribution suggests that local factors were sufficiently strong to maintain large numbers of satellite species and disallow dominance by core species at such small scales (Collins et al. 2002).

Exotic species

Exotic species invasions may be facilitated by the ability to take advantage of unused or fluctuating resources, i.e. the Empty Niche Hypothesis (Davis et al. 2000; Hierro et al. 2005). Thus, exotics may be expected to inflate the number of satellite species, leading to unimodal distributions (Ho_4). We found partial support for this hypothesis as the number of exotics increased the number of satellite species, but did not always lead to unimodal patterns. Nevertheless, we did not observe increased richness of exotics under high levels of resources or in an interaction with disturbance (contrary to Leishman & Thomson 2005). The species occupancy distributions of exotics were often bimodal, enhancing the bimodality of the native species and the total suite of species. This suggests that the exotics at the upland and lowland sites studied here represent a heterogeneous group of taxa with a variety of life history responses to environmental flux. Many of the exotics were core species (Apps. 1 and 2), and perennials so that they dominate the community and affected succession (e.g. *Festuca arundinacea* and *Lespedeza cuneata*; Spyreas et al. 2001; Brandon et al. 2004). However, other exotics were satellite or intermediate species, presumably having only a minor or transient effect on the system. Exotics can thus play a heterogeneous role in the structure of new communities in which they serve a variety of roles based upon their individual life-history characteristics (pre-adaptation model: Wilson et al. 2000).

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