

Sources of Diversity in a Grassland Metacommunity: Quantifying the Contribution of Dispersal to Species Richness

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*Submitted December 21, 2005; Accepted April 27, 2006;
Electronically published July 10, 2006*

ABSTRACT: Metacommunity theory suggests a potentially important role for dispersal in diversity maintenance at local, as well as regional, scales. In addition, propagule addition experiments have shown that dispersal often limits local diversity. However, actual dispersal rates into local communities and the contribution of immigrants to observed local diversity are poorly known. We present a new approach that partitions the diversity of a target community into dispersal-maintained and dispersal-independent components. Specifically, we quantify distances through space and time to the nearest potential seed source for naturally occurring recruits in target communities by using hierarchical data on species pools (local, site, region, and seed bank). Using this “recruit tag” approach, we found that dispersal contributed 29%–57% of the seedling diversity in perennial grasslands with different successional histories. However, both dispersal and seedling mortality remained remarkably constant, in absolute terms, over succession. The considerable loss of diversity over secondary succession (66%), therefore, could be understood only by considering how these processes interact with the decreasing disturbance rate (i.e., frequency of gaps) in later-successional sites. We conclude that a metacommunity perspective is relevant and necessary to understand the diversity and community assembly of this study system.

Keywords: colonization, diversity maintenance, disturbance, gap dynamics, mortality, succession.

The last decade has witnessed a surge of interest in how dispersal may affect the structure and diversity of plant

communities (Clobert et al. 2001; Levine and Murrell 2003; Nathan 2003; Gaston and Chown 2005). This research agenda has been motivated in large part by metacommunity theory demonstrating how spatial dynamics resulting from limited dispersal can affect local diversity (Shmida and Wilson 1985; Hurr and Pacala 1995; reviewed in Leibold et al. 2004; Holyoak et al. 2005). A second motivation has come from conservation biology, as we realize that understanding the role of dispersal is crucial for our ability to predict effects of ongoing environmental changes, such as in land use, climate, or habitat fragmentation (Drake et al. 1989; Tilman et al. 1994; Husband and Barrett 1996; McCarty 2001; Opdam and Wascher 2004; Thomas et al. 2004).

The most common empirical approach to questions of community-level effects of dispersal has been propagule addition experiments (Burke and Grime 1996; Tilman et al. 1997; Stampfli and Zeiter 1999; Shurin 2000; Fargione et al. 2003; Foster et al. 2004; Mouquet et al. 2004). A considerable number of such experiments, conducted across a wide range of habitats and community types, show that diversity of plant communities is often limited by dispersal; that is, when propagules are added, diversity is increased (reviewed by Turnbull et al. 2000; Levine and Murrell 2003; Zobel and Kalamees 2005). This is important information because dispersal limitation is a necessary condition for metacommunity processes to play a role in community structure. However, these experiments do not address the fundamental prediction of metacommunity theory, which is that currently observed diversity is maintained in part by dispersal (Vandvik and Goldberg 2005; see also fig. 1). The latter uniquely predicts that diversity would decline in the absence of dispersal, and the ideal test of the role of dispersal in diversity maintenance is, therefore, to experimentally decrease dispersal into communities. A few such experiments have been carried out (e.g., Williams 1984; Peart 1989; Kalamees and Zobel 2002), but they are technically difficult and subject to a number of artifacts and may therefore be feasible for only

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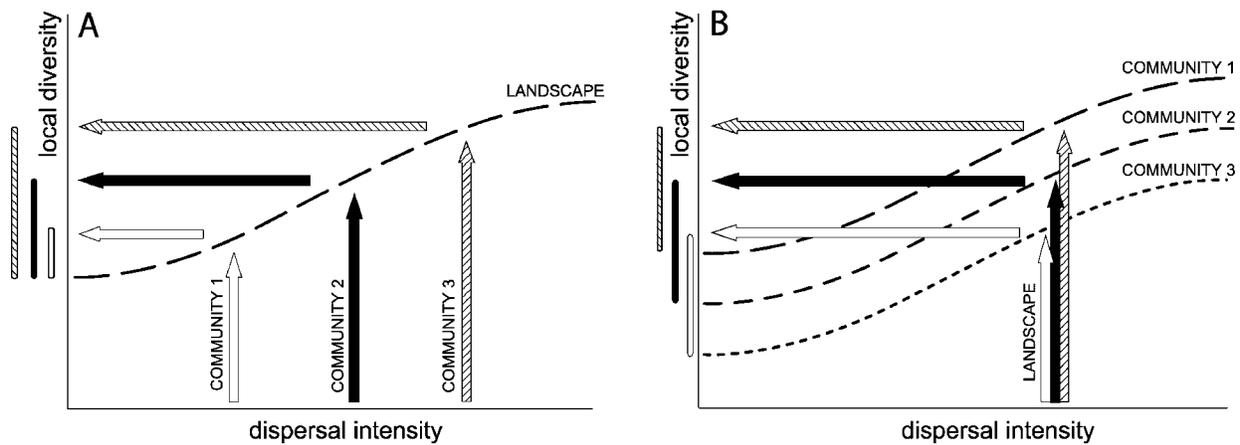


Figure 1: Predicted relationships between dispersal and local diversity in a metacommunity. For any local community, such a relationship divides the observed diversity into a dispersal-maintained component (indicated by the vertical lines parallel to the Y-axis for each community) and a dispersal-independent component (indicated by the intercepts of the curves). The figures illustrate how differences in diversity among communities can be explained by (A) differences in dispersal or (B) differences in local processes. Note that the shape of the dispersal-diversity relationship is generally unknown and may vary among systems and landscapes (modified from Vandvik and Goldberg 2005; see Leibold et al. 2004 for a review of theory that predicts such general relationships).

a narrow subset of species and community types (Klimeš 2005; Thompson et al. 2005; Vandvik and Goldberg 2005). Consequently, despite considerable theoretical evidence that dispersal contributes substantially to local diversity maintenance, empirical evidence is largely limited to demonstrating that dispersal can greatly limit local diversity (Bolker et al. 2003; Levine and Murrell 2003; Gaston and Chown 2005).

Dispersal-maintained and dispersal-limited components of diversity would be tightly correlated only if the relationship between dispersal and diversity depicted in figure 1 is a simple positive linear one (see Haig and Westoby 1988; Vandvik and Goldberg 2005). However, metacommunity theory shows that flat, increasing, humped, or more complex relationships can be predicted, depending on the extent to which diversity is also limited by other factors such as local interactions, resource availability, or niche partitioning (Leibold and Miller 2004). Thus, results of diaspore addition experiments are not necessarily indicative of the importance of diaspore rain for currently observed diversity within communities.

We present an alternative empirical approach that allows a quantitative partitioning of the observed local diversity of natural communities into dispersal-maintained and dispersal-independent (i.e., the diversity that could persist locally in the absence of any dispersal from outside) components. The general idea is to assign individual recruits in a target patch to a particular source (e.g., local or within-community propagule rain; nonlocal, among-community, or landscape-scale dispersal) by means of ex-

haustive surveys of the species pool of the local community and at increasing spatial scales surrounding that community. By using species identities as “recruit tags,” the approach thus allows quantification of the contribution from local versus nonlocal sources to local diversity and also, by tracing individuals over time, testing of predictions about the fate of recruits from these different sources (e.g., survival, growth, fecundity).

Our approach can, in principle, partition the diversity into any number of sources (fig. 1), and the dispersal-maintained component can therefore be further subdivided (e.g., based on dispersal distances). This possibility may be particularly useful when working with organisms that have dormant diaspores, such as the seed banks of many flowering plants, that allow them to “disperse through time” (sensu Harper 1977; Weiher et al. 1999) as well as through space. In metapopulation studies, seed banks are often seen as a nuisance because they introduce errors of “pseudoextinctions” and “pseudocolonizations” into the empirical data (Freckleton and Watkinson 2002; Ouborg and Eriksson 2004; Dostál 2005). However, in temporally and spatially variable environments, dispersal in space and dispersal in time through seed banks can actually be alternative adaptive strategies (Harper 1977; McPeck and Kalisz 1998). Accordingly, dispersal through time and dispersal through space can play analogous roles in mechanisms of coexistence, as exemplified by temporal and spatial storage effects (Chesson 2000; see also Holyoak et al. 2005). A particularly useful feature of our method is that it enables us to quantify the contributions of these

different sources to the maintenance of diversity in local communities, thereby allowing us to evaluate the roles of different mechanisms of coexistence within and between natural communities.

We use this method to test the fundamental prediction of metacommunity theory, namely, that dispersal contributes to observed local diversity rather than just limiting it from being still higher, and this contribution is not simply “weeded out” during early life history (Levine and Murrell 2003; Leibold et al. 2004; Klimeš 2005; Zobel and Kalamees 2005). Our study system is perennial grasslands in the subalpine region of central Norway. These are patchy, species-rich habitats, and it is generally assumed that dispersal, through either space or the seed bank, plays an important role for coexistence in such systems (Grubb 1977; Fowler 1988; Lavorel et al. 1994; Kotanen 1997; Olff and Ritchie 1998; Collins et al. 2002; Vandvik 2004). To evaluate this prediction, we partition the observed local diversity of grassland vegetation into components contributed from local versus nonlocal seeds (i.e., the dispersal-independent vs. dispersal-maintained diversity in fig. 1) and follow the fates of these seedlings over 3 years. While it is beyond the scope of this study to distinguish among particular mechanisms of coexistence (e.g., the four metacommunity perspectives of Leibold et al. [2004]), we nevertheless subdivide the dispersal-maintained components of diversity in our communities into contributions from dispersal across different distances and from the seed bank to illustrate the potential for further applications of the method.

We then evaluate the degree to which dispersal contributes to explaining differences in diversity among communities because strong contributions by dispersal to observed diversity within any particular community do not necessarily imply that differences between communities in diversity are also due to differences in dispersal; differences in local diversity could reflect different frequencies of successful immigration (fig. 1A; Mouquet and Loreau 2003) but also differences in local processes such as competitive exclusion among local communities within the metacommunity (fig. 1B). As indicated by the figure, these two general hypotheses can be distinguished by comparing the magnitudes of dispersal-maintained and dispersal-independent components of diversity across communities.

Our grasslands are seminatural systems, and as is happening in many areas of Europe, the cessation of traditional free-range grazing of these lands is leading to vegetation succession with consequent considerable diversity loss (Fægri 1988; Bernes 1993; Stanners and Bordeau 1995; Lawton 1999; Fremstad and Moen 2001). We explore the mechanisms behind the diversity decline over succession in two steps. First, we ask whether this decline is due to changes in dispersal-maintained or dispersal-independent

diversity by replicating our diversity partitioning along a 40-year successional gradient along which local species richness decreased by 50%. Second, we ask how knowledge of the ongoing processes controlling local community assembly along this gradient can help us understand large-scale, long-term successional dynamics in the landscape.

Methods

Study Area

Our study area, the Vangrøftdalen valley in eastern Norway (62°37'N, 10°49'E) has a subalpine climate with a July mean temperature of 11.4°C and a 5-month growing season (defined as months with mean temperatures above 5°C; 1960–1990 normal period, <http://www.DNMI.no>). The landscape is dominated by subalpine birch forests and extensive mires, with scattered seminatural grasslands. These grasslands were all grazed by free-ranging domestic herbivores (mainly sheep and cattle) until about 1950, but this land use has since been discontinued at many sites. Successional dynamics are slow in this subalpine region, and trees, mainly *Betula pubescens*, typically do not become dominant features of the vegetation until about 70 years after the cessation of grazing (V. Vandvik, unpublished data). The domestic herbivores create gaps within the closed vegetation sward. These gaps are important recruitment sites in these grasslands and are colonized overwhelmingly from seed (Vandvik 2004). The colonization of, and seedling establishment in, such gaps is therefore an ideal system to explore using the recruit tag approach.

Study Design and Sampling of Recruitment

For this study, we chose six grassland sites to represent a replicated successional (time-since-grazing) gradient; two sites that are still grazed, two where grazing was discontinued about 10 years ago, and two where it was discontinued about 40 years ago.

First, we established a set of target gaps where emergence and survival of recruits could be monitored (fig. 2). Within each of the six grassland sites, we established three plots (each 2 × 2 m; $n = 18$) and randomly positioned three target gaps (each 25 × 25 cm; $n = 56$) within each plot, with the constraint that recent disturbance (i.e., bare ground) was avoided. In August 1997, the gaps were created by cutting down to 10 cm below ground level along the edges and removing all above- and belowground plant parts, while leaving the soil and seed bank in place (see Vandvik 2004 for details).

To quantify recruitment, gaps were censused at the beginning and end of the growing season (last weeks of June and August, respectively) in 1998, 1999, and 2000. At each

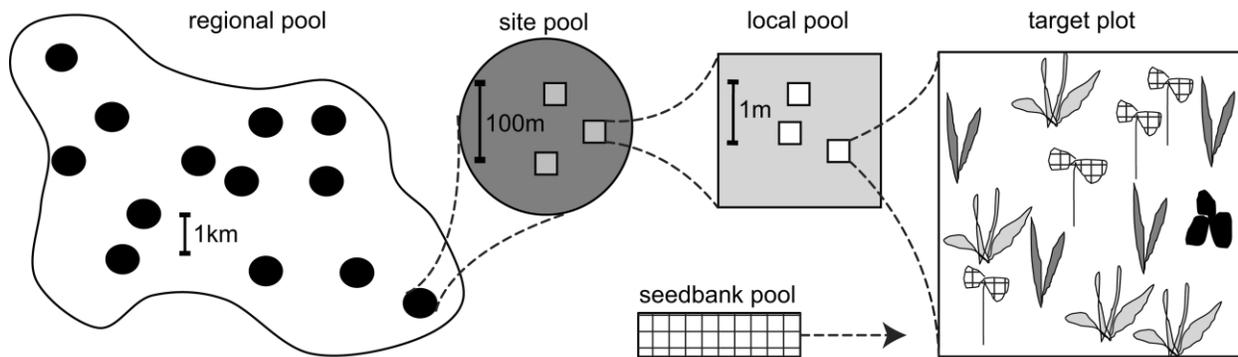


Figure 2: Illustration of our “recruit tag” approach, which enables quantification of the contributions of dispersal across different spatial and temporal scales to local diversity. In a set of target plots, germination, survival, and growth of naturally occurring recruits is monitored. The flora of and around each of these plots is then surveyed at nested spatial and temporal scales, and the species are classified into unique potential sources of recruits depending on minimum dispersal distances, in time or space, from the target plot. The observed seedling recruitment can then be partitioned onto the different sources by using species as dispersal “tags.”

census, all stems were counted, their positions within gaps were mapped, and their origins (seed or vegetative) were determined by looking for remains of seeds or cotyledons, runners, rhizomes, or other belowground connections. In the second and later censuses, we used a lack of juvenile traits (cotyledons), clonal connections, size, and growth characteristics to distinguish ramets that survived from previous censuses from new seedlings of the same species that may have germinated at the same spatial position. Although bulbils of *Bistorta vivipara* are actually vegetative regenerative organs, they function as “seeds” in terms of dispersal and are denoted as such hereafter. Clonal in-growths made up fewer than 2% of the first-year recruits and did not contribute any unique diversity, and therefore, they are not considered further in these analyses.

For this study, we focus our analyses on two seedling life stages: the colonization phase, which we address using data on seedlings emerging the first year ($n = 3,543$ seedlings), and the establishment phase, where we use data on the survival of these seedlings to the second year ($n = 1,083$ seedlings). To evaluate slightly longer-term outcomes, we also report on data from the final census, 3 years after the gaps were created. For all analyses, seedling data were pooled across the three target gaps within each plot (sampled gap area = $0.1875 \text{ m}^2 \text{ plot}^{-1}$; these are referred to as “gaps” hereafter).

Sampling of Species Pools

The total grassland flora was inventoried at nested spatial and temporal scales to identify potential sources of recruits into the target gaps (fig. 2). We assembled the species pools of the current vegetation as complete species lists for all 52 seminatural grasslands found within the valley (the

regional pool), each of the six sampled grasslands (the site pools), and each of the 18 plots (the local pools). The regional and site pools were chosen based on spatial discontinuities in the landscape, and the local pools were chosen arbitrarily to represent the scale of a local plant community. To achieve species lists that were as comprehensive as possible, each pool was surveyed two times, early and late in the 1997 growing season. Each survey was continued until no new species were found (typically about a half-day for each local pool; about 2 days for each site pool [up to about $200 \times 200 \text{ m}$]; total survey time was about 20 days for the regional pool). Species were only considered as potential sources of recruits and hence were included in a pool if they were recorded as flowering or fruiting at least once. A total of 244 taxa of higher plants were recorded. Nomenclature follows Lid and Lid (1994).

The persistent seed bank pools were estimated by the amount of seedling emergence from soil samples (see Thompson et al. 1997). Three soil samples (each a composite of 10 small samples; total sample area, 376.8 cm^2 ; depth, 0–10 cm) were extracted from within each plot in 1997. We collected the soil samples after spring germination but before autumn seed shed (mid-July to mid-August) to ensure that the seed bank recovered reflected the persistent seed bank in these grasslands. After 3 months of storage at $2^\circ\text{--}4^\circ\text{C}$, the samples were sieved and spread in a 0.5-cm layer on top of 5 cm sterile soil in plastic trays. Trays were arranged at random in a heated greenhouse and kept at diurnal temperatures of $15^\circ/25^\circ\text{C}$ under artificial light for two 4-month periods interrupted by 4 months of cold stratification. Emerging seedlings were counted every 2 weeks and removed as soon as they could be identified; difficult taxa (mainly Juncaceae, Cyperaceae, and Poaceae) were potted for later identification. Under

this protocol, an average density of 1,755 seeds m^{-2} from 67 taxa of higher plants germinated from the seed banks. All taxa had also been encountered at least once in the current vegetation surveys. The seed banks were originally divided into two depth strata (0–5 cm and 5–10 cm), but the contributions from the lower seed banks were consistently low, totaling 0.7%–7.4% of the observed seedling recruitment. Therefore, the two seed bank depths were pooled to increase clarity and statistical power in the analyses.

Partitioning Observed Recruitment on Sources

For each target gap, the regional species pool (244 spp.) was classified into unique potential sources of recruits into that gap by assuming that seedlings were most likely to have originated from the nearest possible source in time and space. We thus partitioned the species pools into unique potential sources at three spatial (local = L, site = S, regional = R) and two temporal (current vegetation, seed bank = SB) scales. Species that were present in both current local or site vegetation and seed banks were assigned to combined categories (L/SB, S/SB). While these categories were selected to represent potentially important scales at which dispersal through time and space might occur, we acknowledge that this is a coarse and somewhat arbitrary categorization of a continuous variable. Throughout this article, we will refer to all species present in the local communities (L + L/SB) as “local” and the diversity contributed from these species as “dispersal-independent” and the species in all other pools (S, R, SB, etc.) as “nonlocal” and the diversity contributed from these sources as “dispersal-maintained.”

The validity of our recruit tag approach depends on accurately distinguishing between the various unique sources of individuals that germinate in the target plots. This depends on two assumptions. First, we assume that we have comprehensively surveyed each pool so that we are not, for example, overlooking some adults in a local source and thereby erroneously counting recruits of that species as dispersed in from outside the local community. Given the small area defining each local pool (2×2 -m plot), we are confident that these pools are accurate. Recording errors are more likely in the site pools, defined at the scale of an entire grassland, and in the regional pool, which covers the entire valley. Thus, estimates of the relative contributions from the different nonlocal sources (i.e., site vs. region vs. seed bank) could be affected by survey errors, but such errors should have only minor effects on our estimates of the contribution from within versus outside the local community. Second, we assume that any recruits originated from the nearest possible pool in time and space. Because the vast majority of seeds dis-

perse short distances from the parent plant (e.g., generally less than 50 cm in alpine grasslands; Silvertown and Lovett Doust 1993; Körner 1999), we do not expect that our estimates of local seed recruitment are seriously overestimated due to long-distance dispersal.

Statistical Analyses

The contribution of dispersal processes to local diversity maintenance was evaluated by quantifying the contributions from the different sources of recruits to the newly colonized, established-seedling, and 3-year-old gap communities. Species counts were log transformed before analyses to attain normality. Three-way mixed model ANOVAs were conducted with source and successional stage as fixed independent factors; site was included as a random independent variable. Tukey’s Studentized range test was used to assess the significance of changes in contributions from particular sources over succession (PROC GLM, SAS, ver. 8.02, SAS Institute 2001).

Differences in mortality among recruits dispersed from different sources and changes in mortality over succession were evaluated using data on individual seedlings. This was done by means of logistic regression (PROC LOGISTIC, SAS, ver. 8.02, SAS Institute 2001).

Results

Partitioning Diversity into Dispersal-Maintained and Dispersal-Independent Components

Seedling recruitment was generally high; we registered a total of 3,543 seedlings from 58 taxa of higher plants in the target gaps during the first year, which corresponds to an overall mean density of 1,050 seedlings m^{-2} . The resident communities within local patches (sources L, L/SB) contributed a majority of these recruits (fig. 3A). Nevertheless, 20%–45% of the seedlings could not have originated from the current-year seed rain within communities and therefore must have reached gaps through dispersal across local communities within grasslands, among grassland sites, or from earlier years through the seed bank. This dispersal-maintained component made up 29%–57% of the diversity in gaps. Only 1,083 seedlings from 49 taxa survived to the second year, and both seedling mortality and species loss were generally higher among species dispersed in from outside the local communities, so the relative contribution of the local species increased from the colonization to the established seedling phase (fig. 3A vs. 3B; table 1). Nevertheless, the dispersal-maintained component made up 18%–42% of the diversity of the established seedling communities (fig. 3B).

New seedlings continued to emerge and establish in gaps

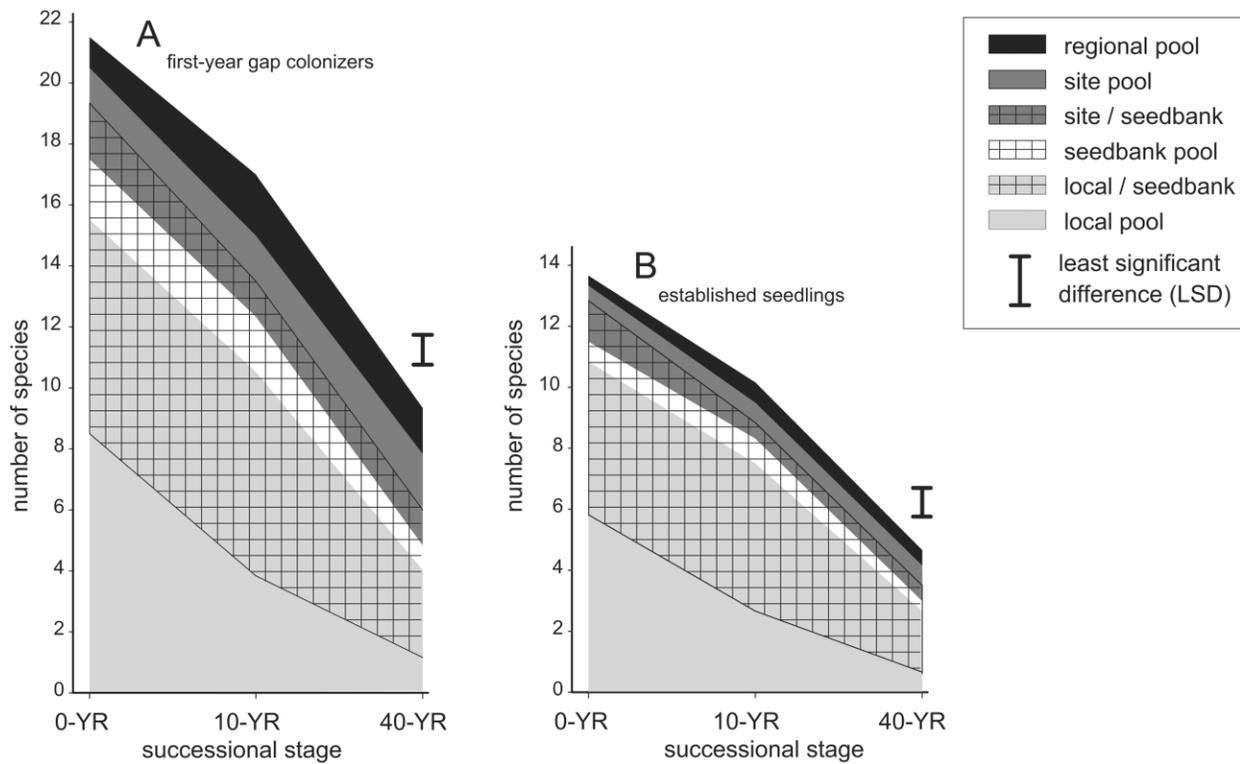


Figure 3: Contributions from different sources of recruits to the diversity of seedlings that colonized gaps (A) and that survived in gaps to the second year (B). For each panel, changes in the contributions to richness from particular sources over succession can be evaluated against the least significant difference (Tukey's Studentized range test; SAS, ver. 8.02, SAS Institute 2001). Data are pooled from three gaps within a plot, representing a gap area of 0.1875 m².

(4,246 and 3,307 in the second and third year, respectively). After 3 years, gaps were indistinguishable from the local matrix vegetation within plots in terms of species richness (fig. 4). This equity of total diversity between gaps and matrix, however, depended on the contributions from all the nonlocal pools, which made up an appreciable fraction of the diversity within the former gaps (27%–47%).

Changes in Diversity Components over Succession

Seedling diversity in gaps decreased significantly along the 40-year successional gradient; in the oldest sites, diversity had dropped by 66%, compared with sites that were still grazed (table 2; figs. 3, 4). This diversity loss over succession could be accounted for by a considerable decrease in the within-patch seed rain. The contribution from local species lacking seed banks decreased substantially ($F = 23.8$, $df = 2, 15$, $P < .0001$, source L; fig. 3A), as did the contribution from local species with seed banks between the 10-year and the 40-year stage ($F = 8.8$, $df = 2, 15$, $P = .0029$, source L/SB; fig. 3A). These among-community patterns persisted in the established

seedling communities ($F = 12.3$, $df = 2, 15$, $P = .0007$, source L; $F = 7.1$, $df = 2, 15$, $P = .0068$, source L/SB; fig. 3B).

In contrast, the dispersal-maintained component of diversity remained remarkably constant over succession, and therefore, site-scale or regional dispersal did not contribute to the changes in diversity over succession (fig. 3A; $P > .4$ in all cases). Seedling mortality also remained relatively constant (table 1). Although mortality within sources differed significantly with successional stage (table 1), pat-

Table 1: Logistic regression testing differences in seedling mortality between seedlings from local versus nonlocal sources and between successional stages

| Effect | df | Seedling mortality | |
|--|----|--------------------|--------------|
| | | Model | Wald X P |
| Recruit source | 5 | 52.7 | <.0001 |
| Successional stage | 2 | .4 | .825 |
| Recruit source \times successional stage | 10 | 27.7 | .002 |

Note: Number of events = 2,460; nonevents = 1,083.

terns were weak and not very consistent within diversity components (results not shown). Accordingly, the general patterns of contributions to diversity over succession persisted from the colonization to the established seedling phase (fig. 3A vs. 3B; table 2).

Discussion

Does Dispersal Contribute to Local Diversity?

Although a majority of the established seedlings originated within the local communities, there was a remarkably consistent flow of individuals and species into these target gaps from other patches within the same grassland sites, from other sites in the region, and from earlier years' seed rain through the seed bank. Both spatial and temporal dispersal processes contribute to local coexistence in these grasslands (see also Kalamees and Zobel 2002); in sum, the nonlocal seedlings contributed a quantitatively significant component, about six species or 29%–57% of the diversity of seedlings that colonized gaps.

Rates of seedling and diversity loss during establishment were high, however, especially from the components contributed by nonlocal sources where about three species per gap, or half of the diversity, were lost during the first year after colonization. This leads to the question of whether dispersal really contributes in any significant way to the local diversity of these communities or this nonlocal contribution will disappear, either because these seedlings are “weeded out” by species sorting or as a result of high random mortality (cf. Klimeš 2005). At least two lines of evidence suggest that dispersal remains important. First, a number of nonlocal species still persisted within the target gaps 3 years after these gaps were created. While new seedlings did emerge in gaps throughout the study period, survivors from the first-year cohort made up a considerable fraction of the third-year gap communities; a few even reached reproductive stages (V. Vandvik, unpublished data). This suggests that long-term survival is sufficiently high for at least some individuals of these nonlocal species to survive to maturity and establish new local populations within the communities. Second, despite this significant immigration from outside local communities, gap diversity after 3 years of recovery did not exceed that of the surrounding nongap matrix. Thus, the establishment and survival of new nonlocal species in gaps does not lead to an accumulation of diversity over time in these communities. This implies that local extinctions must be occurring at a rate high enough to balance (or even overshadow during succession) the observed rates of immigration. These findings indicate that steady state colonization-extinction dynamics play a role and hence that the metacommunity perspective is relevant and nec-

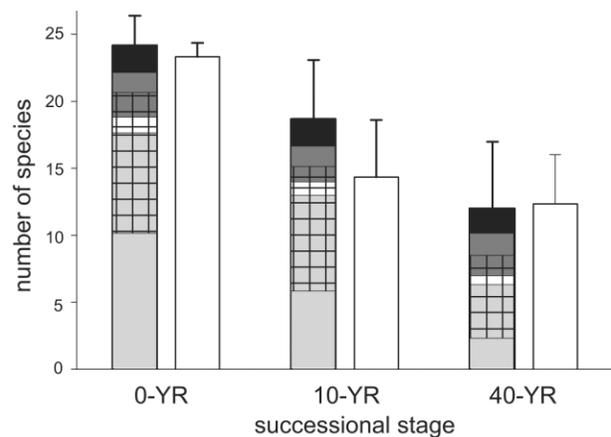


Figure 4: Species richness of gaps (left-hand bar in each pair) versus nongap matrix (right-hand bars) after 3 years (± 1 SD). The diversity in gaps is partitioned on the different sources of recruits; see figure 3 legend. ANOVA results: successional stage: $F = 21.1$, $df = 2, 30$, $P < .0001$; gap: $F = 0.9$, $df = 1, 30$, $P = .35$; successional stage \times gap: $F = 1.2$, $df = 2, 30$, $P = .32$. Data are pooled from three gaps within a plot, representing a gap area of 0.1875 m^2 .

essary to understand the mechanisms controlling community assembly and diversity maintenance in these local communities.

One intriguing finding in this study was that immigrants had consistently higher mortality rates than local species. Such differences in mortality based on dispersal distance would be expected if metacommunities were structured by habitat niche-based processes such as mass effects or life-history niche processes such as competition-colonization trade-offs (e.g., Yu et al. 2001; Mouquet and Loreau 2003) but not if they were governed by purely neutral processes (e.g., Hubbell 2001). In the current debate, niche and neutral models are often put forward as alternative explanatory models for entire communities. However, real communities are subject to both general processes (e.g., Hurtt and Pacala 1995), and we should therefore rather focus on their relative importance; as Hubbell (2003, p. 198) puts it, “How much of species (allele) diversity and abundance is due to asymmetric biotic interactions (selection), and how much is due to neutral, symmetric interactions and ecological drift (genetic drift)?” Although outside the scope of this study, we note that the recruit tag approach, by enabling us to assign individual recruits to dispersal sources and follow the fates of these individuals over time, provides a rich source of data for hypothesis testing and quantification of the roles of different metacommunity processes for local community composition and diversity.

Table 2: Tests of fixed effects in the nested ANOVAs on seedling species richness in gaps in two seedling life-history stages

| Effect | df | | First-year colonizers | | Established seedlings | |
|-------------------------------------|-------|-------|-----------------------|----------|-----------------------|----------|
| | Model | Error | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| Recruit source | 5 | 87 | 15.2 | <.0001 | 24.5 | <.0001 |
| Successional stage ^a | 2 | 3 | 3.4 | .1694 | 3.1 | .1843 |
| Recruit source × successional stage | 10 | 87 | 3.9 | .0002 | 2.9 | .004 |

^a Successional stage is nested within sites.

Does Dispersal Explain Differences in Diversity over Succession?

One striking pattern revealed by the diversity partitioning was the constancy of the contribution from nonlocal sources; at the scale of individual gaps, dispersal from outside the local communities contributed a remarkably stable number of species in all successional stages. This result implies that diversity loss over succession cannot be accounted for by any changes in dispersal processes per se. Specifically, the hypothesis that grazing animals are important dispersal vectors in seminatural landscapes, which predicts that decreased animal density over succession should result in decreased diversity (Olf and Ritchie 1998; Poschlod et al. 2005), is not supported by our data.

Furthermore, there were no consistent differences in total seedling mortality in gaps, which remained constant at about 75% over successional stages. This means that while local processes of stochastic mortality and species sorting are important determinants for diversity within each of the communities, these processes did not contribute to differences among successional stages.

Instead, decreased diversity in gaps over succession could be accounted for by a decreased contribution from the local within-community seed rain (i.e., within 2 × 2-m plots). This decrease in the number of locally contributed species emerging in gaps parallels a decrease in the diversity of the local matrix vegetation (the 0-year, 10-year, and 40-year successional local sources contained on average 27.5, 19.5, and 10.2 species, respectively). This suggests a relatively straightforward causal relationship; the diversity of a gap is limited by the species pool of the local community immediately surrounding that gap (Zobel 1997; Zobel and Kalamees 2005).

This conclusion, however, then begs the question of how these considerable differences in the local species pools have emerged; that is, what determines diversity of the matrix surrounding each gap? To answer this question, we need to scale up from the dynamics within gaps, which have been the focus of this study, to explore the implications of our findings for the larger-scale and longer-term

dynamics of grasslands undergoing secondary succession (i.e., the site scales of fig. 2).

In our grasslands, gap area decreased at least threefold from grazed to successional stages (Vandvik 2004). This means that a later-successional grassland, with fewer gaps per unit area, will “sample” fewer individuals and fewer species from the nonlocal seed rain than a community with higher gap frequency, even though immigration rates are constant and the fraction of immigrant species that successfully establish and become part of the local pool in the next generation is also relatively constant. It is therefore neither dispersal rates from outside the local community nor local demographic processes of stochastic mortality and species sorting that determine the diversity of the grassland matrix, but rather differences in target area for dispersal between grazed and successional stages. We could reach this conclusion only because the recruit tag method allowed us to quantify the arrival and survival of recruits from local versus nonlocal sources. However, while the dichotomy between dispersal-maintained and dispersal-independent was very useful for disentangling these local-scale short-term dynamics, over larger spatial and temporal scales there is obviously an interaction because species from nonlocal sources successfully establish and then become part of the local pool in the next generation.

In our study system (Vandvik 2002), as in perennial grasslands elsewhere (Fenner 1978; Rogers and Hartnett 2001; Forbis 2003; Forbis et al. 2004), seedling recruitment is low in intact vegetation, and one potentially important effect of herbivores is to increase the availability of regeneration niches by disturbance (Olf and Ritchie 1998). Our study illustrates how such gaps function as remarkably efficient “seed traps” that sample the seed rain from local and nonlocal sources at different probabilities, depending mainly on the distances to the source. It has long been acknowledged that changes in disturbance regimes may function as a driving force in succession (Connell and Slatyer 1977; Denslow 1980; Pickett et al. 1987; Milchunas and Lauenroth 1993; Kotanen 1995; Blatt et al. 2001), but these studies have mainly focused on the role of distur-

bance in changing local interactions among species. Our results point to a different explanation for the same phenomenon, namely, a simple species-area relationship: less gap area in later-successional grasslands results in less immigration into the local community, which again results in lower diversity.

The metacommunity perspective points to the importance of interactions between processes operating at different spatial scales (Wilson 1992; Levin 2000; Amarasekare 2003), and our results provide an empirical example of how dynamics at different scales may be intertwined. The diversity loss during secondary succession could be understood only by considering the interaction between gap-scale dynamics due to dispersal and seedling mortality, both of which are constant over succession, with the gap frequency in the grassland site, which decreases over succession.

Implications for the Conservation of Seminal Habitats

The cessation of traditional low-intensity land use is not unique to our system; it is a general trend affecting all seminatural habitats of Europe today (Fægri 1988; Lawton 1999). In fact, successional changes following abandonment have been recognized as the major threat to biodiversity in Europe (Bernes 1993; Stanners and Bordeau 1995; Fremstad and Moen 2001; Eriksson et al. 2002). One important implication of our results in this context is that they point to how land-use change, through its effect on local disturbance rates, may interact with landscape-scale dispersal and metacommunity dynamics. Disturbances provide the microhabitats where dispersed recruits, should they arrive, may establish and survive. The cessation of land use may therefore decrease the rates of successful immigration into local communities. This may be especially important in today's landscapes because dispersal also affects the ability of species to respond to changes in another important environmental factor, climate. The efficiency of "environmental tracking" responses to climate change depends critically on the ability of species to disperse to and establish in new sites (Callaghan et al. 1992; Grabherr et al. 1994; Opdam and Wascher 2004). Our results therefore point to a potentially important interaction between these two global change drivers.

Conclusions

Metacommunity theory shows that dispersal can be of paramount importance for diversity maintenance at local as well as regional scales, yet actual immigration rates into local communities and the contribution of immigrants to local diversity are poorly known empirically (Bolker et al. 2003; Levine and Murrell 2003; Gaston and Chown 2005).

In this article, we present a new recruit tag approach that enables us to partition the observed diversity of our local community into a dispersal-maintained and a dispersal-independent component.

Using this approach, we were able to disentangle the roles of dispersal, local processes, and disturbance in determining the loss of diversity over succession of seminatural grasslands in the subalpine regions of Norway. We found that dispersal contributed significantly to the local diversity within each successional stage and that local community assembly was not neutral. However, neither dispersal processes per se nor local species sorting seemed to be important for determining differences in diversity between communities. Instead, this successional gradient in diversity could be understood as a simple species-area relationship; less gap area in later-successional grasslands resulted in less total immigration into the local community, which in turn resulted in less "trapping" of new species to the community. Thus, the key factor explaining differences in diversity between communities was a change in disturbance regime, while a combination of dispersal and local sorting determined diversity within each community. We suggest that such discrepancies between processes that explain diversity within versus between communities may be very common.

Acknowledgments

We thank K. McGuire, Z. Munzbergová, and other members of Plant Ecology Discussion Group (Ann Arbor, MI) for discussions during the preparation of this manuscript, and B. Foster, P. Geddes, J.-A. Grytnes, S. Harrison, E. Werner, and an anonymous reviewer for comments on previous versions. V.V. was supported by the Norwegian Research Council (grants 73758/410 and 151637/432).

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