

## CENTENARY SYMPOSIUM SPECIAL FEATURE

# Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology

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## Summary

1. Metapopulation and metacommunity theories occupy a central role in ecology, but can be difficult to apply to plants. Challenges include whether seed dispersal is sufficient for population connectivity, the role of seed banks and problems with studying colonization and extinction in long-lived and clonal plants. Further, populations often do not occupy discrete habitat patches. Despite these difficulties, we present case studies to illustrate explicit integration of spatial and temporal data in plant ecology.

2. First, on the population level, we focused on two early successional species that lack discrete habitat patches. Multi-year data sets taken with a grid approach and simple models permit the analysis of landscape dynamics that reflect regional as well as local processes. Using *Silene latifolia*, we examined colonization. We found evidence for seed dispersal and connectivity among populations across a large landscape. With *Helianthus annuus*, a species with seed banks, we determined the degree to which landscape-level patterns of abundance were predicted by local processes (previous year recruitment at a site plus seed banks) vs. seed dispersal. Local processes dominated dynamics.

3. Second, at the community level, we utilized a landscape-level experiment to examine the influence of environmental gradients and spatial processes (dispersal limitation) on community composition during 18 years of succession. Throughout succession, environmental and spatial factors both contributed significantly to spatial variation in species composition (beta diversity). When connectivity was disrupted, space was the dominant factor underlying beta diversity, and this did not change over time. Across more connected communities, spatial effects diminished over succession as the importance of environmental factors increased, consistent with species-sorting metacommunity models.

4. *Synthesis.* Metapopulation/metacommunity concepts emphasize the interaction between space and time in ecological processes. Spatial processes, such as long-distance dispersal, play a crucial role in creating new populations. Temporal processes, including seed banks, may dominate dynamics at both local and regional scales. The relative importance of spatial vs. temporal processes changes as populations persist and communities assemble over time; these patterns may only emerge after many years. Integrating long-term data with spatial data is thus essential for understanding spatio-temporal patterns inherent in metapopulation and metacommunity theories.

**Key-words:** colonization, dispersal, habitat connectivity, local vs. regional dynamics, long-term data, plant population and community dynamics, seed bank, species assembly, species-sorting, succession

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## Introduction

All organisms inhabit spatially and temporally heterogeneous worlds: at any given instant, the habitats that allow survival, growth and reproduction for a particular species are surrounded by habitats that are unsuitable to varying degrees. Furthermore, the spatial pattern of habitat quality can itself vary through time. A hierarchy of spatial and temporal scales is thus superimposed on ecological questions. At small spatial scales and over modest time horizons, one can study population dynamics within suitable habitat patches. However, at larger spatial scales and over longer time-scales, rates of colonization and extinction can determine species persistence across a network of possibly shifting habitat patches. This deceptively simple statement is at the heart of Levin's classic patch model (Levins 1969, 1970) that served as a now historical springboard for the current ecological focus on metapopulations – most simply defined as an assemblage of local populations partially linked by dispersal (Hanski & Gaggiotti 2004; Hanski 2010). Even without local extinction, spatial fluxes of individuals in heterogeneous landscapes can perturb local abundances away from what would be expected given just local processes, as in source-sink or mass effect dynamics (Shmida & Whittaker 1981; Holt 1983; Pulliam 1988). Recurrent immigration from productive to unproductive sites may, for instance, boost a species' abundance in the latter or even permit it to persist when it would otherwise go extinct. In recent decades metapopulation research has grown tremendously, with studies ranging from population dynamics in spatially realistic landscapes, to interactions of a focal species with spatially structured competitors, pathogens, predators and mutualists, to diverse evolutionary questions (Silvertown & Antonovics 2001; Hanski & Gaggiotti 2004; Hanski 2010).

Community ecologists have likewise recognized the importance of spatial processes and regional factors in governing the structure and dynamics of multi-species assemblages. Roughly analogous to a metapopulation, a metacommunity is defined

as a network of local species assemblages linked by dispersal (Leibold *et al.* 2004; Holyoak, Leibold & Holt 2005; Gonzalez 2009). A limiting case of a metacommunity is a mainland-island configuration – the familiar domain of island biogeography. In this case, there is pronounced asymmetry in dispersal, and a clearly defined external source pool from which colonists are drawn. More broadly, all habitats in a region can in principle provide dispersing propagules that can appear in any other habitat. Metacommunity ecology is thus a generalization not just of metapopulations from one to many species, but of island biogeography (Hubbell 2001). Metacommunity dynamics can largely be described by four non-mutually exclusive models that vary in the degree to which environmental factors and dispersal influence community structure at local and metacommunity scales (Table 1, Leibold *et al.* 2004). Two of these models, the patch dynamic model and the mass effects model, extend directly from metapopulation theory. For instance, the patch dynamic model emphasizes stochastic colonization and extinction and invokes trade-offs in species' dispersal and competitive abilities to explain coexistence in a network of environmentally homogenous habitat patches. The mass effects model builds on the metapopulation concepts of source-sink and rescue effects by asserting that dispersal rates among habitat patches are high enough to influence population dynamics. Implicit in the mass effects model (although not strictly necessary for mass effects to operate) is the assumption that habitat patches vary in their quality and that some species outperform others in a given environment. Such differences in local environmental factors provide the basis for the third model, species sorting. This model assumes that all species can reach all habitat patches over some time span, but community composition in the end strongly reflects species' adaptation to environmental conditions. Thus spatial turnover in community composition closely matches environmental gradients as the identity of the top competitor shifts. By contrast, the neutral metacommunity model assumes that all species are demographically and ecologically equivalent; community structure is a function

**Table 1.** Comparison of metapopulation and metacommunity concepts and their applications in empirical studies. These disciplines have separate histories and perspectives; greater integration of approaches is highly desirable

|                                  | Metapopulations  | Metacommunities  |
|----------------------------------|--|--|
| Scale of ecological organization | Population (single species)  | Community (multi-species)  |
| Focus                            | Persistence  | Species composition  |
| Models                           | <i>Homogeneous patches:</i> Levins<br><i>Heterogeneous patches:</i> spatially realistic metapopulation theory, source-sink | <i>Homogeneous patches:</i> patch dynamics, neutral*<br><i>Heterogeneous:</i> mass effects, species sorting              |
| Parameters                       | Focus on colonization and extinction rates   | Focus on colonization, extinction and local growth rates as a function of dispersal rates and interspecific interactions |
| Measurements                     | Population size, occupancy   | Alpha and beta diversity, variance in community composition  |
| Heterogeneity                    | Focus on suitable vs. not suitable habitats  | Focus on resource gradients  |
| Challenges to empirical testing  | Designating patches, defining suitable habitat<br>Estimating colonization and extinction                                   | Designating communities arbitrarily  |

\*Neutrality focuses on equivalence of demographic performance among species and does not necessarily assume all sites are environmentally homogeneous.

of stochastic colonization and extinction dynamics. Collectively, these models represent a continuum of processes, several of which may operate simultaneously.

The rich theoretical literature noted above is often well integrated with empirical research. Most field studies of metapopulations and metacommunities have focused on animals inhabiting distinct habitat patches. Classic metapopulation examples include butterflies in meadows (Thomas & Hanski 2004; Hanski 2010), while empirical applications of metacommunity ideas are common in freshwater ecology (Cottenie *et al.* 2003; Leibold, Economo & Peres-Neto 2010; Winemiller, Flecker & Hoehinghaus 2010). Analogous research on plants restricted to distinct habitat patches does of course exist (e.g. Akasaka & Takamura 2011), and metacommunity perspectives build on long-standing interests in plant ecology (e.g. succession, patch dynamics and disturbance ecology). However, overall, the application of metapopulation and metacommunity theory to plants can be challenging, leading to considerable discussion in the literature (metapopulations: Eriksson 1996; Husband & Barrett 1996; Bullock *et al.* 2002; Freckleton & Watkinson 2002; Ehrlén & Eriksson 2003; Freckleton & Watkinson 2003; Pannell & Obbard 2003; Ouborg & Eriksson 2004; metacommunities: Leibold *et al.* 2004). Controversies arise because many plant and habitat characteristics do not fit comfortably into literal interpretations of theory. Consider four challenges. First, plants are sessile and movement is by seed dispersal, which typically occurs over short distances. Long-distance dispersal – crucial for landscape-scale dynamics to operate – can be rare, highly stochastic, and difficult to estimate (Nathan *et al.* 2008). Second, the common occurrence of seed dormancy (Baskin & Baskin 1998) makes it challenging to identify colonization and extinction events. An observed colonization event could be due to seed dispersal across space or to emergence from buried seeds (dispersal in time). Third, most terrestrial ecosystems are dominated by long-lived plants, and many species have clonal vegetative growth; both features create practical difficulties for collecting data on colonization and extinction. Finally, it is often difficult to define discrete 'suitable' and 'unsuitable' habitat patches for plants. For example, researchers were unable to define suitable habitat patches in over half of the regional studies reviewed by Freckleton & Watkinson (2002). Community ecologists likewise must contend with defining the boundaries of the units they study.

These challenges are daunting, and it might be tempting to conclude that metapopulation and metacommunity theories are simply not applicable and/or feasible to study with plants. We take an alternative view. Following Ouborg & Eriksson (2004), we argue that metapopulation and metacommunity concepts have stimulated interest and novel insights in plant regional dynamics despite the lack of complete concordance between empirical systems and theory. Because colonization and extinction are inherently temporal, as well as spatial, concepts (Chase & Bengtsson 2010), we particularly emphasize the need for explicit spatio-temporal research in plant ecology (Fridley *et al.* 2006; White *et al.* 2010). Further, for plants, the existence of seed banks and long-lived adult plants requires studies across longer time-scales.

Our approach in this paper is twofold and will utilize three case studies, all involving succession. First, at the population level, we use early successional species (*Silene latifolia* and *Helianthus annuus*) to address three challenges of studying landscape-level processes in plants: seed dispersal, seed banks and poorly defined habitat patches. Second, on the community level, we focus on a multi-year field experiment aimed at understanding how habitat fragmentation influences succession. We explore the relative contribution of spatial processes and environmental gradients to the development of spatial structure in communities over time. We conclude by suggesting future research directions and more broadly consider the need for more links between metapopulation and metacommunity research.

### Population-level research

Direct assessment of metapopulation processes requires collection of data at multiple sites for multiple years. Population abundance, persistence, colonization and extinction are then related to habitat patch size, persistence, quality and connectivity. Long-term records of plant population dynamics at the landscape level are biased towards studies of short-lived vascular plants and, especially in the last decade, epiphytes. The latter, with their dependence on host trees, match many of the assumptions of metapopulation (and metacommunity) theory (Snäll, Ehrlén & Rydin 2005; Pharo & Zartman 2007; Burns & Zotz 2010). For long-lived species, metapopulation dynamics can be inferred using statistical relationships between patch occupancy and habitat connectivity (Verheyen *et al.* 2004), although these may require equilibrium assumptions.

A key issue in metapopulation studies is identification of habitat patches: such entities may be effectively static landscape features (e.g. serpentine outcrops, Harrison, Maron & Huxel 2000), where patch arrays are for all practical purposes fixed over the time-scales relevant to colonization and extinction. In such landscapes, extinctions are driven by processes intrinsic to the populations themselves (e.g. small population sizes), or by biotic factors such as herbivory. Alternatively, habitat patches may have their own dynamics over shorter time-scales, leading to relatively determinate changes in colonization potential and extinction risks for plant populations (Menges 1990; Harrison & Taylor 1997; Snäll, Ehrlén & Rydin 2005). Disturbance regimes can often induce successional changes (Watt 1947), which lead to waves of colonization potential and extinction risks, effectively shifting the spatial configuration of patches or successional states. Both static and disturbance-driven successional habitats can strongly affect patterns of connectivity and occupancy in metapopulations (Hodgson, Moilanen & Thomas 2009).

Habitat patches, however, cannot always be delineated. A pragmatic solution to this problem is to superimpose a grid-work over a region and determine occupancy, abundance, colonization and extinction for arbitrarily defined 'populations' within grid squares (Antonovics *et al.* 1994; Thomas & Kunin 1999). Grid-based approaches result in complete coverage of a defined area, so one does not risk missing plants in places

assumed to be unsuitable. However, grid cells may vary in environmental variables, and it is hard to know whether 'empty' cells are 'occupiable'. Several of the most extensive spatio-temporal studies of plant population dynamics have used grid-based approaches and early successional environments. Examples of studies covering 10's–100's of km and 5–20+ years include the following: *Brassica napus* (Crawley & Brown 1995, 2004); *H. annuus* (Moody-Weis *et al.* 2008; Alexander *et al.* 2009); *Lactuca serriola* (Prince, Carter & Dancy 1985) and *S. latifolia* (Antonovics *et al.* 1994; Thrall & Antonovics 1995; Antonovics, Thrall & Jarosz 1998; Antonovics 2004). We will present results for two of these species.

Although the above species may have evolved in permanently open habitats (Marks 1983), they now typically colonize transient, disturbed patches in anthropogenically altered habitats such as roadsides. There has been discussion about whether such landscape-level systems are metapopulations in the narrow sense or are best described as 'spatially extended populations' (Freckleton & Watkinson 2002). Some of the argument is definitional. Interpretations of spatial structure are scale-dependent and any system of spatially interconnected populations lies on a continuum between one extreme of discrete habitat patches of 100% uniformity, suitability and equal interconnectedness (as in Levins 1969, 1970) and the other extreme of a swath of continuously occupied habitat. The important issue is to find an appropriate spatial scale given the study's focus and to develop methods for quantifying spatial and temporal components of relevant processes. For example, connectedness over time, through a seed bank, might be as important for local persistence as spatial interconnectedness (Eriksson 1996). Further, while not all plants have well-defined habitats, aggregated plant distributions do provide discrete habitat patches for pollinators, seed dispersers, pathogens and herbivores that in turn influence their dynamics (e.g. Thrall & Burdon 1997; Thrall, Godfree & Burdon 2003; Ouborg & Eriksson 2004; Antonovics 2004).

#### DISPERSAL, COLONIZATION AND CONNECTIVITY: *SILENE LATIFOLIA*

##### Study design

The colonization process is central to metapopulation and metacommunity dynamics. Estimation of long-distance dispersal is also of critical significance to research on migration, disease spread, gene flow and invasions (Nathan *et al.* 2008; Soons & Bullock 2008; Mundt *et al.* 2009). To estimate long-distance dispersal, we used a multi-year data set of the short-lived perennial white campion, *S. latifolia* (Caryophyllaceae). In the southern USA, this species is largely restricted to roadsides, and discrete habitat patches cannot be clearly defined. Antonovics and collaborators have thus utilized a gridwork approach and counted the numbers of plants in contiguous 40-m roadside segments since 1988 over 150 km of roads in an *c.* 25 × 30 km area of south-western Virginia, USA (for details, see Antonovics *et al.* (1994), Thrall & Antonovics (1995), Antonovics, Thrall & Jarosz (1998), Antonovics

(2004) and Appendix S1 in Supporting Information). Also included was a record of the number of plants in each segment that were diseased with another smut caused by the fungus *Microbotryum violaceum*, which itself was expected to have metapopulation dynamics, superimposed on and to some extent driving, the dynamics of its host. Censuses of this system are continuing, but for the present analysis, we consider data collected from 1989 to 2002.

To identify colonization events, we focused on segments that had been newly colonized within the 1998–2002 period, but which had never previously been occupied since the start of the surveys (mostly a 13-year period, although some sections were only added 9 years previously). Although it thus seems unlikely that seed banks contributed to recruitment into these sites (see Purrington & Schmitt (1995) and Peroni & Armstrong (2001) for studies on seed dormancy), there is a possibility that seeds may have dispersed to empty sites in the past and remained dormant following dispersal, but this effect is likely to be small. We estimated the number of colonized individuals as a function of the number and distance of plants that were flowering in other segments in the previous year. Specifically, we used the following tiered exponential function (Ribbens, Silander & Pacala 1994; Clark 1998):

$$N_j = \sum_{i \neq j} \alpha n_i e^{-\lambda \theta} \quad \text{eqn 1}$$

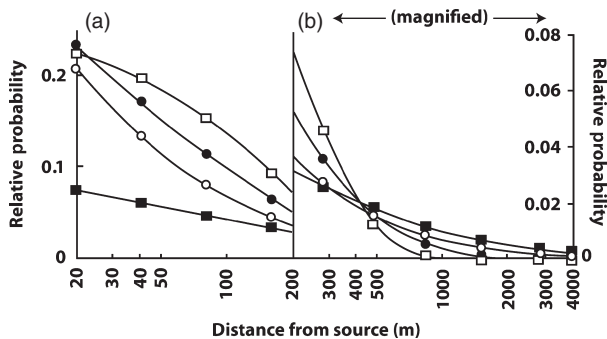
where:  $N_j$ , the number of individuals observed in newly colonized segment  $j$  (the recipient);  $n_i$ , the number of individuals in the  $i$ th (potential source) segment the previous year;  $x$ , the Euclidean distance between the potential source segment and the focal segment (in units of 40-m segments);  $\alpha$ , a parameter determining the average per capita contribution of each individual in the source segment, to the realized population in the recipient segment;  $\theta$ , a parameter determining the effect of distance, allowing for fatter tails if  $\theta < 1$ .

Using maximum likelihood methods, and testing the model over increasing distances of potential colonization, we found that it was possible to get improved model fit and therefore improved estimates of long-distance dispersal by including source populations as far away as 3 km. See Appendix S1 for details of the analyses.

##### Results and discussion

The best parameter combinations were  $\alpha = 0.0025$  and  $\theta = 0.49$ , and we used these values to simulate colonization events given the observed distribution of plants along the roadways. These dispersal parameters (incorporating the potential for long-distance sources of colonists) estimated a much higher frequency of long-dispersal events than if only nearest neighbours were considered (Fig. S2). Moreover, our ML estimates of dispersal were reassuringly consistent with values we had assumed in earlier simulations of spatial dynamics (Thrall & Antonovics 1995; Antonovics, Thrall & Jarosz 1998; Fig. 1). However, a similar analysis (not shown) of the colonization





**Fig. 1.** Dispersal distributions of seeds of *Silene latifolia* (circles) and spores of *Microbotryum violaceum* (squares); graph (b) is a continuation of (a), but with a smaller y-axis for better visualization of long-distance trends. Lines with open symbols are dispersal distances based on the Weibull distribution 'guesstimated' from general natural history (Antonovics *et al.* 1994; Thrall & Antonovics 1995; Antonovics, Thrall & Jarosz 1998) while the lines with closed symbols are from the maximum likelihood models described in this paper. The distribution describes the relative probabilities of dispersed seeds or spores expected at a given distance from the source; the cumulative distributions sum to unity.

process of the associated obligate pathogen showed that these previous models had severely underestimated fungal dispersal distances (Fig. 1).

Long-distance dispersal can thus be inferred from appropriate data sets that contain both spatial and temporal data on abundances. However, because colonization and extinction events may be rare (relative to birth–death processes within populations), such studies have to be carried out on a large enough scale so that they include a large number of such events over the time course of the study. Interpretation of these results in terms of actual dispersal, however, should be viewed cautiously. For example, we did not take into account the spatial structure of 'habitat quality'. If habitat quality declines as one moves away from pre-existing populations, dispersal distances are likely to be underestimated. To address these issues, one should ideally quantify habitat quality using experimental studies of establishment (Ehrlén & Eriksson 2000). Knowledge of dispersal mechanisms is also important. Although the seeds have no special dispersal mechanism, and short-term studies suggest few are dispersed more than a few metres, long-distance dispersal could occur by cars, road maintenance activities (including mowers), farm machinery and by the abundant deer in the area. Recent work on human-mediated seed movement in other systems includes Zwaenepoel, Roovers & Hermy (2006) and Wichmann *et al.* (2009).

We recognize that we cannot completely eliminate the possibility of seed dormancy contributing to rare colonization events; however, the probability of seeds not only surviving for 9–13 years but also occurring in appropriate environments for subsequent emergence seems very remote. Seed longevity studies are insufficient by themselves to address these questions; in future, we will jointly estimate seed dispersal and dormancy using approaches similar to the next section on *H. annuus*.

Despite challenges of interpretation, several features of this work are important to emphasize. First, this methodology can be applied to plants that defy typical metapopulation definitions – *S. latifolia* is found throughout roadside areas, and habitat patches are not obviously delineated. Second, dynamics of populations that have relatively continuous distributions need not be solely the result of local dispersal processes, but may still be influenced by long-distance dispersal events (a point long recognized in studies of population genetic structure). Even rare events can be ecologically relevant: simulations of the *S. latifolia*–*M. violaceum* system, for example, illustrate that occasional dispersal of resistant genotypes has landscape-wide effects on disease persistence (Antonovics, Thrall & Jarosz 1998). Third, in a grid-based study, the spatial scale used will affect the estimated colonization and extinction rates. However, we have shown in both *S. latifolia* and *H. annuus* that colonization and extinction rates calculated at several spatial scales can be predictive of such rates at other scales (Moody-Weis *et al.* 2008).

#### SEED BANKS AND LANDSCAPE-LEVEL POPULATION DYNAMICS: *HELIANTHUS ANNUUS*

##### Study design

The unusually long duration of the *S. latifolia* study allowed us to focus on the spatial component of colonization (=dispersal). We next consider the broader question of population dynamics across a landscape. Abundance patterns over time and space will depend on regional processes of dispersal and local processes (recruitment from seeds produced the previous year at the site and from older seeds in the soil; we define the latter as the 'seed bank' for this system). These processes are challenging to study directly given that above-ground surveys of species with seed banks may record 'pseudo' colonization and extinction events and overestimate the importance of dispersal. Given these difficulties, we parameterized a population model using multi-year data on population abundances. Our data came from roadside surveys of the annual sunflower, *H. annuus* (Asteraceae) (23.8 km roadside survey, 1999–2003, Kansas, USA, Fig. S3). Field methods were similar to the *S. latifolia* study with the exception that segments were 80 m (for details, see Moody-Weis *et al.* (2008) and Alexander *et al.* (2009)).

The ecology of *H. annuus* is well understood (Appendix S2). For example, Alexander & Schrag (2003) found that 10–23% of seedlings under individual plants came from the seed bank; annual seed survival on the soil surface at a second site was 10–30% and up to 83% with seed burial. Most seeds disperse close to maternal plants (< 3.2 m, Appendix S2). However, longer dispersal can occur: Burton (2000) found wind and water could move seeds up to 105 m. We thus constructed a model incorporating both dispersal through space and time with the following dynamics. Initially, plants produce seeds that may disperse. A percentage of the dispersed seeds survive the winter, after which some will germinate, grow and reproduce; the remaining viable seeds remain dormant and may germinate

in subsequent years. This life cycle leads to equations for adult plants ( $N$ ) and seeds in the seed bank ( $S$ ):

$$N_i(t+1) = g\gamma \left[ S_i(t) + \sum_{j=1}^n \alpha N_j(t) f(j \rightarrow i) \right] \quad \text{eqn 2}$$

$$S_i(t+1) = (1-g)\gamma \left[ S_i(t) + \sum_{j=1}^n \alpha N_j(t) f(j \rightarrow i) \right] \quad \text{eqn 3}$$

with probability of a seed germinating, growing and reproducing (hereafter ‘germination’)  $g$ , seed survival in the seed bank  $\gamma$ , fecundity  $\alpha$  (adjusted for pre-dispersal predation and the initial pulse of post-dispersal predation), and dispersal probability from segment  $j$  to  $i$ ,  $f(j \rightarrow i)$ . Dispersal can assume a wide range of forms from long-distance to extremely localized. Equations 2 and 3 can be combined to model the adult dynamics including an implicit contribution from the seed bank:

$$\begin{aligned} N_i(t+1) &= g\gamma \left[ S_i(0) [(1-g)\gamma]^t + \sum_{j=1}^n \sum_{\tau=0}^t \alpha N_j(t-\tau) f(j \rightarrow i) [(1-g)\gamma]^\tau \right] \\ &\quad \text{eqn 4} \end{aligned}$$

We were limited to such a formulation given the absence of seed bank data; such a substitution also makes biological sense given that seed banks cannot exist without plants. Our formulation of the dispersal probability,  $f(j \rightarrow i)$ , follows Ribbens, Silander & Pacala (1994) and Clark (1998),

$$P(j \rightarrow i) = \frac{1}{N} e^{-((d_{ij})/r)^\theta} \quad \text{eqn 5}$$

with  $d_{ij}$ , the dispersal distance and  $N$  a normalization constant. Dispersal is characterized by two parameters,  $r$  and  $\theta$ . While the form of the dispersal function is the same as our work on *S. latifolia*, use of this dynamic model does not restrict the estimation of dispersal and dormancy parameters to only previously unoccupied sites. We made this change both because identification of ‘long-unoccupied’ sites is not possible with the shorter-term study of *H. annuus* and because our goal was to explore population dynamics in general, not just dispersal. The model as presented assumes spatial homogeneity in parameters and lacks explicit density dependence; in future work, it will be useful to relax these assumptions. For full model details, see Appendix S2.

We estimated model parameters that gave the best fit to the observed 2003 abundances using eqn 4 and abundances across the landscape in previous years. We assumed no seed bank prior to 1999 ( $S(0) = 0$  in eqn 4) and generated an implicit seed bank over time. Although this assumption is unrealistic (plants were present in previous years), starting conditions of the seed bank should have little effect on numbers 4 years later (Appendix S2). We obtained parameter estimates by minimizing the sum of (observed plants–expected plants)<sup>2</sup> across all segments for 2003. Estimates of germination,  $g(t)$ , were allowed to vary from year to year, but other parameters ( $\alpha, \theta, r, \gamma$ ) were considered constant through time. The

assumption of no initial seed bank, combined with variable germination over time, changed eqn 4 to:

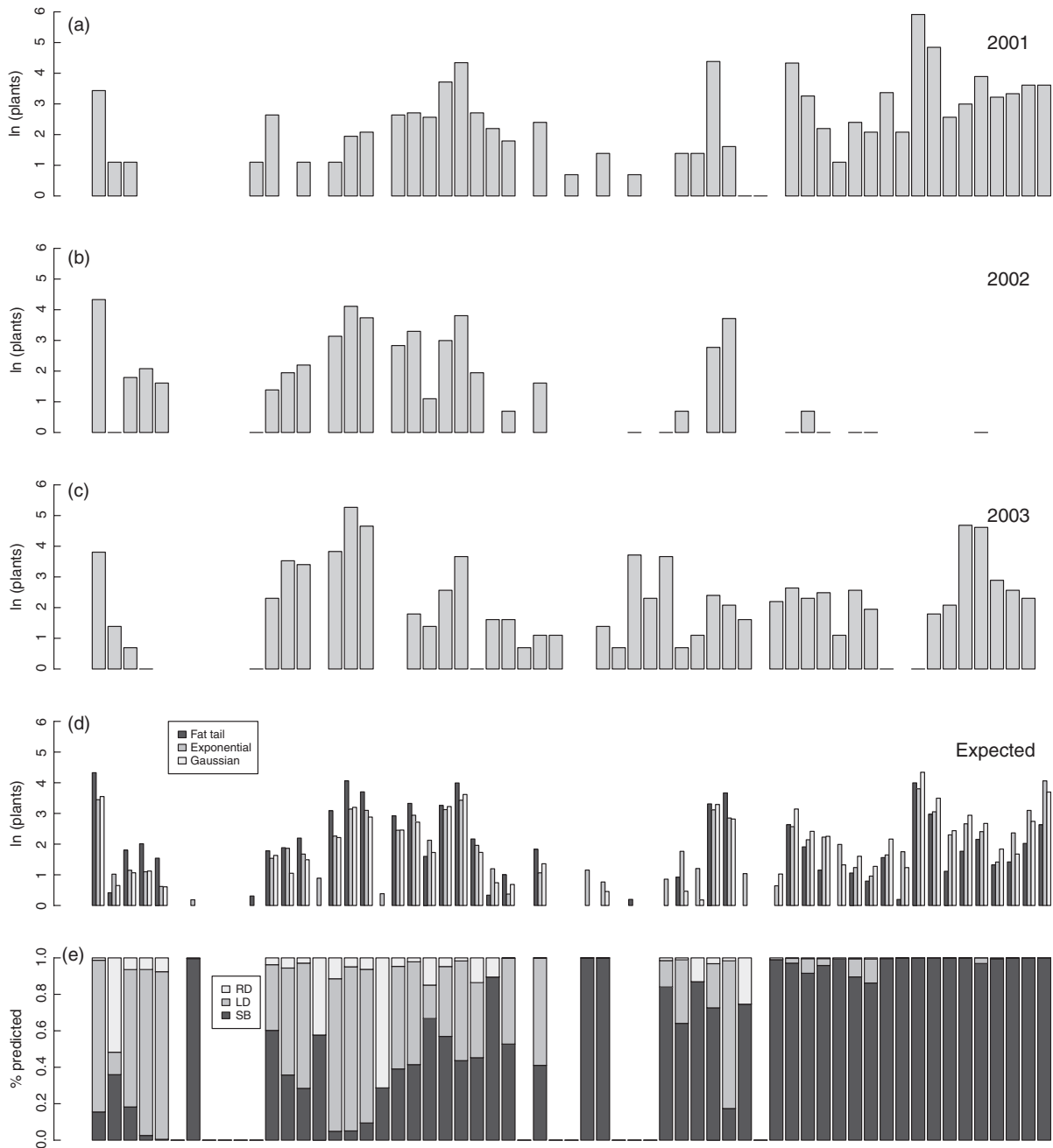
$$N_i(t+1) = g(t)\gamma \left[ \sum_{j=1}^n \sum_{\tau=0}^{t-1} \alpha N_j(t-\tau) f(j \rightarrow i) [1-g(t-\tau)\gamma]^\tau \right] \quad \text{eqn 6}$$

We defined an upper limit for dispersal (10 segments = 800 m). Initial values for the optimizations were based on empirical studies (Appendix S2). We used a combination of the Nelder–Mead Simplex and simulated annealing algorithms in efforts to fully explore the complex error surface and to avoid getting stuck at local minima, which happened easily. All optimizations were performed using the `optim()` function in R.

We explored whether the fit of the model varied across the landscape; such variation would suggest that results depended on the particular site we studied. We then computed the percentage of predicted plants originating from seeds produced in the segment the year before, from seeds present at the segment two or more years earlier (= seed bank), or from seeds that were dispersed to the segment from other locations in the previous year. The former two sources emphasize local dynamics while the latter addresses regional dynamics. We predicted a strong signal from seed banks. For example, the median number of 2003 plants at previously ‘empty’ segments is 4.5, but the upper quartile ranged from 18 to 162 plants (Alexander *et al.* 2009). Such results are more consistent with emergence from dormant seed than with rare dispersal. However, at some level, dispersal must occur to create the distribution of plants along the roadside.

## Results and discussion

The best-fit models had approximately exponential dispersal profiles ( $\theta$  approximately equal to one, with a large dispersion parameter), although other dispersal profiles (Gaussian and fat tail) also had reasonable fit for certain parameter combinations (Fig. 2, Table S1). In particular, exponential dispersal with high dispersion was better than other dispersal profiles at predicting the relatively rare events where sunflowers appeared at a previously unoccupied site. With exponential dispersal, there was considerable spatial variation in the source of the simulated 2003 plants. Local processes were responsible for plants produced in 2003 that had high occupancy in the previous year; the seed bank was most important in areas where 2002 numbers were low relative to numbers in earlier years. Seed dispersal played a minor to moderate role in areas with a patchy historical distribution (Fig. 2). This interpretation is tempered by the observation that for the best-fit exponential model (with high dispersion,  $r = 15$ ), only 6% of dispersed seeds land into the segment from which they originated, which seems unrealistically low. Gaussian dispersal, where 75–90% of seed stays in the ‘home’ segment, resulted in similar patterns of spatial variation in local recruitment vs. seed bank influence, but dispersal barely contributed to landscape abundance patterns



**Fig. 2.** Landscape dynamics of *Helianthus annuus*, expected number of plants in 2003 under three dispersal profiles, and proportion of 2003 expected plants originating from different seed sources using exponential dispersal. For all graphs, the  $x$ -axis refers to positions along the roadside. (a)–(c) refer to observed numbers of plants (note log scale) from 2001 to 2003 in 61 adjacent 80-m segments from the east side of the road (a subset of the entire route). Using eqn 6 and data on population abundances from 1999 to 2002, we computed the expected number of plants across these segments in 2003 using different dispersal profiles (d); we excluded expected numbers  $< 1$  in this panel because of the log scale. (e) shows the proportion of expected plants in 2003 segments (given exponential dispersal) originating from regional processes (RD, 2002 seeds dispersing from other segments), local processes from last year (LD, seeds produced in the same segment in 2002) or from the seed bank (SB). See text, Appendix S2, and Fig. S5 for details.

(Fig. S5D). Gaussian dispersal is also generally more consistent than exponential with small spatial-scale seed dispersal data for *H. annuus* (Appendix S2), but we have quantified dispersal only for short distances. However, for all dispersal profiles, local processes dominated landscape dynamics, and there were large and consistent spatial patterns in seed bank

contributions (Fig. S5). Model fit varied across the landscape (Fig. S5A), highlighting the potential for the relative influence of different processes to vary across space.

Holt (1993) emphasized the value of ‘thought experiments’, where one imagines a world without dispersal and explores the ecological consequences. With this perspective, we

re-estimated the model parameters for two hypothetical scenarios, absence of dispersal and absence of a seed bank (see Appendix S2 for details). Omitting the seed bank greatly reduced model fit; elimination of dispersal reduced fit but to a much lesser degree (see Appendix S2, Table S1). Overall, our results underscore the importance of local processes, including dispersal through time, to landscape-level dynamics of *H. annuus* (as consistent with Freckleton & Watkinson's (2002) concept of spatially extended populations). Even for plants with habitat patches that fit classic metapopulation definitions, local processes should not be ignored (Winkler, Hulber & Hietz 2009). Of course, our results do not preclude the occurrence of rare long-distance dispersal events and some level of connectivity among populations, but accurately characterizing such processes likely necessitates a multi-faceted description of dispersal. We also recognize that if one goes back far enough in time, any local population was surely established by dispersal from an external source. The importance of regional processes thus is likely to increase with increasing span of time included in a study.

A challenge in our work was the issue of identifiability (inability to obtain unique best parameter estimates). This problem arose from implicitly modelling the seed bank. In essence, there are multiple ways to generate sunflower distributions that fit the observed data equally well. The fact that we are estimating nine parameters further complicates the issue, although the identifiability problem would remain even if the number of parameters was reduced or the size of the data set was increased. Simply put, we cannot definitively quantify the role of dormant seed on population dynamics without empirical data on numbers of seeds in the soil and their probability of successful emergence to flowering adult plants. Large spatial-scale data on seed banks are rare (but see Peterson & Baldwin 2004; Bell, Fonseca & Kenworthy 2008; Middleton & Wu 2008). It is therefore not surprising that our knowledge about seed banks across landscapes often comes not from population biology but from community-level studies of species traits. For example, species with seed banks have higher persistence in isolated habitats than those lacking this trait (Piessens *et al.* 2004; Lindborg 2007; Tremlova & Münzbergová 2007). The major challenge in landscape studies of seed bank abundance is effective sampling given spatial heterogeneity in buried seed abundance and dynamics, and long-term observation of these sampled sites with regard to the likelihood of successful establishment. Models such as described here could potentially guide future empirical work by generating testable predictions on spatial variation in the size of the seed bank given historical data on plant abundances.

We are aware of only a few studies that jointly examine the effects of dispersal and seed banks on a landscape spatial scale. Dostál (2005), for example, directly estimated dispersal and seed banks for five annual species that colonize small habitat patches (ant mounds < 1 m wide). Intriguingly, he concluded that seed banks were extensive, but limited soil disturbance meant that they had minor contributions to dynamics. The system thus conformed to metapopulation predictions. Dostál's work highlights that landscape-level research on the

consequences of seed banks must explicitly include processes leading to actual recruitment from the seed such as magnitude and variation in soil disturbance (Amarasekare & Possingham 2001; Claessen, Gilligan & van den Bosch 2005; Alexander *et al.* 2009). More generally, future work requires integration of (i) temporal and spatial data on population abundances, (ii) numbers of buried seed and seed survival rates and (iii) data on environmental variables that affect seedling emergence.

## Community-level research

### SPATIAL AND TEMPORAL EFFECTS ON COMMUNITY STRUCTURE: A METACOMMUNITY PERSPECTIVE ON SUCCESSION

Just as incorporating both spatial and temporal dimensions affords additional insights to population studies, a spatio-temporal perspective in community ecology helps elucidate changing roles of local and regional processes in assembling communities (Whittaker & Levin 1977; Leibold *et al.* 2004; Chase & Bengtsson 2010; White *et al.* 2010). We expect space–time interactions on community composition to be particularly strong in dynamic systems such as those undergoing succession, where many species must colonize from varied external seed sources. Although temporal dynamics are usually emphasized in studies of succession, any community undergoing successional change necessarily also has a spatial dimension (Yarranto & Morrison 1974; Glenn-Lewin, Peet & Veblen 1992; Holt, Robinson & Gaines 1995). Patterns of colonization and extinction, and therefore rates and trajectories of compositional change, are not typically uniform across landscapes. Disturbances that initiate succession for instance leave a spatial footprint on the landscape at particular distances from external source pools for colonists.

Temporal shifts in the spatial structure of vegetation during succession are likely to emerge from the interaction of local and regional processes (Grieg-Smith 1964; Yarranto & Morrison 1974; Cook *et al.* 2005; Cutler, Belyea & Dugmore 2008). The development of spatial patterns in vegetation has commonly been attributed to the influences of underlying environmental heterogeneity. These effects of the environment may arise via abiotic filtering of species pools as well as through environmental mediation of interspecific interactions (Whittaker 1956; Tilman 1987; Ellenberg & Strutt 1988). Such processes, long recognized in plant ecology, form the basis of the species-sorting metacommunity model that can produce shifting species composition along environmental gradients (Leibold *et al.* 2004). However, additional spatial structure in vegetation may develop less predictably and largely independently of the selective influence of the environment. These so-called 'pure spatial effects' may emerge as a result of dispersal limitations and stochastic colonization and extinction events frequently associated with the patch-dynamics and neutral metacommunity models (Chase & Bengtsson 2010). Endogenous spatial structure arising from such processes can potentially be further modified or reinforced during succession by clonal growth of initial colonists, competitive priority



effects, inhibition (Connell & Slatyer 1977) and facilitative nucleation processes (Yarranto & Morrison 1974; Cutler, Belyea & Dugmore 2008).

Although the metacommunity concept was not explicitly developed to address succession (but see Gonzalez 2009), many of its constructs and predictions are highly relevant, particularly when the spatial dimension of succession is of central interest. We explore local and regional controls on the development of spatial heterogeneity in plant species composition (i.e. beta turnover) in the context of vegetation change on abandoned agriculture land. In doing so, we apply a metacommunity perspective to understanding secondary succession using data from a long-term study conducted in north-eastern Kansas, USA. Specifically, we evaluate the contributions of 'pure' (Cottenie 2005) spatial processes (e.g. dispersal limitation, colonization history) and species sorting along environmental gradients to the development of community spatial structure over the course of succession by employing community variance decomposition (Borcard, Legendre & Drapeau 1992; Cottenie 2005). Recently, this approach was employed in a meta-analysis to evaluate alternative models of metacommunity organization for diverse taxa (Cottenie 2005). However, only rarely have these methods been used to investigate plant communities (Freestone & Inouye 2006; Flinn *et al.* 2010; Anderson *et al.* 2011; Burton *et al.* 2011).

We estimate the degree to which spatial variation in species composition across localities in a metacommunity can be explained by pure spatial and pure environmental influences. The components of interest are as follows: variance in species composition among localities explained by environmental variables,  $E$ ; variance explained by spatial location and distance,  $S$ ; variance explained by the joint influences of space and environment,  $E + S$  (total explained variance); variance explained by the environment independent of space,  $E_c$  (conditional or pure effect of the environment); variance explained by space independent of the environment,  $S_c$  (conditional or pure effect of space); and unexplained variation ( $1 - [E + S]$ ). Here, we focus on the conditional effects of the environment and space ( $E_c$  and  $S_c$ ) as they allow assessment of the roles of exogenous processes (species-environment sorting) vs. endogenous processes (dispersal limitation and other pure spatial effects).

The manner in which species-environment sorting and dispersal limitation influence the development of community spatial structure in succession may depend on diverse factors such as the spatial scale and extent of environmental heterogeneity of the area undergoing succession, the dispersal abilities of species in the available species pool, proximity to external seed sources, landscape context and connectivity, and historical agricultural legacies. Acknowledging these complexities, we provide *a priori* predictions; the purpose is not to precisely predict outcomes, but to provide a foil against which to compare our results and to stimulate discussion.

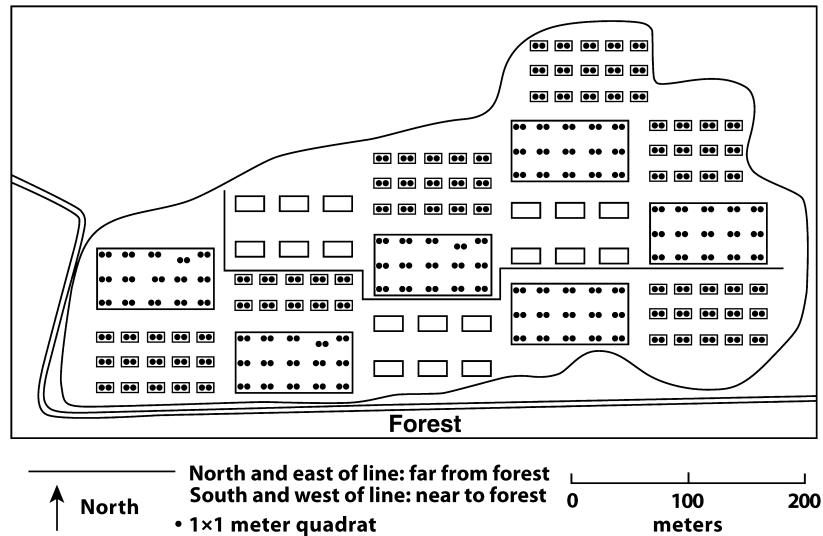
Overall, we expect that the relative influence of environmental gradients and space on community composition will vary systematically across succession. Specifically:

1. Dispersal constraints, evident in the contribution of space  $S_c$  to explaining community composition, will be most dramatic in early succession, and decline through time as species with various dispersal modes and distances from the site eventually arrive, establish and proliferate.
2. Environmental gradients independent of space ( $E_c$ ) will play an increasingly influential role in determining community composition over time. As colonization-competition trade-offs play out over time, the plant community will increasingly mirror underlying environmental heterogeneity due to deterministic species-environment sorting.
3. Where connectivity is disrupted during succession, space will continue to strongly influence community composition throughout the assembly process; in contrast, environmental factors will explain less variation in community structure. Because fragmentation decreases the diversity or abundance of arriving colonists, underlying gradients will not be as strongly expressed as in continuous habitats and species sorting should be less pronounced.

### Study design

We evaluate the influence of pure spatial and environmental effects using a long-term, landscape-scale fragmentation experiment in north-eastern Kansas, USA. The 'fragmentation' experiment was established in 1984 to evaluate the influence of patch size and patch connectivity on secondary succession (Holt, Robinson & Gaines 1995). The experiment consists of replicated patches of three sizes, situated on abandoned cropland (Fig. 3: small patches ( $4 \times 8$  m); medium patches ( $8 \times 12$  m); and large patches ( $50 \times 100$  m)). We focus only on small and large patches due to low numbers of medium-sized patches. The matrix area between patches was mowed regularly while the patches themselves were left to undergo succession. The large patches occupy the same area as the outer perimeter of a cluster of small patches (0.5 ha), allowing assessment of effects of habitat fragmentation and altered connectivity on community development (Holt, Robinson & Gaines 1995). In most years between 1984 and 2002, surveys of plant species occurrence were conducted in sampling stations: a pair of  $1\text{-m}^2$  quadrats separated by 4 m comprises each station. Each small patch contained one sampling station while each large patch contained 15. For this study, we consider individual sampling stations as the local communities, while the assemblage of all sampling stations at the site constitutes the metacommunity (see Appendix S3 for extended methods).

Connectivity (and thus presumably the extent of dispersal limitation) varied at several spatial scales. First, sampling stations within a collection of small patches (a 0.5 ha area) are isolated from other communities by a mowed matrix, whereas the communities within a large patch are connected by continuous habitat. Second, sampling stations differ in their distance to the principal external source of woody plant propagules, an adjacent forest on the southern and western site boundary (Fig. 3) and external sources of herbaceous plants in nearby old-fields. We recorded data on the underlying natural environmental gradient at the study site, including variation in



**Fig. 3.** Fragmentation site experimental design. The study consists of following succession in an experimentally fragmented landscape with large, medium and small patches. Each pair of dots represents one sampling station, or community. Together, these communities comprise the metacommunity. In most cases, collections of small patches cover the same area as a single large patch. The matrix between patches is mowed biweekly.

soil edaphic features along topographic gradients (Appendix S3). The identity and quantity of propagules arriving at the site was subject to natural availability in the species pool and stochastic dispersal. While this experiment does not necessarily fit all metacommunity criteria, the combination of long-term data with the manipulation of connectivity across the landscape allows us to explore the interplay of stochastic and deterministic processes over space and time, ideas that are central to metacommunity theory.

To evaluate the unique contributions of spatial and environmental processes to variation in community composition, we partitioned variance in the plant community similarity matrices into pure spatial ( $S_c$ ) and pure environmental ( $E_c$ ) components using partial redundancy analysis and distance-based linear modelling (DISTLM), in the program PRIMER-E (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008). Environmental data used in the analyses include soil texture variables (% sand, silt and clay) and topographic variables (elevation, slope and aspect). Space was incorporated using third-order polynomials of the  $X$  and  $Y$  spatial coordinates of each sampling location. This approach, which adds terms of a cubic trend surface regression to the model, accounts for spatial dependence of community structure at a variety of spatial scales beyond that which merely corresponds to linear gradients (Borcard, Legendre & Drapeau 1992; Cottenie 2005). Unique models were constructed separately for each year examined, and a variable selection and standardization procedure was employed to facilitate comparison of the models among years (Appendix S3).

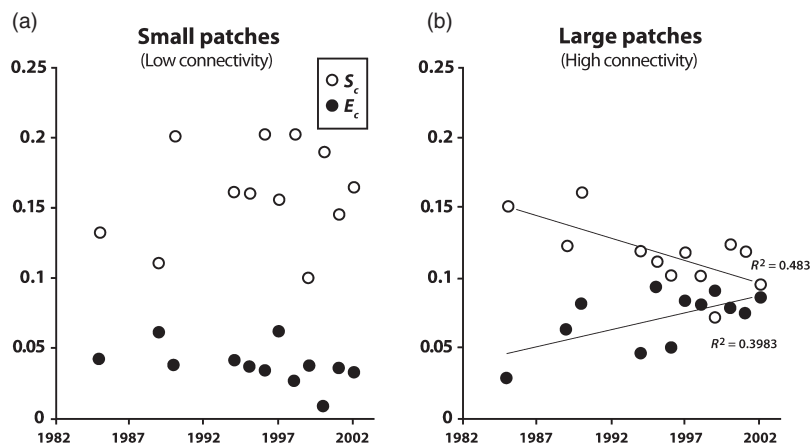
### Results and discussion

Over the course of the study, community composition shifted from being dominated by annuals and short-lived perennials, to

communities of long-lived perennials, including woody species (Fig. S6, Cook *et al.* 2005). The relative contribution of spatial and environmental factors to spatial turnover in plant composition shifted during succession, largely in accordance with predictions (Fig. 4). Consistent with metacommunity predictions, the magnitude of these effects varied with levels of connectivity, as indicated by differences between patch sizes in the degree to which various factors govern community development.

In both small and large patches,  $S_c$  and  $E_c$  were both significant components of variance in all years ( $P < 0.001$ ), except for  $E_c$  in 2000 in small patches, implicating the roles of both stochastic dispersal assembly and species-environment sorting throughout succession.  $S_c$  was the dominant source of variation early in succession in both small and large patches. Typically, a strong spatial signal in the community independent of environmental gradients is taken to indicate dispersal limitation (Borcard, Legendre & Drapeau 1992). Here, spatial variation in the earliest years may reflect differential dispersal of herbaceous plants from sources external to the site, but may also reflect patterns of seed bank emergence and other legacies of prior agricultural land use. Patterns of woody plant colonization likely contributed to the development of spatial structure of the community in later years. For example, Yao *et al.* (1999) and Cook *et al.* (2005) documented greater woody plant recruitment in sampling locations near a forest edge, as found in other studies of old-field succession (Myster & Pickett 1993; Foster & Gross 1999; Briggs *et al.* 2005; Foster & Collins 2009).

When comparing small vs. large patches, we found differences that indicate a substantial influence of habitat fragmentation and connectivity on the spatial structure of the plant metacommunity, and on the degree to which spatial heterogeneity in species composition conforms to underlying environmental gradients (Fig. 4). In large patches,  $S_c$  declined



**Fig. 4.** Spatial and environmental processes both explain significant portions of variance in community composition across successional time.  $S_c$  reflects increasing spatial influences acting independent from the environment, such as dispersal dynamics that vary according to degree of connectivity among communities and distance from external dispersal source.  $E_c$  reflects the environmental effects (elevation, slope aspect and soil texture) on community composition independent from effects of space. In early succession, spatial processes explain more variation in plant communities than do environmental variables in both patch types. In small patches, spatial influences explain more variation than environmental gradients throughout succession. As succession proceeds on large patches, environmental gradients become more expressed in the vegetation, concurrent with a decline in the influence of space on community composition.

significantly ( $r^2 = 0.483$ ;  $P = 0.012$ ) over time while  $E_c$  increased ( $r^2 = 0.398$ ;  $P = 0.028$ ), supporting our prediction regarding the contribution of spatial and environmental factors over the course of succession. In small patches however, these patterns appear to have been disrupted by fragmentation. Unlike in large patches, spatial influences predominated relative to that of the environment over the entire course of succession: in small patches,  $E_c$  showed a non-significant trend of decline over time rather than the predicted increase. By the latter years of succession, the relative contribution of spatial and environmental influences to species composition differed drastically between small and large patches, characterized by relatively equal contributions of space and environment in large patches, but by persistently dominant spatial influences in small patches.

The contrasting responses in small and large patches are consistent with the prediction from metacommunity theory that changes in habitat connectivity and dispersal among localities should alter the spatial structure and dynamics of a metacommunity and modulate the expression of species-environment sorting (Leibold *et al.* 2004). We expect that the level of connectivity and dispersal among localities can influence the extent to which species may consistently reach localities in the metacommunity where they are well suited to local environmental conditions. Connectivity may thus mediate the degree to which community composition assembles so as to mirror underlying environmental gradients. Predictions of metacommunity theory were largely conceived in the context of spatial systems where only internal dispersal is considered (dispersal of propagules among localities in the metacommunity) and where localities are distinct from the surrounding matrix habitat (e.g. archipelagos). Although the observed effects of patch size on the contributions of space and environment to metacommunity structure in our study are consistent with predictions from theory, we cannot unequivocally attribute all of

these effects solely to differences in connectivity *per se* and alterations of internal dispersal dynamics. Observed patch size effects are at least partially due to the way patch size mediates colonization of woody plants from external sources (Yao *et al.* 1999; Cook *et al.* 2005). Further, the different responses of small patches may also reflect biotic and abiotic effects of increased edge-area ratios. For instance, Cook *et al.* (2002) found that patch size effects on species richness were obscured at our site due to 'spillover' of matrix species (mainly weedy grasses and herbs) into small patches. In that study, it was found that 24% of the total species pool at our site was shared between habitat fragments and the matrix in 2001, indicating considerable exchange between the two habitat types. If the matrix can act as a source of immigrants to exposed and isolated patches in a fragmented system (Cook *et al.* 2002; Ewers & Didham 2006), our results challenge general predictions made by the mass effects model of metacommunity theory. Conventional metacommunity theory suggests that mass effects contribute most definitively to community structure (and mask species sorting) in systems with *high* connectivity and dispersal among localities: reducing connectivity via fragmentation should thus reduce the influence of mass effects and source-sink dynamics. Our work suggests that source-sink dynamics and mass effects may limit species-sorting processes where connectivity among habitat fragments is *low*, if the 'matrix' is not entirely inhospitable and can act as a source of colonists. On the one hand, our results suggest that defining experimental patches as discrete plant communities does not fit well with classic metacommunity models, if some species can inhabit the matrix as well as the patches. On the other hand, we do gain insight into the potential importance of edges for mediating community composition and species sorting in fragmented systems.

Our study complements several recent studies investigating the interplay of environmental filters and dispersal in governing

the spatial structure of plant communities using a community variance partitioning approach (Freestone & Inouye 2006; Flinn *et al.* 2010; Burton *et al.* 2011). However, our study is the first we are aware of that evaluates shifts in the relative influence of these factors over substantial periods of time as the plant metacommunity assembles. One potential shortcoming of all studies using this variance partitioning approach is that the influence of important environmental factors left unmeasured may mistakenly be subsumed into the spatial component. We are cognizant of this possibility; for example, soil nutrient content and moisture were not quantified in our study. However, work in a nearby site (Collins & Foster 2008) showed that these soil variables typically covary with topographical features of the landscape and soil texture, both of which were taken into account. It is therefore likely that the major axis of topo-edaphic variability at our site was captured in our analyses. However, because of their potential shortcomings, variance partitioning studies should be interpreted with caution and complemented with other approaches whenever possible.

For example, Foster *et al.* (2011) report a multispecies sowing experiment conducted nearby that complements our findings from the fragmentation study. Here, seeds of 53 plants species were sown to plots undergoing succession and in which nitrogen and phosphorus had been factorially manipulated. We recently analysed these data using variance decomposition (B.L. Foster, unpubl. data). We found that variance in species composition among replicate field plots explained by environmental variables ( $E_c$ ) increased significantly over time as predicted, but that the increase happened more rapidly in sown than non-sown plots, indicative of greater species sorting in the presence of greater propagule availability. In this sowing experiment,  $S_c$  also declined over time as predicted. However,  $S_c$  was substantially reduced by seed sowing, implicating dispersal limitation in the generation of community spatial structure. Importantly, the fact that we see a similar qualitative pattern among studies, regardless of how dispersal limitation is experimentally imposed/ameliorated (seed addition vs. manipulation of habitat connectivity), suggests that the conditional effect of space ( $S_c$ ) as estimated via the variance decomposition procedure is a reasonable surrogate for the role of dispersal limitation in structuring plant communities.

Together, the fragmentation study and seed addition experiment at our research site strongly suggest that habitat fragmentation, altered connectivity and dispersal constraints can have measurable effects on the spatial structure of plant communities undergoing succession and can limit the capacity of communities to assemble in response to environmental gradients via species-environment sorting, as predicted by metacommunity theory. Our findings also support the view that successional systems generally shift over time from a system that is initially strongly dispersal limited, to a system that progressively conforms to the species-sorting model of metacommunity theory, as dispersal limitations from external and internal sources are ameliorated. However, the magnitude of such a shift is itself influenced by landscape structure, not merely the passage of time.

## Conclusions and future directions

It is fitting to focus on successional species in celebrating the 100 year anniversary of the *Journal of Ecology*: research on succession has been critical to the development of ecology. A. G. Tansley stated, “I have always tried to impress on my students, perhaps sometimes *ad nauseam*, the essential importance of the study of succession” (Tansley 1939). Similarly, a major component of A. S. Watt’s research explored temporal changes in communities (Watt 1947). Both Watt and Tansley also appreciated that spatial dynamics (e.g. propagule availability) could affect the direction of succession. We now have the conceptual and modelling tools to address this long-recognized, but hard to investigate, dimension of plant ecology. Further, given the continuing impact of human disturbance, successional systems will continue to play an important empirical role in ecology.

The applicability of metapopulation models for plants has sparked much discussion, especially since the critique by Freckleton & Watkinson (2002). The debate has centred on the ways that plant biology is inconsistent with theoretical assumptions, including the four challenges we note in the Introduction. We have shown that even study systems that do not meet strict definitions of metapopulations and metacommunities are tractable and can therefore inform our understanding of both local and larger-scale processes. For instance, although habitat patches seem at first sight an essential component of classical metapopulation theory, distinct patches are the ‘exception’ and not the ‘rule’ in plant ecology. In our metapopulation studies, spatial dynamics of plants without clear habitat patches could still be studied by combining multi-year grid surveys with models; these approaches allowed us to explore the challenges of long-distance dispersal and seed banks. In the fragmentation study, patches (communities) were initially designated based on dispersal distances of common plants (Holt, Robinson & Gaines 1995), but randomly located on a topographically diverse landscape as part of the experimental design. Our results suggested that these patches are not islands, truly ‘discrete’ from the matrix, but rather the mowed matrix and patches may represent interspersed environments varying in habitat quality. Nonetheless, we demonstrate that even in landscapes with habitat gradients, spatial processes are still operating and important for structuring plant communities. Finally, long-lived and clonal plants were an important component of the fragmentation data set. The long-term nature of the data allowed for dynamics of perennial species to play out, and the use of presence-absence data (as opposed to counts of individuals) minimized clonality issues. Of course, not all study systems provide a way to work around these and other challenges. However, we should still strive to understand the interplay between local and regional processes for a diversity of plant species and communities, including those whose biology does not fit the assumptions of classic theory.

We suggest four general guidelines for future research that can advance the fields of metapopulation and metacommunity ecology:



**1. Strengthen the link between population and community perspectives.** The historical lineages of our disciplines have led to largely independent fields of study (Table 1). Population ecologists, influenced by Harper (1977), study demographic processes, population fluctuations and spatial distributions. Often, population ecologists let the plant provide a plant's eye view of environmental variation (e.g. phytometer method, Clements & Goldsmith 1924; Brandon 1992). In contrast, community ecologists, with a historical lineage including Watt and Whittaker, routinely work with 10's–100's of species, often recording independent measures of environmental variation (e.g. soil types, resource gradients) to tease out the factors that cause shifts in species composition. Metrics frequently used at the community level such as diversity, relative percentage cover or biomass make it challenging to recover data relevant to demography. Conversely, single-species data often neglect the community context of demographic processes. Given these discipline differences, we are impressed by bryophyte researchers whose work spans both the population dynamics of single species and community studies of coexistence (Snäll, Ehrlén & Rydin 2005; Löbel, Snäll & Rydin 2009), and we encourage more such studies. We see less 'cross-over' in research on vascular plant communities. In these study systems, the complexity of species interactions along with the fact that individual species disperse different distances makes it difficult to 'scale up' (metacommunities cannot be seen simply as a collection of metapopulations). To forge links between population and community ecology, we encourage more studies of spatial and temporal dynamics of multiple species within a single community (e.g. Collins, Holt & Foster 2009). A fruitful modelling approach that combines population and community disciplines is to build community modules, by examining dynamics of small sets of interacting species (Holt 1997). Such modelling efforts should be supported by empirical work to determine the degree to which spatially separated plant populations experience the same biotic environments, and how this varies over time.

**2. Integrate spatial and temporal perspectives.** As others have noted (e.g. Preston 1960; White *et al.* 2010), a spatio-temporal perspective is necessary to understand the importance of both local and regional processes on population and community dynamics. Because ecological processes occur at different spatial and temporal scales (in particular, processes that occur at large spatial scales require longer observation times, and *vice versa*, e.g. Fridley *et al.* 2006), data sets that cover many years and more than one location are extremely valuable and versatile for understanding real-world dynamics. Even for annuals, multi-year studies are needed given the combination of dormant seeds and high temporal variation in appropriate conditions for germination (Pake & Venable 1996). As is obvious, long-term studies need long-term commitment. It is perhaps relevant that for all of the studies described here, some portion of the data were recorded without external funding; individual investigators have made it a priority to collect continuous data sets. An increased emphasis of funding agencies on long-term, multi-site data bases

should allow workers to determine at what spatial and temporal scales, and for which taxa, metapopulation and metacommunity dynamics are important.

**3. Quantify dispersal in both space and time.** Although there are many ecologically important processes worthy of study, future work should emphasize dispersal given its central role in metapopulation and metacommunity theory. Long-distance dispersal out of a given source is typically a rare event, but it is important to realize that colonization into a given recipient site may be reasonably high (empty habitat patches and even islands are often colonized relatively quickly). Dispersal is notoriously challenging to quantify. New methods with molecular genetic markers and isotopes offer important empirical insights on long-distance dispersal (Broquet & Petit 2009; Carlo, Tewksbury & Martinez del Rio 2009); modelling approaches can be extended to consider mixed kernels that incorporate both local and long-distance dispersal (Clark 1998). Additionally, researchers interested in spatial ecology have a tendency to avoid species with seed banks, because dormant seed complicates our ability to infer dispersal. However, given the prevalence of seed dormancy across plant taxa, we need to tackle this problem directly.

**4. Integrate research approaches.** In future work, we encourage a diversity of research programs, and not all studies must be long-term. For example, an assumption of metapopulation theory is that dynamics of local populations are not synchronous (Freckleton & Watkinson 2002). Thus, even 1- or 2-year studies of spatial variation in plant demography and/or effects of herbivores or pathogens on seed production provide useful inferences on the degree of spatial autocorrelation in plant fitness, and likely in population dynamics. For long-lived species, incidence function approaches provide an alternative approach to direct observation of dynamics (Verheyen *et al.* 2004). Integrating observational, experimental and modelling approaches is particularly powerful for addressing landscape-level questions. The case studies we presented illustrate the value of combining long-term data (observational and experimental) and modelling (simulation and statistical) to address metapopulation and metacommunity questions. Experimental approaches vary: some focus on manipulating dispersal by altering habitat configuration and connectivity via patch size (e.g. the fragmentation study presented here (Holt, Robinson & Gaines 1995)) or with corridors (e.g. Damschen *et al.* 2006). These approaches allow for natural dispersal processes to occur in the modified landscape, with distance as a surrogate for dispersal limitation. Alternatively, seed addition studies overcome dispersal limitation by directly sowing species from the surrounding species pool (Tilman 1997; Ehrlén & Eriksson 2000; Turnbull, Crawley & Rees 2000; Foster *et al.* 2004; Ehrlén *et al.* 2006). Such studies allow researchers to define 'occupiable' habitat, to determine the degree to which population dynamics is seed-limited and to decipher whether species richness at a site is limited by propagule availability. Directly manipulating the resource environment (such as nutrient addition studies) in combination with landscape configuration or seed addition provides evidence for processes central in metacommunity

theory (Foster *et al.* 2011). A challenge is that seed addition studies require multiple years, both because yearly variability in environmental conditions likely alters seedling establishment and because observations of seedling emergence are not necessarily predictive of population establishment (Ehrlén & Eriksson 2000; Ehrlén *et al.* 2006). In landscape configuration studies, more time allows for rare long-distance dispersal events to be expressed in population and community patterns. While no single approach provides a perfect test of meta-processes, observing similar qualitative patterns via different types of studies provides strong evidence for the role of dispersal in maintaining populations and diverse communities.

We close by stating that the debate should not be whether or not plant metapopulations or metacommunities 'exist', but how spatial and temporal processes interact to determine population and community patterns. Research in this area requires the ecological approaches examined in this paper, and also a genetic perspective that we have not included due to space limitations. Colonization and extinction will have important evolutionary effects that are in turn expressed in population persistence and abundance. For example, a small trickle of immigrants can counter inbreeding depression, reducing extinction risk, or provide a source of adaptive genetic variation. In the metacommunity context, such spatially mediated infusion of variation may be crucial in permitting species to persist in the face of ongoing coevolutionary arms races or environmental degradation (e.g. climate change). Finally, we emphasize that metapopulation and metacommunity research is not just of academic interest: understanding the effect of regional processes is essential as we grapple with the real-world problems of increasingly fragmented landscapes in ever changing environments.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Long-distance dispersal of *Silene latifolia*.

**Appendix S2.** Landscape dynamics of *Helianthus annuus*.

**Appendix S3.** Succession from a metacommunity perspective.

**Table S1.** Summary of different models (*H. annuus*).

**Figure S1.** Observed vs. predicted values for seed dispersal (*S. latifolia*).

**Figure S2.** Number of colonization events at different distances from seed sources (*S. latifolia*).

**Figure S3.** Number of plants from 1999 to 2004 (*H. annuus*).

**Figure S4.** Dispersal profiles (*H. annuus*).

**Figure S5.** Results of model runs (*H. annuus*).

**Figure S6.** Changes in species composition over time in the fragmentation study.

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