

**Supporting Information for Alexander, Foster, Ballantyne, Collins,
Antonovics, and Holt (Metapopulations and metacommunities: spatial and
temporal perspectives in plant ecology)**

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

Distance measures

The roadside survey of *Silene latifolia* used a segment length of 40 m (=44 yards). This value was chosen as a segment size because of ease of locating segments using a mileage-based odometer in the pre-GPS era, and previous local dispersal studies had shown that each segment likely included several, but not many, genetic neighborhoods (Alexander 1990). Euclidean distances were calculated between the start of each segment containing colonists and every potential source segment (within a 3 km distance, see below). Coordinates were estimated by placing the roadside segments onto topographic maps using 3-D TopoQuads program (DeLorme 1999) with CD-rom discs for Virginia. When correlation with topographic maps was difficult because of lack of clear landmarks, we carried out on-site measurements of the coordinates using GPS. Because the census area covered a relatively small geographic area (25 km x 25 km), map coordinates in degrees longitude and latitude were translated into linear x,y coordinates on a meter scale for distance measurement and data presentation.

We made the somewhat arbitrary assumption that a segment on the opposite side of the road was effectively a ½ segment (20 m) away from the focal segment. Actual road widths varied, but were generally 7 – 10 m. However, the populations could extend up to 5 m away on either side of the road if soil disturbance was present. It is also possible that the road itself is a partial barrier to dispersal of seeds.

Model implementation

Using Mathematica, we compared observed colonization events to those predicted from the model with different combinations of the parameters α and θ . We used two ways of calculating error (i.e. deviation of observed from predicted). First, we used error based on data from individual segments. This approach proved problematic because the majority of segments had zero colonists. Because colonization is a rare process, we considered that the model would never be very precise at predicting the exact number of colonists within a given segment, or at predicting which segment might be colonized. There would always remain a large error variance that would be composed of rather indeterminate amounts of process error (stochasticity of dispersal and/or establishment) and observer error (missed early colonizations, or incomplete census of potential sources). As a result, while there were highly significant positive correlations between predicted number and observed number of colonists, the predictions explained very little of the variation.

The second way of calculating error was to identify classes of segments based on their expected number of colonists and to then compare the difference between predicted and observed numbers in these segment classes. We therefore did not attempt to predict exact locations of colonists, but instead evaluated the probability that a colonization event will occur in a set of segments characterized by their expected colonization rates. With this approach, we calculated the expected colonization rate for every focal segment (that had not been previously occupied during the study period) for each parameter combination. Colonization rates were defined as the number of expected colonists per adult plant the previous year. We then pooled these segments into ten classes based on their expected colonization rates. We chose the number

of classes to be ten rather arbitrarily, as this number gave sufficient sample sizes with each group. These predicted colonization rates could be compared to observed colonization rates in the actual roadside segments assigned to each category. We also tried grouping segments by set intervals of expected number of colonists, but the number in these groups was highly skewed, with very few individuals being represented in the classes where the predicted number of colonists was high. In order to determine the best values for α and θ , we took the average across all the predicted colonization rates for the segments within a category, and similarly averaged across all the observed colonization rates for segments within a category. Then, for each of the 10 categories, we calculated the difference between the average predicted and average observed, and chose the values for α and θ that maximized the likelihood (i.e., that minimized the squared deviations of the observed from the expected). Using this model, we cannot accurately predict the number of colonizing individuals for each segment, but we can closely model the average colonization rate for a segment given its proximity to nearby *S. latifolia* individuals. The error variances of the plot of predicted vs. observed were normally distributed, and we therefore did not log transform the data.

For estimation purposes, the distance from the colonization event to possible source populations the previous year was set to a maximum of 3 km. This was done so as to limit the computational time necessary, as well as to limit the magnitude of edge effects. We also tried limiting colonizations to a maximum distance of 1 km, or not having any distance limit at all. The results showed that including only the 1 km scale gave a significantly different result than the 3 km model, indicating that dispersals between 1-3 km did matter. However, the model with all distances was not significantly different from the 3 km model, which suggests that dispersals over 3 km are relatively unimportant to the colonization dynamics of *S. latifolia* in this region.

Edge effects and undetected sources

Because of the finite nature of the census region, focal roadside segments that were near the edge of this area may have had fewer potential source segments recorded. Moreover, particular areas within the census (e.g. roads within the town of Pembroke, and Route 460, a main highway) were excluded as being impractical to census. Populations that were observed away from the roadside (<5% of the total) were included as potential sources of colonists. However, there may have been source populations that went undetected because they were not visible from the road, although given the land-use patterns in the area (forest or grazed meadows), these are likely to have been few. We considered various methodologies for compensating for such incompleteness, but each of the several options we considered had its weaknesses. We therefore chose to use the data “as is”, but to include the possibility that there could be recruitment from a “background pool” of undetected individuals. This background level of colonization can be measured as the intercept of a plot of predicted*observed numbers (see below).

Results

The likelihood surface for the goodness of fit for different parameter combinations showed a clear peak at $\alpha = 0.0025$ and $\theta = 0.49$. There was a highly significant correspondence between observed and predicted values. However, because of the uneven spread of the observed and predicted values, we subdivided the highest predicted category into three equal sized groups, the next highest into two equal groups, and pooled the first five classes which were clustered at the bottom of the graph. The results again showed an excellent correspondence between observed and predicted values (Fig. S1). Because the intercept was not significantly different from zero,

there was no evidence of a detectable level of background colonization from unobserved regions inside or immediately outside the census area.

Fig. S2 compares predictions from the model to assumptions that nearest neighboring segments are the source of colonists; the model predicts greater spread of seeds.

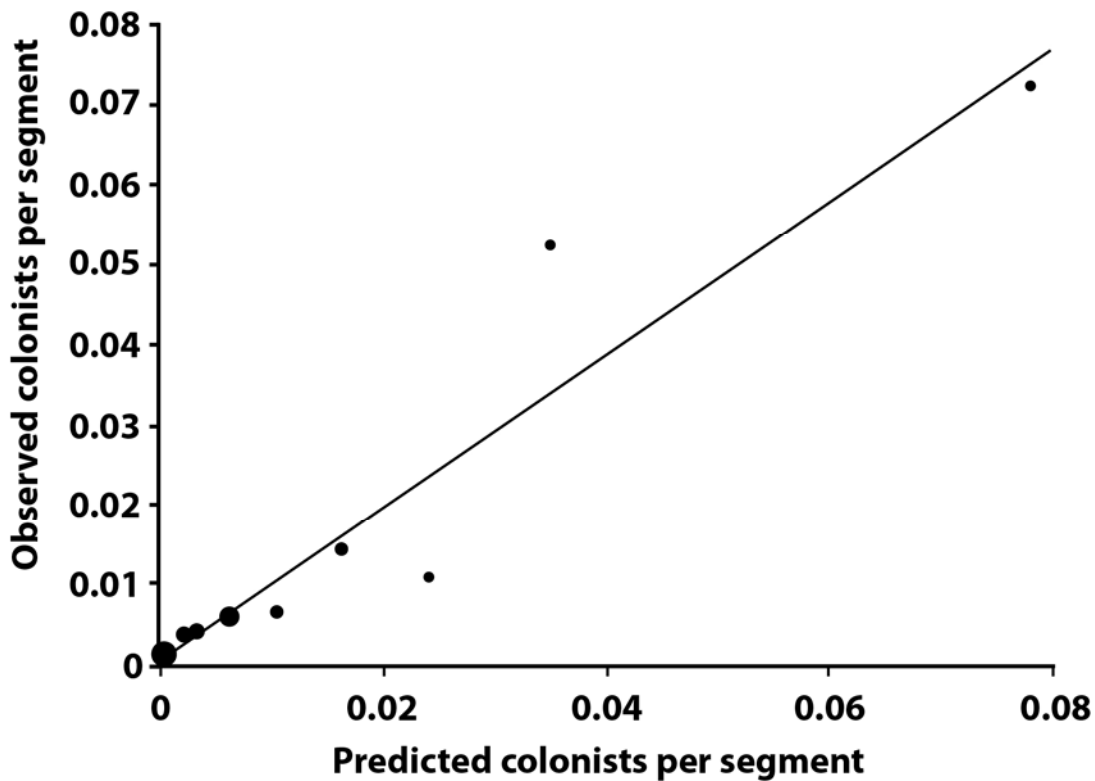


Fig. S1. Observed versus predicted values for seed dispersal (*S. latifolia*). Note that data are presented as numbers of plants per source plant the previous year. The fit for seed dispersal, with predicted classes divided up into different sizes, is represented by different sized points. The largest group has 15225 values, the next three groups have 3045 values each, the next two groups have 1523 and 1522 values, while the last three groups have 1016 values each. The solid line is the weighted regression line, $y = 0.9430x + 0.0009$. The r^2 value is 0.922.

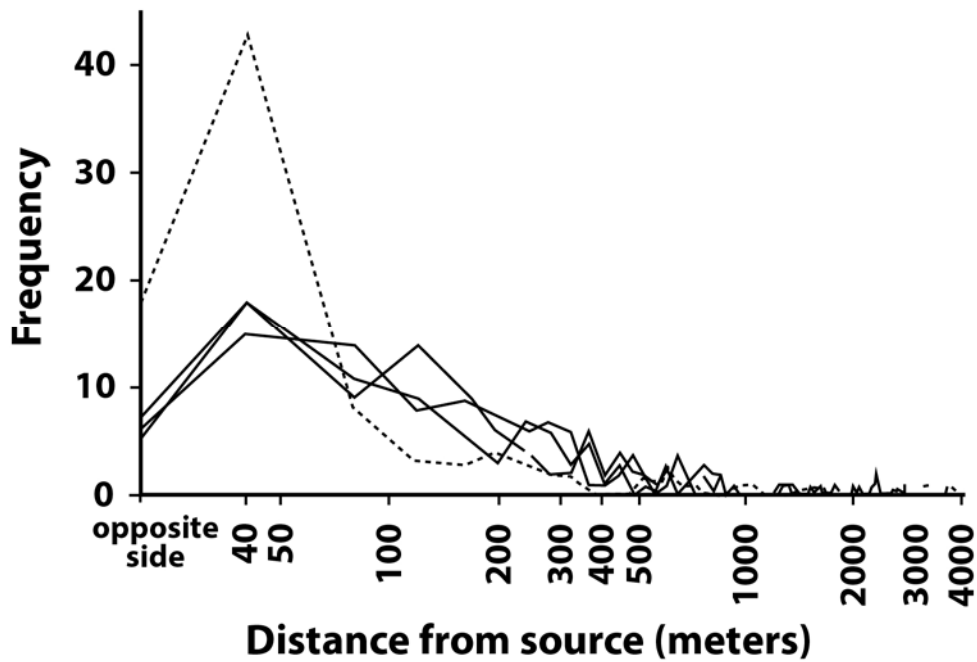


Fig. S2 Number of colonization events at different distances from seed sources (*S. latifolia*).

The dotted line is based on estimates obtained by assuming that colonizations occur as a result of dispersal from the nearest possible colonist source the previous year; specifically it represents the minimum possible dispersal distances for each observed colonist (a total of 105). The three solid lines refer to dispersal simulations generated given the best-fit values of $\alpha = 0.0025$ and $\theta = 0.49$. Note that the peak at 40 m reflects the fact that dispersal from the adjacent segment is defined to be 40 m, even though this could effectively be a distance of a few meters across the boundary between two adjacent segments. The decline in frequency at 20 m reflects dispersal to the other side of the road.

Appendix S2. Landscape dynamics of *Helianthus annuus*

Survey methodology and distance measures

In contrast to *S. latifolia*, the survey route in Kansas, USA for *H. annuus* was essentially linear, with the road oriented in a north-south direction. As described in detail in Alexander *et al.* (2009), the entire route was 23.8 km long and consisted of 298 80 m segments on both the east and west side of the road. The width of each segment was 3-5 m. Numbers of plants were recorded each fall from 1999-2004; Fig. S3 shows the complete set of abundances for the east side of the road over this time period. Off-road populations, or populations along nearby roads, could contribute to population dynamics along the surveyed roadside. We do not anticipate that such effects would be of major importance but we recognize that this is a potential problem for interpretation. In work on other species commonly found on roadsides, off-road populations did not appear to influence roadside dynamics (Crawley & Brown 2004).

In the model, we assumed each segment to be 80 m long and 4 m wide and that the road width was 10 m. To compute dispersal probabilities using equation 5, we assumed that all plants in a segment were located in the center of the north-south and east-west dimensions. We then considered the center of a segment to be the point (0,0) and computed dispersal probabilities to the 10 closest segments on either side of the focal segment along the same side of the road and on the other side of the road. Seeds were allowed to disperse in a 360 degree circle, and we then determined which seeds would reach a particular segment. For example, because segments were 80 x 4 m, the probability of dispersing to an adjacent segment was computed by integrating equation 5 over the rectangle $[-2, 2] \times [40, 120]$ (i.e. the nearest segment was at least 40 m away and as far away as 120 m). Since we put an upper limit of dispersal of 800 m (10 segments), our analyses were focused on a 22.2 km central section of the entire 23.8 km area (i.e. the first and

last 800 m section of the roadside were only included as possible sources of seed). We used Monte Carlo integration with 1000 randomly chosen replicates per segment to compute dispersal probabilities between all potentially “connected” segments.

Model structure and parameter estimation

For a given set of parameters $(\alpha, \theta, r, \gamma, g_{\tau})$, the expected number of plants observed in a given segment in 2003 was computed using equation 6. In other words, observed abundances from 1999 to 2002 determine the abundance in 2003, given a particular set of parameters. We computed the 2003 expected number of plants for all segments on both sides of the road for multiple parameter combinations initially to get a sense for which parameter combinations yielded the best fit to the data. Fit was assessed using the sum of $(\text{observed} - \text{expected})^2$ across all segments for 2003. In efforts to obtain the parameters that yielded the best fit to the data, we performed optimizations with multiple initial seeds in regions of parameter space with initially good fit. We used a combination of the Nelder-Mead simplex algorithms and simulated annealing in attempts to avoid getting stuck at local minima. Parameter combinations used to generate figures in the main text and in this supplement were optimal combinations with close correspondence to the different dispersal profiles. That fact that both algorithms converged to different parameter combinations with different initial seeds underscores the roughness of the error landscape, but also allowed us to obtain multiple parameter combinations that were associated with local minima.

To seed optimizations initially, we used starting values that were biologically reasonable, based on our empirical knowledge of the species. For example, α is determined by fecundity, with adjustments for predispersal predation and the initial pulse of post-dispersal predation. For

fecundity, we used data by Kost and Alexander (unpublished) on six naturally established populations of sunflowers in eastern Kansas, USA in 2009. These data revealed that the median number of seeds per plant was 235 (seed counts excluded seeds with holes from predispersal seed predators). Postdispersal seed predation can be very high. For example, Robel & Slade (1965) document loss of at least one third of seeds on the soil surface from November to December; short term experimental seed predation trials (10 days or less) showed 42% (Alexander *et al.* 2001) and 45% of seeds eaten (Dechaine, Burger & Burke 2010). In a study where seeds were placed on the soil surface in open mesh “baskets” in November or December and then examined in the spring, a average of 0.19 survival was reported (this value is relevant to both estimates of post dispersal predation, as well as seed survival (γ) (Alexander & Schrag 2003). Taken together, these data on fecundity and post-dispersal predation suggest that values of α from 1 – 50 are reasonable. We used this range to constrain our optimizations. Such a range of values for α appear consistent with the lack of a sustained increase in numbers of plants across through time; yearly abundances vary greatly, but there is no evidence for an overall increase in the regional population (Fig. S3). The survival parameter, γ , pertains to survival of seeds in the soil. In the first year, this survival period covers a time from fall seed dispersal to late spring seed germination; if seeds do not germinate their first spring, the time period for this survival term spans a year. Alexander & Schrag (2003, Table 2) provides data on these survival rates; estimates range from 0.12 to 0.45. The parameter g reflects the probability that seeds that are alive in the spring will germinate, grow, and reproduce. We calculated estimates of this probability based on the product of two terms: the probability of germination for seeds that survived the winter (0.59, based on seed bag studies (Mercer and Alexander, unpublished)) and the probability of reproduction for seeds that emerged as seedlings in the spring (approximately

0.35, based on the study reported in Mercer, Alexander & Snow (2011). We lack data to parameterize dispersal profiles, hence our approach of exploring a broad range of dispersal forms (fat tail, exponential, and Gaussian, see Table S1, Fig. S4). Our direct knowledge of seed dispersal in Kansas study sites is limited to an unpublished study, where Alexander observed seed dispersal in 2 m x 2 m plots filled with sunflower plants that were dispersing seed. She placed 12 cm diameter plates covered with a sticky substance directly under the plants (in the center of each plot and at the edge of the plot) as well as at a 60 cm and a 3.2 m distance away from the plants. Most seeds were dispersed directly under the plants; 1.9% of the total seed dispersed were found at the 3.2 m distance. Burton (2000), working in an agricultural landscape, found wind and water movement led to a small number of marked seeds dispersing 105 m from their origin.

In the model, we assumed that there was no initial seed bank and thus effectively the 1999 distribution of plants represents a recent invasion. *Helianthus annuus* is known to colonize new areas through dispersal along roadsides, but there were plants at this particular field site prior to 1999. In the model, the absence of an initial seed bank should have little effect. The initial seed bank contribution to plants in year t decays as $[(1 - g)\gamma]^t$ and is multiplied by $g * \gamma$ in order for seeds in the seed bank to mature into reproductive plants. Even in the most conservative scenario, with g approximately 0.2 and γ approximately 0.4, the initial seed bank is reduced by 99% after four years, and the potential contribution is diminished further by multiplying by $g * \gamma$.

To quantify the influence of regional processes, local recruitment, and seed banks on predicted *H. annuus* abundance across space in 2003, we decomposed the expected number of plants in 2003 into source proportions. We performed this decomposition for each dispersal

profile in Table 1A. To compute the proportion of expected plants generated by regional processes (dispersal), we summed the contributions of dispersal from segments other than the focal segment in 2002. Seeds dispersed from other segments obviously had to survive and germinate (and grow and reproduce) to contribute to the expected number of plants the following year. We considered the proportion of expected plants generated by local plants the previous year to be the fraction of seeds generated by plants in the focal segment in 2002 that survived, germinated, grew, and reproduced. The seed bank source proportion was the proportion of expected plants originating from seeds in the focal segment seed bank that were at least two years old (2001 or earlier).

We also explored two hypothetical scenarios. First, to imagine a situation without seed dispersal, we focused on Gaussian dispersal profiles. Such a profile effectively removes any regional dispersal, since the probability of dispersing to an adjacent segment on the same side of the road with the parameters we used is outside the numerical precision of R and is thus considered zero. Second, we considered a case where there was no seed bank. To model this scenario, we only allowed seeds from year $t-1$ to contribute to year t .

Results

The best fit to the 2003 data was obtained with an exponential dispersal profile with high dispersion and high fecundity (Table S1). Comparing models via ratios of MS, which would have a F distribution if error is roughly normally distributed, would not reject the fat tail or Gaussian tail even though the sums of squares is considerably lower for the exponential. (Note degrees of freedom is the number of segments which cancels out in F ratios in all cases).

Fig. S5 B-D illustrates the sources of the expected numbers of plants in 2003 for the three dispersal profiles. For all three profiles, the regional process of dispersal was a minor component across the landscape, with the notable exception of patchy areas of plants with exponential dispersal. Within the local processes, seed banks dominated in the northern region of the roadside (to the right of the graph, a region with very large numbers of plants in most years, Fig. S3) with considerable variation in seed bank contributions in other locations.

For the exploration of hypothetical scenarios, we found that all dispersal profiles fit significantly (at the $P=0.05$ level for the F -statistic of MS ratios) better with seed banks than without (compare Table S1A to S1B). The absence of seed dispersal (i.e. using the Gaussian profile) leads to poorer fit than for the exponential profile, but not significantly so.

Fig. S5A shows the goodness of fit across the landscape depending on the choice of dispersal profile. More specifically, the $(\text{observed} - \text{expected})^2$ values are plotted for each segment on the east side of the road. On average, fat tailed and Gaussian dispersal profiles tend to deviate more than the exponential from observed 2003 data, with some notable exceptions. Although there are some segments for which exponential is marginally worse than fat and Gaussian, there are two segments in the middle of the transect for which fat and Gaussian tails yield much greater lack of fit.

Table S1. Summary of different models (*H. annuus*). Results are shown for A) with seed bank and B) without seed bank, where we model the hypothetical scenario that there is no seed dormancy. The hypothetical scenario of no dispersal is modeled by using Gaussian dispersal. Dispersal type abbreviations: Fat, fat tail; Exp, exponential; Gau, Gaussian. Estimated parameter values are shown. Note that α , θ , r , and γ are constants, g_τ is allowed to vary. For each model in part A), four values are shown for g in years 2000, 2001, 2002, and 2003 respectively. SS refers to the sum of the (observed-expected)² for 2003 numbers. Each model in part A) corresponds to one of the panels B-D in Fig. S5.

Dispersal							
type	r	θ	α	γ	g_τ	SS	
A) With seed bank							
Fat	0.81	0.75	8.41	0.38	0.444, 0.232, 0.051, 0.996	979245	
Exp	14.58	1.0	32.48	0.43	0.616, 0.377, 0.297, 0.374	917805	
Gau	1.9	1.91	9.53	0.28	0.336, 0.336, 0.284, 0.284	950543	
B) Without seed bank							
Fat	0.98	0.49	8.31	0.4	0.390	1230229	
Exp	1.0	1.0	8.0	0.4	0.400	1181578	
Gau	1.55	2.23	17.79	0.39	0.154	1183598	

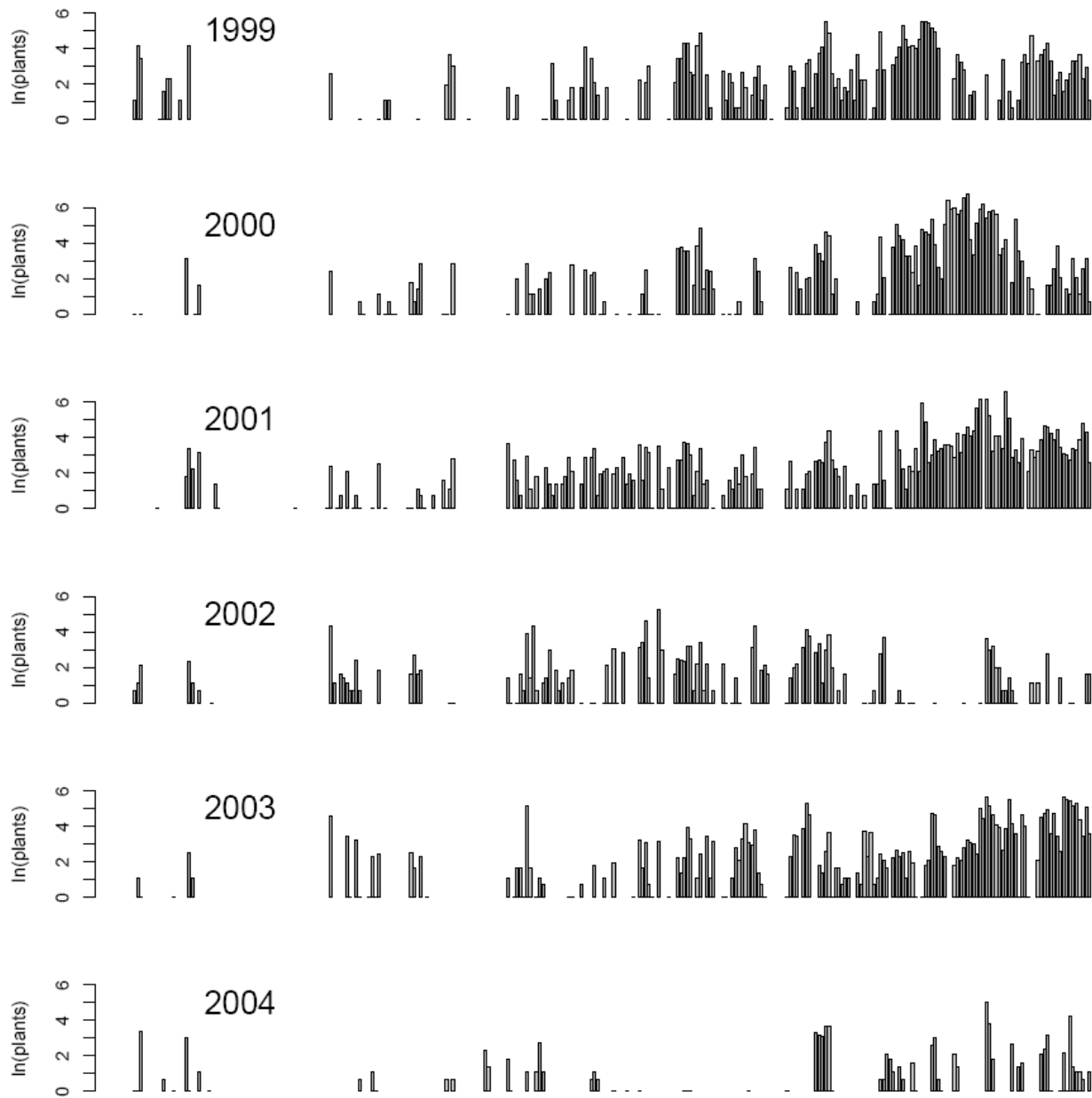


Fig. S3. Number of plants from 1999-2004 (*H. annuus*). Data are shown for the east side of a 23.8 km roadside transect in northeastern Kansas, USA (the southern end is to the left, and the northern end to the right). Each bar refers to the number of plants in an 80 m roadside segment. Note log scale. Although we had six years of data, our model focuses on 2003. We also did

analyses for 2004. However, occupancy and abundance declined dramatically between 2003 and 2004, making it difficult to infer the importance of dispersal and seed banks.

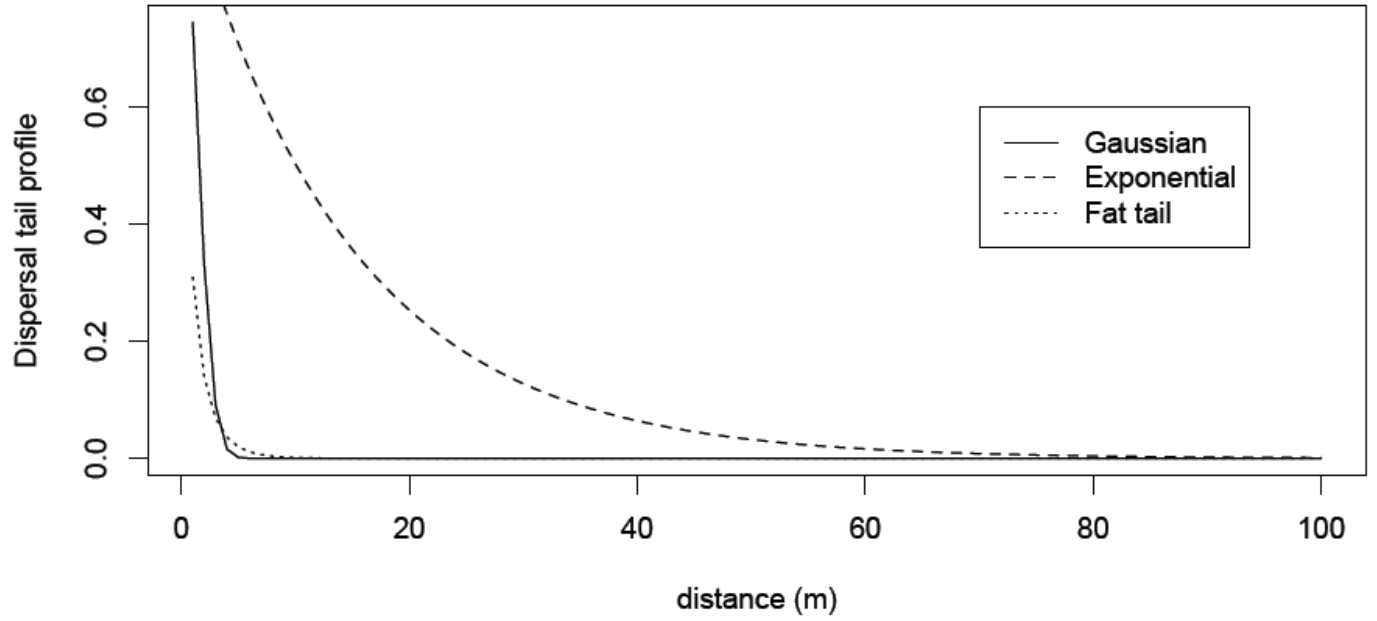


Fig. S4. Dispersal profiles (*H. annuus*). Parameters in Table S1 (A, with seed bank) were used for each profile.

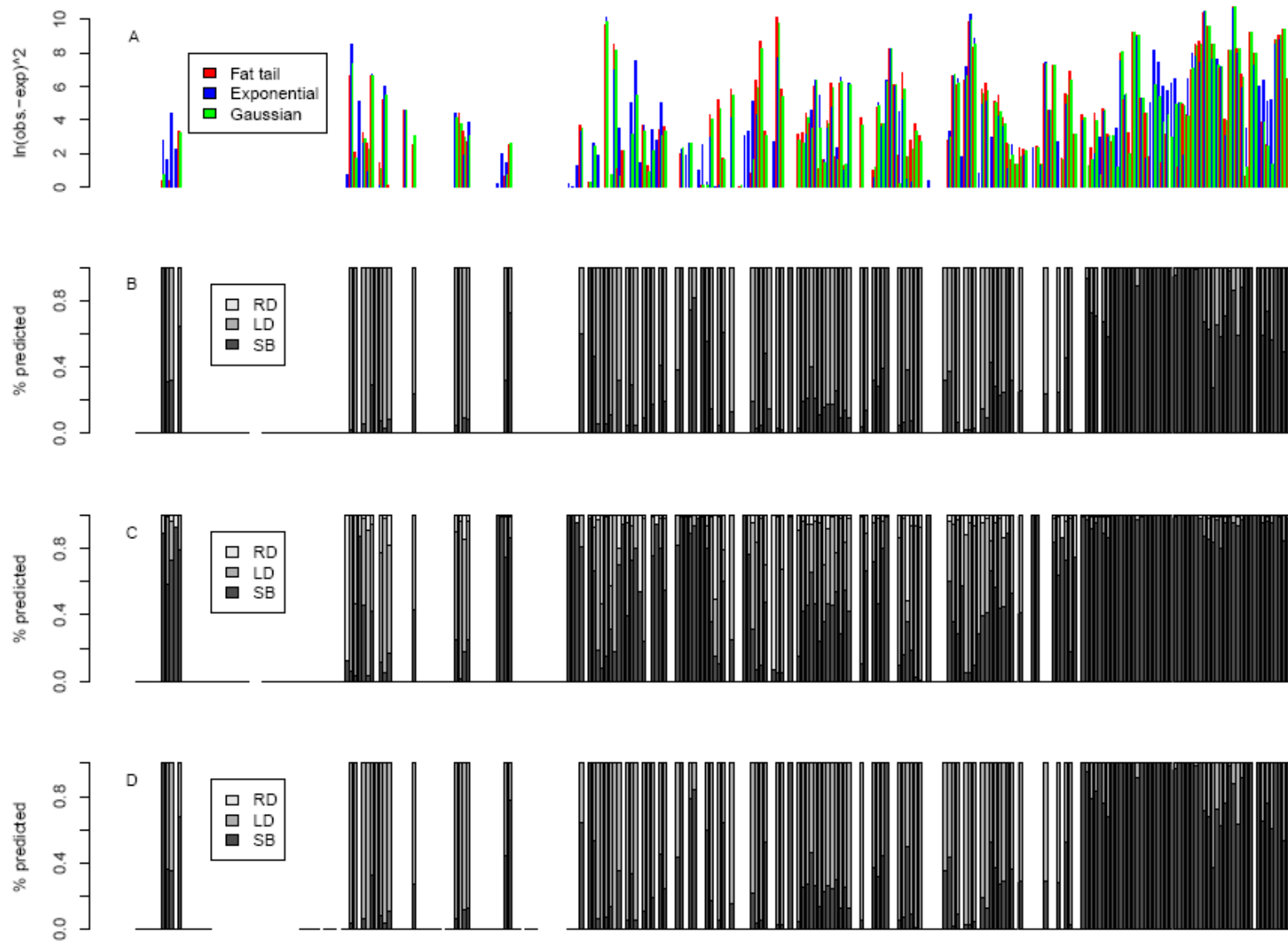


Fig. S5. Results of model runs (*H. annuus*). A) Model fit and B)-D) proportion of 2003 expected plants originating from dispersal from other segments, from seeds at the same segment the previous year, and from the seed bank using different dispersal profiles. For all graphs, the x axis refers to positions along the 298 adjacent 80m segments from the east side of the *H. annuus* survey (see text). For A), note variation in model fit across the landscape. The y axis was calculated as the quantity (observed number of plants – expected number of plants)². B-D refer to the proportion of expected plants in the 2003 segments 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, seeds in the segment older than 2002) under B) fat tail, C) exponential, or D) Gaussian dispersal profiles. See Table S1A for parameter values used in these models.

Appendix S3. Succession from a metacommunity perspective

Study design: The “fragmentation” experiment consists of replicated patches of three different sizes, situated on abandoned cropland (Fig. 3 in main text): small patches (4 x 8 m); medium patches (8 x 12 m); and large patches (50 x 100 m). For the purposes of this study we focus only on the small and large patches due to low numbers of medium-sized patches. The matrix area between patches was mowed regularly while patches were left to undergo succession. Most large patches occupy the same area as a cluster of small patches (0.5 ha), thus allowing an assessment of the effects of habitat fragmentation and altered connectivity on plant 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 m² quadrats separated by 4 m comprise each station. Each small patch contained one sampling station while each large patch contained 15 stations in most cases. For the purposes of this study, individual sampling stations are taken to represent the local communities, while the assemblage of all sampling stations at the site constitute the metacommunity. In total there are 172 sampling stations distributed among small and large patches (82 in small patches, 90 in large patches). Species lists of each quadrat pair in a given sampling station were merged to represent the species composition of that sampling station. In July 2003 soils were collected from all sampling stations to characterize gradients in soil texture (% sand, silt and clay) across the site. Soil samples (2.54 cm diameter x 15 cm deep) were taken from each station using a tube sampler. Soil samples were air-dried and sent to the Kansas State University soil testing lab for analysis. Soil texture was evaluated using the hydrometer method. Topographic variables (elevation, slope and aspect) for each sampling location were estimated from a digital elevation model (DEM)

constructed from a 0.61 m contour topographic survey of the site (Dean Kettle, personal communication).

Statistical analyses: To evaluate the unique contributions of spatial and environmental processes to variation in plant community composition, we partitioned variance in the plant community resemblance matrices into unique spatial and environmental components using Partial Redundancy Analysis (Borcard, Legendre & Drapeau 1992; Legendre & Legendre 1998) and Distance-based Linear Modeling (DISTLM in the program PRIMER-E; (Clarke & Gorley 2006; Anderson, Gorley & Clarke 2008) which are essentially multivariate extensions of linear regression. R^2 values produced by the analysis estimate the percentages of total variation in a community resemblance matrix explained by sets of spatial and environmental variables. The different components partialled out by the analysis include: variance in species composition among localities explained by environmental variables, E ; variance explained by spatial variables, 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 effect of the environment); variance explained by space independent of the environment, S_c (conditional effect of space); and unexplained variation ($1-[E+S]$). The main focus of the analyses in this study are 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) versus endogenous processes (dispersal limitation and other pure spatial effects). Environmental data used for the analyses of the fragmentation experiment included soil texture variables (% sand, silt and clay) and topographic variables (elevation, slope and aspect). The spatial variables were the third-order polynomials of the X and Y coordinates of each sampling location (Borcard, Legendre & Drapeau 1992; Cottenie 2005).

The goal of our analyses was to examine changes in the contributions of E_c and S_c across years. Because the variance explained by sets of predictor variables in a DISTLIM model may vary with sample size and with the number of explanatory variables included, a standardization procedure was employed to make models produced for different years as comparable as possible. First, only years in which all or most sampling stations were sampled were included in the analysis, ensuring relatively constant sample sizes among years. These years were: 1985 (second year of succession), 1989, 1990, 1994-2002. Data were not sufficient for analysis in 1984, 1986-1988 and 1991-1993 due to incomplete sampling (only a subset of sampling quadrats were sampled in these years). Second, a forward selection procedure was conducted for each year separately to eliminate insignificant and co-linear explanatory variables. The *Adjusted R²* selection criterion was used to prevent the inclusion of explanatory variables in the final model that would add no more to the explained sums of squares than would be expected from the addition of a random variable. After forward selection, ten of the twelve DISTLIM models retained between 6 and 8 explanatory variables. However, the other two models both retained more than eight variables and so were subjected to a variable truncation procedure to make the models for these years more comparable with the other ten models in terms of the number of variables included. To do this we used the *BEST* selection procedure in PRIMER-E to select the most parsimonious model in forward selection for a given number of explanatory variables. We set this given number to eight, the maximum number of variables retained among the other ten models. We then compared total variance explained by these truncated models to their non-truncated counterparts (models arrived at via forward selection without using the *BEST* procedure) and found the differences to be negligible.

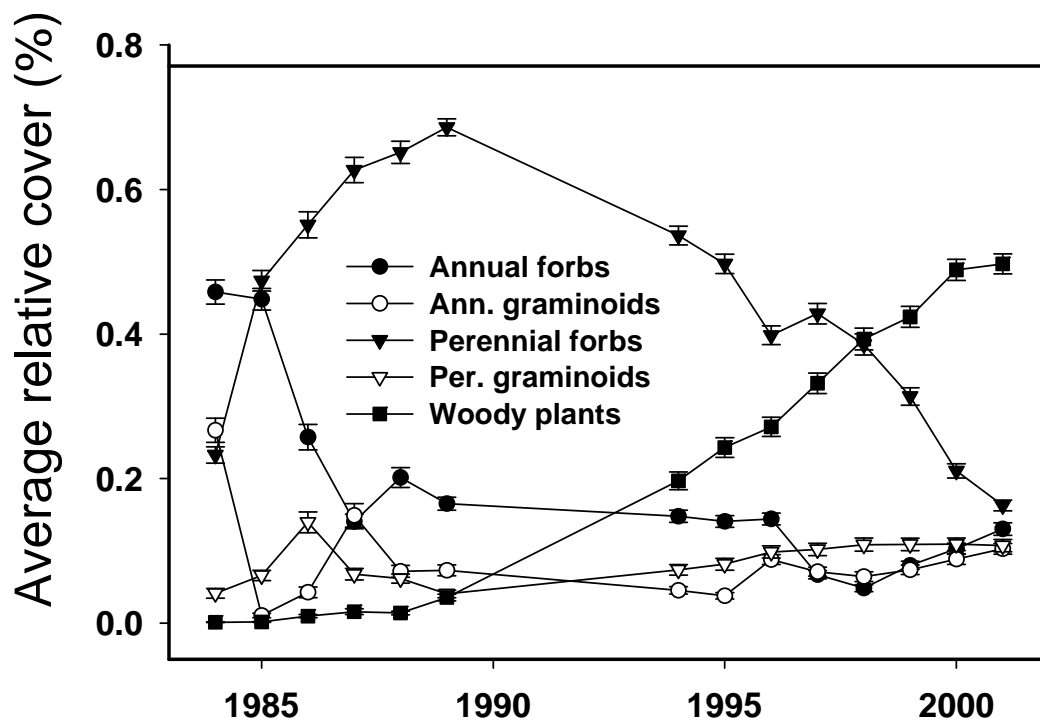


Fig. S6. Changes in species composition over time in the fragmentation study. Yearly changes in relative percent cover (means ± 1 SE) per 1-m² quadrat of the principal life-history groups, averaged across all quadrats and patch types from 1984 to 2001. Key to abbreviations: Ann., annual, Per., perennial). Data from the period 1990-1993 were not collected or were not in comparable format. Modified from Cook *et al.* (2005).

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