Author for correspondence:
Benjamin Gilbert
e-mail: benjamin.gilbert@utoronto.ca

THE ROYAL SOCIETY
PUBLISHING

Ecological drift and the distribution of species diversity

Benjamin Gilbert[1] and Jonathan M. Levine[2]

[1]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada M5S 3B2
[2]Institute for Integrative Biology, Eidgenössiche Technische Hochschule Zurich, 8092 Zurich, Switzerland

(iD) BG, 0000-0002-4947-6822

Ecological drift causes species abundances to fluctuate randomly, lowering diversity within communities and increasing differences among otherwise equivalent communities. Despite broad interest in ecological drift, ecologists have little experimental evidence of its consequences in nature, where competitive forces modulate species abundances. We manipulated drift by imposing 40-fold variation in the size of experimentally assembled annual plant communities and holding their edge-to-interior ratios comparable. Drift over three generations was greater than predicted by neutral models, causing high extinction rates and fast divergence in composition among smaller communities. Competitive asymmetries drove populations of most species to small enough sizes that demographic stochasticity could markedly influence dynamics, increasing the importance of drift in communities. The strong effects of drift occurred despite stabilizing niche differences, which cause species to have greater population growth rates when at low local abundance. Overall, the importance of ecological drift appears greater in non-neutral communities than previously recognized, and varies with community size and the type and strength of density dependence.

1. Introduction

Biologists have long debated the role that stochastic processes play in structuring the diversity and composition of species in ecological communities [1,2]. Chance variation among individuals in their vital rates can have important consequences for ecological communities [3], yet conceptual and theoretical models of community dynamics tend to ignore demographic stochasticity. This factor causes communities to randomly drift from deterministic expectations and reduces local species diversity [4,5]. Hubbell's development of the neutral theory of biodiversity has offered a starting point for understanding the effects of ecological drift among species with identical vital rates [5,6], and forms the basis of testing, and frequently rejecting, the hypothesis that communities are structured by chance demography alone [7,8]. However, this theory does not provide sufficient understanding of how ecological drift influences the dynamics of communities in nature. Natural communities are typically structured by stabilizing niche differences and competitive asymmetries among species, which are expected to modulate the effects of drift and render these systems distinctly not neutral.

Progress towards understanding the role of ecological drift can be aided by lessons from related fields. Theory in population genetics indicates that small, isolated populations are most prone to drift due to the increased importance of sampling effects [9]. Similarly, population ecology and disease epidemic models show that demographic stochasticity has the largest impact on population growth rates and extinction when populations are small, and highlight how density-dependent feedbacks can modify the effects of small population sizes [10–12]. These principles have motivated the major expectations for community drift—the total number of individuals supported in a community must be important for ecological drift, and density dependence should play an important modulating role [6,13–16].

However, some processes affecting drift in natural systems may only emerge at the community level. Of particular interest here, the ecological processes determining the outcome of multispecies competition may have opposing effects on the importance of ecological drift. Stabilizing niche differences between competitors [4], as arise from species differences in the resources most limiting growth, for example, are expected to dampen the effects of drift on dynamics [15,17]. Stabilizing processes benefit species that drift to low relative abundance and harm those drifting to high relative abundance, favouring their return to their quasi-equilibrial abundances [4,17]. Other types of species differences may augment the influence of drift among species that are expected to coexist. In the short term at least, differences between species in their average competitive ability, the ability to deplete a shared limiting resource, for example, may set the stage for drift to operate strongly. Differences in competitive ability drive inferior species to low abundance, where demographic stochasticity is expected to play a strong role. In addition, even when species are apparently excluded, drift processes may dictate the likelihood of population rescue from dormant life stages, such as a seed bank. In sum, complex feedbacks between deterministic processes that maintain diversity and factors that influence the importance of ecological drift make it a particularly important process to address both theoretically and empirically.

Despite several calls for quantifying the importance of drift when deterministic processes also structure communities [18,19], existing empirical approaches provide limited inference. Some observational studies quantify the importance of drift relative to deterministic processes by measuring drift as the 'unexplained' variation after a community dynamics model has been fitted to field data [20]. Such approaches rest on the tenuous assumption that the community dynamics model accurately describes the deterministic processes in the system [7,20]. An alternative approach measures drift as the compositional differences between replicated communities that arise during community assembly [21,22]. However, unless replicate communities experience the same initial conditions and environments, among-community variation in composition can be strongly influenced by community assembly processes such as positive feedbacks [21]. Progress therefore requires novel empirical approaches.

Here, we show how drift can be quantified by measuring how among-community variation in species composition increases with decreasing community size—the key determinant of drift [13,14,16,19]. With this approach, replicate communities need not experience identical environmental conditions so long as communities of all sizes are exposed to the same range of conditions. This approach works because it is not simply the compositional variation among communities that measures drift, but rather how that variation increases with decreasing community size.

In this study, we use this novel manipulation of community size to quantify the effects of three generations of ecological drift in annual plant communities. We selected six native annual plant species that are strong competitors in natural communities [23], and initiated communities of varying sizes with an equal density of these species. We measured the variation in species composition among the replicate communities of differing size and their decline in species richness through time to address three questions: (i) How important is drift in small communities, and how quickly do the effects of drift change with community size and time? (ii) How strongly does drift affect species diversity, extinction rates and recovery from the seed bank? (iii) How does drift operate in the presence of competitive processes that both stabilize dynamics and drive competitive dominance? We explored this final question by measuring species' growth rate advantages when rare and trajectories of species dominance, and by comparing the observed dynamics with those predicted by a neutral model where species lack competitive differences. Our results collectively suggest that the importance of ecological drift in structuring diversity in fragmented ecosystems is far greater than predicted by neutral models.

2. Material and methods

(a) Field experiment

Our experiment was established along level ground in an annual grassland at the University of California Sedgwick Reserve in northern Santa Barbara County, USA (34°40′ N, 120°00′ W), 730 m.a.s.l. (http://sedgwick.nrs.ucsb.edu/). The climate is Mediterranean with cool, wet winters and hot, dry summers.

In September 2010, we created annual plant communities of six sizes: 0.0046, 0.0081, 0.0304, 0.0426, 0.0912 and 0.1885 m^2, each replicated 45 (the smallest size), 30 (the second smallest size) or 15 times (the four largest sizes). One of the challenges of manipulating community size is doing so without altering the edge-to-area ratio of the communities, which can introduce effects of community size separate from drift. We therefore shaped each community as a doughnut lined with 25 cm deep PVC piping at its outer and inner edge (electronic supplementary material, table S1). The sizes of the outer and inner pipes were chosen so as to have a consistent edge-to-interior ratio across community sizes. The two smallest communities (15 and 26 cm^2) did not have PVC centres because their small diameters resulted in edge : interior ratios similar to those of the larger communities (electronic supplementary material, table S1). The communities were arranged in 15 experimental blocks, each of which was roughly 3 × 3 m and held one community of each of the larger four sizes, and two 0.0081 m^2 and three 0.0046 m^2 communities. Simulations indicated that smaller communities have higher expected extinction rates, and therefore higher replication of these smaller systems was necessary to separate compositional variation from mean changes in relative abundance.

All communities were sunk into the ground flush with the soil surface. To homogenize environmental conditions across all communities, soil from the study site was passed through a 1 cm mesh and mixed into a homogeneous pile before being used to fill the experimental communities. We did not include the top 5 cm of grassland soil in order to avoid the existing seed bank, and soil was collected from an exotic-grass-invaded portion of the field site that did not contain the focal species used in our experiment but has been shown to be particularly favourable for the growth of our focal species [24]. We sowed six native annual species into the plots: *Lasthenia californica*, *Chorizanthe palmeri*, *Plantago erecta*, *Vulpia microstachys*, *Navarretia attractyloides* and *Salvia columbariae*. Previous research at the field site has quantified these species' demographic rates, which yield positive long-term average population growth rates in the absence of interspecific competition (i.e. they stably persist in monoculture), and per germinant fecundities in the absence of competition (viable seeds/germinant) which vary from 252 (*Vulpia*) to 26 903 (*Navarretia*) [23,24]. In addition to these demographic differences, research indicates that these species compete interspecifically, and moreover that the strength of this competition is predictable with knowledge of species' functional traits, phenology and life-history traits such as seed mass and dormancy [23,25–27].

An equal density of seeds of all six species was sown into each community, and seed density was constant across community size—each species had 10 viable seeds added per 15 cm^2 surface area (electronic supplementary material, table S1). At the time of seed production, to ensure that the majority of seeds produced in each community would be retained after dispersal, each community was surrounded by a clear plastic barrier affixed at its bottom to the outer PVC liner. The barrier was shaped like an inverted lamp shade and extended 45 cm above the ground. A cone of plastic or metal was affixed to the interior edge of each doughnut plot to have the same effect. These barriers also prevented seeds from dispersing between communities. In early spring of 2011, 2012 and 2013, we counted the number of live plants of each species in each community. These data were the basis of all subsequent analysis, and are available at http://dx.doi.org/10.5061/dryad.kd3p5 [28].

(b) Quantifying compositional divergence

To evaluate how community size affected compositional divergence between replicates, we employed a species-level Fst measure, which standardizes the variation among patches for each species relative to the maximum variation possible, given the observed relative abundance. For Fst and all multivariate measures employed here, raw abundance data were transformed to proportional abundances. Expressing abundance in this way allows comparison of variation among communities with different total numbers of individuals. Three plots (two of the smallest size and one of the second to smallest size) experienced complete mortality by the end of the experiment (no individuals remained)—these were removed from Fst analyses.

In population genetics, Fst measures the genetic variation between populations relative to the total genetic variation. By analogy, when used to analyse species, compositional variation Fst provides a measure of how the relative abundance of a species is distributed within versus between communities. For example, when a species occurs at 30% relative abundance on average, is that because it occurs at 100% relative abundance in 30% of communities, and is absent from the remaining 70% (the maximal between-community variation), or does it occupy 30% of the relative abundance in all communities (no between-community variation)? This species-level analogy of the genetic Fst metric developed by Wright [29] is calculated as

$$\text{Fst}_{\text{species } j} = \frac{\sum (p_{ij} - \hat{p}_j)^2/n}{\hat{p}_j(1 - \hat{p}_j)}, \tag{2.1}$$

where $\hat{p}_j$ is the mean relative abundance of species j for a given treatment, i denotes a community and the summation is across all n communities of the treatment. Fst in ecological communities is analogous to Wright's model if each species is considered analogous to an allele at a multiallelic locus in a haploid population [6]; it is this analogy that we use to generate treatment-specific Fst predictions for a neutral model (below). Because our Fst measure proved unbiased based on a jackknife procedure [30], and errors were unrelated to our treatments, we used this common definition of Fst instead of other derived measures [30].

Fst was calculated for each community size both on a per species basis (equation (2.1)) and for entire communities (equation (2.2)). To calculate Fst for entire communities consisting of S species, the appropriate measure is [30]

$$\text{Fst}_{\text{community}} = \frac{\sum_{j=1}^{S} \sum (p_{ij} - \hat{p}_j)^2/n}{\sum_{j=1}^{S} \hat{p}_j(1 - \hat{p}_j)}. \tag{2.2}$$

In the remainder of the paper, we use the community-level Fst (equation (2.2)) to evaluate differences between communities in their species composition. In the electronic supplementary material, we also present species-level Fst results to quantify

each species's contribution to the overall Fst. Also in the electronic supplementary material, we show that the weighted Fst measure (equation (2.2)) can be calculated in a multivariate dispersion matrix when the data are properly transformed (electronic supplementary material, equation (S1)). This allows us to calculate the distance of each community i from the compositional centroid of each treatment, which can be used in a multivariate test of homogeneity of variances [31].

It should be noted that other distance metrics that are commonly used to calculate β diversity or dispersion in ecological data, such as Hellinger distance and Bray–Curtis distance, are not appropriate for the current dataset because they treat the absence of a species in two communities as uninformative for compositional variation [32]. Nonetheless, because these metrics are commonly used to calculate β diversity, we show their relationship to our Fst metric in electronic supplementary material, figure S1.

We tested the effects of community size on compositional variation with linear mixed models with an autoregressive error correlation to account for repeated measures, with the subject set as the community size treatment. In order to linearize trends and meet assumptions of homogeneity of variances, all Fst measures were log transformed for statistical tests and community size (in area units) was square root transformed.

(c) Neutral model predictions of compositional divergence

We developed neutral models informed by our field data to develop a null expectation for how communities would drift apart in the absence of competitive imbalances and stabilizing niche differences. Specifically, we used simulations to generate neutral predictions for weighted Fst, assuming all individuals of every species had an identical probability of producing offspring in the subsequent generation. In these simulations, each plot was simulated for three generations following an initial even abundance of viable seeds, so that the neutral model simulated what would occur in our experiment if neutral assumptions held. For the neutral simulations, the offspring at year t were drawn randomly from a multi-nomial distribution, with the expected proportion of offspring for each species equal to its relative abundance in the previous year. For example, each species was expected to make up one-sixth of the community in the first year, so that a community with 50 individuals had an expected abundance of 8.3 individuals per species in the first year. Similarly, for a species that occupied 85% of a community in year 2, each individual in year 3 had a probability of 0.85 of being that species. Because the numbers of individuals in our experimental communities increased over the 3 years of the field study, and varied to some degree among communities within treatments, we also included the changing number of individuals in our neutral simulations, thereby accounting for expected changes in compositional variation that occur with changing community size. This formulation of a neutral model follows previous research [5,6], with the addition of including the effect of changing population sizes.

Although neutral models provide a benchmark for ecological drift, they cannot capture deterministic shifts in species' relative abundances. We developed two stochastic non-neutral models to determine if species-specific fecundity without or with competitive asymmetries driven by differences in seed size could explain the deterministic shifts in relative abundance observed. Details of these models are provided in the electronic supplementary material.

(d) Extinction and rescue from the seed bank

In addition to affecting the among-replicate variation in composition, community size should also influence the likelihood of

extinction, and thereby affect species richness. We therefore tested how the size of the community influenced species richness and the extinction rate for each species. For the latter analysis, the response was the extinction of each species in each community (i.e. a binary variable) and this was predicted by the square root of area as a fixed effect, and each species-by-year combination as a random slope effect and as a random intercept. Experimental plot nested within block was also included as a random effect. We used the glmer function in the lme4 library with a binomial distribution to fit the model following [33]; we compared this model with simpler models with random effects removed (first the slope terms, then the intercept terms) using AIC. We subsequently tested the fixed effect (area) of the model with the best random effects structure using the likelihood ratio of the model with and without area included. In these and all other mixed models, we used REML estimation when comparing models with different random effects, and ML estimation to compare models with different fixed effects [33]. Rescue from the seed bank was tested in a manner analogous to extinction, because it too is a binary response. Specifically, each plot that had an apparent extinction event in year 1 or 2 was tested for a rescue (species re-appearing) in the subsequent year. The extinctions were apparent because we could only sample the aboveground community, and thus species lost from the aboveground community could only re-emerge the following year from the seed bank.

(e) Competitive imbalances and stabilizing niche differences

We evaluated the competitive imbalances between the species in the communities by recording how their relative abundances changed over the 3 years of the study. Although our experimental design is better suited to assessing drift than *per capita* competitive effects because we do not manipulate a range of inter- and intraspecific densities [23,34], our data can nonetheless be analysed to provide information on how density affects population growth. We evaluated whether species abundances were stabilized by niche differences that cause higher growth rates when a species drops to low relative abundance by testing how intra- and interspecific density within plots influenced the mean finite rate of increase in each species, R, defined as the number of plants in year $t + 1$ per plant in year t. We used a mixed model with a negative binomial distribution and log link to describe the number of individuals in year $t + 1$ as a function of species crossed with intraspecific density crossed with year plus species crossed with interspecific density crossed with year included as fixed effects, and plot (nested within block) as a random effect. We included the natural logarithm of the number of individuals in year t as an offset, so that the model predicted *per capita* finite rates of increase. From this model, we eliminated terms that did not improve model fit (using likelihood ratios) until we arrived at the most parsimonious model [33]. Models were fitted using the glmmADMB package.

3. Results

We found greater compositional variation among communities, as measured by Fst, as they decreased in size, revealing the role of ecological drift in driving community dynamics (figure 1). The non-zero compositional variation found in our largest plots reflects the combined effects of ecological drift in communities of this size as well as any unavoidable among-replicate variation in environmental conditions that may have occurred despite homogenizing plots (figure 1). However, the increasing variation associated with
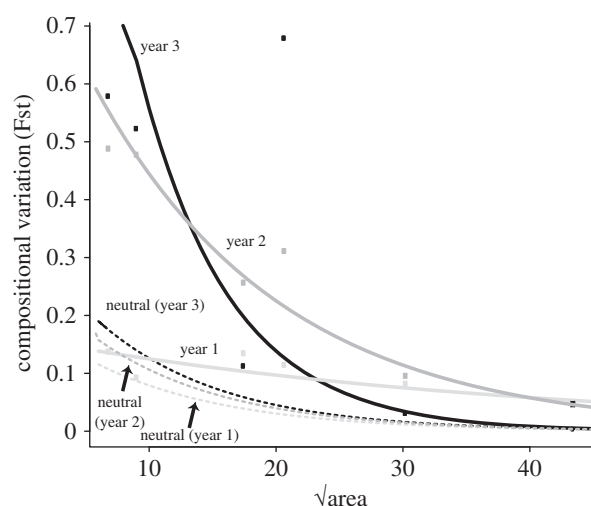

Figure 1. Ecological drift in small communities exceeds neutral prediction. Observed compositional variation among communities (Fst; solid lines) is greatest and increases through time in smaller communities, whereas it decreases in the largest communities. Neutral expectations for Fst are shown with dashed lines, which generally fall below the observed values of Fst. Note the x-axis is the square root of area (cm^2).
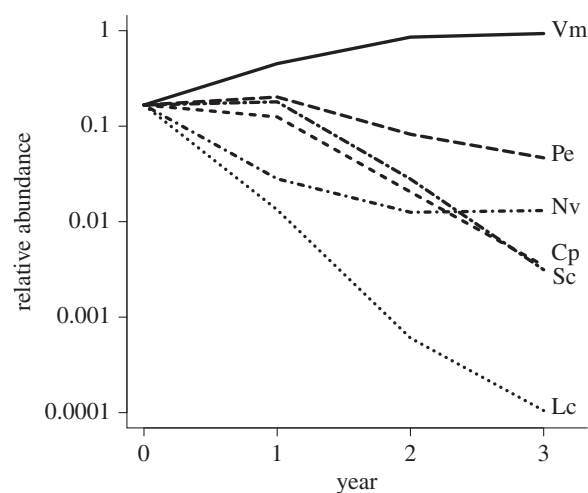

Figure 2. Compositional changes in plant communities through time. Communities were rapidly dominated by *Vulpia* (Vm), which had a relative abundance of 86% by the second year of the study. *Lasthenia* (Lc) rapidly declined and was only present in two communities in the third year. Other species are given by the first letters of the binomial name (genus, species). Relative abundances are averaged for all community sizes, with results for individual sizes given in electronic supplementary material, figure S4.

decreasing community size reflects the effects of drift, because the environmental differences between replicate communities should not change with decreasing community size.

Differences in species composition among communities decreased with community size in all years but also showed a year-by-community-size interaction (figure 1; electronic supplementary material, figure S2; $p = 0.002$). This interaction reflects the fact that small communities diverged from one another in species composition through time, as expected, while larger communities became more similar (figure 1; electronic supplementary material, figures S2 and S3). The reduced compositional variation though time in the larger communities can be partly explained by the fact that all of these communities converged to *Vulpia*-dominated systems by year 3 of the study (figure 2; electronic supplementary material, figure S4).
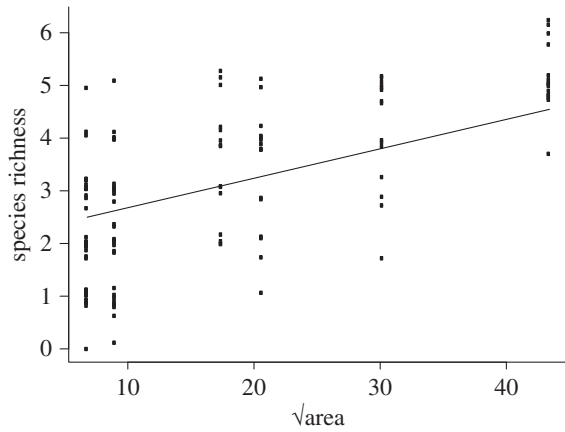
5

Figure 3. Species richness increased with community size. Although all communities were initiated with identical densities of all species, species richness quickly declined in smaller communities. Data shown are from year 2 of the experiment, with points jittered vertically to better visualize the data.

Although *Vulpia* also came to dominate the smaller communities, it sometimes failed to do so, and strong effects of drift enabled different species to co-occur with *Vulpia* in different plots and at varying densities. Species-specific Fst showed similar trends to community Fst (electronic supplementary material, figure S3), with a year-by-size interaction ($p = 0.001$) and differences among species ($p < 0.0001$), but no interactions with species (all $p > 0.1$). Among the competitors, the most abundant species (*Vulpia*) had the greatest species-specific Fst, but abundance was an otherwise poor predictor of species-specific Fst in most years (electronic supplementary material, figure S3). Apart from shifts in relative abundance, increases in absolute abundance occurred in all plot sizes over the course of the experiment (electronic supplementary material, figure S5).

Observed Fst was always greater than predicted by a neutral model, and this was particularly the case for the smaller communities. With *Vulpia* dominating almost all communities, the remaining species were at lower absolute abundances than predicted by the neutral model, allowing demographic stochasticity to have a stronger effect on these species than a neutral model would predict. This was not the only difference between the neutral model predictions and the observed dynamics; Fst in neutral models always increases through time, a trend we observed in our smallest communities but not in the largest communities (figure 1), for reasons stated in the prior paragraph.

Species richness declined most in the smaller communities (figure 3; electronic supplementary material, figure S6), owing to higher extinction rates for the component species (figure 4). The best model for extinction rates showed a significant difference in the slope (effect of community size) and intercept of each species-by-year combination (electronic supplementary material, table S2), with extinction decreasing with community size ($p < 0.0001$) and increasing through time for most species (figure 4).

The probability of rescue from the seed bank increased with community size ($p < 0.0001$). The best model predicted that this increase occurred at a similar rate for all species, but that species differed in their average rescue rates each year (electronic supplementary material, table S3). Estimates of rescue in larger communities were uncertain for some species due to low sample sizes (low numbers of extinctions), but were nonetheless frequently over twice the rate found in the smallest communities (figure 5).

The greater effects of drift observed in the experimental communities than predicted by the neutral model occurred despite evidence that each species showed greater finite rates of increase when rare than when common (figure 6), which should stabilize dynamics. The best model for finite rates of increase (N_{t+1}/N_t) included a species-by-year interaction ($p < 0.0001$), an effect of interspecific density ($p = 0.026$) and a species-by-intraspecific-density interaction (figure 6; $p < 0.0001$; electronic supplementary material, table S4). On average, species appeared to show a stronger response to intraspecific density than interspecific density, although inter- and intraspecific density were strongly correlated in the first year ($r = 0.64$), indicating that this result should be interpreted cautiously. Most species were exposed to much greater densities of heterospecifics in the second year and also had lower finite rates of increase in this year (figure 6), although some species failed to germinate or survive to the census when interspecific densities were very high (*Chorizanthe* and *Navarretia*, figure 6). Our estimates of growth rates may have been lower than actual growth rates due to the extensive seed banks of most species [24]. Nonetheless, species had large differences in mean growth rates (figure 6), with all species increasing in some plots, especially in the first year when at lower overall community density, while the most abundant species had high mean growth rates (*Vulpia*, figures 2 and 6). Incorporating species-specific differences in seed mass and fecundity into our otherwise neutral model provided poor predictions of relative abundances, with all correlations between predicted and observed relative abundances being weakly negative. These results indicate that competitive differences among species were not driven by these differences (electronic supplementary material).

4. Discussion

Our research highlights the important role that ecological drift can play in structuring diversity, and how ecological characteristics of species and communities mediate the effects of drift. In our experiment, small communities showed large variation in species relative abundances and high levels of local extinction (figures 1 and 4). These signatures of ecological drift resulted in lower local (α) diversity but higher among-community (β) diversity in small communities, patterns that have been a longstanding focus of ecological research [5,21,35]. Our results suggest that ecologists must consider the interplay between demographic stochasticity, species interactions and species life-history traits in order to understand species diversity.

Increasing compositional divergence in smaller communities (figure 1) confirms predictions from theoretical models about when drift affects community dynamics [13,15,16,36]. Nonetheless, by the third year of the study, the ecological drift we observed was stronger than we would expect from even a neutral model. Fst in small communities was much greater than in our neutral model, whereas Fst in large communities had decreased but was still as high as the neutral model (figure 1). These high levels of variation among communities suggest that drift is a far more important process than is commonly recognized.
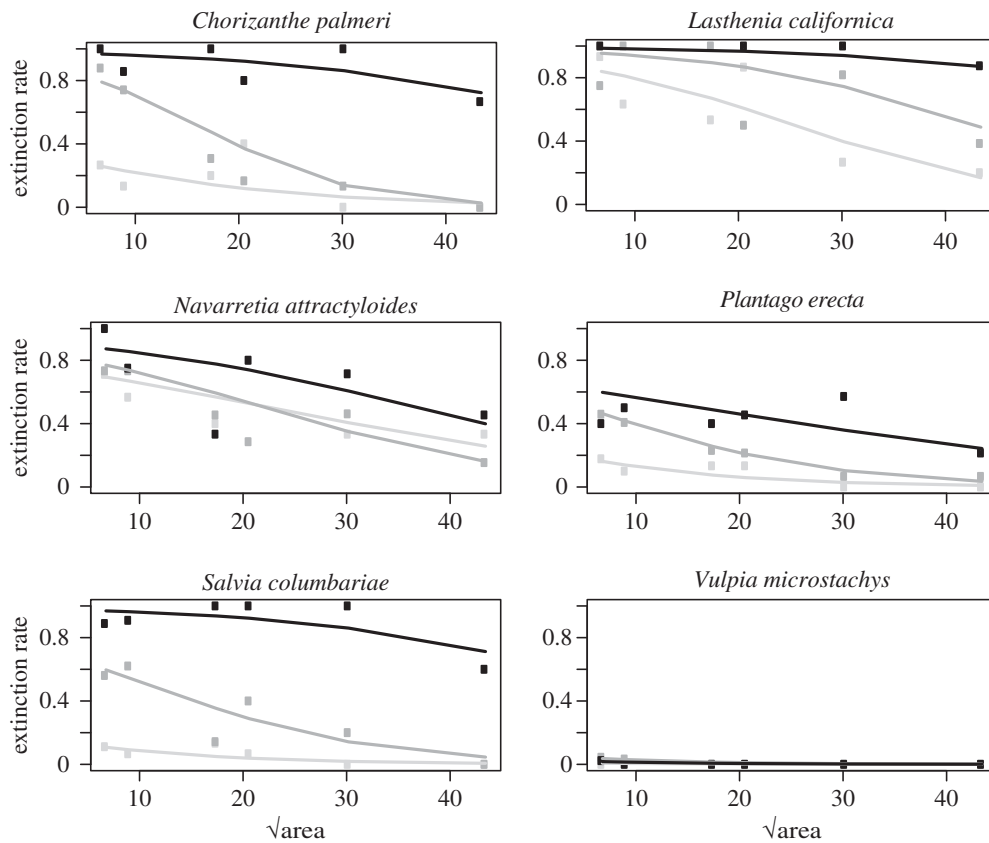
6

rspb.royalsocietypublishing.org   Proc. R. Soc. B 284: 20170507

Figure 4. Apparent extinction with community size. Large communities had lower probability of extinction for all species, with extinction recorded in any year that no germinating individuals of a species were observed. Lines are fitted for each year, with light grey representing year 1, dark grey representing year 2 and black representing year 3.
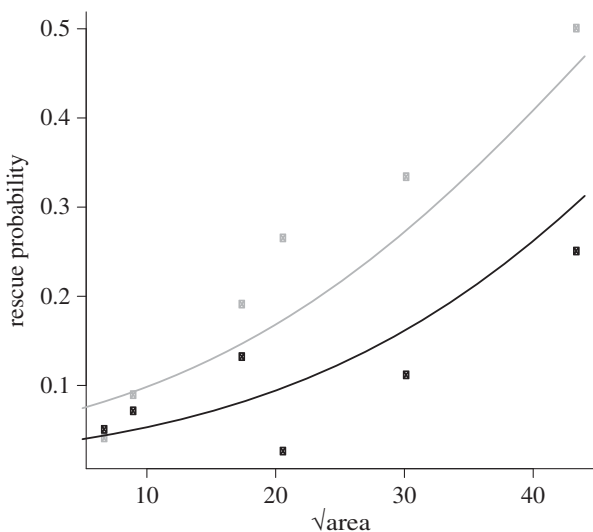

Figure 5. Probability of rescue from the seed bank increases in larger communities. Data shown are for all species combined (species-specific rescue results shown in electronic supplementary material, figure S7). Note that rescue effects could only occur in the second year (grey) and third year (black).

(a) Effects of competition on ecological drift

Our results suggest that rather than dampening the effects of drift, competitive differences between species may create conditions in which drift plays a strong role. Competitive imbalances will generally favour a small subset of species, leaving the majority at small population sizes. One of our focal taxa, *Vulpia*, rose to dominance over the 3 years of the study, which rendered it virtually immune to drift-driven extinctions,

despite relatively high variation in its relative abundance among communities (figure 4; electronic supplementary material, figure S3). Competitive dominance in our study system is driven by a combination of fecundity and insensitivity to competition [25,34,37]; our results, along with published information on these species [23], suggest that *Vulpia*'s success is largely due the latter (figure 6; electronic supplementary material). Despite evidence that all the focal species have high reproductive rates in our system when competition is low [23,24], the rise in *Vulpia* abundance sent the other five competitors to low abundances where demographic stochasticity can more strongly determine dynamics and cause stochastic extinction (figures 2 and 4). Although neutral dynamics also lead to many species having low relative abundances over time [5], our research complements previous work that highlights the ubiquity and consistent effect of competitive imbalances [23,34]. That competitive imbalances can enhance the effects of demographic stochasticity on the inferior taxa is not commonly appreciated [38], but follows from fundamental principles in population ecology [10].

The effect of competitive imbalances on drift emerged despite the operation of stabilizing niche differences, which are predicted to reduce the effects of drift that communities experience by regulating population sizes [4]. In our study, species had the greatest rates of increase when they had low intraspecific densities (figure 6). This evidence for stabilizing niche differences matches other work with the focal species at the field site [23], and is consistent with much more speciose ecosystems [37]. The increasing growth rate when at low abundance found here reduces extinction risk, just as the decrease in growth rate at high abundance reduces
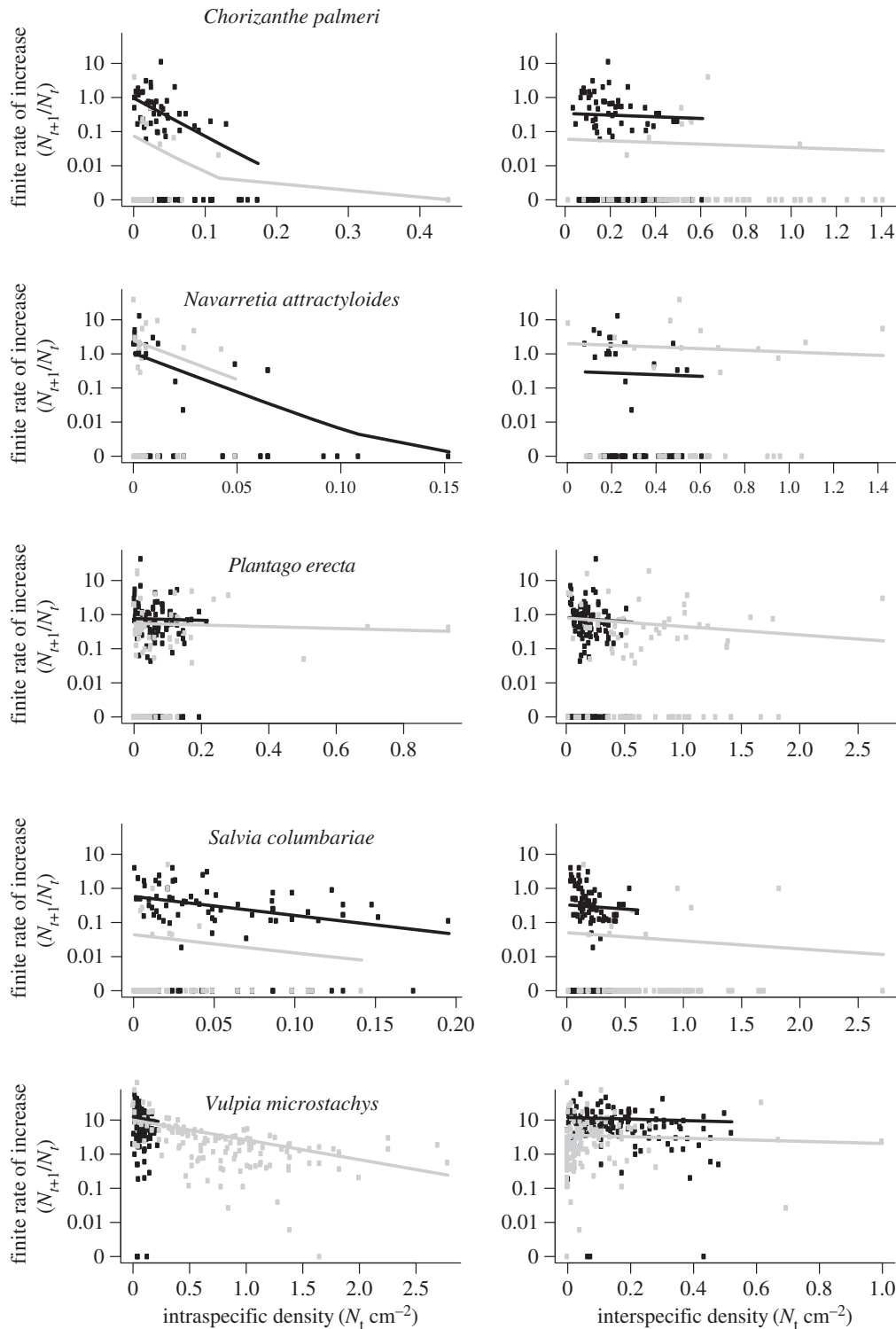
Figure 6. Effects of inter- and intraspecific density on population growth. Species finite rates of increase were predicted by intraspecific density (left side) and interspecific density (right side). All species responded negatively to intra- and interspecific density, but the slope of the relationship varied among species. Data shown are for the year 1–2 transition (black points and lines) and the year 2–3 transition (grey points and lines). The best-fit lines for each type of density were calculated with the other density held constant at the mean level for each species in each year. Note the differences in x-axis ranges, with some species having no germinants when interspecific density was high (*Chorizanthe*, *Navarretia*).

the probability that a single species will exclude others. Ultimately, however, these buffering effects of stabilizing niche differences were much weaker than the drift-amplifying effects of competitive imbalances, contributing to our finding of greater compositional variation than predicted by the neutral model. Although it has been recognized that drift reduces coexistence when stabilizing mechanisms are relatively weak, this 'stochastic limit' to

coexistence has not yet been identified for most theoretical and empirical systems [4,17,39].

(b) Demographic contributions to ecological drift
Factors other than competitive differences probably also contribute to the difference between observed and predicted drift. Demographic stochasticity has several components,

only some of which could be included in our neutral simulation. Recent research has highlighted how demographic heterogeneity, variation between individuals in their innate demographic rates (rather than chance sampling of the same rates), can greatly increase demographic stochasticity if it influences individual fecundities [11,38,40]. In plant communities, large variation in plant size within species is a commonly observed example of demographic heterogeneity that results in large variation in fecundity within species [41,42]. This individual variation can arise from several factors, including early size advantages of individual plants, chance differences in clustering of plants or other microsite differences, and trait variation among species that is not consistently selected for among years [41]. Regardless of the underlying cause of demographic heterogeneity, greater variation among individuals is predicted to increase ecological drift because each demographic transition samples from a population of individuals with vital rates more different from one another.

Random differences among individuals within a population, and among patches within metacommunities, may be further exacerbated by ecological drift at other trophic levels. For example, soil and phyllosphere microbial communities are a critical component of the plant environment [43,44], and there is increasing evidence that these communities may be prone to ecological drift [43,45]. Although we were careful to homogenize soils prior to the start of our experiment, bacterial colonization occurs over weeks to months, and can cause microbial community variation at small and large spatial scales [45], which may contribute to the plant compositional variance observed here. Although it is beyond the scope of this study to test the influences of biotic drift at other trophic levels on our plant community results, mutualistic and consumptive feedbacks between species [44] suggest that further investigations in this area could prove fruitful.

(c) Among year variation and ecological drift

Temporally structured variation in biotic and abiotic conditions is predicted to alter the strength of ecological drift and stabilizing processes [14], making the effects of temporal fluctuations an important avenue for future research on ecological drift. In our experiment, the density of plants within communities increased through time (electronic supplementary material, figure S5), even as relative abundances became increasingly skewed (figure 2). Temporal shifts in climate conditions also appeared to favour different species, with population growth rates for *Navarretia* increasing in the second year but showing the opposite pattern for *Salvia* and *Chorizanthe* (figure 6). Although we do not know the long-term trajectories of these communities, these demographic changes over time suggest the operation of several mechanisms that may either amplify or limit the importance of drift in communities. First, when communities fluctuate in size through time, due to climate or other extrinsic factors [46,47], the effective size of the community is approximately the harmonic mean size over time [14,16,48]. In California, annual variation in rainfall and other conditions relevant to germination are known to drive such fluctuations, reducing the effective size of communities through time [49,50], potentially amplifying the importance of drift. Second, despite the effects of temporal environmental variation on drift via fluctuating community size, these fluctuations may also stabilize communities by favouring the coexistence of species with different temporal

niches [49,51]. For example, seed dormancy may buffer the negative effects of environmental stochasticity through the storage effect [52–54]. Although the extent to which the inter-annual shifts in species' growth rates in our experiment were driven by changing germination biology or variable seed production is unknown (figure 6), both can buffer locally rare species from extinction [54], potentially reducing the effects of drift. Even if such mechanisms operate, however, stochastic extinctions will still be more likely in small communities [16,19], as our extinction and seed bank rescue results illustrate (figures 4 and 5).

(d) Ecological drift in natural and fragmented systems

A large body of research has explored the ecological consequences of fragmentation, and it is well understood that metapopulation processes, edge effects and isolation can combine to have important impacts [24,55,56]. Our study adds to this body of work by removing edge effects and completely isolating communities, allowing us to understand the consequences of demographic variation in the absence of other factors. Importantly, we find that even with density-dependent processes that stabilize diversity, the competitive imbalances observed, along with high levels of demographic stochasticity, greatly increased extinction rates and variation in species abundances beyond what our 'most drift-dependent' community model, a neutral model, would predict. This rapid and variable change within communities has been termed 'hyperdynamic' in the fragmentation literature, and has been observed in butterfly and tree communities [55]. The finding that these effects can occur in the absence of edge effects and without the influence of variable matrix conditions suggests that better characterization of ecological drift may be key to understanding the long-term effects of fragmentation, such as losses in local diversity and creation of extinction debts [6,13,24].

The large effect of ecological drift in our study highlights the need to more formally incorporate drift into ecological theory and empirical research [19]. Relatively few models of ecological drift have focused on the effects of community size [13,14,16,19], even though this factor informs a central underlying assumption of leading spatial metapopulation models [24,57]. Similarly, several theoretical models on drift have combined competitive asymmetries and drift to study extinctions [18,36,39], yet these have not explored impacts on compositional variation, nor have they been matched with empirical research. Given that range shifts and species introductions, two of the greatest conservation challenges, both involve the dynamics of small populations, understanding the distribution of diversity in changing landscapes requires better integration of drift into ecological studies.

8

rspb.royalsocietypublishing.org Proc. R. Soc. B 284: 20170507

References

1. Gleason HA. 1917 The structure and development of the plant association. *Bull. Torrey Bot. Club* **44**, 463–481. (doi:10.2307/2479596)

2. Connor EF, Simberloff D. 1979 The assembly of species communities: chance or competition? *Ecology* **60**, 1132–1140. (doi:10.2307/1936961)

3. Segre H, Ron R, De Malach N, Henkin Z, Mandel M, Kadmon R. 2014 Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecol. Lett.* **17**, 1400–1408. (doi:10.1111/ele.12343)

4. Chesson P. 2000 Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366. (doi:10.1146/annurev.ecolsys.31.1.343)

5. Hubbell SP. 2001 *The unified neutral theory of biodiversity and biogeography.* Princeton, NJ: Princeton University Press.

6. Gilbert B, Laurance WF, Leigh EG, Nascimento HEM. 2006 Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *Am. Nat.* **168**, 304–317. (doi:10.1086/506969)

7. Gilbert B, Lechowicz MJ. 2004 Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Natl Acad. Sci. USA* **101**, 7651–7656. (doi:10.1073/pnas.0400814101)

8. Wootton JT. 2005 Field parameterization and experimental test of the neutral theory of biodiversity. *Nature* **433**, 309–312. (doi:10.1038/nature03211)

9. Kimura M. 1983 *The neutral theory of molecular evolution.* Cambridge, UK: Cambridge University Press.

10. Lande R, Engen S, Sæther B.-E. 2003 *Stochastic population dynamics in ecology and conservation.* Oxford, UK: Oxford University Press.

11. Melbourne BA, Hastings A. 2008 Extinction risk depends strongly on factors contributing to stochasticity. *Nature* **454**, 100–103. (doi:10.1038/nature06922)

12. Bartlett MS. 1960 The critical community size for measles in the united states. *J. R. Stat. Soc. Ser. A* **123**, 37–44. (doi:10.2307/2343186)

13. Orrock JL, Watling JI. 2010 Local community size mediates ecological drift and competition in metacommunities. *Proc. R. Soc. B* **277**, 2185–2191. (doi:10.1098/rspb.2009.2344)

14. Loreau M, de Mazancourt C. 2008 Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.* **172**, E48–E66. (doi:10.1086/589746)

15. de Mazancourt C *et al.* 2013 Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.* **16**, 617–625. (doi:10.1111/ele.12088)

16. Orrock JL, Fletcher RJJ. 2005 Changes in community size affect the outcome of competition. *Am. Nat.* **166**, 107–111. (doi:10.1002/ajpa)

17. Adler PB, Hillerislambers J, Levine JM. 2007 A niche for neutrality. *Ecol. Lett.* **10**, 95–104. (doi:10.1111/j.1461-0248.2006.00996.x)

18. Gravel D, Canham CD, Beaudet M, Messier C. 2006 Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.* **9**, 399–409. (doi:10.1111/j.1461-0248.2006.00884.x)

19. Vellend M. 2010 Conceptual synthesis in community ecology. *Q. Rev. Biol.* **85**, 183–206. (doi:10.1086/652373)

20. Vellend M *et al.* 2014 Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos* **123**, 1420–1430. (doi:10.1111/oik.01493)

21. Chase JM. 2010 Stochastic community assembly causes higher biodiversity in more productive environments. *Science* **328**, 1388–1391. (doi:10.1126/science.1187820)

22. Germain RM, Johnson L, Schneider S, Cottenie K, Gillis EA, MacDougall AS. 2013 Spatial variability in plant predation determines the strength of stochastic community assembly. *Am. Nat.* **182**, 169–179. (doi:10.1086/670928)

23. Levine JM, HilleRisLambers J. 2009 The importance of niches for the maintenance of species diversity. *Nature* **461**, 254–257. (doi:10.1038/nature08251)

24. Gilbert B, Levine JM. 2013 Plant invasions and extinction debts. *Proc. Natl Acad. Sci. USA* **110**, 1744–1749. (doi:10.1073/pnas.1212375110)

25. Godoy O, Levine JM. 2014 Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology* **95**, 726–736. (doi:10.1890/13-1157.1)

26. Germain RM, Gilbert B. 2014 Hidden responses to environmental variation: maternal effects reveal species niche dimensions. *Ecol. Lett.* **17**, 662–669. (doi:10.1111/ele.12267)

27. Kraft NJB, Godoy O, Levine JM. 2015 Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci. USA* **112**, 797–802. (doi:10.1073/pnas.1413650112)

28. Gilbert B, Levine JM. 2017 Ecological drift and the distribution of species diversity. Data Dryad Repository. (http://dx.doi.org/10.5061/dryad.kd3p5)

29. Wright S. 1943 Isolation by distance. *Genetics* **28**, 114–138.

30. Weir B, Cockerham C. 1984 Estimating F-statistics for the analysis of population structure. *Evolution* (NY) **38**, 1358–1370. (doi:10.2307/2408641)

31. Anderson M, Ellingsen K, McArdle B. 2006 Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* **9**, 683–693. (doi:10.1111/j.1461-0248.2006.00926.x)

32. Legendre P, De Cáceres M. 2013 Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol. Lett.* **16**, 951–963. (doi:10.1111/ele.12141)

33. Zuur A, Ieno EN, Smith GM. 2007 *Analysing ecological data.* New York, NY: Springer Science & Business Media.

34. Germain RM, Weir JT, Gilbert B. 2016 Species coexistence: macroevolutionary relationships and the contingency of historical interactions. *Proc. R. Soc. B* **283**, 20160047. (doi:10.1098/rspb.2016.0047)

35. MacArthur RA, Wilson EO. 1967 *The theory of island biogeography.* Princeton, NJ: Princeton University Press.

36. Capitán JA, Cuenda S, Alonso D. 2015 How similar can co-occurring species be in the presence of competition and ecological drift? *J. R. Soc. Interface* **12**, 20150604. (doi:10.1098/rsif.2015.0604)

37. Comita LS, Muller-Landau HC, Aguilar S, Hubbell SP. 2010 Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* **329**, 330–332. (doi:10.1126/science.1190772)

38. Hart SP, Schreiber SJ, Levine JM. 2016 How variation between individuals affects species coexistence. *Ecol. Lett.* **19**, 825–838. (doi:10.1111/ele.12618)

39. Gilbert B. 2012 Joint consequences of dispersal and niche overlap on local diversity and resource use. *J. Ecol.* **100**, 287–296. (doi:10.1111/j.1365-2745.2011.01908.x)

40. Kendall BE, Fox GA. 2003 Unstructured individual variation and demographic stochasticity. *Conserv. Biol.* **17**, 1170–1172. (doi:10.1046/j.1523-1739.2003.02411.x)

41. Weiner J. 1990 Asymmetric competition in plant populations. *Trends Ecol. Evol.* **5**, 360–364. (doi:10.1016/0169-5347(90)90095-U)

42. Freckleton RP, Watkinson AR. 2001 Asymmetric competition between plant species. *Funct. Ecol.* **15**, 615–623. (doi:10.1046/j.0269-8463.2001.00558.x)

43. Maignien L, DeForce EA, Chafee ME, Murat Eren A, Simmons SL. 2014 Ecological succession and stochastic variation in the assembly of Arabidopsis thaliana phyllosphere communities. *MBio* **5**, 1–10. (doi:10.1128/mBio.00682-13)

44. Van Der Heijden MGA, Bardgett RD, Van Straalen NM. 2008 The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* **11**, 296–310. (doi:10.1111/j.1461-0248.2007.01139.x)

45. Nemergut DR *et al.* 2013 Patterns and processes of microbial community assembly. *Microbiol. Mol. Biol. Rev.* **77**, 342–356. (doi:10.1128/MMBR.00051-12)

46. Geritz SAH, Kisdi É. 2004 On the mechanistic underpinning of discrete-time population models with complex dynamics. *J. Theor. Biol.* **228**, 261–269. (doi:10.1016/j.jtbi.2004.01.003)

47. Brännström A, Sumpter DJT. 2005 The role of competition and clustering in population dynamics. *Proc. R. Soc. B* **272**, 2065–2072. (doi:10.1098/rspb.2005.3185)

48. Otto SP, Whitlock MC. 1997 Probability of fixation in populations of changing size. *Genetics* **146**, 723–733.

49. Hobbs R, Yates S, Mooney H. 2007 Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecol. Monogr.* **77**, 545–568. (doi:10.1890/06-1530.1)

50. Suttle KB, Thomsen MA, Power ME. 2007 Species interactions reverse grassland responses to changing

9

rspb.royalsocietypublishing.org *Proc. R. Soc. B* **284**: 20170507

climate. *Science* **315**, 640–642. (doi:10.1126/science.1136401)

51. Adler PB, Drake JM. 2008 Environmental variation, stochastic extinction, and competitive coexistence. *Am. Nat.* **172**, E186–E195. (doi:10.1086/591678)

52. Dyer AR, Fenech A, Rice KJ. 2000 Accelerated seedling emergence in interspecific competition neighbourhoods. *Ecol. Lett.* **3**, 523–529. (doi:10.1046/j.1461-0248.2000.00187.x)

53. Venable DL. 2007 Bet hedging in a guild of desert annuals. *Ecology* **88**, 1086–1090. (doi:10.1890/06-1495)

54. Angert AL, Huxman TE, Chesson P, Venable DL. 2009 Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci. USA* **106**, 11 641–11 645. (doi:10.1073/pnas.0904512106)

55. Laurance WF *et al.* 2011 The fate of Amazonian forest fragments: a 32-year investigation. *Biol. Conserv.* **144**, 56–67. (doi:10.1016/j.biocon.2010.09.021)

56. Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Hermy M. 2006 Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* **87**, 542–548. (doi:10.1890/05-1182)

57. Hanski I. 1994 A practical model of metapopulation dynamics. *J. Anim. Ecol.* **63**, 151–162. (doi:10.2307/5591)

10

rspb.royalsocietypublishing.org   *Proc. R. Soc. B* **284**: 20170507

Supplementary Material

Multivariate measure of community Fst.

The weighted Fst measure (eqn. 2) can be calculated in a multivariate dispersion matrix when the data are properly transformed. By dividing all proportions in a given treatment by the square root of the denominator of eqn. (2), the distance of each community *i* from the centroid of a treatment can be calculated as:

$$\text{Multivariate distance}_i = \sqrt{\frac{\sum_{j=1}^{S}(p_{ij}-\hat{p}_j)^2}{\sum_{j=1}^{S}\hat{p}_j(1-\hat{p}_j)}} \qquad (S1)$$

Equation S1 measures the square root of each community's contribution to the weighted Fst – the average of the square of equation S1 is equal to weighted Fst (eqn. 2) for a given treatment. Equation (S1) is useful in that it can be used in a multivariate test of homogeneity of variances [1]. For our study, we use this this metric to compare to other multivariate approaches (Fig. S1) and note that it is more powerful because it conserves the sample size of the experiment but gives qualitatively identical results to those generated by eqn. 2 (Figs. 1, S2).

Alteration of the neutral model to include species differences

We incorporated species differences into an otherwise neutral model to see if including these differences would better predict the deterministic shifts in species relative abundances that we observed, and thus act as a deterministic frame for a model of ecological drift. To do so, we incorporated two types of differences that have been quantified in previous research – species specific per capita seed production, and species specific seed masses [2].

Our first model allowed species to differ in the number of seeds produced per individual, and then allowing each seed to have equal likelihood of becoming an adult in the subsequent year (as with the neutral model, we restrained the total number of adults to that seen in each plot). The mean and standard deviation of the number of seeds produced were taken from the supplementary material of [2], as their estimates were generated for the same species at the same site. In our second model, we modified seed number by the competitive effect of seed size. In particular, we used the scaling of seed size given in [3,4], where the competitive advantage was given by its relative seed size raised to the exponent 0.62.

Altering our neutral models by adding this species-specific information into our simulations produced a worse fit to the data than the neutral model. The correlation between the relative abundances of species from the simulated data and those observed in our experiment was

negative in both cases (r = -0.221 for seed number only, r = -0.215 for seed mass and seed number). The likely reason for this discrepancy is that *Vulpia,* which rapidly becomes most abundant in our experiment, did so not because of high seed production or large seed mass, but instead due to its excellent ability to tolerate competition from neighbours (Fig. 6; main article).

Supplementary Tables

Table S1: Plot diameters, edge to interior ratios and total number of replicates within experiment.

Outer diameter (cm)	Inner diameter (cm)	Area (cm²)	Number of replicates	Proportion of plot from edge at distances:			Viable seeds per species
				1.3 cm	2.5 cm	3.8 cm	
7.62	0	46	45	0.56	0.89	1.00	10
10.16	0	81	30	0.44	0.75	0.94	18
20.32	5.08	304	15	0.33	0.67	1.00	67
25.4	10.16	426	15	0.33	0.67	1.00	93
45.72	30.48	912	15	0.33	0.67	1.00	200
86.36	71.12	1885	15	0.33	0.67	1.00	413

Table S2: AIC and model rank for models predicting extinction rate that include different random effects. The column AICc weight was calculated using the AICcmodavg package in R.

model rank	df	AIC	Random effects in model* variable slope with intercept	other random intercept(s)	AICc Weight
1	7	1496.52	plot size | year * species	none	0.95
2	5	1502.441	none	species*year	0.05
3	8	1537.777	plot size | year	species	0
4	6	1553.187	none	year, species	0
5	8	1554.885	plot size | species	year	0
6	5	1845.909	none	species	0
7	5	2269.205	none	year	0
8	4	2323.233	none	none	0

*all models included plot nested within block as a random effect to account for experimental design

Table S3: AIC and model rank for models predicting rescue rate from the seedbank that include different random effects. The column AICc weight was calculated using the AICcmodavg package in R.

model rank	df	AIC	Random effects in model* variable slope with intercept	other random intercept(s)	AICc Weight
1	7	1496.52	plot size | year * species	none	0.95
2	5	1502.441	none	species*year	0.05
3	8	1537.777	plot size | year	species	0
4	6	1553.187	none	year, species	0
5	8	1554.885	plot size | species	year	0
6	5	1845.909	none	species	0
7	5	2269.205	none	year	0
8	4	2323.233	none	none	0

*all models included plot nested within block as a random effect to account for experimental design

Table S4: Significance tests of variables included in analysis of finite rates of increase. Model selection was performed by beginning with the most complex model (two 3-way interactions) and subsequently removing higher order terms that were not significant. Significance was tested with Likelihood Ratio Tests (LRT), with the probability (Pr) determined from the Chi-square test with DF degrees of freedom using the 'drop1' function. Lower order terms were not tested if they were included in a higher order interaction. The final model had the following fixed effects: species + year + interspecific density + intraspecific density + species X year + species X intraspecific density.

| Independent Variables	DF	LRT	Pr
intraspecific density X species X year	4	3.3	0.5089
interspecific density X species X year	4	2.42	0.659
intraspecific density X species	4	48.02	9.35E-10
interspecific density X species	4	1.68	0.7943
species X year	4	37.08	1.73E-07
intraspecific density X year	1	1.36	0.2435
interspecific density X year	1	0.16	0.6892
interspecific density	1	4.98	0.02564
intraspecific density	1		Not tested
year	1		Not tested
species	4		Not tested

Supplementary Figures
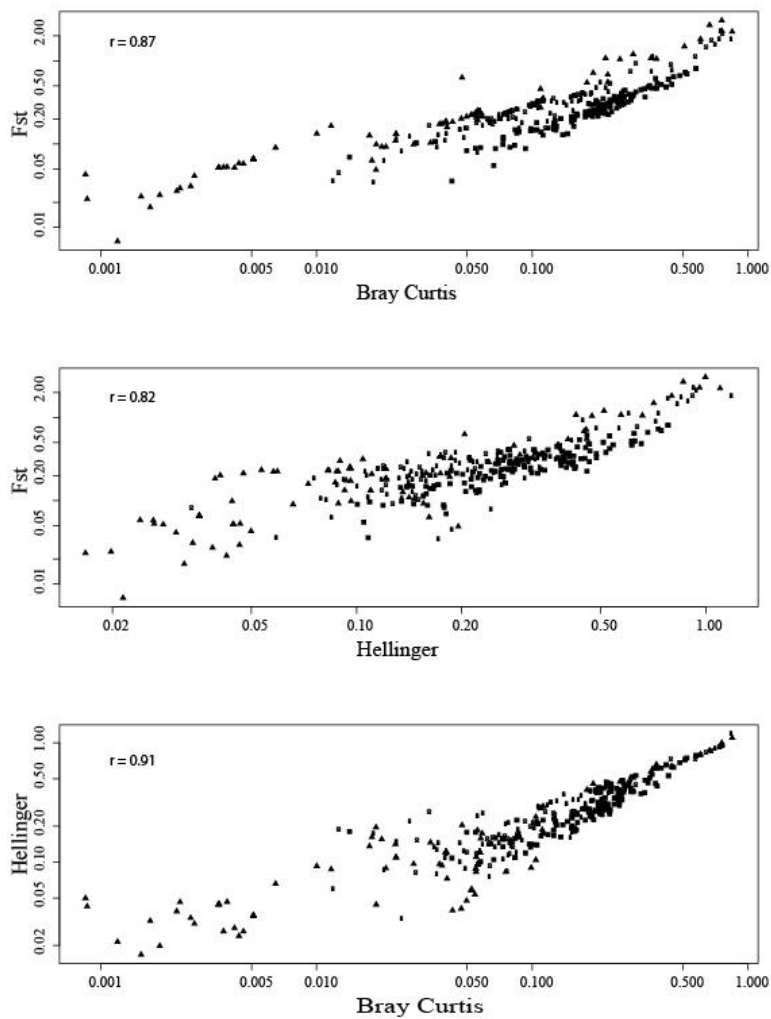
Fig. S1: Relationship between Fst (eqn. 3) and common multivariate distance metrics. The correlation coefficient reported is for log-transformed data, as presented here. Each year of data is represented by a different symbol: squares (year 1), circles (year 2) and triangles (year 3).
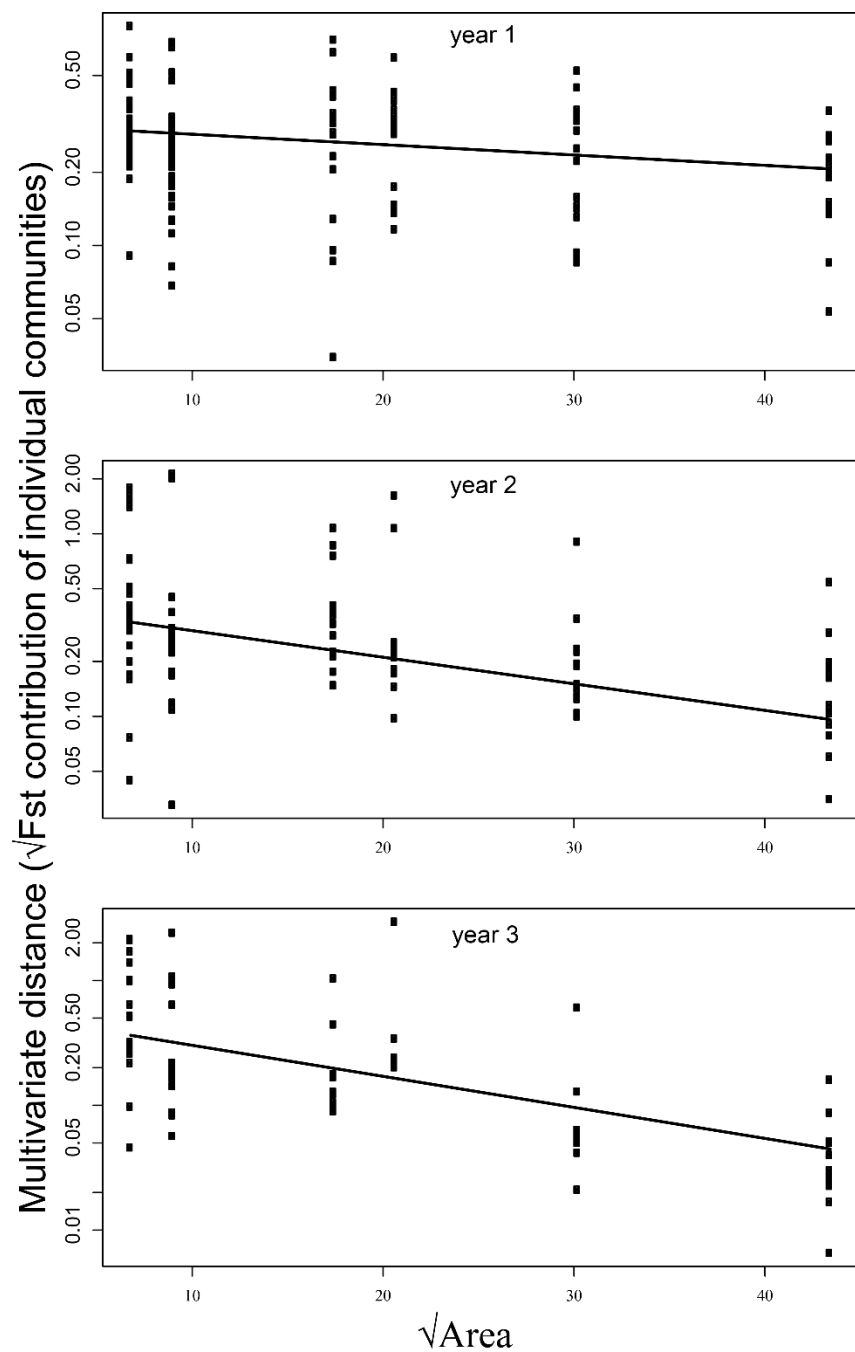
Fig. S2: The effect of community size (area) on the multivariate analogue of Fst (eqn. S1) shows a significant year x community size interaction (p<0.0001). Note the log-scaled y-axes and the differences in y-axes among years.
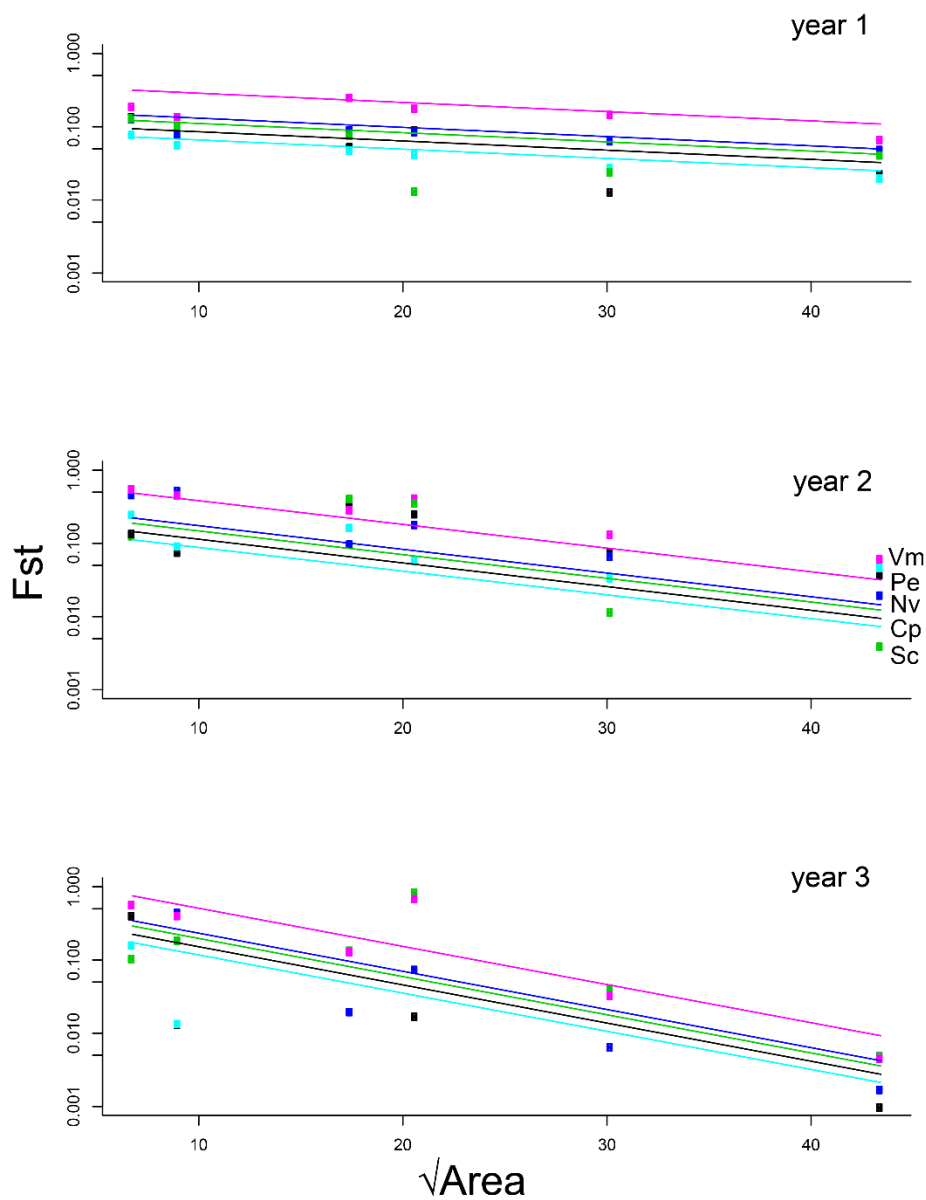
Fig. S3: Fst versus square root area calculated by year for each species (eqn. 1). Species abbreviations are given on the right side of the middle panel, and correspond to the genus (capital) and species name.
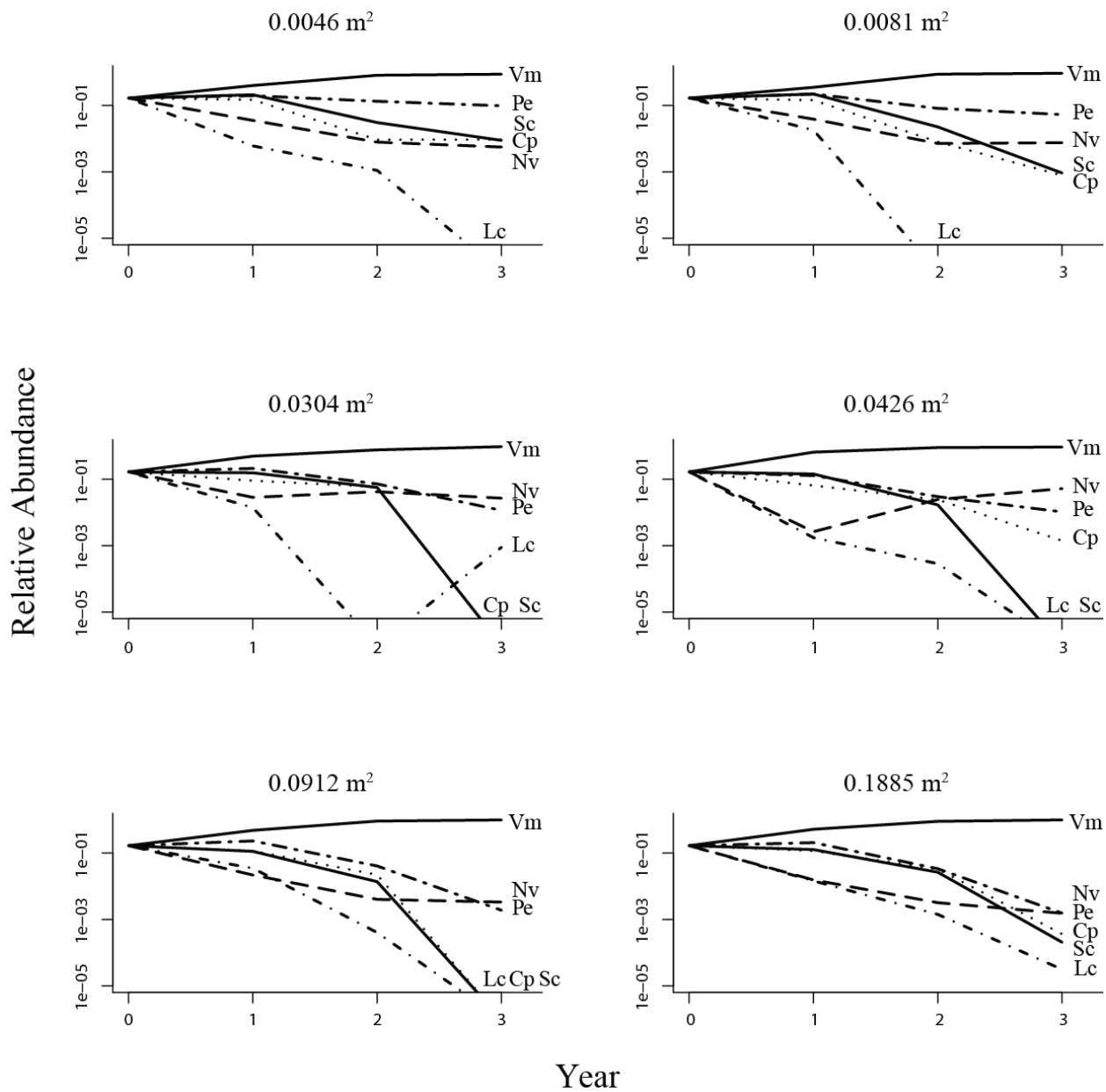
Fig. S4: Relative abundances of species over the experiment by treatment (community size in m^2). Lines dropping below 1 x 10^{-5} had apparent extinctions (i.e. no plants in a given year although seeds may still have persisted in the soil). The largest four communities had fifteen replicates, whereas the second smallest had 30 replicates and the smallest had 45 replicates.
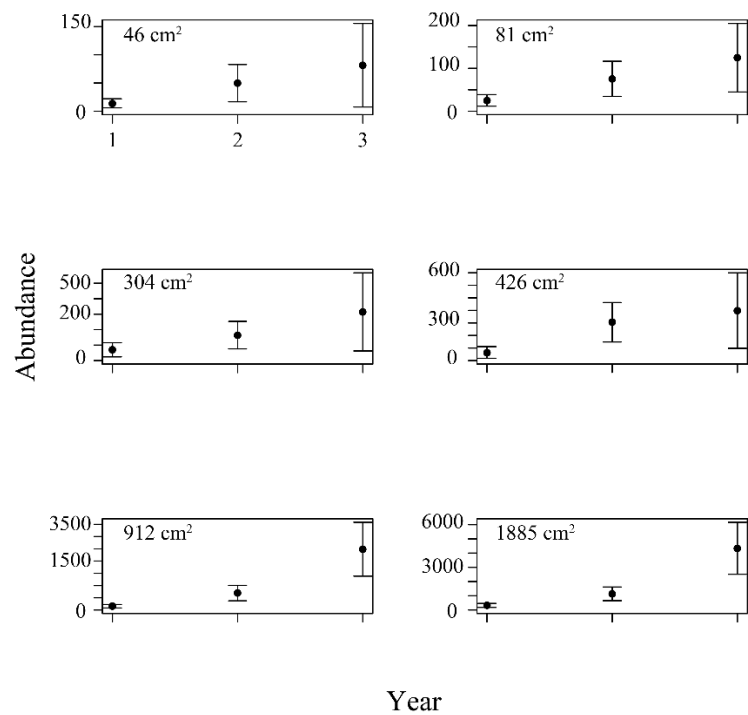
Fig. S5: Changes in abundance through time for each plot size, with error bars showing one standard deviation. Note differences in scale (y-axis) among plots of different sizes.

Fig. S6: Species richness increased with community size. Although all communities were initiated with identical densities of all species, species richness quickly declined in smaller communities. Data shown are from year three of the experiment (year two shown in main text), with points jittered vertically to better visualize the data.
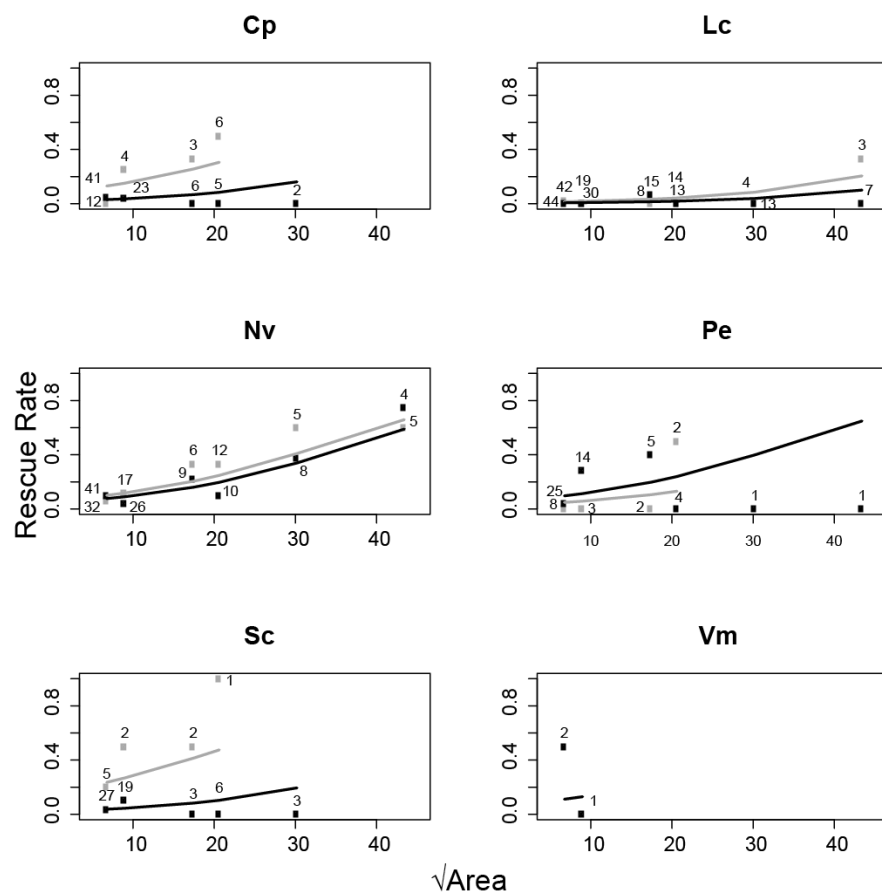
Fig. S7: Rescue rates from the seedbank for each species in the second (grey) and third (black) year of the experiment. Numbers above data points give the number of observations included for each species and year, as only plots with a species previously absent could be included.

Literature Cited

1.   Anderson, M., Ellingsen, K. & McArdle, B. 2006 Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* **9**, 683–693. (doi:10.1111/j.1461-0248.2006.00926.x)

2.   Levine, J. M. & HilleRisLambers, J. 2009 The importance of niches for the maintenance of species diversity. *Nature* **461**, 254–7. (doi:10.1038/nature08251)

3.   Levine, J. M. & Rees, M. 2002 Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *Am. Nat.* **160**, 452–67. (doi:10.1086/342073)

4.   Freckleton, R. & Watkinson, A. 2001 Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. *Ecol. Lett.* **4**, 348–357.