

Testing the roles of competition, facilitation and stochasticity on community structure in a species-rich assemblage

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Summary

1. There is an ongoing debate about whether communities are closely integrated and bound together via interactions such as competition or facilitation, or are disintegrated and dominated by chance. We still lack community-wide data on the intensities of interactions and randomness, and measurements of their impacts on community structure.

2. Using a long-term data set, we sought to measure the effects of interactions and stochasticity in structuring a highly diverse (>100 species) semi-arid grassland plant community, testing for positive and negative interactions at different stages of population growth of all species.

3. During the colonization of new patches, most species were facilitated or inhibited by several others. These opposite effects can potentially have a large effect on species abundances, but they were correlated and cancelled out at the community level. Nevertheless, competition during colonization was strong enough to cause poor competitors to have small population sizes.

4. The subsequent phase of population growth (increase and subsequent change in numbers within occupied patches) was mainly driven by intraspecific density dependence, and we found little evidence for interspecific interactions.

5. Model results showed that stochasticity and recurrent colonization of transient, favourable patches maintained diversity, keeping poor competitors from becoming extinct.

6. *Synthesis:* Our results, taken together with recent studies on tropical forests, suggest that weak interactions among established plants may be a general phenomenon, but that local interactions during colonization are important drivers of community composition. Most of the variance in species abundance in our community was explained by intraspecific competition and stochasticity, with interspecific interactions playing a minor role due to their overall weakness, interaction changes over ontogeny, and the cancellation of opposite-sign interactions when all the species in the community are considered. Despite this, some species were rare seemingly because they cannot withstand interspecific competition. Thus, to untangle the effects of interactions on community structure, future research should focus on interactions occurring at different phases of population growth and on whole communities.

Key-words: coexistence, colonization-competition trade-off, community assembly, density dependence, facilitation, intraspecific competition, interspecific interactions, model, plant population and community dynamics, positive interactions

Introduction

There has been a long-term debate about whether communities are structured by the interactions among constituent species or instead by chance and individual responses of species

to the abiotic environment. Community-level assessments of stochasticity and interactions are required to distinguish between the various models of community structure and relevant data and techniques are now beginning to emerge (Levine & HilleRisLambers 2009; Adler, Ellner & Levine 2010; Comita *et al.* 2010; Mangan *et al.* 2010). However, sufficiently detailed measurements of the quantitative effects

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of randomness and interactions on whole communities are largely lacking.

Theories of community structure have been dominated by models of resource competition on the assumption that plants of all species compete for the same limited pools of key nutrients (Tilman 1980; Chesson 2000b; Keddy 2001; Silvertown 2004; Tilman, 2007). In general, the species with the largest long-term population growth rates should outcompete the others, unless strong negative dependence on conspecific density limits their populations before competitive exclusion takes place (Chesson 2000b). Differences in resource requirements among species, that is, niche differentiation (Tilman 1980), and specialist natural enemies (e.g. Janzen-Connell effects; Chesson 2000a; Freckleton & Lewis 2006) have been frequently advocated as the mechanisms behind such species-specific negative feedbacks. Strong negative feedbacks may also arise from limited dispersal, which inflates the frequency of interactions with conspecifics and their demographic impact, regardless of their *per capita* intensity (Rees, Grubb & Kelly 1996; Turnbull *et al.* 2007).

In resource-poor communities, it has been suggested that positive interactions (frequently referred to as facilitation) may be particularly significant because established plants ameliorate the negative effects of environmental stress on their neighbours (Brooker & Callaghan 1998; Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008). Facilitation seems to be especially important during establishment, vanishing or even turning competitive during later phases of population dynamics (Miriti 2006; Valiente-Banuet and Verdú, 2008, Verdú, Jordano & Valiente-Banuet 2010). This highlights the importance of considering different life stages when interactions are studied. There is still debate about the impact of positive interactions on community structure: they seem to increase species richness in some cases (Valiente-Banuet *et al.*, 2006; Bruno, Stachowicz & Bertness 2003; Cavieres & Badano 2009), but also tend to destabilize communities and thus lead to species extinction (May 1973; Butterfield 2009).

In contrast, it has also been proposed that local communities are largely the outcome of chance, and that we should not expect interspecific competition (which is thought to be weak or unimportant; Ricklefs 2008, 2009) or niche differentiation to determine membership in the community (Hubbell 2001). According to this view, a local community is largely a draw from a larger species pool. The composition of the local community is determined by regional abundance, random extinction, colonization and dispersal events. The neutral model shows that if species are equivalent in every possible respect (interactions, dispersal, fitness, etc.), a community may be extremely diverse if speciation and immigration from the regional biota are sufficient to balance the stochastic extinction rates inherent to the model (Hubbell 2001). At small scales, these same processes still dominate. Demographic stochasticity (population variability that arises from random events such as birth or death that affect its individuals) becomes more important as fewer individuals are considered, and may result in local extinctions (Menges 1992). The re-colonization of the gaps so opened is largely determined

by chance events during dispersal and by the distance to seed donors (Hubbell 2001). Because random events drive community structuration in such models, stochastic processes are often labelled as neutral, despite the fact that neutrality more usually refers to species equivalence.

Most ecologists would agree that interactions and stochasticity occur concurrently in ecological communities. Neutrality may operate within subsets of closely related or convergent species (Leibold & McPeck 2006; Scheffer & van Nes 2006; Vergnon, Dulvy & Freckleton 2009), or among species pairs with similar fitness (equalizing mechanisms). However, increasing niche differentiation is required for coexistence to occur as asymmetries in competitive ability become greater (stabilizing mechanisms; Chesson 2000b; Adler, HilleRis-Lambers & Levine 2007). Furthermore, immigration may counteract competitive exclusion in interconnected metacommunities, reducing the degree of niche organization required for diversity maintenance (Gravel *et al.* 2006). Nevertheless, stochasticity is expected to set more restrictive conditions to coexistence in interaction-driven communities (May 1973; Tilman 2004; Adler & Drake 2008).

Empirical evidence is still insufficient to settle the conflict between these theories. Community patterns expected from theories based on interactions and stochasticity are frequently indistinguishable (Hubbell 2001; Chave, Muller-Landau & Levin 2002; Rosindell, Hubbell & Etienne 2011), so direct assessments of the effects of both mechanisms on community structure are required (Freckleton, Watkinson & Rees 2009). In contrast with the huge body of evidence from experiments that shows the potentially powerful effects of competition on individual plant performance, when the strength or demographic importance (i.e. the impact on species abundance) of interspecific interactions in plant communities have been measured in the field, often only weak effects are found (Rees, Grubb & Kelly 1996; Law, Herben & Dieckmann 1997; Freckleton *et al.* 2000; Ives *et al.* 2003; Adler *et al.* 2006; Lamb & Cahill 2008; Mutshinda, O'Hara & Woiwod 2009; Villarreal-Barajas & Martorell 2009; Adler, Ellner & Levine 2010; Comita *et al.* 2010). The reasons for this are still unclear. There are currently too few systems in which interactions have been measured *in situ*, and only a handful for which this has been done for separate stages of the life cycle.

In order to fully understand the community-level effects of interactions, several issues need to be addressed. First, the demographic importance of interactions has to be evaluated separately from the intensity of interactions via their effects on individuals in pairwise interactions (Rees, Grubb & Kelly 1996; Freckleton & Watkinson 1999, 2001b; Freckleton, Watkinson & Rees 2009; Rees, Childs & Freckleton 2012). Secondly, the model should allow for the negative and positive components of interactions to act simultaneously (Brooker & Callaghan 1998; Brooker *et al.* 2008). Thirdly, it is necessary to look at how the effects of interactions manifest at different stages of population growth, as interaction shifts seem to be common (Miriti 2006; Valiente-Banuet and Verdú, 2008, Verdú, Jordano & Valiente-Banuet 2010). Fourthly, stochasticity needs to be acknowledged, as it may affect substantially the

outcome of interactions (Tilman 2004; Adler & Drake 2008). An appropriate structure that accounts for different forms of randomness (e.g. demographic stochasticity, dispersal and colonization probabilities) is required in the model for it to be realistic and informative (Clark 2009). Finally, data are required that encompass all species within a community, or else a random sample. The selection of species because they appear a priori to interact strongly may induce a considerable bias in our perception of how interactions structure communities.

In this study, we assess the role of interactions and stochasticity in structuring an ecological community, focusing on species abundances and not just their presence or absence. For the first time, we analyse all the pairwise interactions (positive and negative) that drive two phases of population growth: the recruitment phase, in which areas previously devoid of the species are colonized, and the population growth phase in which there are changes in the numbers of established plants. Stochasticity during colonization (non-neutral random colonization, i.e. with species-specific probabilities) and population growth (demographic stochasticity) was also assessed. Finally, we measure the degree to which population sizes are affected by interactions and stochasticity. Our overall aim was to document the intensity and demographic importance of interactions and stochasticity in terms of *per capita* effects, and to set them in a community context. We discuss how these results may then relate to different theories of coexistence.

Materials and methods

DATA

Data come from a semi-arid grassland in Concepción Buenavista, Oaxaca, Southern Mexico. Annual precipitation is 579 mm and mean temperature 16.3 °C. Soil is very shallow (depth <20 cm) and develops over a continuous andesitic-tuft pan. The community is very rich, with about 200 species, comprising perennial, annual and facultatively annual taxa in more or less equal proportions. The vast majority of species are herbaceous and minute (≤ 5 cm in height and diameter, with the exception of a few tussocks and shrubs which may cover an area up to 0.15 m in diameter but are usually much smaller). As a result, a large number of individuals (up to 135) and species (up to 22) can be found in a 0.1×0.1 m area.

In four 1 ha sites, we randomly placed 16 1×1 m quadrats. We recorded the number of individuals of all species in 20 randomly chosen 0.1×0.1 m squares in each quadrat. This sampling unit was selected because it probably reflects the scale over which interactions occur given the extremely small sizes of plants in this grassland (Freckleton & Watkinson 2001b; Villareal-Barajas & Martorell 2009). Only presence-absence was recorded for three highly clonal species (*Bouteloua polymorpha* and *Tripogon spicatus*). The squares were followed over seven annual transitions (2001–2008). In total, 103 species occurred in our squares, so we have 1.05×10^6 abundance records in our data base.

POPULATION MODEL

The structure of a community can be defined as the composition and abundances of the species that co-occur. In this sense, understanding

the effects of interactions and stochasticity on community structure arises from the analysis of how these factors affect the population sizes of the community's constituent species. To do so, we developed a discrete-time model that projects population size for each species in the community at time $t + 1$ from the population sizes of all species at time t in 0.1×0.1 m squares. The model was selected from a large set of alternatives using the Akaike Information Criterion (AIC; See Appendix S1).

The model considers five different factors that affect population dynamics:

(i) Interactions: these change over the life cycle (Miriti 2006; Valiente-Banuet and Verdú, 2008; Verdú, Jordano & Valiente-Banuet 2010), so we modelled separately the data from squares where the focal species was present or absent at time t . In herbs, once the plant becomes established, survival is relatively independent of the density of con- or heterospecific neighbours; in contrast, density dependence is presumed to mainly affect growth and fecundity of established individuals (Watkinson, 1980; Crawley 2007), and thus population size at time $t + 1$. Therefore, the colonization of empty squares should depend heavily on the outcome of interactions occurring during germination and early growth, while the population growth in occupied squares reflect the interactions over the whole life cycle.

(ii) Positive interactions: Since our study site is a stressful, semi-arid environment, facilitation can be expected to play an important role (Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008). However, even positive interactions may have a negative component (Brooker & Callaghan 1998; Brooker *et al.* 2008), so our model contains separate terms for both positive and negative interactions.

(iii) Annual stochasticity: Interannual variability in rainfall plays an important role in dryland-plant population dynamics (Schwinning *et al.* 2004).

(iv) Dispersal: Squares are linked through seed dispersal. Population density in the neighbourhood of any square and the distance that seeds may travel are expected to determine the chances of immigration. Dispersal limitation is central to the neutral theory (Hubbell 2001), and failure to include it in the model may result in biased interaction coefficients (Freckleton & Watkinson 2000).

(v) Intra-annual stochasticity: Colonization and population growth are subject to stochasticity. Seeds move randomly during dispersal, and established plants are subject to events such as predation, disturbances or pollinator visits that result in stochasticity.

Colonization probability and number of colonizers were modelled as functions of the densities of the interacting species at time $t + 1$. Densities at time $t + 1$ (rather than t) were used because germination and survival of seedlings are enhanced by nurse plants in semi-arid ecosystems (Valiente-Banuet *et al.*, 1991, Flores & Jurado 2003), and it would be those plants present at the time of germination that act as nurses or inhibit seedlings. To account for stochasticity, the colonization probability of the focal species j ($P_{j,t+1}$) was assumed to follow a binomial distribution with the following mean:

$$P_{j,t+1} = \frac{\exp(y_{c,k} + \sum_{i \neq j} \gamma_i N_{i,t+1} + m_c \bar{N}_t)}{1 + \exp(y_{c,k} + \sum_{i \neq j} \gamma_i N_{i,t+1} + m_c \bar{N}_t)} \quad \text{eqn 1}$$

$y_{c,k}$ is a year-specific term determining the effect of the k th year on colonization, $N_{i,t}$ is the density of the interacting species i at time t , γ_i is the effect of species i on species j (i.e. interaction intensity) during colonization, m_c determines the intensity of dispersal and \bar{N}_t is the mean density of individuals of the focal species in the neighbouring squares in the same 1×1 m quadrat weighed by the reciprocal of the Euclidean distance between them and the focal square. Such weighting was included because distant squares are expected to

contribute fewer seeds to the focal squares (Nathan 2001, see Appendix S1 for further details). Given that a square was colonized, the number of colonizers $N_{j,t+1}$ was modelled as follows:

$$N_{j,t+1} = \exp(y_{n,k} + \sum_{i \neq j} \delta_i N_{i,t+1} + m_n \bar{N}_t) \quad \text{eqn 2}$$

This number was modelled using a zero-truncated Poisson distribution, and $y_{n,k}$, δ_i and m_n are year specific, interaction and dispersal coefficients, respectively, and thus are equivalent to $y_{c,k}$, γ_i and m_c in eqn 1.

The dynamics in occupied squares were modelled by modifying the Akçakaya & Ferson (1990) population-growth model for Allee effects in order to accommodate facilitation and interactions between several species:

$$N_{j,t+1} = (1 - m_j) N_{j,t} \frac{\lambda_{j,k} \prod_{i \neq j} (1 + N_{i,t})^{\beta_i}}{1 + \sum_i \alpha_i N_{i,t}} + m_j \bar{N}_{j,t} \frac{\lambda_{j,k}}{1 + \alpha_j \bar{N}_{j,t}} \quad \text{eqn 3}$$

m_j is the dispersal rate of the focal species, $\lambda_{j,k}$ is the population growth rate during the k th year in the absence of interactions, and α_i and β_i are, respectively, a measure of competition and facilitation of species i on the focal species. Large values of these parameters imply high interaction intensity. In this equation, a species may have positive and negative effects on the other simultaneously but competition will dominate at high densities (see Appendix S1). This prevents the occurrence of ‘orgies of mutual benefaction’ that drive population sizes to infinity (May 1981).

The first term on the left hand side of eqn 3 describes the ‘local’ dynamics in a 0.1×0.1 m square as it includes only the proportion $1 - m_j$ individuals that do not undergo dispersal. Note that eqn 3 includes intraspecific competition and that we assumed that there is no intraspecific facilitation. The right-hand part of the sum accounts for immigrants from neighbouring squares. No interspecific effects were included in this term as preliminary tests showed that this had a negligible effect on parameter estimation, but frequently precluded convergence in the fitting procedure. Demographic stochasticity was included by assuming a negative binomial distribution of recruits about the mean predicted by eqn 3 with dispersion parameter d_j for species j . Finally, for species for which only presence–absence data were available, the probability of persistence (1–extinction probability) was modelled using an equation with the same form as (1), but with different parameters (See Appendix S1). Cactus and shrub densities per square were so low that they were also analysed as presence–absence data.

MODEL FITTING

Model parameters were estimated from the dynamics of the number of individuals of each species observed in each square (Rees, Grubb & Kelly 1996; Freckleton & Watkinson 2001b). All the species were included in the analyses. The 18 most common species (350 or more occurrences, mean $n = 731$) were treated individually, and the remainder was pooled into nine functional groups depending on their possible responses to the environment (drought and grazing) and effects on neighbours. Accounting for the response to drought is important because most facilitative effects in dry lands occur through stress amelioration and thus depend on tolerance (Flores & Jurado 2003; Brooker *et al.* 2008), so functional groups separate succulent and non-succulent plants. Grazing modifies competitive relationships (Le Bagousse-Pinguet, Gross & Straile 2012) and should increase demographic stochasticity by removing individuals and opening gaps for colonization. Tall and erect plants are more frequently eaten than

small or prostrate ones, and hemicryptophytes are specially resistant to grazing (Díaz *et al.* 2007). Architectural traits affect interactions among plants, as those that have greater basal areas usually have a greater impact on their neighbours (Freckleton & Watkinson 2001a) or plants that develop canopies may facilitate seedlings of other species (Valiente-Banuet *et al.* 1991; Flores & Jurado 2003; Leger & Espeland 2010).

We recognized three groups of succulents: cacti (stem succulents), leaf succulents and bulb rosettes (rosette plants with underground succulent bulbs and no above-ground tissue during the dry season). Hemicryptophytes include solitary graminoids (small solitary rosettes in the Poaceae and Cyperaceae) and tussocks (which are taller and have large basal areas). Small plants unlikely to be grazed comprise vines (diffuse prostrate plants), mats (compact prostrate plants forming dense plates), while erect plants prone to grazing were classified either as shrubs or erect forbs. The last two groups, as well as solitary graminoids, tussocks and bulb rosettes form canopies that project shades and thus may facilitate their neighbours. Pooling reduced the data set size to 276 480 records. For simplicity, we will refer to the groups of pooled taxa (e.g. ‘rare erect forbs’) as species, unless stated otherwise.

Equation 1 was fitted to the data using binary regression via procedure glm in R (R Development Core Team 2009). Only squares for which $\bar{N}_t > 0$ were used in this analysis (mean $n = 2562$). The same was done for persistence probability in species with presence–absence data (mean $n = 709$). Equations 2 and 3 were fitted using ADMB (Fournier *et al.* 2012). The parameters for eqn 2 were obtained through maximum likelihood, but Markov-Chain Monte Carlo was required for equation (3) due to the complexity of the likelihood surface (Bolker 2007).

DEMOGRAPHIC IMPORTANCE OF THE INTERACTIONS

In order to assess the joint net effect of the interactions, we simulated the changes in population size of focal species over time. We generated a sequence of 100 years by randomly and independently choosing one of the seven observed transitions at a time. The densities of all interacting species, with the exception of that of the focal species, and the coefficients λ_c , λ_n and λ were set to those observed in each year. The number of individuals of the focal species at time $t + 1$ was estimated for each 10×10 cm square. If the square had no individuals of the focal species at time t , we used eqn 1 to determine if it was colonized, and the number of individuals was obtained from eqn 2. If the square was occupied at time t , we used eqn 3 to predict the numbers at time $t + 1$. Equations (1–3) provide mean values, to which stochasticity was incorporated via binomial, zero-truncated Poisson and negative binomial distributions respectively (see Model fitting). Extinctions may occur in a square due to the stochasticity related to eqn 3. For each species, 20 series of 100 years were simulated.

In order to measure the relative demographic importance of positive, negative or the combination of all interspecific interactions, the previous model was run again setting the negative, positive or all the interaction coefficients to zero. The intraspecific competition (α_j) and dispersal coefficients were always set to their estimated values.

We measured the demographic importance (I_n) of the different interactions in terms of their impact on population densities. This was measured by dividing the density predicted by each model by that predicted without interspecific interactions. As a measure of the effect that competition or facilitation have on the actual community, their importance was also measured with respect to the model with all interactions by removing the respective interaction. Thus, we

measured the importance of interspecific competition for density, I_c , as follows:

$$I_c = \frac{\text{population density without competition}}{\text{population density with all interactions}}$$

The demographic importance of facilitation for population densities, I_f , was similarly defined as follows:

$$I_f = \frac{\text{population density with all interactions}}{\text{population density without facilitation}}$$

Note that both measures increase as the effect of the respective interaction increases. Although some authors describe such measures as confusing (e.g. Brooker *et al.* in press), the interpretation is quite simple: a value of one indicates that there is no impact of interactions; values >1 indicate that there are effects, for example, a value of two implies that there is a doubling of population size by removing competition (importance of competition) or through the presence of facilitators (importance of facilitation).

To assess the effects of stochasticity, a final set of models was run. All interspecific interaction coefficients were set to zero. In occupied squares, the removal of demographic stochasticity precludes extinctions because eqn 3 can only approach zero asymptotically. In the absence of randomness, the expected number of colonizers in a square equals $P_{j,t+1} \times N_{j,t+1}$ (see eqns 1–2). As this product is always different from zero and no extinctions occur, all squares would be immediately colonized and inordinate increase in population sizes would follow. To circumvent this rather uninteresting and uninformative result, and to compensate for the lack of local extinctions, we did not allow any new squares to be colonized. Individuals that undergo dispersal were distributed equally among all occupied squares to avoid loss into squares that can no longer be colonized. Such loss would lower population sizes as an artefact of suppressed colonization. Thus, eqn (3) was modified

$$N_{j,t+1,p} = (1 - m_j)N_{j,t,p} \frac{\lambda_{j,k}}{1 + \alpha_j N_{j,t,p}} + m_j \frac{\sum_{s \neq p}^s N_{j,t,s} \frac{\lambda_{j,k}}{1 + \alpha_j N_{j,t,s}}}{S - 1}$$

At the start of each simulation, one randomly chosen year was selected and the initial densities were set to those observed in that year. Population densities were recorded after 100 iterations, and averaged over 1000 simulations. The importance of stochasticity was measured as follows:

$$I_s = \frac{\text{Density without stochasticity and interspecific interactions}}{\text{Density without interspecific interactions}}$$

Results

INTERACTION INTENSITY

A large number of intense positive and negative interactions were detected during the colonization of 0.1×0.1 m squares. Positive interactions were more frequent than negative ones during colonization. 20.8% of the standardized interaction coefficients for the colonization probability were found to be significantly different from zero. This was significantly more than the 5% expected by chance indicating a departure from random (6.1% were negative, $P < 0.001$, and 14.7% were positive, $P < 0.001$), while for the number of colonizers 25.5% of coefficients were statistically significant (negative: 11.6%, $P < 0.001$; positive: 13.9%, $P < 0.001$).

In contrast, the number of interspecific interactions detected for squares that were already occupied by the focal species was dramatically lower, and nearly no positive interactions were found. Intraspecific competition was consistently the most intense interaction determining population growth in occupied squares (Fig. 1; interaction coefficients are reported in Appendix S2).

The effect that species exerted on their neighbours was found to vary between functional groups (Fig. 2 and Table 1). Prostrate species that cover large areas (mats) had the largest proportion of species acting as competitors, reducing the probability and number of colonizers. Most of the species with growth forms that are characterized by forming above-ground canopies that project shade (erect forbs, solitary graminoids, bulb rosettes, tussocks and shrubs) exerted significantly more positive effects on their neighbours than expected by chance, both in terms of colonization probability and the number of colonizers (Table 1). Most of the few facilitative effects detected in occupied squares were still exerted by erect forbs. However, most of the interactions occurring during colonization became competitive or negligible once the focal species was established (Fig. 1).

We found no difference in the frequency of positive and negative coefficients when comparing within and between functional-group interactions, regardless of whether coefficients were measured during colonization or population growth (Fisher's exact test). The differences between the mean intensities of the interactions within and between functional groups were not significant, except for colonization probability. For this variable, the within group interactions were more negative among species that belong to the same functional group (mean interaction coefficient = -0.083) than among species from different groups (-0.039 , Mann–Whitney U -test $z = 4.176$, $P < 0.001$).

Despite being statistically significant, most of the interactions taking place during colonization were weak. With the exception of a few species that compete strongly with each other, interspecific effects were rarely symmetric (Fig. 3a). One would expect that if the effect of species i on species j was strong (e.g. that species i was a superior competitor over species j) then, reciprocally, the effect of species j on species i should be weak. However, this asymmetry of interactions is not evident in Fig. 2a, regardless of whether effects on colonization or population growth were considered.

Two-thirds of the pairwise interactions that took place during colonization were weak for both species involved, with most of the remaining interactions being either commensalistic (+/0) or ammensalistic (–/0). Competitive (–/–), mutualistic (+/+) or parasitic (+/–) were very infrequent (Fig. 3b).

DEMOGRAPHIC IMPORTANCE OF INTERACTIONS AND STOCHASTICITY

When the interactions occurring during colonization and in occupied squares were combined to simulate population dynamics, our model was able to reproduce community structure remarkably well. The complete model including all

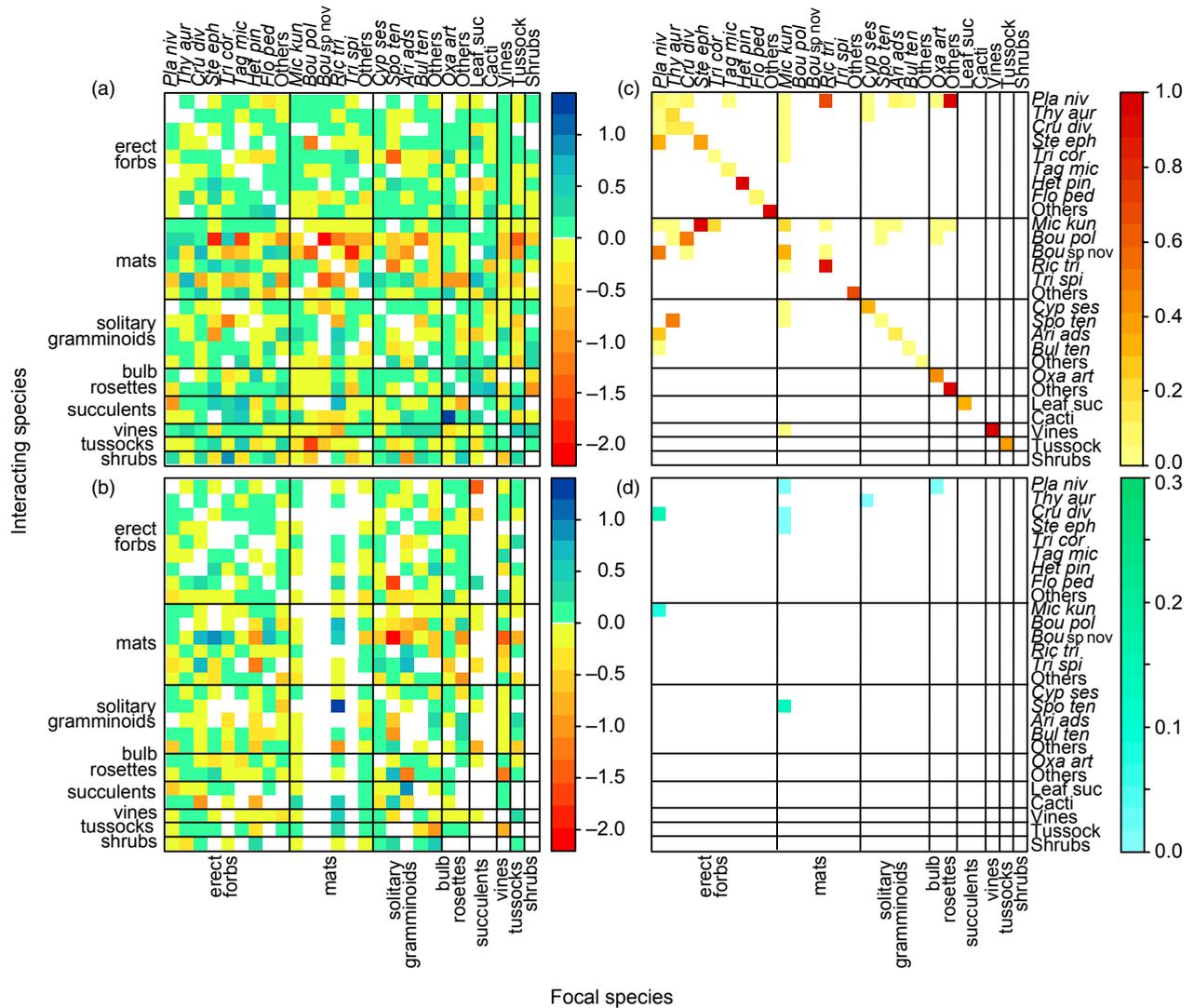


Fig. 1. Per capita interaction coefficients for pairs of species during colonization (left column; (a): Interactions affecting the colonization probability. (b): Interactions affecting the number of colonizers) and in occupied squares (right column; (c): Competition coefficients. (d): Facilitation coefficients). White squares correspond to interaction coefficients that were negligible or set to zero due to lack of convergence. Species and groups of rare species are arranged according to functional group (left and bottom labels, black lines). See Appendix S2 for species names (right and top labels).

Table 1. Fraction of the species in each functional group that exerted significantly more significant positive or negative interactions than expected by chance

Species	Colonization probability		Number of colonizers	
	Negative	Positive	Negative	Positive
Erect forbs	–	0.89	0.33	0.89
Mats	0.50	0.50	0.67	0.33
Solitary gramminoids	–	0.80	0.17	0.33
Bulb rosettes	–	1.00	0.50	1.00
Succulents	–	–	0.50	0.50
Vines	–	1.00	–	1.00
Tussocks	–	1.00	–	–
Shrubs	–	1.00	–	–

intra- and interspecific interactions, dispersal and demographic stochasticity was able to explain 71.1% of the variation in population sizes among species (Fig. 4a). However, after removing interspecific interactions the model still accounted for 57.0% of the variation in population sizes (Fig. 4b). When all interactions were included in the model, population sizes were at most doubled or halved, but far more frequently the changes were much smaller (leftmost box in Fig. 5). Nevertheless, when positive and negative interactions are analysed separately, their effects on population size were found to be much larger (up to a 20-fold change). Interactions taking place during the colonization phase were responsible for most of that variation (Fig. 5).

Rare taxa (i.e. those with the lowest densities) were more affected by interspecific competition (Spearman correlation between observed densities and competition importance I_c :

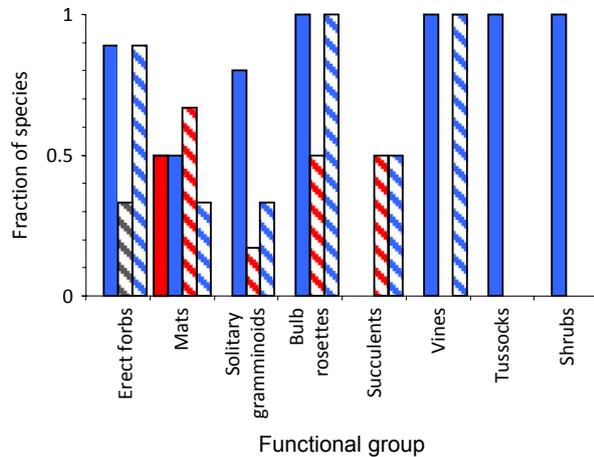


Fig. 2. Fraction of the species in each functional group that exerted negative (dark grey) or positive (light grey) interactions significantly more frequently than expected by chance. Solid bars correspond to effects on colonization probability, and cross-hatched bars to effects on the number of colonizers.

$\rho = -0.666$, $P = 0.001$; Fig. 6a). No correlation was found between density and facilitation (correlation between observed densities and facilitation importance I_f ; $\rho = -0.141$, $P = 0.481$), but there was a significant trend for rare species to suffer reductions in size and common ones to increase when all interactions are considered in the model (correlation between observed densities and importance of all interactions I_n ; $\rho = 0.551$, $P = 0.003$; Fig. 6b). The demographic importances of facilitation and competition were also correlated (correlation between I_c and I_f ; $\rho = 0.589$, $P = 0.006$; Fig. 6c).

When stochasticity and interspecific interactions were removed from the model, a further decrease of 0.03 in the R^2 value of the model compared with that of the model with only intraspecific interactions and demographic stochasticity (Fig. 4c). Nevertheless, the estimated population sizes were systematically lower for all species (mean reduction: 46.9%, range: 9.3–99.6%) with only one exception. Reductions were greater for rare species (correlation between observed densities and stochasticity importance I_n ; $\rho = 0.8836$, $P < 0.001$; Fig. 6d), so many of them became quasi-extinct (Fig. 4c). To discard any possible bias, all the correlation analyses were repeated without the sets of pooled species. All tests became more significant, except that for density- I_n , which had a $P = 0.320$.

Discussion

Studies of communities ranging from tropical rain forests to sand dunes are beginning to yield remarkably similar results in terms of the effects of interactions and stochasticity on species composition and population growth (Rees, Grubb & Kelly 1996; Law, Herben & Dieckmann 1997; Comita *et al.* 2010; Johnson *et al.* 2012). Among these shared properties, our analyses highlight a number of key outcomes: (i) Intraspecific competition is the main driver of local population

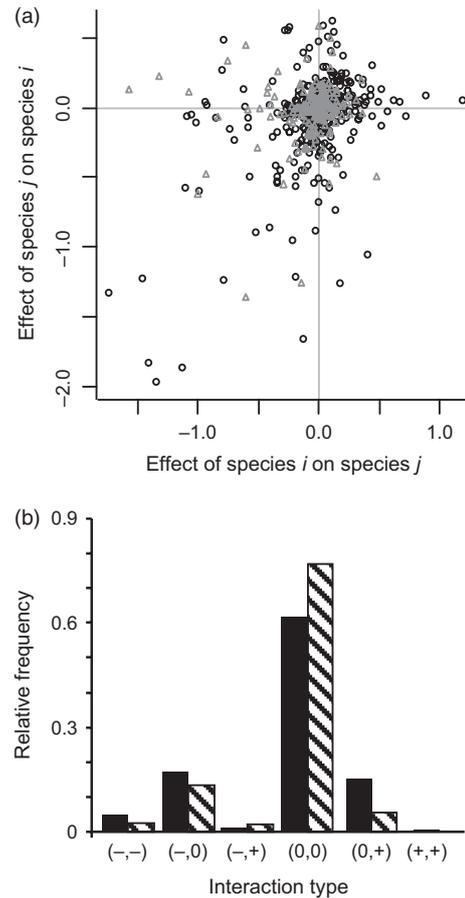


Fig. 3. Pairwise interactions during colonization. (a): Reciprocal interaction coefficients for all the possible pairs of species i, j (b): Relative frequency of interaction types. Interaction coefficients were classified as “0” if smaller than 0.2, but changing this boundary had little effect on the predominance of weak interactions shown in panel B (Appendix S3). Triangles and solid bars: Interactions affecting colonization probability. Circles and cross-hatched bars: Interactions affecting the number of colonizers.

growth once individuals are established, as expected by niche-differentiation models. (ii) Interactions play a role in the initial stage of local population growth, with both positive and negative effects of species on each other. (iii) Competition during this stage sets limits to population size. (iv) Interaction coefficients show little pairwise structure with the result that $+/+$ and $-/-$ interactions are exceptionally rare and $0/0$ interactions dominate. (v) Stochastic events occurring at small scales promote diversity.

INTRASPECIFIC EFFECTS

Theory states that differentiation among species is required for long term, stable coexistence (Chesson 2000b). The signature of differentiation is typically stronger intraspecific density dependence compared to interspecific effects (Chesson 2000b; Levine & HilleRisLambers 2009). Several recent papers have found evidence of such pattern (e.g. Turnbull, Manley & Rees 2005; Adler *et al.* 2006; Levine & HilleRisLambers 2009; Adler, Ellner & Levine 2010). Our results also show that once

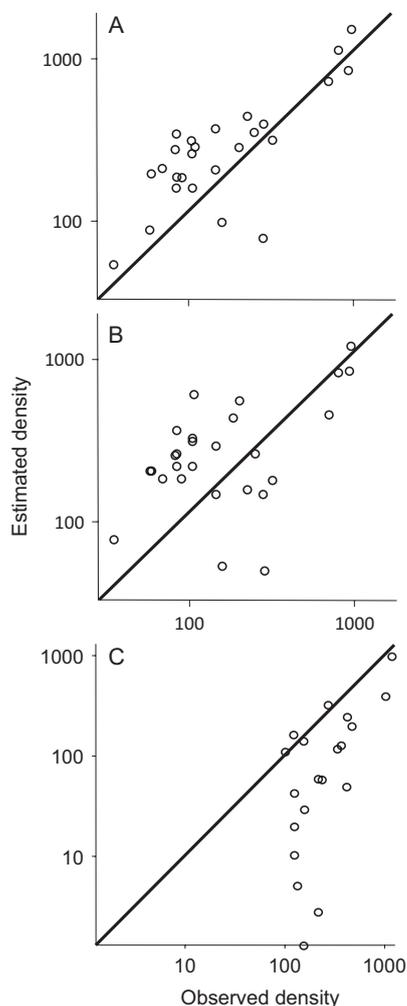


Fig. 4. Observed and predicted population sizes using different models. (a): Populations sizes predicted by a model with all interactions and stochasticity. (b): Populations sizes predicted by a model with intraspecific competition and stochasticity. (c): Populations sizes predicted by a model with intraspecific competition only.

a species becomes established, strong negative density dependence drives population dynamics. It has been suggested that rare taxa are more likely to exhibit neutral dynamics (Turnbull, Manley & Rees 2005), but stronger intra than interspecific interactions (see *per capita* interaction coefficients in Fig. 1c) were also found among low abundance species. It is impossible to tell whether the strong coefficients for the pooled species were due to inter- or intraspecific interactions. However, given that these taxa are very infrequent, it seems unlikely that interspecific encounters contribute significantly to the estimated interaction coefficient.

It has been suggested that strong self-limitation is needed for rare species to persist in a community (Yenni, Adler & Ernest 2011). This is because if a species is rare due to intraspecific competition, a very steep increase in population growth rate as the density diminishes is required to prevent extinction. Although there is evidence for this phenomenon in nature (Yenni, Adler & Ernest 2011), the opposite pattern, that is, positive density dependence in rare species, has also been

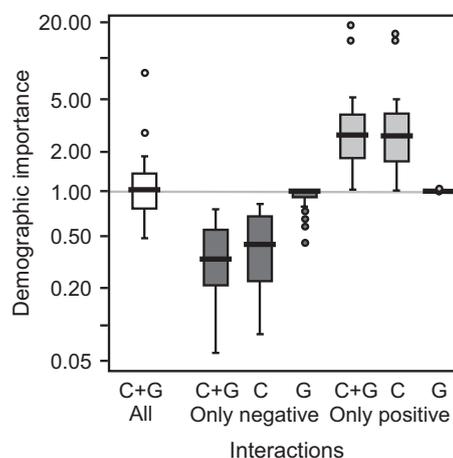


Fig. 5. Demographic importance of interactions during different phases of population growth: colonization (C), growth in occupied patches (G) or both (C+G). Importance was estimated as the ratio of population size affected by interactions to the size expected if only intraspecific interactions and stochasticity are included in the model. White: Importance of all the interactions combined. Dark grey: Importance of negative interactions. Light grey: Importance of positive interactions.

observed (Levine & HilleRisLambers 2009). We found evidence for greater self-limitation in rare species. They showed the strongest intraspecific competition (Fig. 1c), and became nearly extinct when stochasticity and dispersal were removed. It would seem that negative density dependence is so strong in these species that once a patch is occupied, dispersal to new sites is required to avoid extinction. Most of these species occupied any given square for very short periods of time (1–2 year), typically experiencing a local population burst before becoming locally extinct. Bursts may cause species-specific nutrient depletion in the soil or the accumulation of specialized natural enemies (i.e. Janzen–Connell effects; Ehrenfeld, Ravit & Elgersma 2005; Kulmatiski *et al.* 2008) that lead in turn to local extinction. Such plant–soil feedbacks are strongest in annual grasses and forbs (Kulmatiski *et al.* 2008), which were the species that suffered the most when we precluded dispersal. Negative plant–soil feedbacks mediated by pathogens are known to regulate population sizes in many communities (Freckleton & Lewis 2006; Mangan *et al.* 2010; Johnson *et al.* 2012), and have been reported for several grassland species (Ehrenfeld, Ravit & Elgersma 2005; Casper *et al.* 2008; Petermann *et al.* 2008).

INTERSPECIFIC EFFECTS

The frequency of interspecific interactions among established populations may be underestimated in Fig. 1, as we may not have had enough statistical power to detect some of them. For 12% of the species pairs we had <20 co-occurrences in the data set (3% had <10 co-occurrences, the minimum number for interaction intensity estimation, Freckleton & Watkinson 2001b; See Appendix S1). Nevertheless, the high proportion of very weak interactions found in larger data sets (species close to the top-left corner of graphs in Fig. 1c) sug-

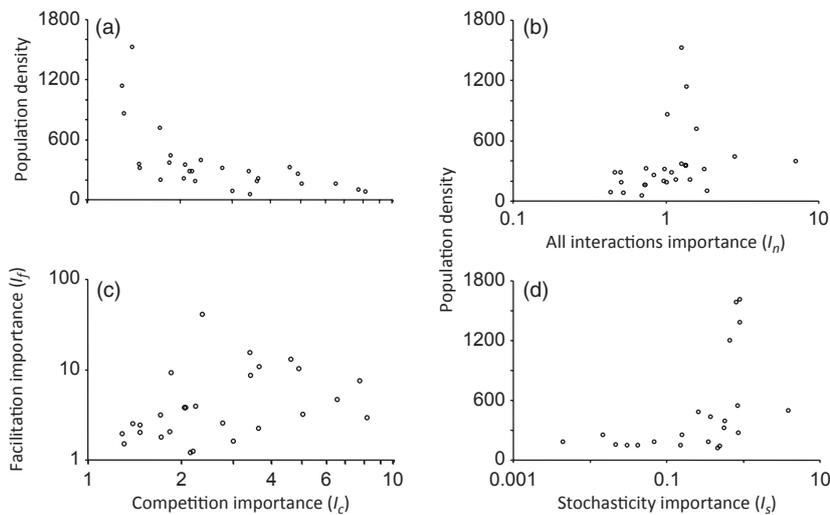


Fig. 6. Relationships between the importance of different interactions, stochasticity importance and population densities. All the shown relations are significant (Spearman's ρ , $P < 0.05$).

gests that many of the interactions that we may have missed are likely to be weak as well. Moreover, if species do not co-occur frequently, their interaction would not be expected to have a significant effect on community structure.

Although they were weak overall, interspecific interactions did occur in the initial stages of population growth and affected community structure. It seems that, from the point of view of a colonist, the rest of the community acts as a physical matrix within which it attempts to establish. The mechanisms for both positive and negative effects of different species on colonizers are straightforward to envisage. Negative interactions arise when one species occupies space prohibiting another species from establishing, as it happens with mats, but positive interactions can arise when, for example, nurse plants create a microclimate that small seeds and seedlings can recruit into. Drylands are the ecosystem in which nurse-protégé interactions are most frequent due to shading that ameliorates temperature extremes and increases water availability (Valiente-Banuet *et al.* 1991; Flores & Jurado 2003). Such effects have also been documented in our study system (Vergnon, Dulvy & Freckleton 2009). Species such as erect forbs or solitary graminoids have a reduced basal area, thus pre-empting a small area, but produce shade that may ameliorate stress (Fayolle, Violle & Navas 2009). The effects of species on each other are thus likely to be primarily through habitat modification.

In recent studies, it has been found that competition during colonization sets limits to population size either by direct competition between conspecific seedlings or because of apparent competition with the mother plant mediated by natural enemies (Comita *et al.* 2010; Mangan *et al.* 2010; Johnson *et al.* 2012). In our system, rare species were also the ones most affected interspecific competition (Fig. 6a), whose demographic importance was largest during colonization (Fig. 5). This provides evidence in favour of the idea that interspecific interactions do play a role in structuring communities.

Nevertheless, these observations beg the question of why local-scale interspecific interactions should have a relatively small effect at the population level. This paradox is at least

partially solved by our approach, which bridges the gap between individuals and the community. It shows that dramatic changes in population sizes may be observed in removal experiments if the right species are suppressed (see, for instance, the large impact of competitive release in the light-grey boxes of Fig. 5), but not if the whole community is analysed (white box, same figure).

One reason for the differences between studies performed on individuals and populations becomes clear in our study. Species may be locally facilitated or out-competed depending on the neighbourhood composition, but these effects cancel out at the population level because the importances of facilitation and competition are correlated. This correlation may be expected in several systems because large-seeded species are superior competitors (Rees & Westoby 1997; Turnbull, Rees & Crawley 1999; Leishman 2001) and more tolerant to stress (Leishman & Westoby 1994; Facelli 2008; Muller-Landau 2010). In contrast, small-seeded species would depend more on stress amelioration by neighbouring plants, so facilitation should be more frequent in them, but they would also be more affected by competition. Furthermore, as it happens in many other systems (Flores-Martínez, Ezcurra & Sánchez-Colón 1994; Miriti 2006; Schiffers & Tielbörger 2006; Valiente-Banuet and Verdú, 2008; Fayolle, Violle & Navas 2009), interactions shifted over ontogeny. Intense, positive interactions that occurred during colonization turned weak or competitive on occupied patches. Such changes may also contribute to the cancellation of the interactions at the population level (Fayolle, Violle & Navas 2009; Leger & Espeland 2010; Verdú, Jordano & Valiente-Banuet 2010).

This neutralization of interactions with different signs highlights several issues. (i) The outcome of interactions depends on the composition of the neighbourhood and its variability. Accounting for the interactions among several species may significantly affect our perception of their effects on community structured compared to studies based on a few pairwise interactions. (ii) The correlation between positive and negative effects would have important implications for the emerging research into positive interactions, as it would set important constraints upon the evolution of facilitation. Coexistence models based

solely on competition may also require revision. (iii) The effects of interactions on community structure need to take into consideration the whole life cycle and the demographic importance of interactions. Shifts over ontogeny are common, so studies based on individual-level performance over short periods cannot be readily extrapolated to the community.

STOCHASTICITY

Due to strong self-limitation, recurrent colonization of empty patches increased population sizes in nearly every species in spite of the concurrent removal of stochastic extinctions from the model. Recolonization allowed the persistence of rare species that were vulnerable to intra- and interspecific competition. From a community assembly viewpoint, it seems that the only poorly competitive species in the regional biota that were able to invade our grassland were those that are able to colonize new patches continuously. Evading competition through the colonization of favourable patches has recently been shown to promote coexistence under a wide set of circumstances. Fugitive species take advantage of windows of opportunity unlocked by disturbance or stochastic extinctions of superior competitors. Facilitators may also create sporadic, benign patches that fugitive species may also track, thus preventing their extinction (Valiente-Banuet *et al.*, 2006).

It has been proposed that subsets of similar species in the community may coexist due to neutral (equalizing) mechanisms even in the absence of niche differentiation because of a slow random drift (Leibold & McPeck 2006; Vergnon, Dulvy & Freckleton 2009). Within such subsets interspecific competition should be similar to intraspecific feedbacks. This is in accordance with the fact that competition during colonization was greater within functional groups than among them. Species in the same group have similar functional traits and thus are expected to have similar requirements. However, this likeness seems to be restricted to the regeneration niche, as the same pattern was not identified in already occupied squares. Tailored tests are required to address the question of neutral subsets in the community unambiguously.

In conclusion, our data illustrate that the community is strongly non-neutral, as very strong asymmetries between intra- and interspecific interactions were found. Neutrality did not operate even within functional groups, where we only found weak evidence that such asymmetry is attenuated. According to Ricklefs (2008), communities are disintegrated because they can be broken down into individual species and still retain their essential features. The fact that intraspecific competition (altogether with stochasticity) was able to explain most of the variance in species abundance in our community would appear to support his claims. Nevertheless, the same pattern would be expected if the community were structured by interspecific competition, which would cause extinctions until only a set of species that are more limited by conspecific than heterospecific interactions remained (Chesson 2000b). A deeper understanding of the community-assembly process is needed to discern between both alternatives. Despite the leading role of self-regulation, interspecific interactions had an

effect on community structure: some species are rare seemingly because they cannot withstand interspecific competition and are strongly self-regulated, and thus appear to undergo a life of vagrancy in search of competition-free patches. Moreover, the potentially large effects of interactions on population size were neutralized because the magnitude of positive and negative interactions was correlated. To fully understand community functioning, we need to discern whether the effects of interactions on population sizes is small in other systems because interactions are weak or because they cancel each other out. Community-level assessments such as ours are needed to deliver the correct answer.

Are our results likely to be general? We would argue that this is indeed likely to be the case. The most intense interactions occur mostly during the early stages of the life cycle even within complex communities at the other end of the productivity spectrum, such as tropical rain forests. For example, shade-adapted species will recruit only beneath existing canopies, and poorly competitive pioneers can recruit only into gaps and thus depend strongly on stochastic events. In line with our findings, recent research in Panama's rainforests found evidence for direct and indirect interspecific interactions during recruitment (Comita *et al.* 2010; Mangan *et al.* 2010), but that population sizes are mainly determined by intraspecific competition (Villarreal-Barajas & Martorell 2009; Comita *et al.* 2010). That strong self-limitation pervades community structure and allows for coexistence is a general result in several ecosystems (Silverton 2004; Adler *et al.* 2006; Levine & HilleRisLambers 2009; Villarreal-Barajas & Martorell 2009; Adler, Ellner & Levine 2010; Johnson *et al.* 2012). The colonization phase of any community is likely to have a complex outcome depending on the recruitment requirements of the species present, the local balance between positive and negative interactions during early growth, and on how stochasticity determines the rates of appropriate environment formation and colonization.

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Statement of authorship

CM collected the data. CM and RPF conducted the analyses and wrote the manuscript.

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Supporting Information

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

Appendix S1. Model selection and parameter estimation.

Appendix S2. Interaction coefficients.

Appendix S3. Frequency of interactions using different cut points for zero interaction intensity.