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The effect of space in plant–animal mutualistic networks: insights from a simulation study

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The topology of plant–animal mutualistic networks has the potential to determine the ecological and evolutionary dynamics of interacting species. Many mechanisms have been proposed as explanations of observed network patterns; however, the fact that plant–animal interactions are inherently spatial has so far been ignored. Using a simulation model of frugivorous birds foraging in spatially explicit landscapes we evaluated how plant distribution and the scale of bird movement decisions influenced species interaction probabilities and the resulting network properties. Spatial aggregation and limited animal mobility restricted encounter probabilities, so that the distribution of animal visits per plant deviated strongly from the binomial distribution expected for a well-mixed system. Lack of mixing in turn resulted in a strong decrease in network connectance, a weak decrease in nestedness, stronger interactions, greater strength asymmetry and the unexpected presence/absence of some interactions. Our results suggest that spatial processes may contribute substantially to structure plant–animal mutualistic networks.

There has been much recent interest in the topology of plant–animal mutualistic networks. This interest is warranted, because network topology has potentially important consequences for the ecological and evolutionary dynamics of interacting species (Thompson 2005, Montoya et al. 2006). Several apparently pervasive topological patterns have been described. For example, connectance (the proportion of possible links that are actually realized) is generally low, and it tends to decrease with increasing network size (Jordano 1987, Olesen and Jordano 2002). Plant–animal mutualistic networks are also characterized by high interaction asymmetry, both in terms of number of links per species (degree) and the relative strength of interactions. Degree asymmetry means that specialists (species with low degree) tend to interact with generalists (species with high degree; Bascompte et al. 2003, Vázquez and Aizen 2004); this asymmetry results in a nested pattern of the interaction matrix, in which specialists tend to interact with a subset of the species that interact with generalists (Bascompte et al. 2003). Strength asymmetry means that species that have strong effects on other species tend to interact with species that have weak effects on them, so that pairwise interactions have highly uneven strengths (Bascompte et al. 2006).

The determinants of the above patterns are the subject of an ongoing debate. Network structure has been hypothesized to result from phylogenetic and phenotypic matching between interacting species (Jordano 1987, Jordano et al. 2003, Rezende et al. 2007, Santamaría and Rodríguez-Gironés 2007, Stang et al. 2007). For example, a plant and a frugivore with non-overlapping phenologies will not be able to interact, whereas only pollinators with a long proboscis may reach the nectary of flowers with long, narrow corollas. These sort of 'forbidden links' may impose structural constraints on the network, thus generating the observed topology (Jordano 1987, Jordano et al. 2003, Santamaría and Rodríguez-Gironés 2007). However, mechanistic explanations of these ubiquitous network patterns should be confronted with null models. Under a neutral scenario, abundant species should have frequent encounters with individuals of many other species, most of which are relatively rare and specialized, given the pervasive right-skewed distribution of abundance (Preston 1962a,1962b, May 1975). Thus, if individuals of all species are identical and encounter each other randomly in the environment, species abundance would determine interspecific interaction frequency and strength and the resulting network structure (Vázquez et al. 2005, 2007).

The simple null models used to represent the above neutral hypothesis have sufficed to match some observed patterns, but not all. For example, null models have so far constrained connectance (the proportion of nonzero cells in the interaction matrix) to be the same as observed in the real

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networks they are compared with (Vázquez and Aizen 2004, Stang et al. 2007); relaxing this constraint usually results in networks with much greater connectance than observed (Fig. 1). These simple null models also result in lower occurrence of 'unexpected interactions' (lack of interaction among some abundant species and occurrence of interactions among rare species) compared to real networks (Fig. 1, Blüthgen et al. 2008).

Here we argue that the ongoing debate about the structure of mutualistic networks has so far ignored one key dimension of ecological communities: space. Given that species are composed by individuals that must meet in space and time in order to interact, we expect that the spatial distribution of plant species and animal mobility will play an important role in structuring interaction networks. In any community, individuals of plant and animal species are likely to exhibit patchy distributions, which means that interactions will be restricted by their location and the scale of animal movements. Thus, the spatial distribution of individuals in a community may influence species interaction probabilities, which in turn will determine network patterns. Although there have been some attempts to make mutualistic networks spatially explicit (Lázaro et al. 2005, Fortuna and Bascompte 2006, Carlo et al. 2007), to our knowledge spatial structure has not been formally considered as a potential explanation of network topology.

We used a simulation model of frugivorous birds foraging in spatially explicit landscapes to evaluate how plant spatial distribution and the scale of animal movement decisions influenced the buildup of species interaction networks. The model recorded every event in which a particular bird consumed fruit at a particular plant. Once the simulation had ended individual birds and plants were assigned to species according to relative abundances drawn from a log-normal distribution (below). Apart from abundances, there were no species-specific parameters in the model, so as to preserve its neutral nature. From these data we constructed plant–frugivore species interaction networks, on which we evaluated the distributions of interaction events per individual, the pairwise species interaction probabilities and several network statistics including connectance, nestedness, the distribution and asymmetry of interaction strengths, and the occurrence of unexpected interactions. Our simulation experiments consisted in varying the spatial distribution of individual plants in the landscape, the degree of spatial autocorrelation in species identities and the spatial scale at which simulated birds made their foraging decisions.

Material and methods

Plant–frugivore simulation model

We modified Morales and Carlo's (2006) plant–frugivore simulation model to study the effects of the spatial distribution of individuals and animal mobility on interaction networks. The model is a spatially explicit, event driven, stochastic simulation of bird foraging and fruit production, originally developed to study seed dispersal. The model assumes that animals may detect and track fruit abundance at multiple spatial and temporal scales, as has been shown to occur in nature by several field studies (Levey 1988, Aukema and Martinez del Rio 2002, Saracco et al. 2004). Here we present a summarized description of the model; a full description, together with default parameter values, can be found elsewhere (see Morales and Carlo 2006, particularly Appendix A).

In the model, simulated birds move from plant to plant as they forage for fruits; it is possible to keep track of the number of fruits consumed by each animal at each plant. For simplicity, birds moved from plant to plant in straight

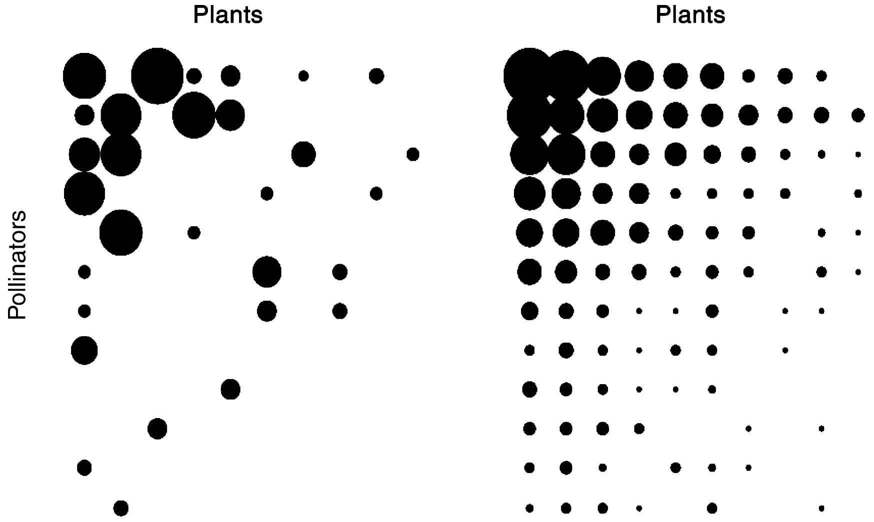

Figure 1. Real plant–animal mutualistic network and expectations from a spatially unconstrained null model. Plots depict quantitative matrices representing interactions among species of plants (columns) and animal mutualists (rows). Left matrix: observed plant–pollinator interaction matrix from a study by Olesen et al. (2002). Right matrix: quantitative matrix predicted by a model assuming random interactions among individuals, so that the probability of interaction between pairs of species is proportional to species' abundance. The model assigns the total number of interactions observed in an interaction matrix according to probabilities proportional to species abundances as done by Vázquez et al. (2007), but without constraining connectance.

lines and at constant speed. When choosing where to perch next, individual birds sampled from an attraction distribution that was compiled by weighting fruit abundance and distance from current location (below). Simulated birds spent a variable amount of time (sampled from a probability distribution) perching and eating at fruiting plants. We kept perching time independent of fruit abundance because many factors other than resource availability can influence how much time a bird spends at a perch. Fruit consumption followed a hyperbolic functional response but was kept within the limits of gut size. Simulated birds kept moving, eating and dispersing seeds until they accumulated six hours of daily activity. At the end of each simulated day, every plant produced new ripe fruits according to a regrowth model. All birds had identical parameter values and hence reacted in the same way to fruit abundance, number of fruits per plant, etc. Similarly, all plants had identical parameter values and produced fruits at the same rate.

Distribution maps

We manipulated plant spatial distribution at two levels, which we believed could affect network structure simultaneously: the spatial distribution of individual plants and the spatial autocorrelation of individual identities (Fig. 2). We reasoned that even if all plants in a landscape were randomly distributed over space, species identities could still be autocorrelated, so that the identity of neighboring individuals is likely to be the same. Conversely, even if individual plants formed clearly defined patches over the landscape, species identities could be well mixed.

To construct distribution maps of plant individuals, we first distributed individual plants throughout the landscape either randomly (random landscape) or spatially aggregated (clustered landscape). To generate clustered maps, a fixed number (500) of 'parents' were randomly located within the landscape, which served as centers for plant clusters. From these centers the remaining plants were located sequentially at random angles, with distances following a Weibull distribution with scale determined by the desired degree of aggregation and with shape set to two.

To assign individual plants to species we started by defining the number of individuals per species (n_i), by discretizing a lognormal distribution and then generating a list of species probabilities so that the i-th species has probability $p_i = n_i/\Sigma n$. An individual plant from the map was then randomly chosen and assigned an identity i sampled from the species probabilities. We then randomly selected another individual among those within a 100 m radius from the previous plant. Before assigning an identity to this new plant, the species probabilities were updated by removing an individual from the i-th species and normalizing. Furthermore, to manipulate the autocorrelation of species identities according to a parameter ρ, the probability of assigning species i was increased as $p_i' = p_i + (1 - p_i)\rho$, whereas the probability of assigning other identities j was reduced by $p_i' = p_j(1 - \rho)$. By changing the scale of the Weibull distribution that modeled distance from parents and the autocorrelation parameter ρ we controlled both the degree of aggregation of individuals and of species identities in the landscape.

The starting location of bird individuals was randomly determined, and their identities were assigned according to a probability $p_i = n_i/\Sigma n$ derived from a discretized lognormal distribution of abundances, as explained above for plants.

Simulation experiments

We used simulation experiments to assess the effects of animal mobility and plant spatial distribution on network statistics. Simulations were run with 200 individual birds that foraged in landscapes consisting in a 10 × 10 km area populated by five thousand plants. Our choice of the number of simulated individuals was dictated by both realistic plant:frugivore ratios and computational efficiency. The dimensions of the species interaction network (i.e. the number of plant and frugivore species) was set to 30 plant species and 20 bird species (plant:frugivore ratio 1.5). These numbers are representative of described networks. For example, for the seven networks used in Bascompte et al. (2006), the mean number of plant species per network was 20.28 (range: 7–35), mean number of frugivore species was 15.86 (range: 6–33), and the mean plant:frugivore ratio was 1.55 (range: 0.76–3.44). The number of individuals assigned to each species was determined from log-normal distributions with mean of one and standard deviation of two.

The area covered by birds as they foraged for fruits was regulated by an interaction between the spatial distribution of plants and the distance component in their decision process. Attraction to a particular plant increased with the number of fruits and decreased with distance. The number of ripe fruits (F) in a particular plant was translated to an attraction value (A_f) between 0 and 1 as $A_f = \tanh(a_f F_f^b)$ where a_f and b_f are parameters. The decay of attraction with distance was modeled with a hyperbolic tangent, $A_d = \tanh(-kd^2) + 1$, where A_d is attraction due to distance, d is distance in meters from current bird location and the plant of interest, and k is a parameter. The hyperbolic tangent, tanh(x), is a sigmoidal function between −1 and 1 with inflection at $x = 0$. Since F and d are always positive, A_f will be zero for small F and will go to one as F increases, and A_d will be close to one for small d and will go to zero as d increases. Note that A_d effectively limits the scale at which movement decisions are made. To assess the effect of animal mobility on network structure we changed the value of k so that the attraction A_d was reduced to 0.05 at 200, 500 and 700 m. This manipulation of k resulted in simulated birds making their foraging movement decisions at three different spatial scales.

We performed a full factorial experiment with the three levels of bird foraging decision scales (i.e. 200, 500 and 700 m), two levels of individual plant spatial distribution (random or clustered), and ten levels of autocorrelation in plant identities (ρ 0 to 0.9). For each combination of factors we generated 30 species interaction networks. Although model output included over 500 000 interaction events, our analyses were based on 10 000 consecutive interaction events in order to match the scale of observational studies. For example, for the five plant–frugivore

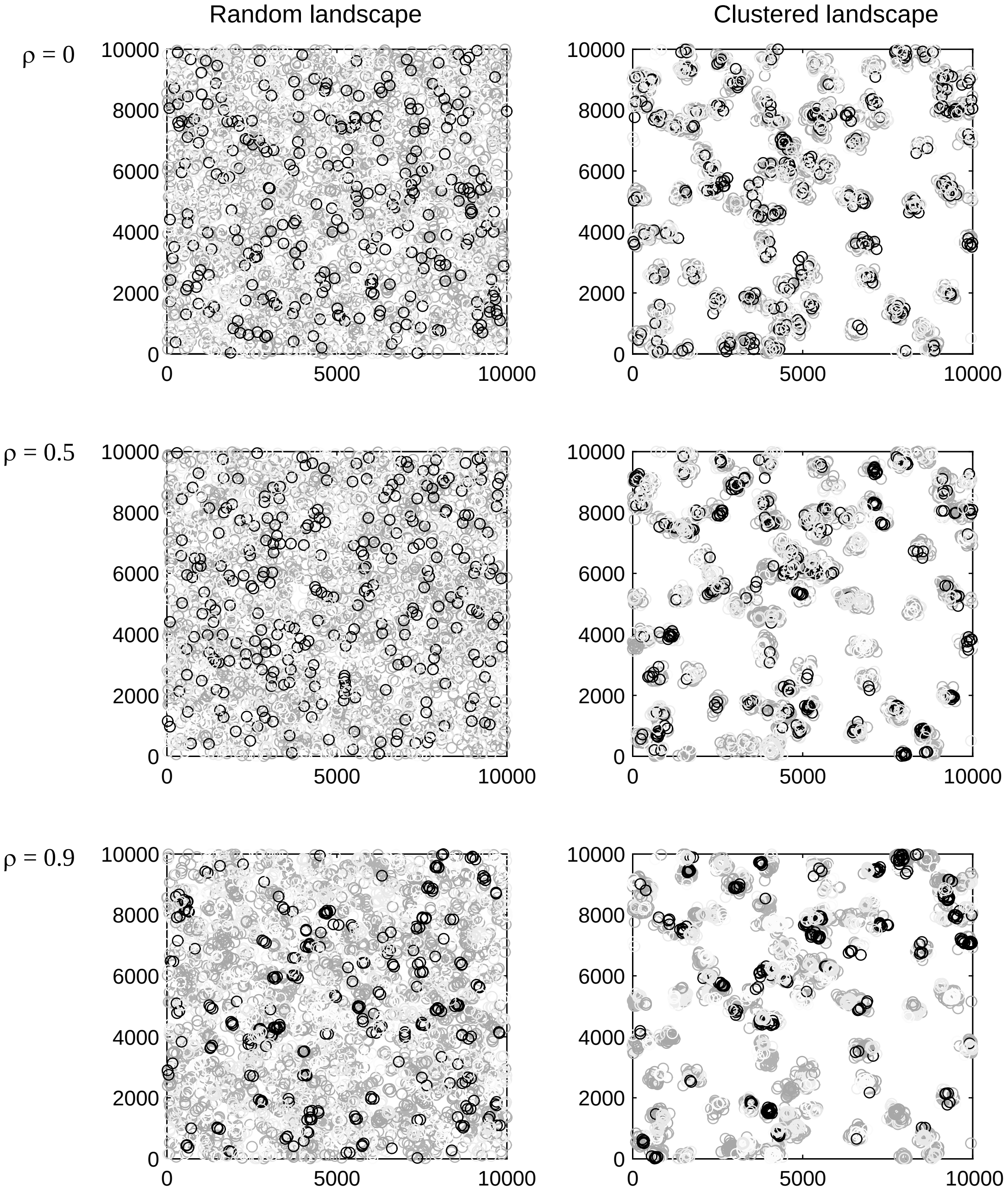

Figure 2. Examples of simulated maps to illustrate different plant spatial distributions and autocorrelation in the assignment of plant individual identities to species (ρ). The six most abundant species (out of 30) are represented by different grey tones. When $\rho = 0$, individual plants are randomly assigned to species while for $\rho > 0$ species identities are spatially autocorrelated.

networks considered in Vázquez (2005), the mean number of recorded interactions was 3332 (range: 292–7434); thus 10 000 recorded interactions seems a reasonable number for a well-sampled network. The starting point of the consecutive events used for each replicate was randomly chosen after discarding the first 10 000 interactions to avoid potential initial conditions effects. To check if this level of sampling effort could affect results, we repeated the simulation with 50 000 interaction events instead of 10 000; results were qualitatively unaffected, and thus we report only results for 10 000 interaction events.

Distribution of interaction events

We hypothesized that spatial structure and restricted animal movement impose constraints in individual mixing, in turn affecting species interaction probabilities and network properties. In a well-mixed system the number of interaction events (fruits removed) per plant should follow a binomial distribution,

$$p(h|N,\theta) = \binom{N}{h}\theta^{h}(1-\theta)^{N-h}$$

where h is the number of interaction events per individual plant, N is the total number of events and $\theta = 1/$(total number of plants) is the probability of choosing an individual plant in each of the N events (Carlo and Morales 2008). We evaluated spatial effects by comparing the fit of this expected distribution with a zero-inflated negative binomial (ZINB), which assumes heterogeneity in the distribution of interactions (Martin et al. 2005). The ZINB has a parameter z indicating the probability of zero visits in excess to those expected under the negative binomial and parameters μ and s for mean and overdispersion, respectively. As the overdispersion parameter s increases, the negative binomial approaches a Poisson distribution. We evaluated the relative fits of the binomial and ZINB distributions with Akaike's information criterion (AIC), comparing the AIC differences, $\Delta AIC_i = AIC_j - AIC_{min}$, where AIC_{mim} is the AIC value for the best-fitting model (Burnham and Anderson 2002).

Network statistics

For every animal–plant species pair we calculated an interaction probability as the quotient between the observed number of interaction events between the species pair and the total number of interactions. We calculated these interaction probabilities for all replicates and report median values and the coefficient of variation as well as the evenness of the probability distribution (using the interaction eveness measure proposed by Tylianakis et al. 2007, which is based on the Shannon evenness index of diversity Magurran, 2004).

For each species interaction network generated from the simulation model we calculated several network statistics frequently used to characterize the structure of binary and quantitative mutualistic networks. For binary networks, we calculated connectance, $C = L/(AP)$, where L is the number of realized links in the binary matrix and A and P are the numbers of animals and plants, respectively (Jordano 1987, Olesen and Jordano 2002), and nestedness, N (Atmar and Patterson 1993, Bascompte et al. 2003). To calculate nestedness we used the R package 'bipartite' (Dormann et al. 2008), which implements the Rodríguez-Gironés and Santamaría (2006) BINMATNEST algorithm for nestedness calculation. BINMATNEST solves some limitations of the nestedness temperature calculator (Atmar and Patterson 1993) used in many studies (Rodríguez-Gironés and Santamaría 2006). Package bipartite returns the statistic T (matrix temperature), a measure of the 'disorder' of the matrix; a matrix with $T = 0$ would be perfectly nested, whereas one with $T = 100$ would be completely random. Following Bascompte et al. (2003), we defined nestedness as $N = 100 – T$. For quantitative networks, we calculated animal and plant interaction strengths, d_{ij}^{A} (termed 'dependences' by Bascompte et al. 2006), which measures the fraction of all plant visits made by animal species i to plant species j (Vázquez et al. 2007), and d_{ij}^{P} (which measures the fraction of all frugivore visits made by animal species j to plant species i), and strength asymmetry, $A_{ij} = \mathrm{abs}(d_{ij}^{A} - d_{ij}^{P})/\max(d_{ij}^{A}, d_{ij}^{P})$ (Bascompte et al. 2006).

Results

The distribution of interaction events among plant individuals was strongly influenced by plant spatial aggregation and animal mobility. The zero-inflated negative binomial model for the distribution of interaction events per plant clearly outperformed the binomial model in all cases (Table 1). However, the differences between the expected binomial distribution for a well mixed system and the observed distribution of interactions per plant were greater for clustered landscapes with limited bird mobility (Fig. 3A, B, Table 1). As the scale of bird movement decision increased the observed distribution of interactions per plant became more similar to a binomial, especially for random landscapes (Fig. 3C–F, Table 1).

Pairwise species interaction probabilities were also affected by plant spatial aggregation and animal mobility: interaction probability evenness decreased with increasing autocorrelation of species identities and decreasing animal mobility. In other words, high spatial aggregation and low animal mobility meant higher interaction probability for abundant species and lower interaction probability for rare species than in a well-mixed system. For random landscapes, the decrease in evenness with increasing autocorrelation was approximately linear with intercept and slope depending on the scale of animal movement decisions (Fig. 4A, red symbols). In contrast, evenness changed faster than exponentially for clustered landscapes with small to moderate animal mobility (Fig. 4A, blue symbols). Thus, as autocorrelation of plant identities increased and animal mobility decreased, interactions involving rare species

Table 1. Model comparison for the distribution of interactions per plant as a function of plant patchiness (random landscape vs clustered landscape) and the scale of bird movement decisions (Scale). The zero-inflated negative binomial (ZINB) was always the best fitting model so that $\Delta AIC = AIC_{binomial} - AIC_{ZINB}$.

Landscape	Foraging scale (m)	Parameter P	AIC	Parameter			AIC	ΔAIC
				μ	s	z		
Random	200	0.0002	42481.8	14.6	4.5	1.00	34120.5	8361.3
	500	0.0002	29012.0	14.3	43.4	1.00	28793.8	218.3
	700	0.0002	28516.6	13.5	51.71	1.00	28374.7	141.9
Clustered	200	0.0002	53091.1	15.3	3.5	0.94	35263.8	17827.3
	500	0.0002	46190.9	15.0	4.7	0.96	34462.2	11728.7
	700	0.0002	30399.9	13.7	21.3	1.00	29747.2	652.8

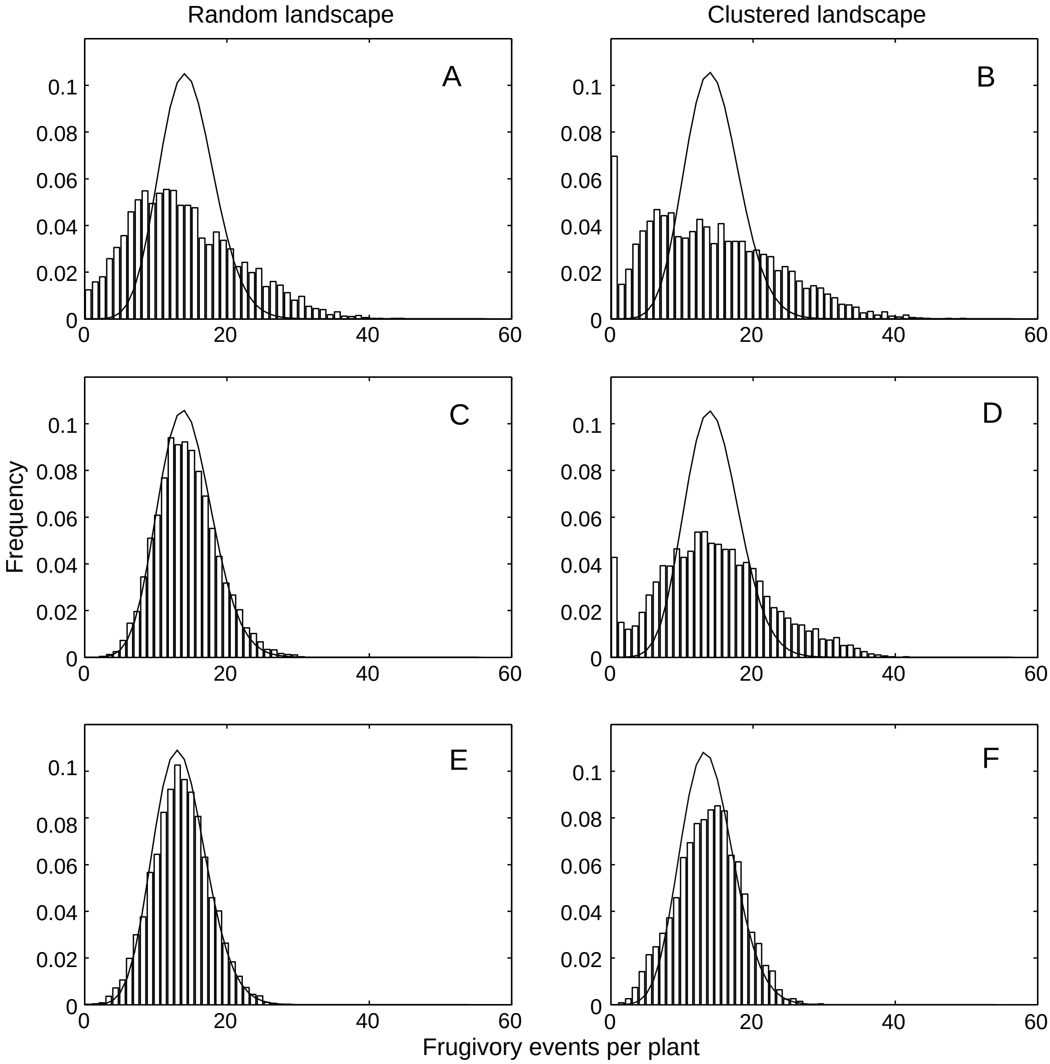

Figure 3. Distributions of interaction events per plant as a function of landscape patchiness and the scale of bird movement decision. Bars are observed frequencies in the simulation experiments; solid lines represent the expected distribution for a well mixed system. (A, C and E) random landscape with increasing scale of movement decisions (200, 500 and 700 m, respectively). (B, D and F) clustered landscape with increasing scale of movement decisions as above.

became less likely and those involving abundant species became more likely, especially for clustered landscapes.

The above effects on interaction probabilities were reflected in matrix connectance and strength asymmetry. Changes in connectance showed similar trends to those observed for interaction probability evenness. Connectance was high for random landscapes, decreasing with increasing autocorrelation in plant species identities; the intercept and slope of this reduction in connectance was determined by the scale of bird movement decisions (Fig. 4B, red symbols). In contrast, under aggregated landscapes and low to moderate animal mobility, connectance decreased sharply with increasing autocorrelation, but this effect disappeared when animal mobility was high (Fig. 4B, blue symbols). Strength asymmetry remained low under random landscapes and moderate to high animal mobility, but increased with increasing autocorrelation parameter when animal mobility was low (Fig. 4C). In contrast, in aggregated landscapes strength asymmetry increased with increasing ρ for low to moderate animal mobility, but remained low when animal mobility was high (Fig. 4C). Thus, networks became less connected and more asymmetric as plants were more spatially aggregated and animals foraged more locally.

Spatial distribution of individual plants, autocorrelation of individual identities and animal mobility also influenced variability of interaction probabilities among simulation replicates. Under random landscapes and low autocorrelation of individual identities interaction probabilities varied little among simulation replicates (Fig. 5A). In contrast, under aggregated landscapes and high autocorrelation of individual identities there was high variability of interaction probabilities, particularly for interactions involving rare species (Fig. 5B). A similar effect was found for contrasting levels of animal mobility, with variability of interaction probabilities being highest under low animal mobility (not shown). High variability in interaction probabilities among replicates suggests that spatial aggregation may contribute

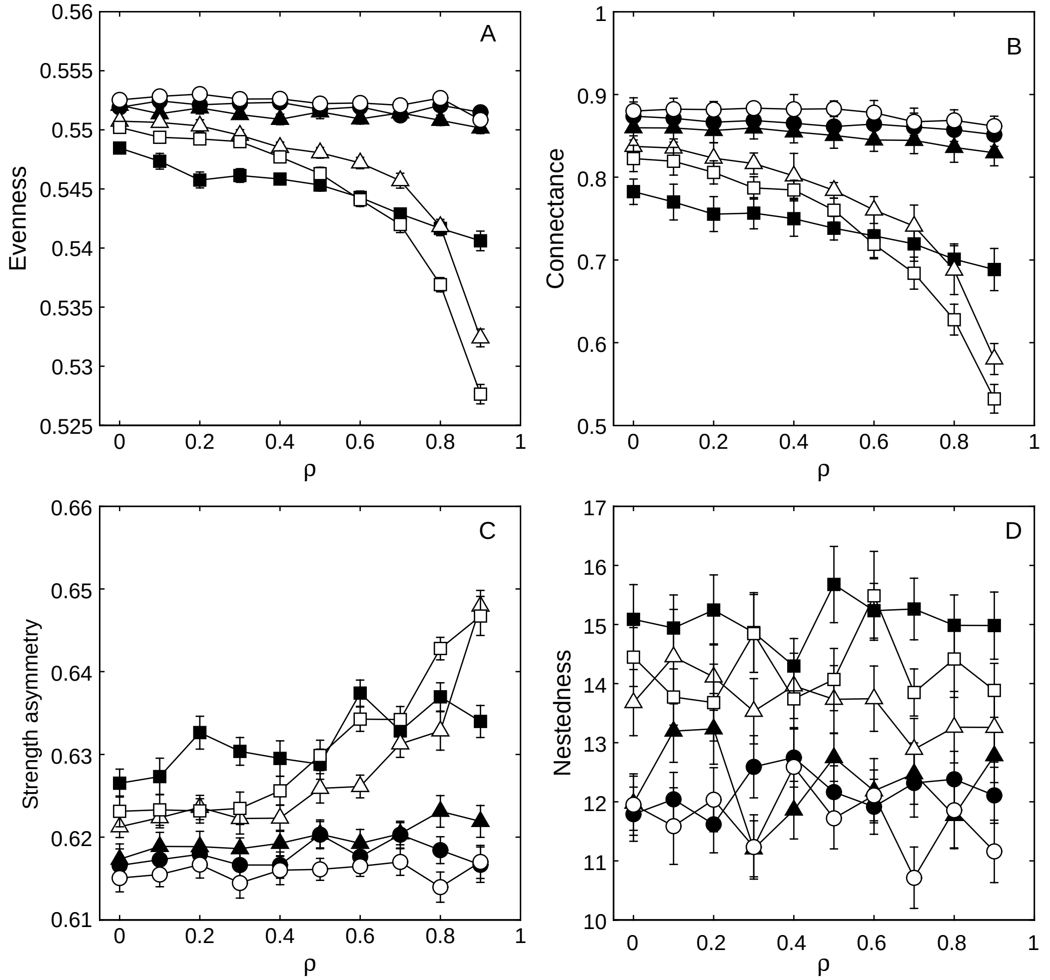

Figure 4. Changes in interaction evenness (A), connectance (B), strength asymmetry (C) and nestedness (D) with changes in spatial autocorrelation of plant individual identities (ρ, abscissa), landscape structure and animal mobility. Symbol filling indicates the underlying spatial distribution of individual plants: solid symbols, random distribution; open symbols, aggregated distribution. Symbol types indicate mobility: circles, high mobility (scale of decision about 700 m); triangles, moderate mobility (scale of decision about 500 m); squares, low mobility (scale of decision about 200 m).

to generate some of the unexpected absence of interactions between highly abundant species and the unexpected occurrence of interactions among rare species usually observed in real networks (Fig. 5C–D, cf. Fig. 1).

Although the increased unevenness of interactions resulting from high spatial aggregation and low animal mobility should lead to increased matrix packing and hence greater nestedness, increased frequency of unexpected interactions should produce the opposite effect. Thus, spatial aggregation and animal mobility should have only a minor net effect on nestedness; this is in fact what our simulation shows (Fig. 4D).

Discussion

We have shown that the spatial aggregation of plant individuals and their identities, as well as the limited movement of animal mutualists, can influence the structure of plant–animal mutualistic networks. Under high spatial aggregation and low animal mobility, simulated networks exhibited lower connectance, higher strength asymmetry and a greater frequency of 'unexpected' patterns (such as the lack of interaction among some common species and the occurrence of interactions among some rare species), compared to cases with low spatial aggregation and high animal movement. Although other mechanisms, particularly phylogenetic and phenotypic constraints, are likely to contribute to generate structural patterns observed in mutualistic networks (Jordano 1987, Jordano et al. 2003, Rezende et al. 2007, Santamaría and Rodríguez-Gironés 2007, Stang et al. 2007), our study shows that even in the absence of such constraints spatial structure can result in a network structure which resembles that observed in real-world networks. Given the pervasive occurrence of spatial aggregation in the distribution of individuals in ecological communities, and the inherently local nature of animal foraging patterns, our results strongly suggest that spatial effects may contribute to generate the observed structure of mutualistic networks.

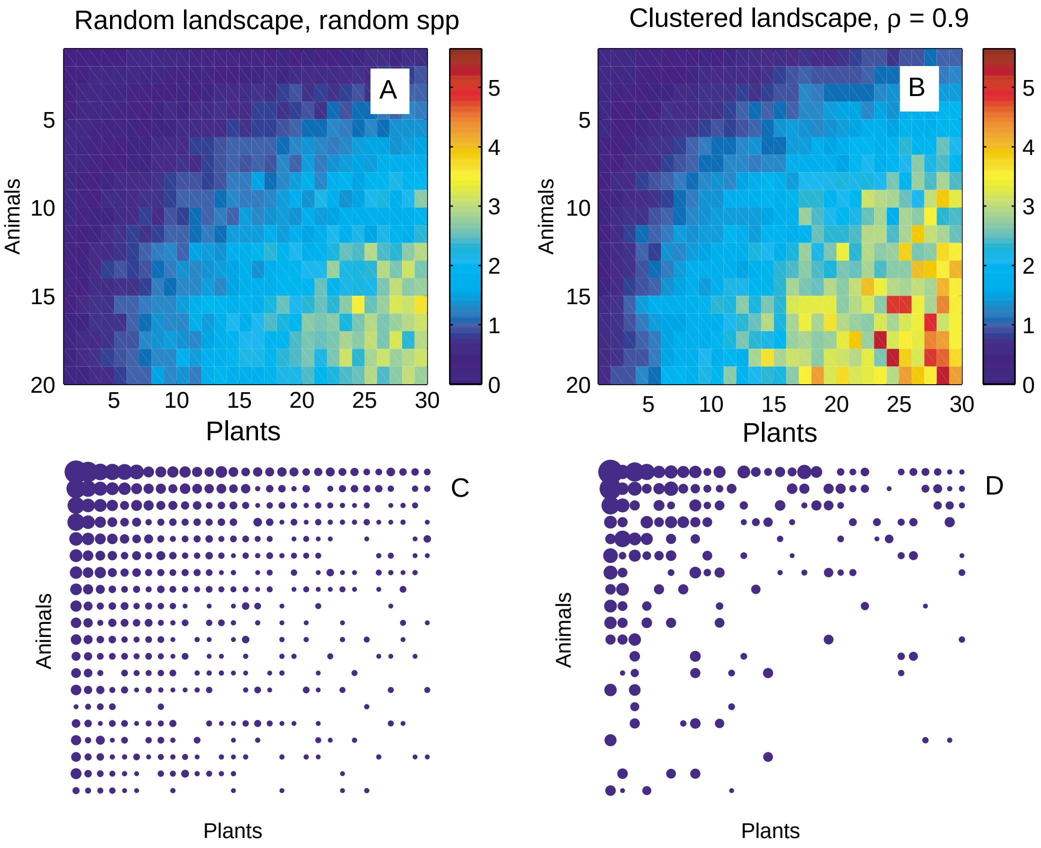

Figure 5. Spatial aggregation, the coefficient of variation of interaction probabilities and the structure of the interaction matrix. (A and B) coefficient of variation of interaction probabilities calculated across 100 replicates, with species sorted in decreasing order of abundance from top to bottom (birds) and left to right (plants). (C and D) examples of simulated quantitative interaction matrices. Quantitative matrices represent interactions among species of plants (columns) and frugivores (rows) for a randomly chosen replicate for each combination of treatments. (A and C) random landscape, low autocorrelation of individual identities (ρ). (B and D) aggregated landscape, high autocorrelation of individual identities. The scale of bird movement decisions was about 200 m for all cases.

Spatial structure and animal movement influenced network structure by affecting the degree of mixing of the system. In a spatially-structured system, individual animals must move in order to interact with plants, which imposes a constraint on encounter probabilities. Our simulated birds interacted only with plants within their mobility range, which meant only a few plant individuals and species under spatial aggregation and low animal mobility. This effect of spatial structure resulted in greater unevenness of both interaction events among plant individuals (Fig. 3) and species interaction probabilities (Fig. 4A). Note that although we manipulated only the spatial distribution of plant species, we could have also classified birds according to the location of their areas of activity. Clearly, clustered distributions of bird individuals would exacerbate the observed effects of clustered plant distribution on interaction probabilities.

Because the clustered landscapes of our study are substantially more fragmented than the random landscapes (Fig. 2), our study allows making specific predictions about how habitat fragmentation may influence species interaction probabilities and the resulting network structure. For example, all else being equal, we expect that mutualistic networks in fragmented landscapes are less connected, more asymmetric and less predictable from species abundances alone than networks in less fragmented landscapes.

Available data on mutualistic networks are not spatially explicit, and thus it is currently not possible to confront the predictions of our model with real data. It is thus highly desirable that future studies describing mutualistic networks consider the spatial component of interactions. However, even in the absence of such spatially explicit data, studying the distribution of interaction events per individual plant (Carlo et al. 2007) may allow evaluating the degree of mixing of the system, which, as we have shown (Fig. 3), is a direct result of the spatial distribution of individuals and animal mobility. More abitiously, making mutualistic networks spatially explicit would at least involve recording the spatial location of plant individuals in the studied community, as well as the location of observed interactions and the movement patterns of foraging animals. Although making mutualistic networks spatially explicit would thus represent substantial additional work, we think it is well worth the effort, because it would allow a more mechanistic understanding of topological patterns.

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