

The role of frugivory in plant diversity maintenance- a simulation approach

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Abstract

Frugivores may play a key role in plant species coexistence by equalizing the species' representation in the seed rain. Rare species may benefit from enhanced dispersal if frugivores prefer locally scarce fruits, or if rare plants are found in neighborhoods of high fruit density. Using a simulation model of frugivorous birds foraging on landscapes we tested if increased diversity in the seed rain could emerge from rare-biased fruit selection, from the spatial configuration of plants, or both. In the absence of rare-biased fruit selection, frugivores were not able to increase the diversity of the seed rain in any of our simulated landscapes. In contrast, when frugivores were attracted to locally scarce fruits, we found increased diversity in the seed rain whenever frugivore mobility across the landscape was high and plant species were well-mixed in the fruiting neighborhoods. Irrespectively of the behavioral mechanism involved, landscape fragmentation lead to losses in diversity and species richness of simulated communities. In all simulations, density-dependent mortality of dispersed seeds increased diversity in the community of seedlings. However, landscape homogenization at the scale of frugivores movements decreased the magnitude of this diversification effect. In summary, our study shows that frugivory has the potential to increase diversity in the seed rain when frugivores display rare-biased fruit choices, provided that rare and common plants form heterogeneous neighborhoods. They also show that fragmentation is a major threat for diversity maintenance in the early-regenerating community. Finally, they show that rarity confers advantages during regeneration only if it occurs at the scale of frugivores' foraging decisions.

Key words frugivory, diversity, rarity

Introduction

Understanding ecological processes driving the maintenance of plant diversity is a fundamental goal in community ecology (Vellend 2010). The persistence of rare plant species in communities has intrigued ecologists for a long time, particularly in highly diverse communities where rare species constitute the bulk of the species richness (Terborgh et al. 2002). Ecologists have identified several post-dispersal processes that may confer “advantages to the rare” via density-dependence (reviewed by Terborgh 2012) and act as equalizing and stabilizing forces (Chesson 2000). Still, the seed dispersal stage is the critical initial step that sets the recruitment templates (Nathan and Muller-Landau 2000). Fruit-eating animals or frugivores disperse the seeds of high numbers of species (Herrera 2002), generating recruitment templates that are influenced by their foraging decisions (Jordano 2000). However, the underpinning mechanisms by which frugivory shapes community composition remains poorly understood.

Rare-biased or anti-apostatic fruit selection (*sensu* Allen 1988) by frugivores has been recently suggested as a potential mechanism explaining diversity enhancement in the seed rain and regeneration stages (Carlo and Morales 2016). Frugivores may be attracted to rare fruits for several reasons including diet complementation (Murphy 1994, Whelan et al. 1998), neophilia (Greenbert and Mettke-Hofmann 2001, Sol et al. 2011) or conspicuity with respect to the background (Cooper and Allen 1994, Shaefer et al. 2006). In any case, per-capita fruit-frugivore interactions are expected to increase with rarity. When faced to frequency-dependent food selection, wild birds tend to preferentially consume rare items at moderate to high food densities (25-100 food items m^{-2}); while the opposite occurs when food is scarce (<10 food items m^{-2}) (Church et al. 1997, Allen 1998, Weale et al. 2000). Fruit density in actual plant communities is

usually within the ranges that favor rare-biased selection (>10 fruits m^{-2} – 140 fruits m^{-2} , Jordano 2000, Carlo and Morales 2016). Thus, rare-biased frugivory may constitute another density-dependent process conferring advantage to rare species that warrants study.

However, because plant-frugivore interactions are highly context-dependent, rare species over-representation in the seed rain may be affected by or solely due to the spatial arrangement of plants (Carlo et al. 2007, Cortes and Uriarte 2013). For instance, rare fruiting species could experience enhanced dispersal in the absence of rare-biased fruit selection due to the effects of spatial position or neighborhood facilitation (Saracco et al. 2004, Carlo 2005, Carlo and Morales 2008). Since areas of high fruit availability attract more frugivores (Rey 1995, Carlo and Morales 2008), rare species may benefit from enhanced dispersal services if they are located in dense interspecific neighborhoods, provided that they share the frugivore agents. Therefore, rare-biased dispersal may not necessarily imply a behavioral mechanism involving rare-biased fruit selection by frugivores.

Irrespectively of the mechanism involved in rare-biased dispersal, the spatial distribution of plants also affects the way frugivores move around in the landscape, and consequently, the dispersal services they provide (Cortes and Uriarte, 2013). Usually, landscapes are composed of clusters (patches, neighborhoods) of resource plants whose spatial distribution may affect the probability that frugivores move from patch to patch, which in turn depends on their movement capacity relative to the spatial scale of plant aggregation. For example, if clusters of fruiting plants are separated beyond the normal movement range of frugivores, then the landscape would be effectively fragmented. Since frugivores' mobility across the landscape is tightly linked to their capacity to

interact with all plant species in the community (Morales and Vazquez, 2008), fragmentation is expected to decrease the positive effects of frugivory on diversity maintenance. The degree to which plant species are spatially-mixed is also important because it would determine how available are different fruit resources at the spatial scale at which birds decide what to eat. Finally, plant spatial patterns also influence where seeds are deposited, and therefore determine post-dispersal processes such as density dependent mortality of seedlings, which may be key in structuring plant communities (Janzen 1970, Nathan and Muller-Landau 2000, Schupp et al. 2002, Terborgh 2012). Thus, to assess the potential of frugivory in structuring plant communities it is necessary to evaluate the interaction between the motivations of frugivores, and their movement capacity in relation to the spatial scales of intra and interspecific aggregation of resource plants (Carlo et al. 2007, Cortes and Uriarte 2013, Morales et al. 2013)

Here we use a spatially-explicit simulation model (Morales and Carlo 2006) to test if rare-biased seed dispersal emerges from the fruit-selection behavior of frugivores, from the spatial configuration of plants, or both. We also evaluate the effects of frugivore behavior and landscape properties on the strength of density dependent mortality on the diversity of seedlings. We expected that spatial configurations in which plants are located in neighborhoods that are dense, and where common and rare species are mixed within the scale of frugivore foraging, will provide dispersal and recruitment advantages to rare species.

Material and Methods

Morales and Carlo model (2006) developed a spatially explicit, event driven, stochastic plant-frugivore model, in which individual birds choose the next foraging plant according to their distance from the current position and their fruit availability but irrespectively of plant species. Because frugivores are blind to the relative abundance of plant species, it can serve as a null model with respect to *rare-biased* selection – or any form of fruit selection – in a multi-species system. Here we present a summarized description of the model, a full description can be found elsewhere (see Morales and Carlo 2006). In the *rare-biased* selection scenario we slightly modified this model in order to include higher attractiveness of fruits when they are locally scarce.

Landscape generation

Since one of our main goals was to test if diversity enhancement in the seed rain could arise from landscape properties, we performed a preliminary sensitivity analysis to choose the most relevant landscape features. Using a design of experiment methodology (DoE) (following Thiele et al. 2014) we manipulated- plant density, degree of aggregation, autocorrelation of plant species identities, bird:plant ratio and evenness of the plant community. Our analysis consisted in a full factorial design, in which all factors had two levels that corresponded to extreme values (Supplementary Table S1). Model output was difference in effective number of species (Jost 2006) between seed availability and seed rain ($\Delta H'$). Effective number of species represents the number of equally abundant species necessary to produce the observed value of diversity. It was calculated as $\Delta H'_{fi} = ((\exp H_f - \exp H_i) / \exp H_i) \times 100$; with “f” being the final stage of recruitment and “i” the initial stage. H represents Shannon diversity index. All parameters showed similar first and second order sensitivity indexes except for evenness which explained little variance in the model (Supplementary Table S1). We

decided to keep bird:plant ratio in 1:10 values in order to avoid dispersal vector limitation within the landscape (see Fig. 16 Carlo et al. 2007). Therefore, our simulation experiment consisted in varying plant density, degree of plant aggregation and spatial autocorrelation of species identities (see below).

Our landscape consisted of a square of 25 km², in which we generated different levels of plant aggregation following a Neyman-Scott process (Zollner and Lima 1999). Firstly, we distributed “parent” plants over space randomly (following a Poisson process). Secondly, one of the “parent” plants was chosen and a “daughter” plant was located at random directions and at a distance sampled from a Weibull distribution. Shape parameter of the Weibull distribution was fixed to 2 and the scale parameter defined the degree of desired aggregation. This process was repeated until the number of plants within the landscapes was achieved.

To create the plant community, we first defined the number of individuals per species (n_i) by discretizing a lognormal distribution. The number of plant species was fixed to 5 and community evenness to 0.5 (logmean = 0.23, logsd = 0.43). This way the dominant species showed a proportional abundance of 0.75 and the rarest species of 0.02. To generate different degrees of spatial autocorrelation we followed (Morales and Vazquez 2008). We first created a list of species probabilities according to their abundance ($p = n_i/N$, N = number of plants). We chose an individual plant from the map and assigned it a species identity (i) sampled from species probabilities. Before assigning an identity to a new plant, species probabilities were updated by removing one individual of the i th species. Then, we randomly selected another individual within a 250 m radius from the previous plant. The probability of assigning the i -th species to this new individual was increased as $p_i = p_i + (1-p_i)\rho$, whereas the probability of

assigning a new species identity decreased by $p_j = p_j(1-\rho)$. High values of ρ imply high aggregation of species in the landscapes while ρ equal to 0 imply that species identity is assigned only based on their abundance (Supplementary Fig. S2 for landscape examples).

Simulation model

In the *unbiased scenario*, birds decide which plant to visit next by sampling from a destination distribution that weights fruit availability and distance from the current position of all potential destinations (eq 1-2).

$$\beta_i = [\tanh(-a_d d_i^2) + 1] \times [\tanh(a_f F_i^2)]$$

$$\beta = \beta_i / \sum_1^n \beta_i \quad (1-2)$$

β_i measures the bias towards the i -th plant given its current distance (d_i) and fruit abundance (F_i). Parameter “ a_f ” of the fruit attraction curve was set so that it saturated at 100 fruits (maximum crop size, see below). Besides, parameter of distance curve “ a_d ” was set so that attraction for a particular plant dropped to 0.05 at 200 m. Thus, simulated birds made most of their foraging decisions within a radius of 200 m from their current location.

In the *rare-biased* scenario birds were more attracted to locally scarce fruits (3),

$$\beta_i = [\tanh(-a_d d_i^2) + 1] \times [\tanh(a_f F_i^2)] \times [\tanh(-a_a A_j^2)] \quad (3)$$

where A_j is the relative abundance of fruits of the j -th plant species within the decision radius. By multiplying attractiveness vectors, *rare-biased* selection is stronger when fruit availability is high (according to density-dependent rare-biased selection; Allen et al. 1998). Parameter “ a_a ” was fixed so that bias due to abundance saturates (>0.99) when relative abundance is low (0.2%). These values match previous observations in which plants with relative abundance below 0.2% experience increased seed dispersal

(Carlo and Morales 2016). Finally, birds balance their movement decisions according to gut fullness (Sasal and Morales, 2013). If their gut is full, they will not be able to consume fruits in the next location, and hence, they minimize travel costs by preferentially moving on the basis of distance.

For the sake of simplicity, once birds decide where to go they move at a constant speed (6 meters per second) and in straight lines. When perching in the next plant fruit consumption follows a hyperbolic response kept within the limits of gut size (15 fruits). Perching time is determined drawing from a gamma distribution (shape=4 and scale=1.25) with a mean of 5 min (Carlo and Aukema 2005). Each fruit has a single seed with a gut passage time sampled from a gamma distribution with a mean of 27 minutes (shape =2.8, scale = 12.7) that broadly match gut-passage rates reported from several frugivorous bird species (Wahaj et al. 1998).

Plants produced 100 fruits at the beginning of the simulation but no new fruits were produced in order to take into account resources depletion and frugivores satiation (Rey 1995, Hampe 2008). Simulation stops when thirty percent of the fruits available are consumed. Preliminary analysis revealed that fruit depletion overrides landscape characteristics when fruit consumption exceeds fifty percent of available fruits (Supplementary Fig. S1).

Once seeds are deposited, the probability of survival depends on the density of conspecific seeds in a radius of 1 m (Janzen 1970, Connell 1971). A probability of survival was assigned to each seed according to the logistic function $logit(P_s) = a_s - \beta_s \times N_c$; where P_s is the probability of survival, a_s corresponds to a baseline probability of survival of 0.2 ($a_s = -1.38$) and β_s was selected so that in the most extreme landscapes negative density dependence processes at least promoted diversity maintenance

($\beta_s = 0.2$). We also simulated density-dependent mortality with $\beta_s = 0.4$ and 0.05 to test for this parameter sensitivity.

Experimental design

Our experimental design consisted in varying number of plants from 200 to 2500, scale of plant aggregation from 10 to 170 m and species identities autocorrelation ($\rho=0$ and $\rho=1$). In total 40 landscapes were evaluated per behavioral scenario. Each landscape simulation was run 15 times (DoE analysis showed variance stabilization at 15 replicates). Since dispersal services provided by frugivores depend on their landscape perception (Cortes and Uriarte 2013), we translated raw landscape characteristics (plant density, aggregation and autocorrelation) into values of bird mobility across the landscape and plant community representation at the scale of bird decision radius (Table 1, Fig. S3).

First, we calculated bird mobility across the landscape as the ratio between frugivores decision radius (200 m) and the minimum distance between clusters of plants ($B_m = \text{decision radius} / \text{mean distance among-cluster distances}$). Values of B_m below 1 indicate that clusters of vegetation are separated beyond the decision radius of birds, and hence, landscape is perceived as fragmented by frugivores. Thus, landscapes with $B_m < 1$ were classified as fragmented, and the contrary for those with $B_m \geq 1$.

Secondly, to assess if plant community was well-represented at the scale of bird foraging decisions (local heterogeneity, hereafter) all plants calculated the diversity of their neighborhood (200 m, hl). Then, local diversity was averaged and normalized by landscape diversity (normalized local diversity = $N_{LD} = \bar{hl} / H_{landscape}$). N_{LD} ranges from 0 to 1. Zero values imply monospecific co-fruiting neighborhoods while values of 1 imply that plant community is well represented at the scale of bird foraging decisions.

Landscapes were classified into three categories of local heterogeneity: low, intermediate and high ($N_{LD} < 0.25$, $N_{LD} [0.25, 0.75]$, $N_{LD} > 0.75$, respectively). Our estimates of local heterogeneity and fragmentation are not an inherent property of landscapes but arise from the interplay between landscape configuration and the specified bird motion parameters. Thus, biological interpretations of results are less dependent on particular distances than on the ratio of the scale of plant aggregation, and the scale at which birds are able to choose what they eat (Table 1).

Data analysis

For each mechanism (*unbiased* and *rare-biased selection*), we evaluated how local heterogeneity and animal mobility across the landscape could modify seed rain outcomes.

Regarding seed availability-seed rain transition, for each landscape we calculated- (1) difference between effective number of species between seed availability and seed rain ($\Delta H'$), (2) whether there had been species loss during dispersal and (3) the relative change in abundance of each species (ΔAb). Since plant species showed very different abundances in the landscape (from 0.75 to 0.02), we normalized their change in abundance by their initial availability as $\Delta Ab_i = \frac{(Ab_1 - Ab_0)}{Ab_0}$. In the seed rain-to-seedling transition we calculated difference between effective number of species ($\Delta H'$). In all cases, for each landscape we firstly calculated average and standard error across repetitions. Then, we obtained mean and standard errors across landscapes with similar levels of local heterogeneity (low, intermediate and high) and fragmentation (1, 0). Besides, within each fragmentation-heterogeneity category we calculated the proportion of landscapes with significant changes in diversity or rare species abundance (according to 0.95 confidence intervals) and species loss.

Results

Impacts of frugivore behavior on diversity maintenance

In the absence of rare-biased selection, we did not observe increments in diversity in the seed rain-seed availability transition in any of our simulated landscapes (Fig. 1, Table 2, $\Delta\text{diversity} > 0$) despite showing contrasting local diversity and permeability to bird movements (Supplementary Fig. S2 and S3). In contrast, in the presence of *rare-biased* selection frugivory fostered diversity whenever animal mobility across the landscape was high and species were well-mixed in the fruiting neighborhood (Fig. 1, Table 2, $\Delta\text{diversity} > 0$).

Landscape characteristics effects on diversity maintenance

In the absence of *rare-biased* selection, diversity in the seed rain depended on both- bird mobility across the landscape and plant community representation at the scale of bird foraging decisions. When bird mobility was high, diversity in the seed rain was maintained in most spatial configurations (Fig. 1, Table 2). In contrast, in fragmented landscapes diversity loss occurred when local heterogeneity was low. Under such conditions diversity significantly decreased in 50% of simulated landscapes (Table 2, $\Delta\text{diversity} < 0$). Moreover, the probability of species loss in the seed rain rapidly increased with low local heterogeneity (Table 2, Species loss).

When birds preferentially consumed locally scarce fruits, only 13% of fragmented landscapes suffered diversity loss. However, diversity was retained due to increased equitativity in the seed rain (25% higher) and not to richness maintenance. Similarly to the unbiased selection scenario, in fragmented and homogeneous landscapes species loss occurred (Table 2, Species loss).

Landscape characteristics effects on species abundances

Changes in diversity in the seed rain were not driven by changes in the abundance of dominant species. In both scenarios and in all simulated landscapes, relative abundance of dominant species remained mostly unchanged while relative abundance of rare species in the seed rain declined in spatially-structured landscapes (Fig. 2, black bars, Table 2). Preferential consumption of rare fruits caused rare species over-representation in the seed rain in 80% of landscapes with high frugivores' mobility and local heterogeneity. However, rare-biased selection was not able to prevent under-representation of rare species in the seed rain when plants were located in monospecific neighborhoods and animal mobility was low (Table 2).

Seed rain to seedling transition

In both scenarios (*rare-biased* and *unbiased selection*), density dependent mortality always promoted diversity enhancement in the seedling community. These effects were stronger in well-mixed and fragmented landscapes (25% and 7% higher respectively, Fig. 3). Different values of beta parameter (β_s), which dictates the strength of density dependent mortality, did not vary the observed pattern (Supplementary, Fig. S4).

Discussion

Seed dispersal is an important process driving the spatial structure and diversity of plant communities by mechanisms such as colonization-competition trade-offs (Tilman 1994), density-dependent processes (Janzen-Connell hypothesis, Janzen 1970, Connell 1971), ameliorating competitive exclusion (Pacala and Levin 1997), and incorporating species from the regional pool (Cadotte 2006, Myers and Harms 2009). However, the role of frugivores as potential promoters of plant community diversity via

rare-biased fruit selection has not been studied until recently (Carlo and Morales 2016), and remains theoretically unexplored.

Contrary to our expectations, *unbiased selection* did not increase diversity in the community of dispersed seeds in any of our simulated landscapes. This suggests that in the absence of *rare-biased selection*, frugivores are not able to promote diversity in the seed rain even under very favorable conditions (i.e when the density of birds is high, co-dispersal of different species occurs, and disperser mobility across the landscape is ensured). In contrast, when birds were attracted to locally scarce fruits, we found increased diversity in the seed rain. These findings point out that, preferential consumption of uncommon fruits is needed to enhance the diversity of the seed rain, supporting the idea that *rare-biased selection* can play a crucial role in plant species coexistence (Carlo and Morales 2016).

In the absence of fruit-selection, the composition of the seed rain was mainly determined by the spatial structure of landscapes. The spatial distribution of plants can have a dual effect, one determining how easily birds can move through the landscape, and another affecting the species mix at the scale of frugivores' foraging decisions. When landscapes were fragmented, and had high aggregation of plant species, there was a decrease in diversity and even species loss in the seed rain. Low animal mobility and clumped distribution of species constrained the probability of plant-animal encounters, and hence, uncommon species become more dispersal limited (see Morales and Vazquez 2008 for similar results in the context of plant-frugivore networks). In contrast, in well-mixed systems in which most fruit resources were available at the scale of frugivores' foraging decisions neither diversity reduction nor species loss occurred. This suggests that plant communities well represented at the scale of frugivores'

movement decisions are more resilient to the negative impacts of fragmentation in diversity maintenance.

When frugivores were attracted to locally scarce fruits, diversity enhancement in the seed rain occurred whenever they were able to easily move through the landscape and species were mixed in hetero-specific neighborhoods. Even when landscapes were perceived as fragmented, we found loss of diversity in the seed rain in only 13% of our simulations. It is important to point out, however, that *rare-biased* fruit selection by itself was not able to prevent species loss in the seed rain of fragmented landscapes with high spatial aggregation of plant species. Under such circumstances, diversity was maintained thanks to an increase in the evenness (25% higher) of the impoverished seed rain community. High spatial aggregation of plant species meant that local neighborhoods were in general more or less homogeneous, and hence, species that were rare at the landscape level were not perceived as locally rare by frugivores. Lower bird densities than those used in our simulations (Carlo and Morales 2008) and higher spatial aggregation of rare species (Condit et al. 2000) would accentuate limitations in seed dispersal for rare plant species.

As expected, density-dependent mortality acted as a stabilizing force in the seed to seedling transition (*sensu* Chesson 2000) increasing diversity in all simulated landscapes. The net effect of this mechanism depended on the spatial configuration of plants. On one hand, landscape homogenization at the scale of dispersers' movement decisions decreased the "advantages of the rare" because both rare and common plants suffered high intra-specific competition. As a result, diversity enhancement was 25% lower than in well-mixed systems (Figure 3). On the other hand, landscape fragmentation had positive effects on diversity. Though these findings could appear

counterintuitive, they reflect the effects of fragmentation on frugivores' movements. In fragmented landscapes, birds moved more within clusters of vegetation, leading to more aggregated seed-deposition patterns. Consequently, seeds suffered higher density-dependent mortality (see Sasal and Morales 2013 for similar results). It should be noted, however, that positive effects of fragmentation may not be sustained at the sapling stage since the probability of survival is expected to be lower in seedlings close to conspecific trees (between 13 and 58% lower Comita et al. 2014).

It has been advocated that landscape effects on plant-frugivore outcomes are scale-dependent, and consequently, landscape properties should be evaluated from the dispersers' perspective (reviewed in Cortes and Uriarte, 2013). Similarly to fragmentation effects, which depend on the balance between the scale of animal mobility and distances between clusters of vegetation (Saura 2011), here we show that rarity confers advantages during recruitment only when it occurs at the scale of dispersers' foraging decisions.

Conclusions

Three main points emerged from our simulations- (1) *rare-biased* frugivory is needed to increase diversity in the seed rain; (2) but it cannot always override the negative effects of landscape fragmentation, and (3) rarity will confer advantages during dispersal only if it occurs at the scale of dispersers' movement decisions. In sum, our theoretical explorations support recent empirical work that highlights the importance of frugivory as an early-stage diversifying mechanism (Carlo & Morales 2016). A better understanding of the behavioral mechanisms determining frugivores preferences for rare species and quantifying its effects in community recruitment will provide valuable

information on the capacity of plant communities to maintain diversity under global change scenarios.

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References

- Allen, J. A. 1988. Frequency-Dependent Selection by Predators — *Philos. T Roy. Soc. B.* 319: 485-503.
- Allen, J. A. et al. 1998. The influence of density on frequency-dependent selection by wild birds feeding on artificial prey. — *P Roy. Soc. Lond. B Bio.* 265: 1031-1035.
- Cadotte, M. W. 2006. Dispersal and species diversity: A meta-analysis. — *Am. Nat.* 167: 913-924.
- Carlo, T. A. 2005. Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. — *Ecology* 86: 2440-2449.
- Carlo, T. A. and Aukema, J. E. 2005. Female-directed dispersal and facilitation between a tropical mistletoe and a dioecious host. — *Ecology* 86: 3245-3251.
- Carlo, T. A. et al. 2007. Plant-frugivore interactions as spatially explicit networks: integrating frugivore foraging with fruiting plant spatial patterns. — In: Dennis, A. J. S., E. W.; Green, R. J.; et ál. (ed), *Seed dispersal: theory and its application in a changing world* pp. 369-390
- Carlo, T. A. and Morales, J. M. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. — *J. Ecol.* 96: 609-618.
- Carlo, T. A. and Morales, J. M. 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. — *Ecology* 97: 1819-1931.
- Church, S. C. et al. 1997. Does prey dispersion affect frequency-dependent predation by wild birds? - *Oecologia* 111: 292-296.
- Comita, L. S. et al. 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. — *J. Ecol.* 102: 845-856.
- Condit, R. et al. 2000. Spatial patterns in the distribution of tropical tree species. — *Science* 288: 1414-1418.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. — In: PJ den-Boer, G. G. (ed), *Dynamics of Populations. Cent. Agric.*, pp. 298–312.
- Cooper, J. M. and Allen, J. A. 1994. Selection by wild birds on artificial dimorphic prey on varied backgrounds. — *Biol. J Linn. Soc.* 51: 433-446.
- Cortes, M. C. and Uriarte, M. 2013. Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. — *Biol. Rev.* 88: 255-272.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. — *Annu. Rev. Ecol. Syst.* 31: 343-366.
- Greenbert, R. and Mettke-Hofmann, C. 2001. Ecological aspects of neophobia and neophilia in birds. — In: Nolan V Jr, e. (ed), *Current Ornithology*. pp. 119-178.
- Hampe, A. 2008. Fruit tracking, frugivore satiation, and their consequences for seed dispersal. — *Oecologia* 156: 137-145.
- Herrera, C. M. 2002. Seed dispersal by vertebrates. — In: Herrera, C. M. a. O. P. (ed), *Plant-animal interactions. An evolutionary approach*. Blackwell Science, pp. 185-208.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. — *Am. Nat.* 104: 501-+.
- Jordano, P. 2000. Fruits and Frugivory. — In: Fenner, M. (ed), *Seeds: the ecology of regenerating plant communities*. p. 125.
- Jost, L. 2006. Entropy and diversity. — *Oikos* 113: 363-375.
- Morales, J. M. and Carlo, T. S. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. — *Ecology* 87: 1489-1496.
- Morales, J. M. et al. 2013. Frugivore Behavioural Details Matter for Seed Dispersal: A Multi-Species Model for Cantabrian Thrushes and Trees. — *Plos One* 8:
- Morales, J. M. and Vazquez, D. P. 2008. The effect of space in plant-animal mutualistic networks: insights from a simulation study. — *Oikos* 117: 1362-1370.
- Murphy, M. E. 1994. Dietary complementation by wild birds - considerations for field studies. — *J. Bioscience* 19: 355-368.
- Myers, J. A. and Harms, K. E. 2009. Seed arrival, ecological filters, and plant species richness: a meta-analysis. — *Ecol. Lett.* 12: 1250-1260.
- Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. — *Trends Ecol. Evol.* 15: 278-285.

- Pacala, S. W. and Levin, S. A. 1997. Biologically generated spatial pattern and the coexistence of competing species. — In: D. Tilman, P. K. (ed), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. University Press, pp. 204–232.
- Rey, P. J. 1995. Spatio-Temporal Variation in Fruit and Frugivorous Bird Abundance in Olive Orchards. — *Ecology* 76: 1625-1635.
- Saracco, J. F. et al. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. — *Oecologia* 139: 235-245.
- Sasal, Y. and Morales, J. M. 2013. Linking frugivore behavior to plant population dynamics. — *Oikos* 122: 95-103.
- Saura, S. et al. 2011. Network analysis to assess landscape connectivity trends: Application to European forests (1990-2000). — *Ecol. Indic.* 11: 407-416.
- Schaefer, H. M. et al. 2006. The role of chromatic and achromatic signals for fruit detection by birds. — *Behav. Ecol.* 17: 784-789
- Schupp, E. W. et al. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. In.: *Seed dispersal and frugivory: Ecology, evolution and conservation*, 19-33.
- Sol, D. et al. 2011. Exploring or Avoiding Novel Food Resources? The Novelty Conflict in an Invasive Bird. — *Plos One* 6:
- Terborgh, J. 2012. Enemies Maintain Hyperdiverse Tropical Forests. — *Am. Nat.* 179: 303-314.
- Terborgh, J. et al. 2002. Maintenance of tree diversity in tropical forests. — In: Levey, D. J. et al. (eds), *Frugivory and Seed Dispersal: Ecology, Evolution and Conservation*. CABI, pp. 1-17.
- Thiele, J. C. et al. 2014. Facilitating Parameter Estimation and Sensitivity Analysis of Agent-Based Models: A Cookbook Using Net Logo and R. — *Jasss-the Journal of Artificial Societies and Social Simulation* 17:
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. — *Ecology* 75: 2-16.
- Vellend, M. 2010. Conceptual synthesis in community ecology. — *Q. Rev. Biol.* 85: 183-206.
- Wahaj, S. A. et al. 1998. Control of gut retention time by secondary metabolites in ripe *Solanum* fruits. — *Ecology* 79: 2309-2319.
- Whelan, C. J. et al. 1998. Are bird-consumed fruits complementary resources? — *Oikos* 83: 195-205.
- Zollner, P. A. and Lima, S. L. 1999. Search strategies for landscape-level interpatch movements. — *Ecology* 80: 1019-1030.

Table Legends

Table 1. Summary of experimental design (raw parameters) and parameters that represent landscape perception by dispersers

Raw parameters	Range	Perception parameter	Definition	Landscape classification
Number of plants	200-2500	Mobility (Bm)	Bird decision radius/ average distance among clusters of plants	Bm \geq 1 Not fragmented Bm < 1 fragmented
Aggregation	10-170 m	Normalized local diversity (N_{LD})	Neighborhood diversity* / Landscape diversity	$N_{LD} < 0.25$ low heterogeneity (at scale of bird foraging decisions)
Autocorrelation	0/1			$N_{LD} [0.25, 0.75]$ intermediate het. $N_{LD} > 0.75$ high heterogeneity

*Neighborhood was defined with respect to birds' decision radius.

Table 2. Summary table of the effects of fragmentation and local heterogeneity on the proportion of simulated landscapes with significant changes in diversity (ΔDi), rare species abundances (ΔAb_R) and species loss.

Fruit choice	Fragmentation	Local heterogeneity	$\Delta\text{Di}_{v < 0}$	$\Delta\text{Di}_{v > 0}$	$\Delta\text{Ab}_R < 0$	$\Delta\text{Ab}_R > 0$	Species loss
Unbiased	Fragmented	Low	0.50	0	0.5	0	0.50
		Medium	0.44	0	0	0	0.07
		High	0	0	0	0	0
	Not fragmented	Low	0	0	0	0	0.02
		Medium	0.15	0	0.08	0	0
		High	0	0	0	0	0
Rare-biased	Fragmented	Low	0.13	0	0.32	0	0.44
		Medium	0.11	0	0	0	0.07
		High	0	0	0	0	0
	Not fragmented	Low	0	0	0	0	0
		Medium	0	0.17	0.08	0	0
		High	0	1.00	0	0.8	0