

Linking frugivore behavior to plant population dynamics

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Despite the acknowledged importance of frugivores as seed dispersal agents we still lack a general understanding of the mechanisms by which these animals could shape plant populations and communities. We used a spatially explicit stochastic simulation to explore how frugivore movement decisions interact with landscape properties, thus affecting plant population dynamics through dispersal. The model simulated bird movement, foraging, seed deposition and plant recruitment. We assumed that plants lived only for one season and that recruitment was a function of local seed density. We also considered the effect of perches as non-food landscape features. Our simulation experiments consisted in varying the parameters governing bird foraging decisions in relation to 1) how fruit abundance biased their movement, and 2) how the willingness to visit a plant or perch decreased with distance to current location. Simulated plant population dynamics was strongly influenced by bird behavior. The scale of foraging decisions had a much stronger effect on plant dynamics than biases due to fruit abundance. Birds tended to concentrate their activities in the center of the landscape where plants became more abundant, increasing local competition. The presence of perches reduced this tendency resulting in larger population sizes. The importance of perches highlights the fact that behaviors other than foraging can have a strong impact on the patterns of seed deposition and hence on plant population dynamics. Several recent studies have combined animal movement data with seed retention time in order to predict seed dispersal kernels. These studies usually emphasize the ecological implications of the scale and shape of such kernels. However, our simulation results reveal that movement directionality and the fact that birds moved mostly among plants and perches can have a major impact on plant population dynamics.

Current theoretical work on spatial plant dynamics assumes for simplicity and tractability that all plants within a population have the same dispersal kernel (Bolker and Pacala 1999, Law et al. 2003, North and Ovaskainen 2007). Another important assumption is that of isotropy, meaning that seeds are dispersed in any possible direction (Ribbens et al. 1994). These studies often emphasize the importance of the scale and shape of dispersal kernels and have been quite useful in promoting our understanding of how the interplay between scales of dispersal and competition can lead to different population trajectories through their effects on the spatial distribution of individuals (Bolker and Pacala 1999, Law et al. 2003), and in clarifying the effect of space in species coexistence (Murrell and Law 2003). However, these assumptions about dispersal are challenged by field data (Levey 1988, Russo and Augspurger 2004, Russo et al. 2006, Schurr et al. 2008, Anderson et al. 2011) which show heterogeneity and multimodality in dispersal kernels, especially when such kernels are generated by frugivorous animals.

For many plant species frugivores move seeds away from the parent plant affecting how seeds are deposited in space (Herrera and Jordano 1981, Herrera 2002) and generating the templates for plant recruitment (Schupp and Fuentes

1995, Nathan and Muller-Landau 2000). Often, frugivores show complex behavioral patterns which translate into seeds being more likely to be deposited in some places than others (Wenny and Levey 1998, Jordano et al. 2007). Habitat selection, the uses of leks, latrines or sleeping sites can concentrate seed deposition and influence recruitment patterns (Fragoso 1997, Wenny 2000, Russo and Augspurger 2004, Santamaría et al. 2007, Whelan et al. 2008, Rodríguez-Pérez et al. 2011). For example, frugivorous birds use perches for vigilance, resting, shelter, and to maintain territory or attract a mate (Wenny and Levey 1998, García et al. 2010). Thus, perches may receive a disproportionate number of seeds after repeated use by frugivores.

Clearly, seed deposition patterns by frugivores would depend on their movement decisions (Schupp 1993, Jordano and Schupp 2000, Cousens et al. 2010). Relevant behavioral processes include habitat selection at different scales, post-feeding microhabitat use and the directionality and rate of movement away from the fruiting plant (Herrera 1985). These processes would interact with landscape structure such as the abundance and distribution of fruit-resources (Levey 1988, Loiselle and Blake 1991, Rey 1995) and non-fruit resources like sitting perches (Wenny and Levey 1998, Deckers et al. 2008). Therefore, the behavior

of frugivorous animals with respect to the spatial and temporal distribution of resources together with other landscape features such as perches should be taken into account to link seed dispersal with plant recruitment.

The complexity of the process and the time-scales involved makes the task of empirically relating frugivore behavior with seed dispersal and plant population dynamics a difficult one indeed (Wang and Smith 2002, Russo et al. 2006). Mechanistic models of seed dispersal that incorporate realism to the process have improved our ability to predict dispersal (Nathan and Muller-Landau 2000, Cousens et al. 2010). Mathematical or simulation models are useful tools to estimate seed trajectories from its origin to recruiting site, allowing us to develop and test our understanding of the process affecting the seed dispersal cycle. When we ask long-term questions, such as how seed dispersal will affect vegetation structure over 10, 50 or 100 generations, it is really necessary to use some modeling approach. Although models require more assumptions than empirical measures of dispersal, they can be applied to larger spatial and temporal scales and to different landscape configuration and be used to gain insight about the relative importance of different processes (Grimm and Railsback 2005).

Recently, Morales and Carlo (2006) developed a spatially explicit stochastic model to simulate frugivores feeding on fruit and dispersing seeds in a plant population. This model is based on rather simple behavioral rules where simulated animals bias their movements toward plants with more fruits and – all things being equal – prefer to visit nearby plants rather than distant ones. The main result from this theoretical work is that seed dispersal depends strongly on the spatial distribution of plants (Morales and Carlo 2006, Carlo and Morales 2008). Plants in denser fruiting neighborhoods would experience higher fruit-removal rates compared to more isolated ones (although fruit-removal could saturate or even decrease at very high densities). Furthermore, dispersal distances are predicted to be shorter for plants in dense neighborhoods, while isolated plants would often show longer and fatter dispersal tails.

Several field studies have documented how fruiting plant neighbors affect fruit-removal rates by creating facilitation or competition among plant neighbors that share frugivores (Manasse and Howe 1983, Sargent 1990, García et al. 2001, Carlo 2005, Saracco et al. 2005, Blendinger et al. 2011). The effects of neighborhoods and crop size on seed dispersal distances are notably harder to investigate. Consistent with theory, a recent study of mistletoe dispersal by a marsupial found that mean dispersal distance decreased for plants growing in dense neighborhoods (Morales et al. 2012). Also, it is important to note that many studies of seed rain (i.e. seed deposition) indirectly document neighborhood effects on dispersal. Dispersal of zoochorous plants is contagious and patchy (Schupp et al. 2002), with both seed rain and plant recruitment usually increasing in areas where fruiting resources are more dense or diverse (Howe and Smallwood 1982, Aukema and Martínez del Río 2002, Fragoso et al. 2003, Kwit et al. 2004, Hampe et al. 2008).

As mentioned above, these theoretical and empirical findings are at odds with the way seed dispersal is represented in theoretical plant population dynamics models. Despite

the importance of frugivores as seed dispersal agents, we still lack a general understanding of the mechanisms by which these animals potentially shape plant populations and communities. It is not immediately clear how the interplay between frugivore behavioral decisions and the spatial distribution of plants would unfold over time in a plant population. Seed dispersal will affect future plant spatial distribution, which in turn will influence frugivore movement decisions, and hence the pattern of seed deposition in the following generations. The dependence of dispersal on the spatial distribution of plants can have important consequences for plant population dynamics but as far as we are aware these effects have not been studied. Our aim here is to fill this gap using a simulation model in order to gain insights about the interplay between frugivore behavior and plant population dynamics.

Here we extend the simulation model of Morales and Carlo (2006) of frugivorous birds foraging in a spatially explicit landscape closing the dispersion cycle including post-dispersal plant recruitment as a function of local density and considering the effect of perches as non-fruit features in the landscape. Even though the model was developed for frugivorous birds, it can be argued that the general processes should be applicable as a first approximation to other fruit-eating animals.

Several aspects of frugivore behavior and physiology can affect dispersal. In their extensive sensitivity analysis, Morales and Carlo (2006) found that mean dispersal distance was mostly affected by parameters controlling perching time and gut passage time but also by the degree of plant spatial aggregation. Furthermore, the number of frugivores in a landscape was an important determinant of the shape of the dispersal kernel. However, here we are mostly interested in behavioral features that relate directly to the way animals respond to the spatial structure of the plant population and the presence of non-fruiting features such as perches. We decided to keep gut passage and perching time distribution as well as other model properties at baseline parameter values in order to explore the effects of movement bias due to distance and fruit abundance. Our simulation experiments consisted then in varying the parameters governing bird foraging decisions in relation to 1) how fruit abundance bias their movement, and 2) how the willingness to visit a plant or perch decreased with distance from current location to such plant or perch. Finally and to test the importance of lack of isotropy and directionality in dispersal we ran simulations where seed dispersal distance was resampled from observed distances in the bird-dispersal models, but with dispersal direction set at random. These simulations represent the case where some aspects of seed dispersal by animals such as dispersal distances are taken into account (say from animal tracking and observations) but a simplistic assumption is made regarding directionality.

Given that frugivore movement decisions interact with plant spatial distribution and with other landscape features, we expect that: 1) increased selectivity for fruit abundance will result in seeds being spread more evenly in space and hence in reduced plant competition. Similarly, 2) if bias towards plants decreases slowly with distance, frugivores could cover large areas while foraging, again reducing plant

competition. And 3), the presence of perches in the landscape could also serve to modify frugivore space use and hence the patterns of seed deposition and plant competition.

Methods

We modified Morales and Carlo (2006) plant–frugivore simulation model to study the effects of disperser behavior on plant population dynamics. The model is a spatially explicit, event-driven, stochastic simulation which represents plant spatial location, fruit production, bird foraging and movement, seed dispersal and plant recruitment for an annual plant. Our choice of functional forms and parameter values was guided by bird behavioral observations and data reported in literature, although some aspects were chosen for simplicity and flexibility. We model bird and plant populations in general and none in particular, so we used general functions for competition, probability of establishment, fruit production, etc.

Initial plant distribution and fruit production

The simulated landscape was defined for simplicity as consisting of a single annual plant species and fixed perches. We started the simulation by placing 1000 plants at random on a 100×100 m area. Each plant started bearing 100 ripe fruits, which was the maximum crop possible. Each fruit had one seed; hence fruit-removal was equivalent to the number of dispersed seeds. At the end of each simulated day, every plant could produce up to 50 new ripe fruits according to a regrowth model (see Morales and Carlo 2006 for details). We assumed that plants produced fruits during 30 days, which was considered as one fruiting season. Simulated landscapes also included a variable number of perches (see (Simulation experiments) below) which increased spatial structure. Perches represented structures such as dead trees or posts on which birds could alight in order to rest or to perform other activities other than foraging. These perches, unlike the fruiting plants, were fixed in space over time producing a landscape feature with a rate of change much slower than that of annual plants.

Frugivory and gut passage time

Simulated birds spent a variable amount of time at each visit to a fruiting plant or perch sampled from a Gamma distribution (shape 4, scale 1.25) with a mean time of 5 min. This function produced visiting times similar to those reported by field studies of frugivorous birds (Carlo and Aukema 2005). Fruit consumption followed a hyperbolic functional response, but was kept within the limits of gut size. Bird gut had a capacity of 15 fruits/seeds (Murphy et al. 1993). Every time a frugivory event occurred, the fraction of gut filled and the number of available fruits at the focal plant were updated. The maximum number of fruits eaten per visit was 10, which was based on observations by Carlo (2005) on *Mimus*, *Tyrannus* and *Turdus* birds feeding on *Solanum* spp. and *Cestrum* spp. plants. After ingestion, gut passage time was sampled from a Gamma distribution with parameters chosen to broadly match seed gut-passage rates

reported for several frugivorous bird species (Wahaj et al. 1998) with a mean time of 35 min (shape 2.8, scale 12.7). For simplicity, all seeds from a frugivory event had identical gut passage time. Seed defecation by birds was dictated by gut passage time, irrespective of whether the animals were perching or flying.

Foraging decisions and bird movement

Our simulated frugivores moved among plant or perches, as it is usually observed in real birds (Howe and Vande Kerckhove 1980, Murray 1987). In our model this movement allowed two kinds of basic behaviors: feeding and not feeding such as resting, territory holding, singing, etc. Once visiting time at a plant or perch expired, birds had to decide where to move. When choosing where to move next, birds sampled from a destination distribution (B), that combined the effects of distance from current location to all potential future destinations, fruit abundance, perch quality and gut fullness:

$$\beta_j = \left(\tanh(-\kappa d_j^2) + 1 \right) \times \left((1-G) \tanh(\phi F_j^2) + G Q_j \right) \quad (1)$$

$$B = \beta / \sum_{j=1}^N \beta_j$$

where β_j measures the bias towards the j -th plant or perch given current distance d to it. G is the proportion of the bird's gut currently filled by seeds, F_j is fruit abundance on the j -th focal plant and Q_j is a measure (between 0 and 1) of the plant or perch quality as a place for resting, singing, scouting, etc. Note that birds balanced the importance of fruit abundance depending on gut fullness. When G is close to 1, the contribution of F to β vanishes and Q becomes more relevant. The opposite occurs when G is close to zero. For all simulations we set $Q = 1$ for perches and $Q = 0.5$ for plants, this enables birds to differentiate the two landscape features and their functions: perches for resting or other activities and plants for feeding. Finally, κ and ϕ are parameters that govern how fast bias changes with distance and fruit abundance respectively. As we sought to understand how movement decisions could impact on plant populations, we focused on these two parameters in our simulation experiments. For simplicity, we assumed that birds moved between plants and perches in straight lines and at a constant speed of 6 m s^{-1} (Marcum et al. 1998). All birds in a simulation had identical parameter values and hence reacted in the same way to fruit abundance, number of fruits per plant, etc.

Plant recruitment

The simulator recorded the spatial coordinates of each dispersed seed. Once the dispersal phase ended, seed survival probability was calculated as a function of seed density using a Gaussian competition kernel (Law et al. 2003), where the influence of neighboring plants decreases with distance d as $\exp(-d^2/2\sigma^2)$. Surviving seeds then grew and matured to produce fruits during the following generation. Thus, our simulation model allowed for the spatial distribution of plants to affect how birds moved and foraged in

the landscape. Bird movement, in turn, determined the patterns of seed removal, dispersal and the spatial distribution of dispersed seeds, which then determined the degree of competition among growing plants and hence the spatial distribution of the next generation of fruiting plants.

Simulation experiments

We performed simulation experiments to assess how disperser movement decisions could interact with landscape structure and affect plant population dynamics. As detailed in ‘Foraging decisions and bird movement’ above, our simulated birds based their movement decisions on fruit abundance and distance to potential destinations. We changed the parameter ϕ in Eq. 1 so that movement bias was maximized at different fruit abundances. Thus, we changed how sensitive the birds were to differences in the fruit crops of individual plants when making their movement decisions. We also manipulated parameter κ in Eq. 1 so that bias due to distance to a potential destination was reduced to a small value (0.05) at different distances. In essence, these values of κ resulted in simulated birds making their foraging decisions at three different spatial scales.

Following a factorial design, we considered three levels of scales of bird foraging decision (about 190, 60 and 19 m) and three levels of bias due to crop size (maximized at 90, 30 and 10 fruits). This factorial design was repeated in three types of landscapes differing in the number of perches available (0, 50 and 100) reflecting varied levels of ‘exogenous’ or ‘fixed’ landscape structure. For each combination of factors, we ran 10 replicates of 100 plant generations. Landscapes started with 1000 plants distributed at random and 10 birds sitting at randomly chosen plants. When perches were present, they were randomly placed in the landscape. For each replicate we tracked changes over time in mean seed dispersal distance and population size. To quantify the relative effects of the scale of foraging decision and bias due to crop size on dispersal distance and population size, we used a two-way ANOVA model with fixed effects, and then partitioned the variance separately for each landscape.

Comparison with random dispersal

An important characteristic of seed dispersal by animals is local seed aggregation (Schupp and Fuentes 1995, Schupp et al. 2002, Russo and Augspurger 2004), in the case of birds seeds are clustered around foraging plants and perches (García 2001). For birds, this pattern is the natural consequence of animals moving mostly among plant and perches (Graham 2001, Wenny 2001). To evaluate the importance of this effect of frugivore behavior, we ran simulations where seed dispersal distance was resampled from observed distances in the bird-dispersal models, but with dispersal direction set at random. We kept the total number of dispersed seeds per generation equal to the maximum observed in the bird-dispersal simulations (ca 5500 seeds).

Results

Simulated plant population dynamics was strongly influenced by bird movement behavior (Fig. 1). Variation partition

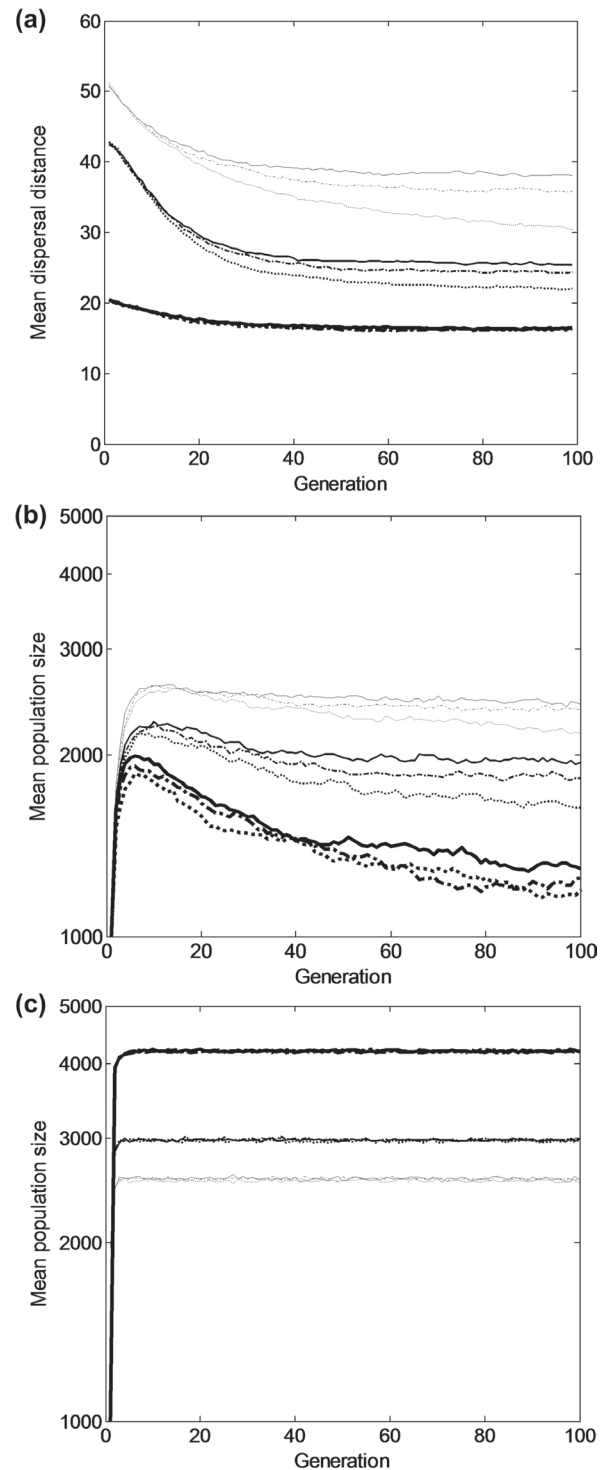


Figure 1. (a) Mean dispersal distance along generations for different frugivore scales of movement decisions. Population size along generations for (b) full model including simulated bird foraging and seed dispersal, and (c) reduced model where dispersal distance was resampled from the full model output but dispersal direction was random. Thin lines corresponded to a scale of movement of 190 m, medium width lines to 60 m, and thick lines to 19 m. Black continuous lines were for landscape with 100 perches, dark grey long-dashed lines for landscapes with 50 perches, and light grey dashed-lines for landscapes without perches. Data shown corresponds to the average of 10 replicate runs of each combination of parameters and number of perches.

indicates that in all landscapes, the scale of foraging decision had a much stronger effect on seed dispersal distances than biases due to fruit abundance at plants. The scale of foraging decision explained 94.2% of the variability in the final mean dispersal distance for landscapes with no perches ($ss = 3290.4$, $F_{2,81} = 701.3$), 99.3% for landscapes with 50 perches ($ss = 5785.9$, $F_{2,81} = 6150.7$), and 99.5% in landscapes with 100 perches ($ss = 7190.0$, $F_{2,81} = 8261.2$). Bias due to fruit abundance and its interaction with the scale of movement explained less than 1% of the variability in mean dispersal distance on each landscape.

In general, mean dispersal distance was higher at the start of the simulation (i.e. first generations) when plants were randomly distributed (Fig. 1a). Then, it decreased with time and reached relatively stable values depending on parameter κ , which controlled the scales of movement decisions (Fig. 1a). For a given value of the parameter κ , mean dispersal distance was always relatively larger in landscapes with 100 perches, intermediate with 50 perches and lower with no perches (Fig. 1a).

Variation partition also indicates that in all landscapes, the scale of foraging decision also had a stronger effect on plant population size than biases due to fruit abundance at plants. The scale of movement decision explained 90.5% of the variability of the population size in the landscapes with no perches ($ss = 16892175$, $F_{2,81} = 419.5$), and 97.6% of the variability of the population size for landscapes with 50 perches ($ss = 19094468$, $F_{2,81} = 1678.9$), and 97.4% for landscapes with 100 perches ($ss = 20329929$, $F_{2,81} = 1606.2$). Bias due to fruit abundance and its interaction with the scale of movement explained less than 1% of the variability in plant population size on all landscapes.

In all landscapes, plant population size increased during the first few simulated generations, peaked and then started to decline (Fig. 1b). As the scale of movement decision increased, plant populations peaked at higher values, declined at slower rates, and had higher numbers at the end of the simulations (Fig. 1b). For each scale of movement decision, population size was comparatively larger in landscapes with 100 perches, intermediate with 50 perches and smaller without perches (Fig. 1b).

Simulations where we used seed dispersal distances from the full simulation model but set dispersal direction at random produced plant populations that quickly stabilized at different sizes depending on the scales of bird movement decision (Fig. 1c). In all cases these values were much larger than the corresponding full bird dispersal simulations. No noticeable differences were found due to the presence of perches (Fig. 1c). The pattern of increased population size with increasing scales of movement was reversed as plant populations were largest for the small scales of movement decisions (Fig. 1c).

Plant spatial distribution at generation 100 was visibly different as we changed parameter κ , which controlled the scales of movement decisions (Fig. 2). The clumped spatial distribution increased with decreasing scale of movement and the area covered by plants varied with landscape structure (Fig. 2). In landscapes with 100 perches, plants covered larger areas than landscapes with 50 perches and plants only (Fig. 2).

Discussion

Understanding the relationship between frugivore movement, seed dispersal, and plant dynamics should contribute to the general goal of linking the behavior of organisms to population and community dynamics (Morales et al. 2010). Our simulation experiments show how plant population dynamics can be controlled by frugivore behavioral rules as they interact with plant spatial distribution and other landscape features such as perches. Bird movement decisions were simulated by first computing biases towards all potential destinations (plants or perches) combining the effect of distance, number of fruits, perch quality and gut fullness, and then sampling from the distribution of such biases. Our experiments consisted in varying parameters κ and ϕ which govern how quickly biases change with distance and fruit abundance respectively. We did not find any meaningful effect of changes in the strength of movement bias due to fruit abundance (ϕ) for the scenarios considered here, this could be because in our simulations we work with a low number of frugivores (i.e. 10) and with a lot of plants (i.e. initially 1000), which had a large capacity to replace removed fruits (maximum fruit maturation was 50) so dispersers always found plants with many available fruits. However, preliminary explorations (results not shown) with reduced fruit production and a large number of frugivores suggest that the effect of bias due to fruit abundance is more subtle than that of the scale of movement decisions. Consequently the following discussion deals mainly with the effects of changing the scale of movement decisions due to changes in the bias parameter (κ). As we changed this parameter in different scenarios, we obtained different values of mean dispersal distances (Fig. 1a) and also different plant population sizes (Fig. 1b).

Mean dispersal distances were larger during the first generations, when plants were randomly distributed in the landscape (Fig. 1a). Then, as simulated birds dispersed seeds, plants became more and more aggregated in space and dispersal distance decreased over generations. Interestingly, plant population size increased during the first few generations even though mean dispersal was decreasing. After the initial increase in size, populations then peaked and started to decline (Fig. 1b). This decline was due to a combined effect of reduced mean dispersal distance (hence stronger local competition) and because birds concentrated their activities in the center of the landscape where plants were more abundant. The presence of perches in the landscape attenuated this latter effect as birds would often visit perches near the landscape edge (Fig. 2). Thus, the addition of perches in the simulation arena while holding other things equal resulted in increased mean dispersal distances and larger plant populations.

The progressive concentration of plants within the simulated area and the dramatic effects of the scales of movement decisions are a consequence of our simulated animals moving only among plants or perches. Accordingly, seeds were deposited either under plants or perches or (more rarely) somewhere in the route among plants or perches. In essence, some areas of the landscape became empty as they became outside the movement paths of frugivores.

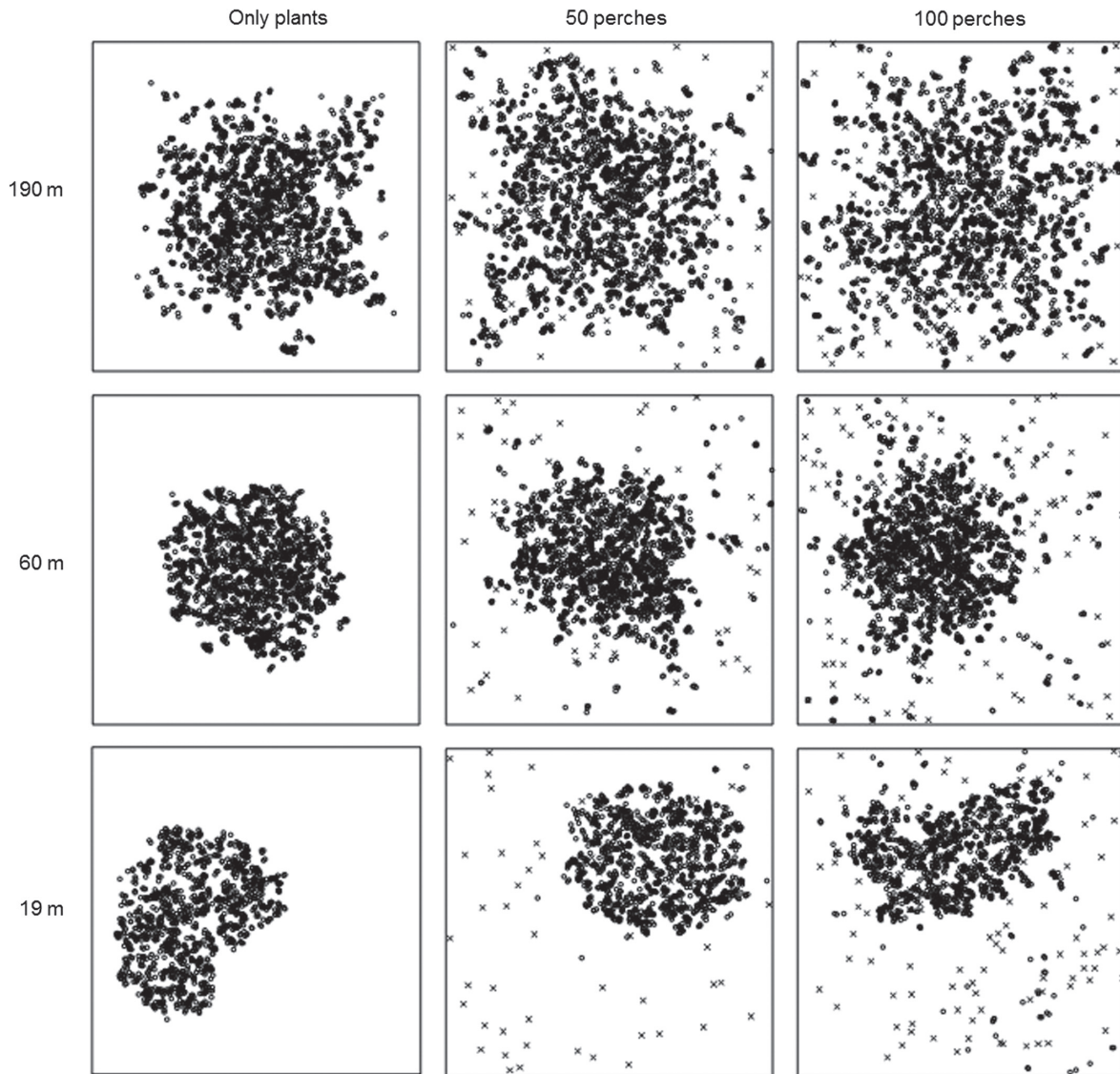


Figure 2. Final spatial distribution of plants (o) and perches (x) for scales of movement of 190 m, 60 m and 19 m and landscape complexities of only plants, with 50 perches and 100 perches. All simulations started with 1000 randomly located plants and had 10 individual birds foraging for fruits and dispersing seeds. We only show results corresponding to bias due to fruit abundance reaching its maximum at 90 fruits because different values of parameter produced very similar spatial distributions.

Perches being fixed in space through plant generations, gave birds the opportunity to move away from the area where plants were becoming concentrated, extending the plants spatial distribution. Several recent studies have combined animal movement data with seed retention time in order to estimate seed dispersal kernels (Westcott and Graham 2000, Westcott et al. 2005, Spiegel and Nathan 2007, Anderson et al. 2011, Lenz et al. 2011). Such studies usually emphasize the ecological implications of the scale and shape of such dispersal kernels. However, our simulation results reveal that movement directionality and the fact that birds moved mostly among plants and perches can have a major impact on plant population dynamics.

The behavioral rules of our simulated frugivores are quite simple but it is important to note that they result in patterns of seed removal and dispersal consistent with empirical observations. As mentioned in the Introduction,

several studies have documented neighborhood effects on fruit removal (Manasse and Howe 1983, Sargent 1990, García et al. 2001, Carlo 2005, Saracco et al. 2005, Blendinger et al. 2011) while the effects on dispersal distance have been recently confirmed in a mistletoe–marsupial system (Morales et al. 2012).

In nature, birds exhibit spatial memory and usually perform regular movements within their home ranges (Westcott and Graham 2000) generating a non-random seed rain with aggregation in space (Jordano and Godoy 2002, Jordano et al. 2007, Herrera et al. 2011). In our simulations birds had no memory, nor home ranges, nor other complex behaviors which might also have an impact on plant population dynamics. In essence, the importance of perches highlights the fact that behaviors other than foraging can have a strong impact on the patterns of seed deposition and hence on plant population dynamics.

As birds alternate between foraging for fruits and other activities such as performing displays for territory holding, chasing intra and inter-specific competitors, foraging for supplementary resources, etc. the chances of seeds being deposited in places other than directly below plants will increase.

In simulations where we sampled observed seed dispersal distances but set direction at random, population size stabilized quickly and at very different values than those obtained with the full bird foraging model (Fig. 1c). By setting dispersal direction at random, we eliminated the effect of movement directionality and the consequent seed aggregation below plants and perches. Thus, in these simulations landscape features (i.e. perches) did not affect population sizes (Fig. 1c). In effect, these simulations also break the feedback between plant spatial distribution and dispersal distance, thus greatly reducing the transient time needed to reach population stability. Furthermore, population sizes showed a reverse order in relation to the scale of movement decision, with larger population values attained at the shorter dispersal distances. This result was due to the fact that many seeds landed out of the simulated arena when dispersal distance increased. Other boundary conditions could produce different results (results not shown) but the main message of the randomization exercise is that bird behavior influences plant population dynamics not merely through dispersal distances but through the spatial pattern of seed deposition (see similar discussion by Spiegel and Nathan 2010 regarding directed dispersal).

We have simulated bird behavior because they are ideal endozoochorous seed dispersers, highly mobile, typically swallow fruits and seeds intact, and occur nearly everywhere (Whelan et al. 2008). However, other frugivores could also produce similar seed rain patterns where most seeds are deposited under plants or other 'special' places such as latrines, sleeping sites, etc. Spider monkeys produce clusters of dispersed seeds associated with their sleeping sites and their resting places on foraging routes (Russo et al. 2006). Many plant species deposited on Gorillas nests were found to have higher survival than in other sites of the forest (Rogers et al. 1998). Latrines sites of rhinoceros and tapirs also provides recruitment sites (Dinerstein 1991, Fragoso 1997). Clearly, every plant–frugivore system will have its own idiosyncrasies and particularities but our results highlight the fact that when seed dispersal is mediated by frugivores landscape structure and movement bias will have a strong impact on plant population dynamics. Furthermore, the effects on plant dynamics are beyond what is expected due to dispersal distance per se.

Being a first attempt at relating frugivore behavior with plant population dynamics, our simulation model has several simplifying assumptions. Further studies are needed to explore additional complexities of plant–frugivore dynamics. In particular, the presence of other fruiting species in the landscape could have important effects, as the spatial distribution of different fruits could interact with frugivore preference (Carlo et al. 2007). The importance of plant longevity and fruit production should also be explored. Furthermore, our simulation might be overemphasizing competition among seedlings because we have all seeds effectively starting to grow at the same time. In nature however, seeds could start developing soon after

being dispersed so that seeds dispersed earlier might not experience strong competition. Despite these limitations, we believe that our simulations highlight important features of plant population dynamics when seed dispersal is mediated by animals and draw attention to differences with other dispersal systems.

In conclusion, in our simulations we found that frugivore behavior interacts with landscape features affecting plant population dynamics. Frugivore non-foraging behavior and movement directionality impacts strongly on the seed deposition patterns and hence on plant population dynamics. These results can be applicable to other frugivores with their particular behaviors.

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