Frugivores and cheap fruits make fruiting fruitful

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Abstract

Animal seed dispersal provides an important ecosystem service by strongly benefiting plant communities. There are several theoretical studies on the ecology of plant–animal seed–disperser interactions, but few studies have explored the evolution of this mutualism. Moreover, these studies ignore plant life history and frugivore foraging behaviour. Thus, it remains an open question what the conditions for the diversification of fruit traits are, in spite of the multitude of empirical studies on fruit trait diversity. Here, we study the evolution of fruit traits using a spatially explicit individual-based model, which considers the costs associated with adaptations inducing dispersal by frugivory, as well as frugivore foraging behaviour and abundance. Our model predicts that these costs are the main determinants of the evolution of fruit traits and that when the costs are not very high, the evolution of larger fruit traits (e.g. fleshy/colourful fruits) is controlled by the choosiness and response thresholds of the frugivores as well as their numerical abundance.

Introduction

The survival and reproduction of most angiosperm plants highly depend on the ecological dispersal service provided by frugivorous animals (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982; Herrera, 1989). Around 90% of tropical tree species produce fleshy fruits dispersed by vertebrate animals, such as mammals and birds (Jordano, 1992). Frugivores consume fruits produced by the plants and actively disperse their seeds over long distances (Howe & Smallwood, 1982). In this study, we focus on the most widespread biotic dispersal syndrome, endozoochory, where frugivores regurgitate, defecate and release the seeds, although benefiting themselves from the energy and nutrients of the fruits (Herrera, 1989). This mutualistic interaction seems to be responsible for the establishment and radiation of angiosperm plants in terrestrial ecosystems (Howe & Smallwood, 1982; Herrera, 1989; Fleming & Kress,

2011). Frugivores thus represent a predominant selective force on the evolution of flowering plants (Jordano, 1987).

The 'dispersal syndrome' hypothesis argues that evolutionary convergence of fruit traits (e.g. colour, size, aromas, nutrients) in different plant species is driven by a set of similar frugivorous species (Voigt *et al.*, 2004; Lomáscolo & Schaefer, 2010). Therefore, the diversification of fruit traits might be the outcome of different selective pressures from frugivores with different visual/ olfactory perceptions (Kalko & Condon, 1998; Schaefer & Schmidt, 2004; Schaefer *et al.*, 2007, 2008; Valido *et al.*, 2011), social behaviour (Howe, 1989; Russo & Augspurger, 2004; Russo *et al.*, 2006) and/or morphology (e.g. gape width) (Janson, 1983; Flörchinger *et al.*, 2010). However, little is still known about what ecological conditions and evolutionary forces drive the diversification of fruit traits (Bolmgren & Eriksson, 2010; Lomáscolo & Schaefer, 2010). Several studies support the dispersal syndrome hypothesis (Janson, 1983; Gautier-Hion *et al.*, 1985; Voigt *et al.*, 2004), and others reject it (Fischer & Chapman, 1993). Furthermore, there are many empirical studies on fruit diversification stating different hypotheses and predictions that have not been considered in the theoretical literature (Willson & Whelan, 1990; Schaefer *et al.*, 2007;

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Lomáscolo & Schaefer, 2010; Valido *et al.*, 2011). Thus, it remains an open question whether seed dispersal syndromes can explain the evolution of fruit diversity (i.e. diversity in terms of size, colour, nutrient content) (Flörchinger *et al.*, 2010).

To our knowledge, there are few mathematical models specifically dealing with the evolution of animal seed dispersal. There are models that explain the evolution of seed dispersal kernels (Hovestad *et al.*, 2001; Starrfelt & Kokko, 2010), but they do not consider animal-induced dispersal. Moreover, most mathematical models do not consider the trade-offs affecting plant investments in traits promoting frugivory, nor, even more importantly, the consequences of animal behaviour for the quality of the dispersal service. In summary, key features of this mutualistic interaction remain unexplored in theoretical studies investigating their evolutionary dynamics, in spite of their importance for the ecology of angiosperm plants (Herrera, 1989) and evolution of fruit traits (Valido *et al.*, 2011).

In this study, we will investigate the evolution of fruit traits involved in frugivory and dispersal by endozoochory. For this, we will use a simulation model incorporating key aspects of plant life history. This will allow us to assess the effect of different life cycle parameters on population viability and to determine under which conditions frugivory benefits plants and fruit traits can evolve. Our model combines three important features not considered together in previous models. First, by considering the plant's life cycle, we can study the effect of trade-offs related to fruit production costs on plant fitness. Second, the mutualism is treated as a consumer–resource interaction, where the extent of consumption affects the benefits for the plants. And third, it accounts for the effect of density dependence in the cost–benefit balance for the plants. We will study the evolution of endozoochorous adaptations, that is, metric traits that induce or facilitate frugivory, such as fruit size, fruit pigmentation, chemical attractants (Howe & Smallwood, 1982; Gautier-Hion *et al.*, 1985; Willson & Whelan, 1990). On the one hand, the investment in such traits has costs and leads to trade-offs (Eriksson & Jakobsson, 1999; Alcántara & Rey, 2003; Pakeman & Small, 2009). On the other hand, aspects of frugivore behaviour, such as choosiness and the threshold to respond to fruit traits, and seed release patterns, will determine whether such investments contribute to plant fitness (Russo *et al.*, 2006).

Model and methods

Statement of the problem

Consider a fruit-producing species. There are three paths on the plant's life cycle that cause population changes from one year to the next: survival of adult trees (path '0'), recruitment from fruits not consumed by frugivores (path '1') and recruitment from fruits consumed by frugivores (path '2'). The plant's growth rate would be:

$$R = \underbrace{p}_{"path\ 0"} + f\Big[\underbrace{(1-c)g_1}_{"path\ 1"} + \underbrace{c\epsilon g_2}_{"path\ 2"}\Big] \qquad (1)$$

where P is the annual survival probability of an adult tree, f is the number of fruits made by a tree in a year, each containing a single seed, c is the probability that a fruit is eaten by a frugivore and ϵ is the probability that a seed survives the frugivore treatment (e.g. gut passage, seed handling). The quantity in brackets is the average seed survival probability from paths '1' and '2'. The probability that a seed from path $i = 1, 2$ survives and develops into an adult tree is g_i. Several hypotheses (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982) argue that seeds dispersed by frugivores have higher chances to become adults, that is, $\epsilon g_2 > g_1$, otherwise frugivory would not have any benefit at all and should be avoided instead.

If frugivory is beneficial because of seed dispersal, then we should expect c to simply evolve towards larger and larger values such that average seed survival and thus fitness increases. This is a necessary condition for frugivory to evolve, but it is not a sufficient condition. Traits that affect attractiveness of the fruit to frugivores, such as their size, nutrient content or pigmentation that makes them more visible, are also expected to be costly in terms of energy and resources that could instead be directed towards making more fruits. In addition, the response from the frugivores towards such traits also depends on the frugivore abundances, physiology and foraging behaviours, thus making plant investments range from highly profitable to unrewarding.

Fitness optimization is further complicated because of the spatial context where dispersal takes place, because this affects the survival probabilities g_i in intricate ways. The chance of a seed becoming an adult depends on several contingencies such as finding and securing space that is free from other plants, the densities and distances from other plants that compete for resources such as light, and the number of seeds against which a seed can potentially compete during its development. This means that the g_i are variable both in space and in time. In addition, seeds dispersed by frugivores may encounter seeds not dispersed by them, so the independence of paths 1 and 2 suggested by Fig. 1 and eqn 1 is not the most general scenario, and the probabilities g_1 and g_2 are conditional on the amount of overlap caused by the pattern of frugivore dispersal.

To study the evolution of traits that the plants use to profit from animal dispersal services, we therefore constructed an individual-based model. In the next two sections, we first explain the mechanics of the model in space and time, and then we give the details about the
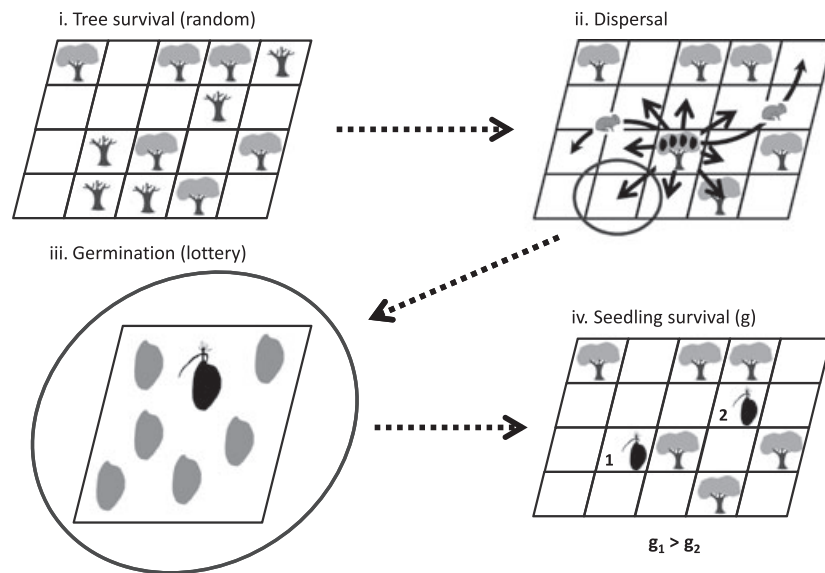
Fig. 1 Sequence of events in the spatially explicit model of seed dispersal. (i) Adult tree survival: according to annual survival probability P some adult trees survive (trees with leaves) or die (trees without leaves), (ii) passive and animal seed dispersal: each tree disperse their seeds passively to the nearest neighbour cells and actively to different cells in the lattice by frugivores, (iii) lottery competition: seed germination in a patch occurs by lottery competition, that is, the more abundant phenotype (e.g. small-seed phenotype) has a higher probability of germination and (iv) seedling survival: once lottery competition is completed, we evaluate the probability of seedling survival (black seeds) in each patch. Seedling 1 has higher probability of survival than seedling 2 ($g_1 > g_2$) because seedling 1 has fewer surrounding tree neighbours than seedling 2.

trade-offs relating fruit traits with fruit production and foraging behaviour of the frugivores.

Spatially explicit individual-based model

We model space as a lattice of $n \times n$ sites with absorbing boundaries. Figure 1 describes the events that can take place in this spatial context, and Table 1 lists the variables and parameters involved. A site can be empty or occupied by at most one tree with a phenotype or trait value z. At the start of year t, a tree survives death with probability P. Trees produce seeds and with a probability m the trait of a seed can mutate, changing its value to $z + \delta$, where δ is a normally distributed mutational step with mean zero and standard deviation σ. The trait value, changed or not, determines the number of fruits f of a tree and the proportion of fruits c that will be eaten by frugivores. The dependence of f and c on the trait z is explained in the next section 'Fruit production costs and frugivore foraging behaviour' (eqns 4 and 7), and the number of fruits is discrete ($f = 1, 2, 3, \ldots, \phi$). We assume that there is one single seed per fruit.

Seed dispersal takes place in two different ways. By passive dispersal, for example by gravity or wind, $(1-c)f$ seeds from a tree disperse evenly to the eight neighbour sites (Moore neighbourhood). By active dispersal, that is, by frugivores, $cf\varepsilon$ seeds disperse across the landscape, where ε is the fraction of seeds that survive

Table 1 Variables and parameters employed in the simulation model.

Quantity	Definition	Default values
z	Trait value, for example fruit size or pigmentation	$0 < z < 1$
$f(z)$	Number of fruits per tree, discrete variable	$\{1, 2, \ldots, \phi\}$
ϕ	Maximum value of f	100
θ	Cost parameter. Low (high) value means costly (cheap) trait	0.5, 2
$c(z)$	Fraction of fruits eaten by frugivores	$0 < c < 1$
ε	Fraction of seeds surviving frugivory	0.9
A	Frugivore abundance	10, 100
ρ	Frugivore choosiness	10
ζ	Frugivore response threshold	0.5
κ	Number of sites where the seed of a tree is released	5
p	Adult tree survival probability	0.5
g_0	Maximum of seed-to-tree survival (i.e. germination) probability	1
α	Effect of adjacent trees on seed survival	0.01
P	Number of trees is the neighbourhood of a site	$\{1, 2, \ldots, 8\}$
m	Probability of mutation on z per tree per year	0.0001
σ	Standard deviation of mutational changes in z	0.025
n	$n \times n$ gives the number of lattice cells	100

frugivore treatment (scarification, digestion, etc.). For each tree, the frugivores release their seeds at k randomly and independently chosen sites. We explored

two types of seed dispersal behaviour related to quality of service (Schupp, 1993): (i) seed dispersers only release seeds to sites without trees (empty/unoccupied patches) and (ii) they release seeds to any site (free or occupied by a tree). In the main text, we only focus on behaviour (1), and we explored the differences between both behaviours in the Appendix. We assume that $k < cf\varepsilon$ because the number of fruits per tree is discrete and much lower than the number of sites ($f \ll n \times n$), so a tree cannot spread all its seeds across the entire landscape because this leads to fractioned seed numbers per site. Seed release patterns can range from clumped (small k values) to scattered (large k values).

At each site, a single seed is chosen for further development into a tree. The phenotype of the winning seed is decided by simple lottery, where the probability of a given phenotype winning is equal to its frequency (i.e. proportion of seeds having the phenotype). If the site happens to be already occupied by a tree (this only happens when seeds are dispersed passively), then nothing else happens and the winner is wasted. If the site happens to be empty, then the chances of the winner becoming a tree in year $t + 1$ depend on the number of trees P ($= 0, 1, \ldots, 8$) in the eight neighbouring sites according to the formula $g = g_0 \exp(-\alpha P)$, where g_0 is a density-independent maturation rate and α is a coefficient giving the strength of density dependence. This assumption reflects the Janzen–Connell effect (Janzen, 1970; Connell, 1971) whereby a higher density attracts a disproportionate number of host-specific seed predators or pathogens.

The equilibrium of the simulations was checked by estimating whether there were significant differences between replicates of thirty simulations for different parameter combinations and by extending the simulation time to 20 000 generations. We found that a simulation time of 10 000 generations was always enough to reach an equilibrium.

Fruit production costs and frugivore foraging behaviour

Some adaptations are more costly than others, so the number of fruits per tree may depend on the fruit trait under selection in different ways. For example, following Smith & Fretwell (1974), suppose that there is a fixed amount of resources Q per plant set aside for the production of mesocarp, and z is the mass or volume of mesocarp per fruit. Fruits with more mesocarp will be more attractive for animals. Hence, $f(z) \propto Q/z$. Thus, at low values of z, an increase in z induces a rapid decrease in f, and we conclude that fruits are very costly. By contrast, suppose that z is the amount of fruit pigment; and more pigment means easy detection and more frugivory. We can argue that pigments are metabolic by-products from the production of compounds that benefit other life-history aspects of the plant (e.g.

photosynthetic pigments, secondary metabolites, Cipollini & Levey, 1997). In these circumstances, the increment in z is not very costly, and the functional form for f may be more like $f(z) \propto a - bz$ where $b \ll a$. Hence, f drops slowly with z, and we conclude that pigmentation is not costly. In general, $f(z)$ must have two properties. The first is that f declines with z:

$$\frac{df}{dz} < 0 \tag{2}$$

where the maximum fruit production $f = \phi$ occurs when $z = 0$, that is, when plants do not invest in attracting frugivores. The second property is that the curvature of $f(z)$ reflects how costly it is to increase the trait, that is,:

$$\frac{d^2f}{dz^2} \begin{cases} > 0 & \text{high costs} \\ < 0 & \text{low costs} \end{cases} \tag{3}$$

For the simulations, we need a function $f(z)$ having these properties. A functional relation such as $f(z) \propto Q/z$ satisfies (2) and is curved (but only as in $d^2f/dz^2 > 0$); the problem with this function is that it allows the production of infinite numbers of infinitesimally small fruits ($f \to \infty$ as $z \to 0$) and zero production of infinitely large fruits ($f \to 0$ as $z \to \infty$). The functional form $f(z) \propto a - bz$ satisfies (2) and keep fruit numbers and trait values bounded, but does not satisfy (3) because it lacks curvature. A simple way to model curved trade-offs and bounded fruit production $[0, \phi]$ is by means of the function (see e.g. Rueffler *et al.* (2006)):

$$f(z) = \phi\left(1 - z^\theta\right)^{1/\theta} \tag{4}$$

where $f = \phi$ is the maximum fruit production when $z = 0$, and $f = 0$ when z attains an extreme large value that we choose to be 1, without loss of generality. This is represented in Fig. 2a. When $\theta < 1$, the number of fruits falls rapidly at low values of z, which means high costs ($d^2f/dz^2 > 0$). When $\theta > 1$, the number of fruits falls more slowly at low values of z, which means low costs ($d^2f/dz^2 < 0$). In the simulations, f is rounded to the nearest integer.

The probability c that a fruit is eaten by a frugivore is expected to increase with z, but the rate of increase also depends on the abundance of the frugivores as well as on their consumption patterns or behaviour. If on the one hand frugivores are very rare, one should expect very low values of $c(z)$ no matter how large the trait, and in fact $c = 0$ if frugivores are absent. If on the other hand frugivores are extremely abundant, fruits have a higher chance to be picked up by at least one frugivore provided of course that the frugivores like the fruits. This last fact depends in turn on the frugivore response to fruit size, colour, nutrients or whatever trait z of interest. If the frugivores are not choosy, $c(z)$ is a saturating function of z, but if the frugivores are choosy, then $c(z)$ has a sigmoid shape that becomes more
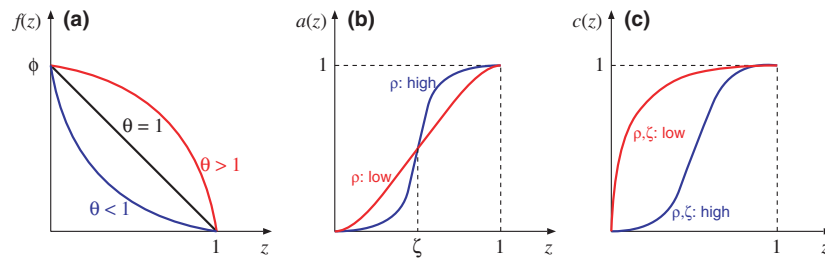
Fig. 2 (a) Trade-off between fruits per tree f, and the trait that promotes frugivory z (e.g. fruit size or pigmentation). The parameter θ is inversely related to the cost of the trait, for example $\theta > 1$ 'cheap' (red solid line), $\theta < 1$ 'costly' (blue solid line). (b) Fruit consumption rate a as a function of the trait z. The shape parameter ρ ($\rho_{low} = 5$, $\rho_{high} = 20$) measures the frugivore's choosiness: the higher the ρ the steeper the curve and the choosier the frugivores. ζ is the response threshold of the frugivores. (c) Probability c that a fruit is eaten by a frugivore as a function of the trait value z. A high and low ρ curve is shown as a blue and red solid line, respectively.

step-like with frugivore choosiness, as shown in Fig. 2c. Thus, $c(z)$ will have the following properties:

$$\frac{dc}{dz} > 0 \qquad (5)$$

$$\frac{d^2c}{dz^2} \begin{cases} <0 & \text{: non choosy frugivores} \\ \begin{cases} >0 & z \text{ small} \\ <0 & z \text{ large} \end{cases} & \text{: choosy frugivores} \end{cases} \qquad (6)$$

We propose an analytical form for $c(z)$, following the reasoning behind the Nicholson–Bailey functional response (Nicholson & Bailey, 1935). Given A animals per unit area, with per frugivore consumption rate a (i.e. fruits eaten per frugivore, per unit time, per unit area scanned), the probability that a fruit is found and eaten by a frugivore is:

$$c(z) = 1 - e^{-a(z)A} \qquad (7)$$

The dependence of the consumption rate on the fruit trait is given by a scaled sigmoid function:

$$a(z) = \frac{\frac{1}{1+\exp(-\rho(z-\zeta))} - \frac{1}{1+\exp(\rho\zeta)}}{\frac{1}{1+\exp(-\rho(1-\zeta))} - \frac{1}{1+\exp(\rho\zeta)}} \qquad (8)$$

where $a(0) = 0$ when the fruit trait is zero, and $a(1) = 1$ when the fruit trait takes its maximum viable value $z = 1$ (since $f(1) = 0$ in eqn (4)). Substituting (7) in (8), we obtain an explicit formulation for $c(z)$. The steepness ρ of the consumption rate determines the choosiness of the frugivores, and the inflection point ζ denotes the frugivore response threshold to the fruit trait. Low values of ζ means that frugivores already start to consume fruits at low values of the fruit trait whereas high values of ζ means that frugivores have high requirements for fruits, that is, they will start to consume fruits only if they are highly attractive (e.g. colour, size). It is important to stress that the response threshold is less important when frugivores are less choosy and more important when they are very choosy. Fig. 2b shows the shape of $a(z)$ and Fig. 2c the final shape of $c(z)$.

Results

### Effect of trait costs and frugivore's foraging behaviour

Costs largely determine the extent of trait evolution (Fig. 3). Under high costs ($\theta < 1$), the trait remains very low or evolves towards very low values, and there is little influence of the frugivore choosiness (ρ) on this outcome. This means that the advantages of attracting the frugivores for dispersal do little to compensate for the associated loss in seed numbers. By contrast, if costs are low or moderate ($\theta > 1$), the trait evolves towards values that are significantly larger (i.e. far from $z = 0$).

Frugivore choosiness appears to be an important driver of evolution when the costs are low or moderate. If the costs are low ($\theta > 1$), the trait tends to evolve to higher values when frugivore choosiness (ρ) increases (Fig. 3). A similar pattern occurs when the threshold of the consumption rate (ζ) is increased. For lower costs, the highest values of the trait occur for large values of the threshold (Fig. 4). A possible explanation for these outcomes is that when costs are not an issue, choosy frugivores and/or frugivores with larger thresholds (large ρ and/or ζ) raise the amount of investment that the plants need to profit significantly from their seed dispersal service. By contrast, for nonchoosy frugivores and/or frugivores with lower thresholds (small ρ and/or ζ), low values of the trait are already sufficient to cause a large fraction of seeds to be dispersed by frugivores (see Fig. 2c), so selection for large trait values is rather weak.

Both seed dispersal behaviours we explored (i.e. either dispersing seeds only to free sites or to any site) promote the evolution of frugivory. However, as expected, when frugivores only disperse to free sites (high-quality service), there is a higher evolution of the frugivory trait than when frugivores disperse seeds to any site (see Appendix 1). This difference between seed dispersal behaviours becomes larger when the maximum seed-to-tree survival probability is decreased ($g_0 < 1.0$) (see Appendix 1).
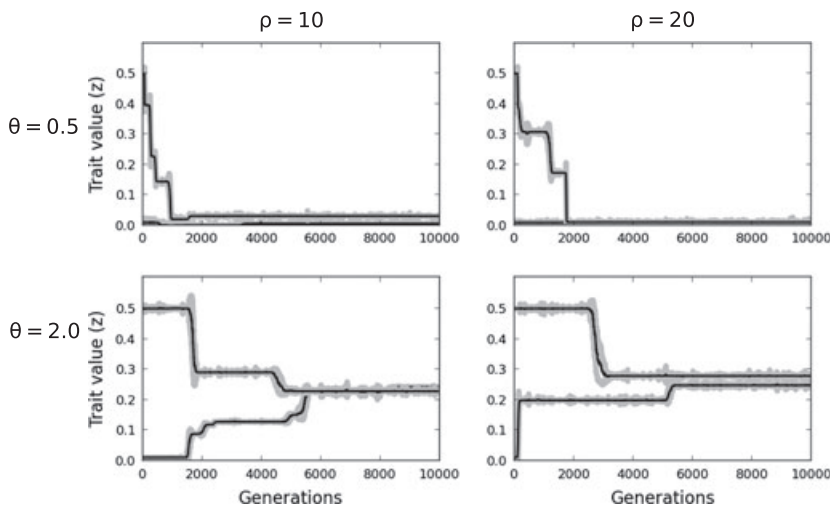
Fig. 3 Typical trait evolution for two different initial conditions under different values of the cost parameter θ and frugivore choosiness ρ. Black lines correspond to the mean trait in the population and grey lines to the standard deviation. Fruit production costs and choosiness have an important effect on the evolution of frugivory. Costly fruits do not favour the evolution of frugivory, but choosy frugivores can promote it, especially when costs are low. For parameters values used, see Table 1.
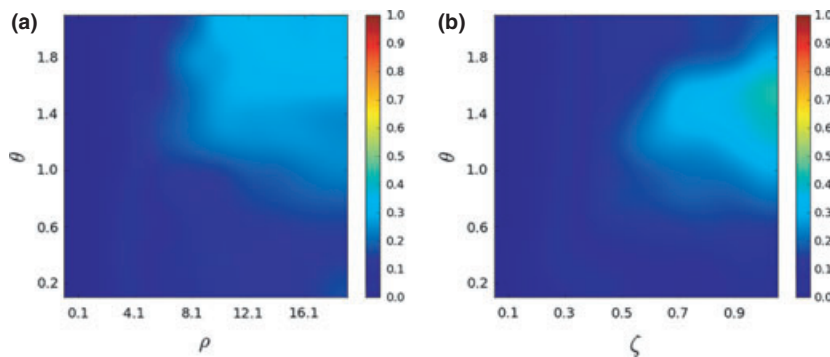

Fig. 4 Average frugivory trait ($\bar{z}$) values as a function of the cost parameter θ and (a) the frugivore choosiness (ρ) and (b) response threshold. ζ. The average value was taken from ten simulations for each parameter (θ, ρ) and (θ, ζ) combination. In general, decreasing fruit costs and increasing choosiness ($\rho \gg 0$, $\zeta > 0.5$) promote the evolution of frugivory. The initial value of the trait was $z_0 = 0.1$. For other parameters values used, see Table 1.

Effect of frugivore abundance

When the cost of the trait is low ($\theta < 1$) and the frugivores are not choosy (low value of ρ), the trait evolves towards a simple dynamical equilibrium, that is, there is always a single, global, evolutionary stable strategy (Fig. 5). In all simulations, we find that the equilibrium value of the trait increases as the number of frugivores decreases. This can be understood as follows: if we consider that when frugivores are rare, passive seed dispersal into neighbouring sites predominates over dispersal by frugivores (Fig. 5a, top panel), then lottery competition is more intense and seed survival is more difficult due to higher concentration of adult trees around seeds. Under these circumstances, there is a strong selective pressure towards increasing the trait inducing frugivory to increase the chances of germination and development (Fig. 5a, bottom panel). By contrast, if frugivores are abundant, dispersal by frugivores is already very frequent without requiring much investment by the plant (Fig. 5b, top panel). Thus, there is weak selection for larger trait values (Fig. 5b, bottom panel).

Discussion

Seed dispersal and survival are crucial processes for plant recruitment and population dynamics (Levin *et al.*, 2003). These early developmental stages are critical for plant community dynamics and numerous factors, such as competitive trade-offs (Tilman, 1994), pathogens (Gallery *et al.*, 2010), seed predators (Avgar *et al.*, 2008) and seed–disperser agents (Schupp *et al.*, 2010) are mediating the evolution of plant dispersal strategies. Several theoretical studies have focused mostly on the ecology of plant recruitment patterns (Nathan & Muller-Landau, 2000) and the evolution of seed dispersal kernels (Hovestad *et al.*, 2001; Starrfelt & Kokko, 2010), and only few studies have explored the evolution of plant-specific traits in connection with dispersal (Geritz *et al.*, 1999). However, most plants need animal seed dispersers to survive and reproduce; these animals can even be necessary for the germination of the seeds (Robertson *et al.*, 2005). This is the case for many plants that establish mutualistic interactions with a high diversity of animal frugivores (Traveset *et al.*, 2001). Our study aims to understand how this mutual-
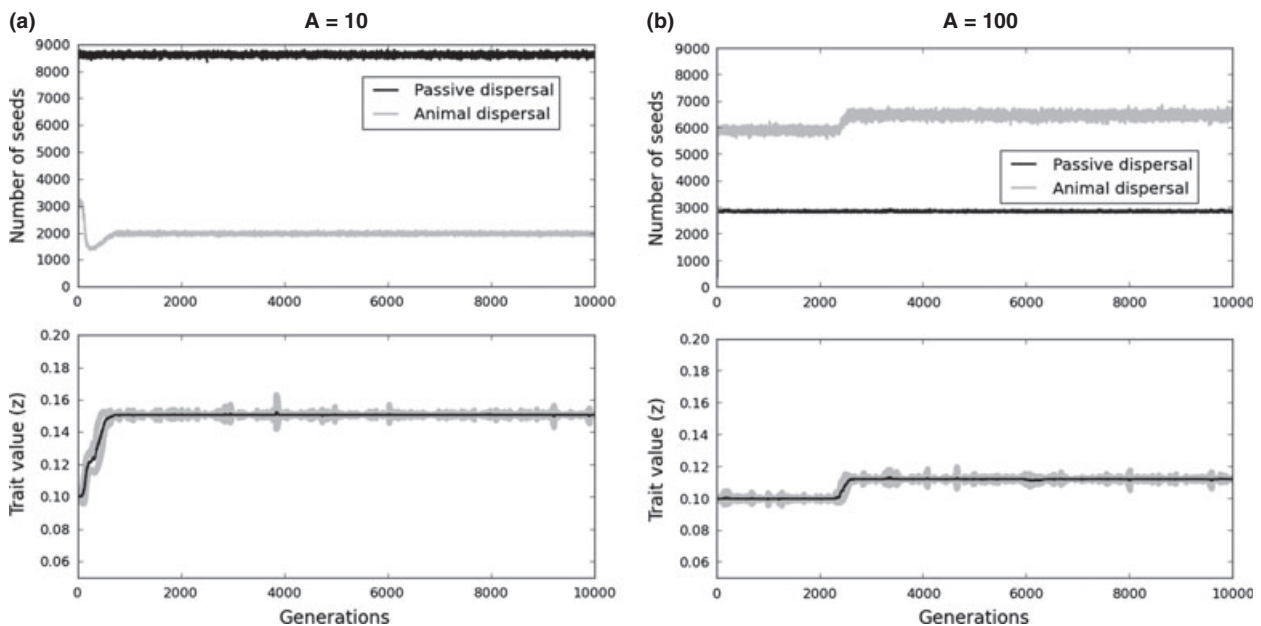
Fig. 5 Trait evolution (z) and proportion of passive and frugivore-dispersed seeds under two scenarios of frugivore abundance (A) using cheap fruit costs ($\theta = 2$): (a) low abundance ($A = 10$) and (b) high abundance ($A = 100$). Decreasing animal abundance promotes the evolution of frugivory. For parameters values used, see Table 1.

istic interaction could evolve, in order to explain the high diversity of cryptic fruit traits (e.g. colour, aromas) to attract frugivores (Julliot, 1996; Schaefer & Schmidt, 2004; Schaefer et al., 2007, 2008). Our results indicate that the evolution of traits involved in the attraction of frugivores depends on how costly such traits are for the plant and more interestingly, on the abundance and foraging patterns of the frugivores.

Our model has three important advantages compared with previous models. First, it considers different stages in a plant's life cycle, allowing us to account for trade-offs affecting fitness. Second, the plant–animal mutualism is treated as a consumer–resource interaction with benefits for the plants (e.g. dispersal service), enabling us to use principles of consumer resource theory (e.g. functional response, consumer abundance and preferences). And third, it accounts for differences in population regulation encountered by frugivore versus nonfrugivore-dispersed seeds (e.g. competition for space, seed predation risk, competition with parentals). Foraging decisions form an important feature of the model because frugivores can be highly variable in terms of choosiness and response threshold (Levey, 1987; Schaefer et al., 2003), influencing the extent of dispersal. Our approach is an important step in the direction of 'closing the seed dispersal loop' (Wang & Smith, 2002) by merging plant demography and animal foraging behaviour. Although we focused on the evolution of fruits, we think that our approach and findings can be applied, with proper modifications, to

the evolution of other adaptations required for plant–animal seed dispersal mutualisms, such as the elaiosomes involved in dispersal by ants (Hughes & Westoby, 1990; Giladi, 2006) or the fruit-supporting structures in dispersal by bats (Kalko & Condon, 1998).

Drivers of fruit evolution

Fruit production should evolve only if average seed survival increases as a consequence of frugivory, that is, the probability of recruitment from seed to adult is higher in the frugivore recruitment path compared with the nonfrugivore path. However, the extent of the evolution is strongly affected by fruit production costs and the availability and foraging behaviour of the frugivores (choosiness, response threshold). Moreover, the availability of alternative food sources for frugivores can trigger changes in the frugivore's choosiness, which in turn can generate changes in fruit trait selection. The picture is further complicated by the fact that the effects of density dependence on survival are heterogeneous in time and space, making the strength of selection for larger fruit production traits very variable.

When the costs associated with traits involved in promoting frugivore dispersal are too high, the traits do not evolve towards significantly larger values in our model, even if frugivore dispersal increases seed survival. However, larger trait values may arise by causes not considered in our model. For example, fruits may have originally evolved as adaptations to protect seeds

from predation rather than for dispersal (Mack, 2000), with further evolution driven by the advantages of endozoochory. If the traits are not very costly, then the features (e.g. abundance, choosiness) of the frugivore population will determine the extent of the evolution of traits involved in fruit production: if frugivores are very abundant and not very choosy, natural selection favours very small and less colourful fruits, but it favours large and colourful fruits if frugivores are rare and choosy. To understand this outcome, remember that the earliest stages of a plant life cycle, such as seed and seedling, are subject to enormous risks of predation and disease (e.g. granivory, fungi), competition among members of the same cohort (e.g. seedlings competing for nutrients) and competition with other cohorts (e.g. with adults for space and light). Only when a plant attains the adult stage, it becomes relatively free from many of these risks. Frugivore dispersal provides an attractive escape route from these risks. If frugivores become rare and choosy, it pays to invest in attracting them, and natural selection favours larger fruit production traits. If frugivores are very abundant and not choosy, dispersal services would be almost cost-free for plants with small and large fruit traits, and there is no selection for larger fruit production traits. A good empirical example of the extent to which plants can adjust to the demands of their dispersers is the plasticity displayed by plants producing watery fruits in summer and nutrient rich ones in winter (Herrera, 1982), both actions would be considered costly, but the changing preferences of the animals force the plants to do so. Selection for larger fruits will be possible if we consider other selective advantages related to large fruits, for example larger fruits with large seeds having more resources and hence higher recruitment probability (Armstrong & Westoby, 1993).

An important factor in the evolution is the form of frugivore dispersal, which determines the quality of the service. Seed dispersal service not only depends on the number of seeds dispersed but also on how and where they are dispersed (Schupp, 1993). In our model, we explored two extremes of seed dispersal quality: (i) the frugivore release the seeds only in sites that do not contain trees (i.e. high-quality dispersal (Anderson *et al.*, 2009)) and (ii) the frugivore release seeds to any site (i.e. low-quality dispersal). Both seed dispersal behaviours promote the evolution of frugivory. However, high-quality service produces a larger increase in the frugivory trait than low-quality service. In summary, it is more advantageous to disperse away from the parental tree, even though seeds might land in less suitable sites, than to stay beneath the parent tree (Hamilton & May, 1977).

The quality of seed dispersal can vary greatly between frugivores due behavioural differences (Russo *et al.*, 2006). Garcia & Martinez (2012) found that the richness of frugivore assemblages have a positive effect on the probability of tree colonization. They suggest

that functional complementarity is an important aspect of diverse frugivore communities. Thus, it would be interesting in a future study to explore the effect of frugivore assemblages and quality of service on the evolution of frugivory.

There is still another factor that could determine dispersal quality: the relative degree of clumpiness in the seed release pattern. In our simulations, we kept this parameter fixed at five sites per adult tree, and we have not yet studied the consequences of changing it. Increasing the number of release sites (large k) raises the chances that some seeds recruit far from the vicinity of adult trees, but this also leads to fewer seeds per site which lowers the chances of winning the lottery competition against other phenotypes. It remains to be explored whether this is beneficial or not.

It has been empirically shown that clumped dispersal can severely hinder seed and seedling survival in plants dispersed by monkeys (Russo & Augspurger, 2004), thus creating a potential conflict where frugivore dispersal could be harmful instead of beneficial. The question remains whether or not clumped dispersal suffices to cause disruptive selection and polymorphism. What has been at least hypothesized in this respect is that clumped-dispersed plants can develop mechanisms to overcome density dependence and thus coexist with scatter-dispersed plants (Howe, 1989). Alternatively, plants may induce scattered dispersal by altering gut passage times (which is one of many functions of secondary metabolites (Cipollini & Levey, 1997), such as capsaicin (Tewksbury *et al.*, 2008)).

Beyond simple assumptions

Our model makes several simplifications. We considered scenarios where only mutualists drive the evolution of fruits, but it is important to consider the opposing effects of mutualists and antagonists (i.e. herbivores). We expect that this promotes trait diversification (Gautier-Hion *et al.*, 1985) and that it has a strong influence on the co-evolution between plants and frugivores, as in the case of plant–pollinator interactions (Ferriere *et al.*, 2007). Furthermore, we have not yet considered more specific characteristics of social frugivores, such as monkeys and birds (Russo *et al.*, 2006). They may spend some time travelling between trees compared with the time they spend on foraging in a tree. This will likely cause many frugivores to release seeds closer to a tree in comparison with seeds that disperse passively. In this situation, the frugivore may be 'cheating', because they obtain the rewards but perform a very poor dispersal service by aggregating the seeds (Russo & Augspurger, 2004).

Fruits are very complex structures that are the product of 'phenotypic integration' (Valido *et al.*, 2011), where traits such as colour, size and nutrients among others might be signalling for multiple receivers: mutu-

alists and antagonists (Schaefer & Schmidt, 2004). Fruit traits are known to correlate with other plant traits constraining selection by frugivores (Flörchinger *et al.*, 2010). Accordingly, instead of single traits considered one at a time, a linear combination (e.g. principal component) could realistically represent the trait axis along which evolutionary changes happen, and a potential object of study can be the joint evolution of fruit and seed size (Bolmgren & Eriksson, 2010). Mathematical models of seed evolution assume large but costly seeds as adaptations for competition (Geritz *et al.*, 1999), and our model assumes large fruits as dispersal adaptations. It would be interesting to investigate these effects simultaneously.

The co-evolution between plant and animal traits was not explored in this model. However, if we also consider evolutionary changes in the animal traits (e.g. choosiness, response threshold) and animal demography, this might promote co-evolutionary changes in plant and animal traits and the evolution of dispersal syndromes.

Our model predicts that fruit evolution is determined by frugivore abundance, treated here as a parameter. Realistically, frugivores respond to plant population dynamics, as assumed in most consumer–resource models (e.g. Rosenzweig–MacArthur model). Consumer–resource dynamics will have important ecological and evolutionary consequences, because changes in the composition of frugivore guilds affect plant fitnesses and population viability (Asquith *et al.*, 1999; Wright, 2003; Guimarães *et al.*, 2008). Changes in frugivore's density and/or consumer–resource cycles could potentially generate diversification in fruit traits by, for example, evolving unattractive and highly attractive fruits. This is analogous to the evolution of different levels of resource specialization in consumer–resource interactions (Abrams, 2006).

We predict that the evolution of fruit diversification by frugivory is mainly driven by fruit production costs, but more importantly by frugivore foraging behaviours (i.e. choosiness Janson, 1983; Kalko & Condon, 1998; Schaefer & Schmidt, 2004; Schaefer *et al.*, 2007; Flörchinger *et al.*, 2010) and the effects of frugivore seed release patterns on seed survivability and density dependence (Russo & Augspurger, 2004; Russo *et al.*, 2006). We contend that our approach of considering life-history and consumer–resource theories is essential for the creation of models that seek to explain the evolutionary origin of plant diversification and dispersal syndromes.

Acknowledgments

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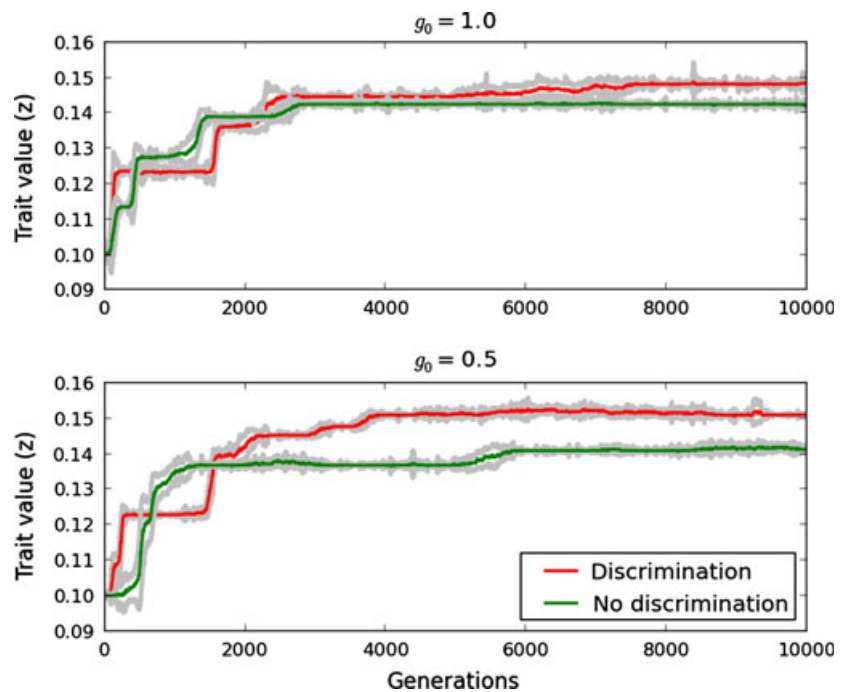
Appendix 1

Effect of frugivore's seed dispersal behaviour and germination cost

Frugivore's seed dispersal behaviour can have an important effect on the evolution of frugivory. In the main text, we only studied a single seed dispersal behaviour: *frugivores only disperse seeds to empty (unoccupied) sites*. Here, we will explore the effect of frugivores that do not discriminate between sites, that is, they can disperse seeds to any site (empty or occupied). This can be seen as a more realistic behaviour of frugivores that, for example, can disperse seeds under the canopy of a tree. Both seed dispersal behaviours are probably the extremes of a broad spectrum of seed dispersal quality service: from no discrimination (low-quality service) to full discrimination (high-quality service).

As shown in Fig. A1, both dispersal behaviours (with and without discrimination) promote the evolution of frugivory. However, frugivores only dispersing seeds to empty sites produce larger values of fruit traits. The difference between both dispersal behaviours on the evolution of frugivory becomes larger if we decrease seed's germination probability ($g_0 = 0.5$). The reason is that with low germination probability, it becomes more difficult for mutants to invade, particularly in the case of frugivores with no discrimination. Therefore, it is more advantageous to colonize a site where the probability of becoming an adult is at least higher than zero than landing on an occupied site where the probability of survival is zero.

Effect of tree survival

The probability of tree survival (P) determines the amount of free space available for seed colonization. Therefore, P is crucial for the process of extinction–colonization, as in classic models of metapopulation dynamics (Levins, 1969). For high values of P
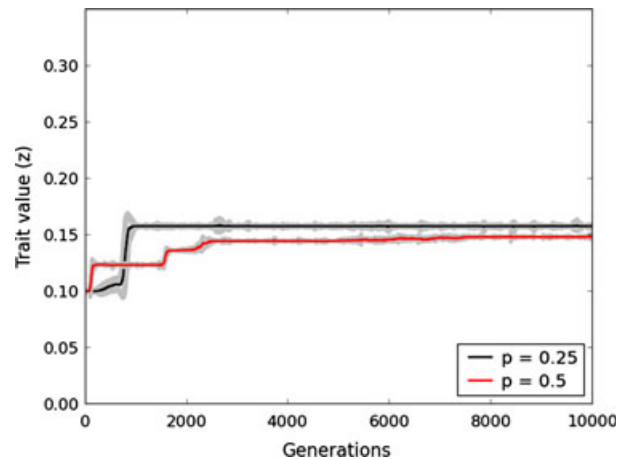
Fig. A2 Effect of tree survival probability on the evolution of frugivory. The average trait value was taken from twenty-five simulations for each value of tree survival probability: $P = 0.5$ (red solid line) and $P = 1.0$ (black solid line). Solid lines correspond to the mean trait in the population and grey lines to the standard deviation. Parameters used: $\rho = 10$, $\theta = 2.0$, $z_t = 0 = 0.1$, $A = 10$. For the rest of parameters used, look at the Table 1 in the main text.

Fig. A1 Effect of frugivore seed dispersal discrimination and germination probability. The average trait value was taken from twenty-five simulations for each value of germination probability ($g_0 = 0.5$ bottom panel and $g_0 = 1.0$ top panel) and two types of dispersal behaviour: frugivores dispersing only to free sites (red solid line) and to any site (green solid line). Solid lines correspond to the mean trait in the population and grey lines to the standard deviation. Both seed dispersal behaviours, that is, when frugivores discriminate or not between sites, promote frugivory. Parameters used: $\rho = 10$, $\theta = 2.0$, $z_t = 0 = 0.1$, $P = 0.5$, $A = 10$. For the rest of parameters used, look at the Table 1 in the main text.

($P > 0.5$), the evolutionary process is extremely slow because there are very little opportunities for the invasion of mutants, the space fills in very rapidly. When $P < 0.5$, the evolutionary dynamics can occur faster (i.e. taking less generations) to reach the evolutionary equilibrium (see Fig. A2). This is because there is a fast turnover of free sites through the extinction–colonization process, which gives more opportunities in a short time for mutants to invade. Furthermore, with low tree survival probabilities, it seems to reach a slightly higher evolutionary equilibrium than when $P = 0.5$ (see Fig. A2).

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