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Diet complementation as a frequency-dependent mechanism conferring advantages to rare plants via dispersal

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Abstract

1. We used an agent-based model to test the hypothesis that diet complementation by frugivores can promote the persistence of rare plant species in communities (DCH).
2. Models simulated bird movement, frugivory, seed dispersal and plant recruitment on landscapes that differed in their degree of fragmentation and in their degree of fruiting species mixing at the scale of frugivores' foraging decisions.
3. Diet complementation promoted the dispersal of rare species without the need of a priori preference from birds. The effects of landscape structure on the dispersal of rare plants were small (<5%) compared to positive effects of diet complementation because birds tracked the nutrients contained in rare fruits to balance their diets. However, resource-tracking of rare fruits increased foraging costs up to 20% of net energy intakes.
4. During postdispersal stages, density-dependent mortality only conferred advantages to rare plants when located within heterospecific plant patches. Still, thanks to rare-biased dispersal, rare plants showed the highest seed dispersal effectiveness irrespectively of landscape configuration.
5. Our theoretical approach presents a behavioural mechanism by which fruit choice can act as a frequency-dependent mechanism conferring rare species advantages as important as classic postdispersal density-dependent processes.
6. We hope that this study stimulates future work aimed at evaluating the importance of diet complementation in structuring the composition and spatial patterning of plant communities.

KEYWORDS

advantage of the rare, diet complementation, frugivory, negative frequency-dependent, rarity

1 | INTRODUCTION

Understanding how rare species persist in communities despite the demographic challenges posed by rarity has been a central question in community ecology and conservation biology (Espeland & Emam, 2011). By definition, rare plant species experience stronger recruitment limitation than common ones because they produce proportionally fewer seeds at the community scale, and hence, the per-capita probability of seeds reaching suitable recruitment sites is slim (Schupp, Milleron, & Russo, 2002). Theory predicts that diversity should decrease in the absence of compensatory mechanisms because common and dominant species win recruitment sites by competitive exclusion or by forfeit (Chesson, 2000; Terborgh, 2012).

Well-studied postdispersal compensatory mechanisms that confer advantages to rare plant species mostly involve density-dependent mortality by enemies and intraspecific competition for

light, space and nutrients (Barot, 2004; Comita et al., 2014; Janzen, 1970; Terborgh, 2012; Turner, 2001). However, it has not been until recently that the dispersal process itself, as mediated by the behaviour of frugivorous animals, has been proposed as another frequency-dependent mechanism conferring advantages to rare plants (Carlo & Morales, 2016). Recently, the overrepresentation of rare species and increased evenness in bird-generated seed rains—as compared to seed availability in the environment—has been documented for a tropical forest (Carlo & Morales, 2016). Moreover, it has been shown that such patterns cannot arise as a by-product of plant spatial structure but require that fruit choices are biased towards rare species (Morán-López, Carlo, & Morales, 2018). As frugivore-dispersed plants dominate tropical and other terrestrial plant communities (Herrera, 2002), fruit choice by birds may have a strong and yet overlooked impact on plant community assembly (Almeida-Neto, Campassi, Galetti, Jordano, & Oliveira, 2008; Carlo & Morales, 2016; Jordano, 2000). Thus, assessing which behavioural mechanisms can underpin rare-biased dispersal becomes a key question to achieve an integrative understanding of plant species coexistence.

A recent theoretical study shows that negative frequency-dependent fruit selection (antiapostatic selection Allen, 1988) can provide rare species dispersal advantages provided that frugivore movements are unconstrained and plant species are well-mixed at local scales (Morán-López, Carlo, & Morales, 2018). This mechanism is based on visual cues from fruits and searching behaviour. Although chromatic and morphological traits can modify fruit choice (Schaefer, Levey, Schaefer, & Avery, 2006), fruits have an intrinsic value as food. Frugivorous birds interact with fruit resources that differ in the content of sugars, lipids and secondary compounds (Cazetta, Galetti, Rezende, & Schaefer, 2012; Levey & Del Rio, 2001). Because no plant species provides all nutritional requirements for

frugivores (Levey & Del Rio, 2001), frugivores commonly eat from multiple fruiting species (Murphy, 1994) and combine fruits with other food items (Carlo, Pérez-Rivera, & Gelditsch, 2012; Izhaki & Safriel, 1989). The need to feed on multiple fruit resources over short time-scales to obtain proper nutrition has been suggested to promote complementarity among fruiting plant species (Whelan, Schmidt, Steele, Quinn, & Dilger, 1998). Food resources are considered complementary when they provide nutrients not found in either food alone or, when consumed jointly, result in a balanced animal diet (Whelan et al., 1998). If complementary fruit resources vary in relative abundance in the community, the rarer species will be consumed at proportionally higher rates because the nutrients offered by their fruits are more difficult to obtain. Therefore, diet complementation may constitute a frequency dependence mechanism conferring advantages to rare species in plant communities.

However, seed dispersal services provided by frugivores are not independent from the spatial context in which plant–animal encounters occur (Cortes & Uriarte, 2013; Morales & Carlo, 2006). Two main landscape properties may affect the role of frugivory in structuring plant community regeneration—fragmentation and the spatial association of plant species. On the one hand, fragmentation determines the capacity of frugivores to move through landscapes and, consequently, their ability to interact with all plants in the community (Morales & Vazquez, 2008). As a result, fragmentation can interfere with the role of frugivory on diversity maintenance (Morán-López, Carlo, & Morales, 2018). On the other hand, the degree of mixing of plant species within neighbourhoods affects the availability of different types of fruits at local scales, modifying the immediate fruit choices made by frugivores (Carlo, 2005; Morán-López, Carlo, & Morales, 2018). Moreover, the spatial configuration of fruiting resources affects the way frugivores
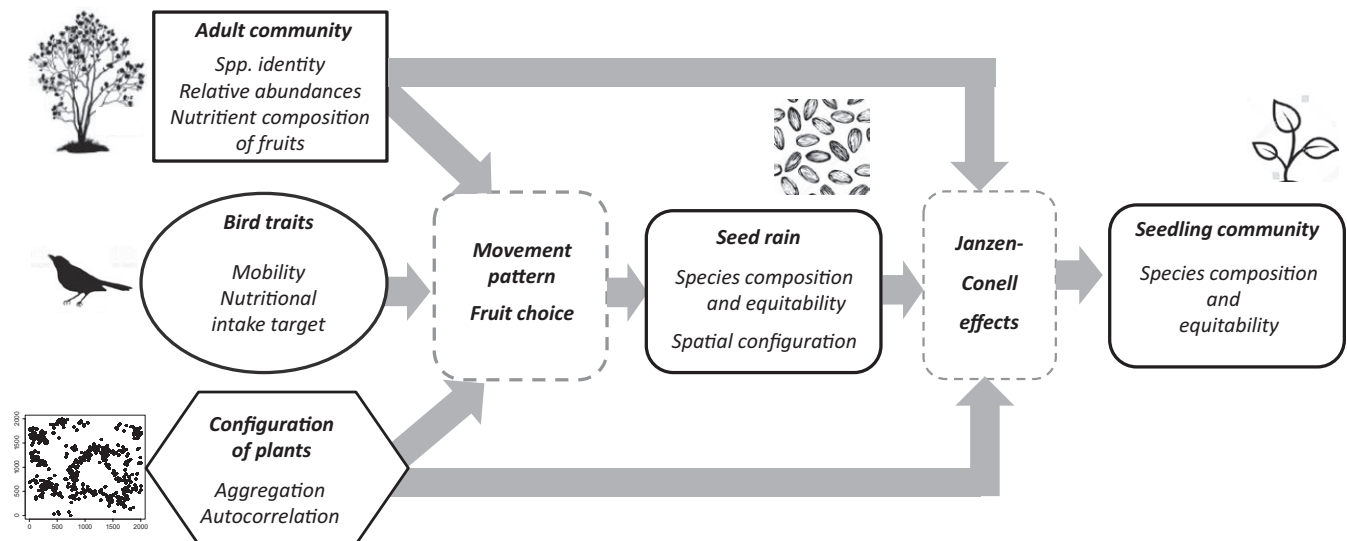

FIGURE 1 Model process connecting birds' foraging decisions to the composition and equitability of regenerating plant communities. Frugivorous birds decide where to move and which fruits to consume according to the spatial configuration of fruiting resources and their nutritional adequacy. Foraging decisions affect the composition and equitability of the seed rain as well as spatial patterns of seed deposition. Depending on how seeds are deposited, the strength of density-dependent mortality on seedlings will vary, modifying the final composition and equitability of the regenerating plant community

move across the landscape, and hence, modifies seed deposition patterns (Morales & Carlo, 2006). The way seeds are deposited, in turn, influences postdispersal density-dependent mortality, which affect recruitment rates of plant species (Janzen, 1970; Nathan & Muller-Landau, 2000; Sasal & Morales, 2013; Spiegel & Nathan, 2010). Thus, to understand the role of diet complementation in rare-biased dispersal, we need also to assess the inescapable effects of landscape configuration on frugivores' foraging behaviour.

Here, we use a spatially explicit simulation model, modified from Morales and Carlo (2006), to test the hypothesis that diet complementation is a behavioural mechanism that could increase seed dispersal effectiveness (Schupp, Jordano, & Gómez, 2010) of rare plants (diet complementation hypothesis, DCH). For this purpose, we examined diet complementation within landscapes that vary in their degree of fragmentation and the spatial autocorrelation of fruiting plant species (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Model development

2.1.1 | Process overview

The composition and spatial configuration of fruiting plants interacts with frugivores' characteristics influencing their movement and diet selection, with consequences for seed rain, postdispersal effects and the resulting community of seedlings (Figure 1). Simulations first generate an adult plant community with different equitability in species abundances and nutritional composition of fruits. Then, individual plants are located in space creating landscapes with contrasting degrees of fragmentation and spatial autocorrelation of plant species. Frugivorous birds are simulated with two main state variables—(a) intake target, which represents their nutritional demands and (b) foraging decision radius. Once birds are randomly located within the landscape, the simulation begins. During the simulation, frugivores decide where to forage following two objectives—minimizing travel costs and meeting their nutritional demands. According to these behavioural rules, they forage across the landscape, eating from different fruiting resources and dispersing seeds, thereby creating the seed rain community. The spatial configuration of the seed rain then serves as the template for positive density-dependent mortality effects when generating a community of seedlings. Our main model outputs are seed dispersal effectiveness of focal species (SDE, number of seeds dispersed x probability of postdispersal survival; Schupp et al., 2010) and resource provisioning effectiveness of foraging birds (RPE, number of fruits consumed x energy gain per gram of fruit consumed; Schupp, Jordano, & Gómez, 2017).

2.1.2 | Modelling frugivores' decisions

To model birds' decisions, we modified the spatially explicit, event-driven, stochastic simulation model of Morales and Carlo (2006). In our model, birds choose where to go next by sampling from an attraction distribution that balances travelling costs, fruit availability and nutritional adequacy of available fruits.

$$\beta_{ij} = [\tanh(-a_d d_i^2) + 1] \times [(1 - ND_j)\tanh(a_f F_i^2)] \quad (1)$$

where β_{ij} measures the relative bias towards the i-th plant belonging to the j-th species according to its distance to bird location (d_i), its number of fruit (F_i) and the nutritional adequacy of its fruits ($A_j = 1 - ND_j$). ND_j represents birds' nutritional deficiency after ingesting fruits of the j-th species (see below). For all plant species, parameter "a_f" was set so that the bias due to fruit abundance is maximum at 100 fruits (maximum crop size of simulated plants). The parameter governing bias due to distance "a_d" was set so that the relative attraction for a particular plant dropped to 0.05 at 100 m. Thus, simulated birds decided where to go next within a radius of 100 m from their current location. Following Morán-López, Carlo, and Morales (2018), landscape properties such as fragmentation and autocorrelation were measured at the scale of frugivores' foraging decisions (see below). Thus, biological interpretations of landscape effects are not dependent on particular bird movement distances but on the ratio between the scale of plant aggregation and the scale of bird decision radius. Finally, nutritional adequacy of fruits ($1 - ND_j$) controls the level of fruit attractiveness. For the same number of fruits offered by the i-th plant, its attractiveness increases as the nutritional adequacy of their fruits (belonging to the j-th species) is greater (Figure 2b). β_{ij} is then standardized and converted to a multinomial distribution

$$\beta = \beta_{ij} / \sum_1^n \beta_{ij}, \quad (2)$$

from which birds sample a plant to move next.

Birds assess nutritional adequacy of fruits according to the so-called geometric framework (Raubenheimer, 2011; Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Raubenheimer & Simpson, 1993). This framework explores how animals may solve the problem of mixing multiple food sources, each providing a nutritionally imbalanced meal, to meet their nutritional demands. Nutrients are represented along the axes of a Cartesian space in which food resources and the animals' intake target are located according to their nutritional composition. The intake target denotes the proportion of nutrients an animal should ingest to reach its nutritional demands (T_{xy} being x and y nutrients, Figure 2a). Thus, the distance between the current position of birds in the Cartesian space and the intake target determines the animal's nutritional status. Distances between food resources and the intake target represent food imbalance, and the distance among food resources represents overall nutrient dissimilarity (Figure 2a). The nutritional adequacy of fruits of the j-th species (A_j) depicts the potential of fruits to allow the bird consumer to meet its current nutritional demands. It is given by the nutritional distance (ND_j) between the new position of the bird in the nutritional space after ingesting "n" fruits of j-th species (B_j', Figure 2a) and its intake target (T_{xy}) according to Equation 3. Nutritional adequacy is not
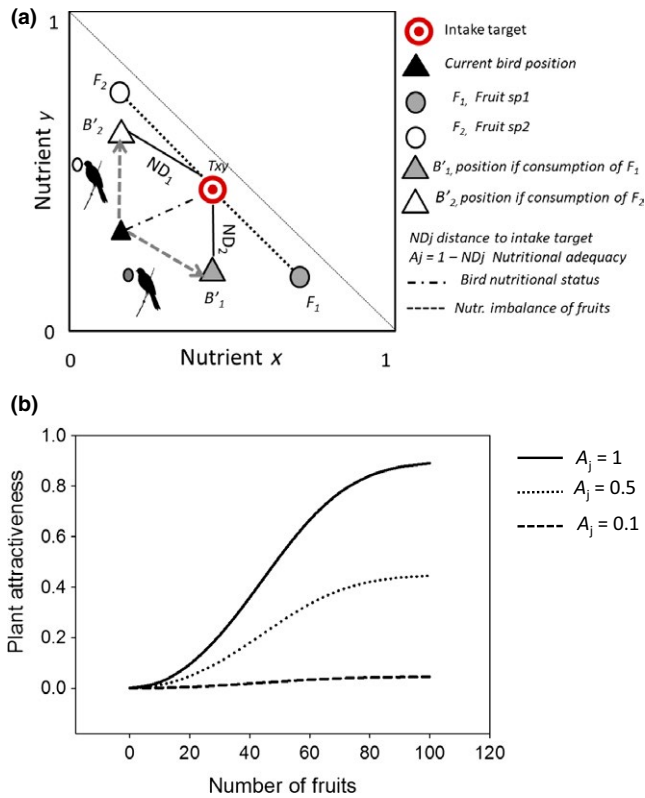
FIGURE 2 Representation of bird decision process in the diet complementation model. (a) When birds decide where to forage next, they take into account the nutrient adequacy ($A_j = 1 - ND_j$) of the different fruit resources. For each plant species (j), they assess their new position in the nutrient Cartesian space after ingesting "n" fruits of the j-th species ($[B']_j$). Next, they calculate ND_j, which is the distance between this new position and the intake target. (b) For the same amount of offered fruits, plant attractiveness is higher as the nutritional adequacy of fruits increases

an inherent property of fruits, but changes over time as a function of birds' current nutritional status and the ability of fruits to meet the bird's nutritional demands. See supplementary material Supporting Information Appendix S1-*Nutritional status assessment* for further details.

$$ND_j = \sqrt{\left(\frac{B'_{jx} - T_x}{T_x}\right)^2 + \left(\frac{B'_{jy} - T_y}{T_y}\right)^2} \quad (3)$$

To gain generality, ND_j is expressed relative to the intake target (T_{xy}). ND_j saturates to 1 ($A_j = 0$) whenever excess of nutrients in the new position of birds exceeds 100% of its nutritional demands. Whenever a bird's nutritional status for a certain nutrient falls below 25% of the quantity required by its intake target (extreme nutritional deficiency, E_{ND}), the nutritional adequacy of fruits with the maximum content in that limiting nutrient is maximal ($1 - ND_j = 1$), while the opposite occurs for nutrient-poor fruits ($1 - ND_j = 0$). This way, birds "defend" their intake target (according to Raubenheimer & Simpson, 1993) by

searching for alternative foods. The importance of this assumption was assessed by a sensitivity analysis with E_{ND} equal to 0.1 and 0.75. Changes in this parameter did not affect simulation results (Supplementary material, Supporting Information Appendix S3, Figure C5). Behavioural parameters such as flight speed, perching and gut passage times were obtained from Morales and Carlo (2006). Simulations were run with a bird plant ratio of 0.01. To reduce computational time, instead of simulating one fruiting season (30 days, Sasal & Morales, 2013), at the beginning of each simulation every plant produced 100 fruits and simulation stopped when thirty per cent of available fruits at the landscape scale were consumed. We opted for this strategy because a preliminary analysis revealed that both types of approaches (fruiting season and thirty per cent depletion) lead to similar patterns of frugivory effects on rare species dispersal (Supporting Information Appendix S3, Figure C8). For further model details, see Supporting Information Appendix S1.

2.1.3 | Postdispersal seed survival

Once seeds are deposited, the probability of survival depends on the density of conspecific seeds in a radius of 1 m (Connell, 1971; Janzen, 1970). The probability of survival depends on a logistic function $-\text{logit}(p_s) = a_s - \beta_s \times N_c$, 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 set to 0.2 according to Morán-López, Carlo, and Morales (2018). N_c depicts the number of conspecific seeds within a 1 m^2 radius. We also simulated density-dependent mortality with $\beta_s = 0.4$ and 0.05 to test for this parameter sensitivity.

2.1.4 | Resource effectiveness assessment

To illustrate landscape effects on seed dispersal outcomes, we assessed resource provisioning effectiveness (RPE) (Schupp et al., 2017). RPE measures the benefits of the mutualism from the animal's perspective. As in seed dispersal effectiveness (SDE), RPE can be divided into a quantity (number of fruits consumed) and a quality component (energy assimilated per gram of fruit consumed). Because in our simulation number of fruits consumed was prefixed due to 30% depletion, the quantity component was very similar among birds and RPE depended on energy assimilation efficiency.

To estimate the quality component of RPE, we assumed that glucose and lipids were the main macronutrients offered by simulated fruits (Galetti, Pizo, & Morellato, 2011; Levey & Del Rio, 2001). During simulations, birds assessed their net energy gain according to

$$E_{gain} = E_{assim.} - (BMR + E_{flying} + E_{perching} + E_{night}) \quad (4)$$

E_{gain} is the net energy gain (kJ). It is obtained by discounting from energy assimilated during foraging (E_{assim}), basal metabolic costs (BMR), energetic costs of flying (E_{flying}), perching ($E_{perching}$) and overnight

energy expenditure (E_{night}) The amount of energy assimilated during the simulation is calculated according to

$$E_{assim}(kJ) = [(G \times 15.70) + (L \times 39.56)] \times 0.40 \quad (5)$$

where G and L depict grams of glucose and lipids consumed. They depend on the nutritional composition of simulated fruits (experimental design input), fruit mass and percentage of dry weight. For all plant species, we assumed a fruit mass of 2 g and a water content of 80% (Galetti et al., 2011). Parameters correspond to 15.70 and 39.56 kJ/g of glucose and lipids, respectively (Witmer & Van Soest, 1998). Parameter 0.4 represents energy assimilation efficiency of fruits by frugivorous birds (Castro, Stoyan, & Myers, 1989).

Energetic costs were calculated as a function of body size using allometric relationships. As bird mobility is tightly linked to their body size (Haskell, Ritchie, & Olff, 2002), we assessed the energy balance of a frugivorous species that showed a decisions radius similar to the one implemented in our model (100 m). We chose *Turdus merula* for this purpose (Body mass = M_b = 0.01 kg, Morales, Garcia, Martinez, Rodriguez-Perez, & Herrera, 2013). Basal metabolic costs (BMR) were calculated according to McKechnie and Wolf (2004) energetic costs of flying (E_{flying}) and perching ($E_{perching}$) according to Nudds and Bryant (2000) and Aschoff and Pohl (1970) and overnight energy expenditure following Nudds and Bryant (2000). See Supporting Information Appendix S1, resource provisioning effectiveness assessment.

Once net energy gain was assessed, the quality component of RPE was calculated as $E_{gain}/Mass_{fruits consumed}$ (kJ/g) (Schupp et al., 2017). Furthermore, to better contextualize daily energetic costs of simulated birds, we estimated field metabolic rates (FMR = $10.5 \times M_b^{0.681}$, FMR in kJ/day, M_b in grams; Nagy, 2005). Finally, to evaluate whether energy expenditure by birds surpassed the physiological limits of energy assimilation, we calculated sustainable energy budgets (SEB = 7 × BMR; Weiner, 1992), which represent a ceiling of energetic expenditure an animal can maintain without losing body weight.

2.2 | Experimental design

Regarding landscape generation, we followed a full factorial design considering two levels of fragmentation (yes/no) and spatial autocorrelation of plant species (well-mixed and autocorrelated; four landscapes in total). When landscapes were not fragmented, they consisted of 500 plants with a scale of clustering of 170 m. This way, minimum distance between clusters of vegetation was around 50 m, which is half of the decision radius of foraging birds (100 m). Thus, birds could move easily between clusters of vegetation within these landscapes. Fragmented landscapes, in turn, consisted of 500 plants with a scale of clustering of 10 m. In this case, clusters of plants were usually separated by more than 100 m (birds' foraging decision radius), and hence, the landscape was perceived as fragmented by frugivores. In both scenarios of fragmentation (yes/no), we changed the spatial autocorrelation of species identities creating well-mixed ($\rho = 0$) and highly autocorrelated plant communities ($\rho = 1$). This results in a low and high spatial aggregation of plant species at the scale of birds' foraging decisions (100 m) (see supplementary

material, Supporting Information Appendix S2, Landscapes generation, Figure B1).

One of our objectives was to evaluate whether species overrepresentation in the seed rain can emerge from the interplay between their relative abundance in the community and the nutritional imbalance of fruits (with respect to birds' requirements). For this purpose, we varied the relative abundance of a focal plant species (from 0.5 to 0.05) and the nutrient imbalance of fruits (from 0.2 to 1). To avoid a priori fruit preference, fruits were equally distant from the intake target (see Supporting Information Table B1 in Appendix S2). This way, no plant species offered fruits more appropriate for birds' nutritional demands and we could test for pure diet complementation effects. It is important to note that because nutrients are equally distant from the intake target, higher nutrient imbalance of fruits also entails greater differences in their nutritional composition. A total of five nutrient imbalance levels were run in five relative abundance levels in the four simulated landscapes (N = 4 landscapes × 5 abundances × 5 unbalances = 100 landscape-abundance-imbalance scenarios).

2.3 | Data analysis

In each simulation, the model tracked how the relative abundance of the focal species changed from seed availability to seed rain (ΔAb). As our experimental design consisted in varying the abundance of focal plant species (from 0.5 to 0.05), we relativized change in abundance by initial seed availability in the landscape as

$$\Delta Ab = (Ab_{seed rain} - Ab_{seed avail.})/Ab_{seed avail.}$$

Also, for each plant, the program recorded the number of fruits dispersed and the probability of survival of dispersed seeds. Subsequently, we calculated seed dispersal effectiveness (SDE) as the product of the number of seeds dispersed and the probability of postdispersal survival (Schupp et al., 2010).

During the simulation, in each bird movement, the program recorded the difference between the nutritional adequacy of fruits of the focal species with respect to nonfocal one as a measure of focal fruits preference ($P_f = A_f - A_{Nf}$). Higher values of P_f imply that all else being equal, focal plants become more attractive (according to Equation. 1, Figure 2b). The program also recorded bird nutritional status (1—distance to its intake target, Figure 2a) and kept track of mean seed dispersal distances as a proxy of bird mobilization radius. At the end of each simulation, P_f and birds' nutritional status were averaged and median dispersal distances were estimated. In addition, each bird calculated the quality component of RPE (kJ of energy gained per gram of fruit consumed). For each scenario, we run 15 replicates and calculated their average and standard error.

To evaluate the importance of relative abundance of focal species (codominant/rare), nutrient imbalance (high/low) fragmentation (yes/no) and spatial autocorrelation (well-mixed & autocorrelated) on ΔAb, postdispersal survival and RPE, we performed a regression analysis. Then, we calculated lmg metrics, which partitions R^2 among
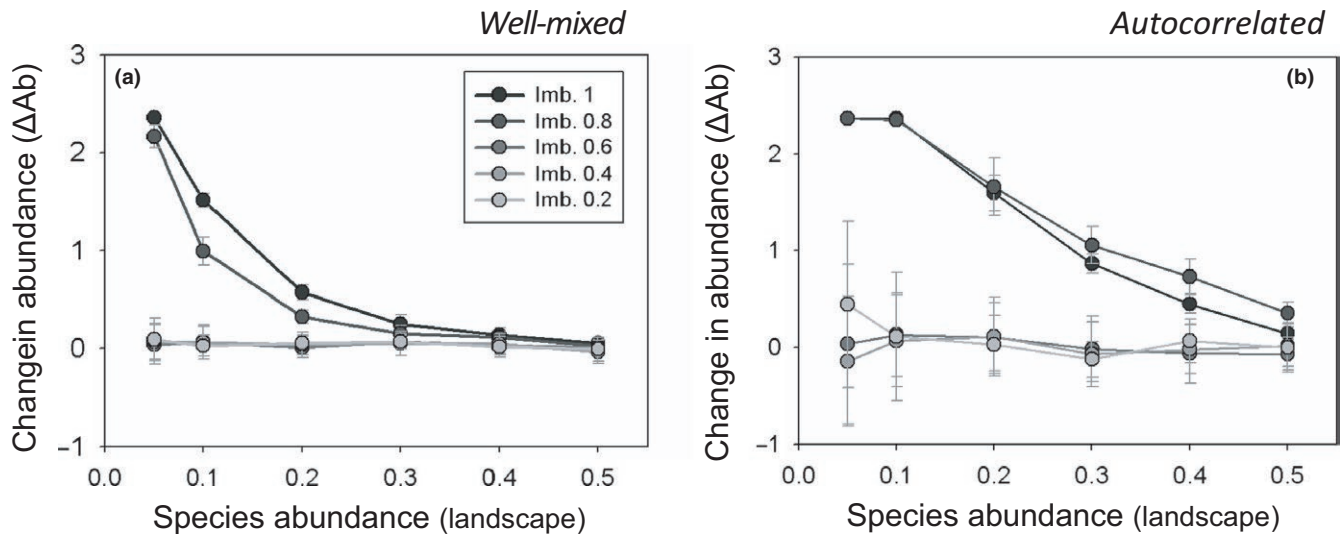
Well-mixed   Autocorrelated

FIGURE 3 With diet complementation operating, rarity and nutrient imbalance (imb.) promoted species overrepresentation in the seed rain ($\Delta Ab > 0$). ΔAb depicts the relative change in species abundances in the seed availability-seed rain transition. Abundance of focal species at the landscape scale is represented in the x-axis (from 0.5 to 0.05). Note that higher nutrient imbalance of fruits also entails higher nutritional differences between fruit species. Bars show mean (±SD) of 15 replicates. See Supporting Information Figure C1 for fragmented landscapes
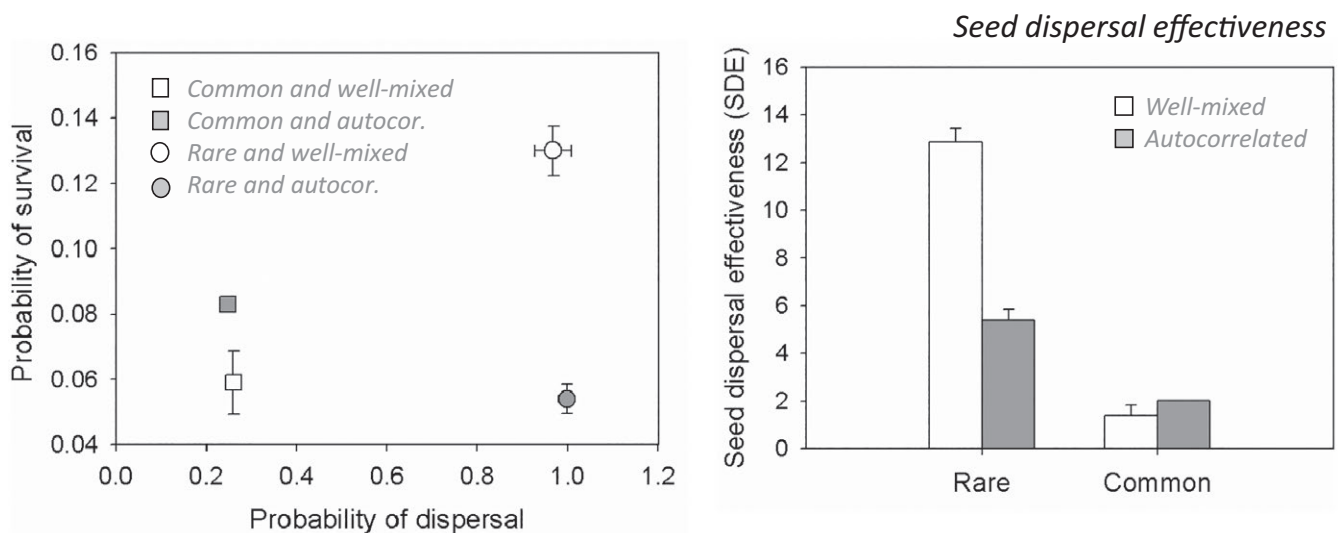
Seed dispersal effectiveness

FIGURE 4 (a) When rarity and nutrient imbalance were high, in all landscape scenarios, the probability of dispersal of rare species was much higher than common ones. In contrast, the probability of postdispersal survival was landscape-dependent. Only when plant species were well-mixed, density-dependent mortality conferred dispersal advantages to rare species (white dots) (b) However, as frugivorous almost depleted crops of rare plants, rare species showed the highest seed dispersal effectiveness in all landscape scenarios. Bars show mean (±SD). See Supporting Information Figure C2 in Appendix S2 for fragmented landscapes

fixed effects (Lindeman, Merenda, & Ruth, 1980). For this purpose, we used relaimpo package (Gromping, 2006).

3 | RESULTS

3.1 | Seed rain community

In any landscape scenario, plant species were overrepresented in the seed rain when they were rare and their fruits were complementary in nutrients from those of the surrounding fruiting community. (Figure 3 and Supporting Information Figure C1 in Appendix S3, $\Delta \bar{Ab} = 2.12$). Overrepresentation of rare species was due to the increased attractiveness of fruits with rarity and nutrient imbalance (Supporting Information Appendix S3, Figure C4). Forest fragmentation and spatial autocorrelation of plant species had a small effect on seed dispersal outcomes (Figure 3 and Supporting Information Figure C1 in Appendix S3). According to lmg metrics, most of the variance explained by the model ($R^2 = 0.80$) was due to nutrient
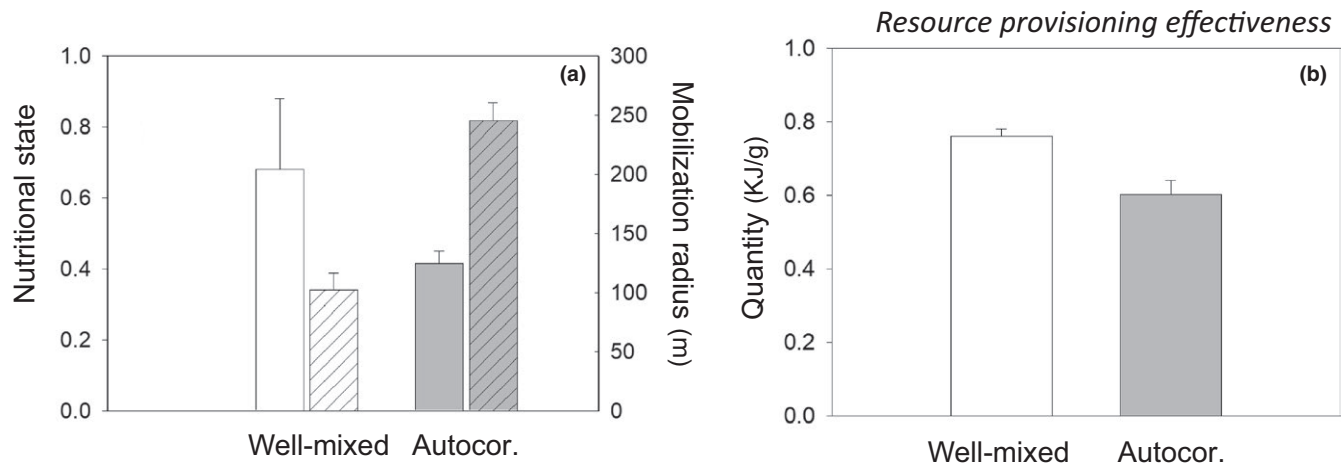
FIGURE 5 (a) In autocorrelated landscapes, birds were forced to fly further to balance their diet. Nonetheless, as they could not feed from different food resources at local scales, their nutritional status was on average poorer. Mob. depicts bird mobilization radius during the simulation (stripped bars) and nut. nutritional state. (b) Due to the extra energy expenditure in flights, energy assimilation per gram of fruits consumed declined. Bars show mean (±*SE*). See Supporting Information Figure C3 in Appendix S3 for fragmented landscapes

imbalance and plant species abundances (36.4 and 35.6%, respectively), while landscape properties explained less than a 5% of the variance.

3.2 | Seedling recruitment and seed dispersal effectiveness

In contrast with the dispersal process, the probability of postdispersal survival was strongly affected by landscape structure. In particular, it depended mostly on the spatial autocorrelation of plant species. When landscapes were well mixed at the scale of frugivores' movement decisions, the probability of survival of seeds of rare species was on average eight times higher than for common species (Figure 4a). In contrast, in spatially autocorrelated landscapes, the advantages of rare species disappeared. In fact, according to lmg metrics, most variance of postdispersal survival ($R^2 = 0.83$) depended on relative abundance of the plant species (32%) and autocorrelation (38%) in the community.

However, because depletion of rare fruits was nearly absolute in all landscape configurations (Figure 4a *x*-axis), diet complementation always resulted in higher seed dispersal effectiveness of rare plants (Figure 4b and Supporting Information Figure C2B in Appendix S3, 8.52 vs. 1.70 S$\bar{D}$E of rare and common species, respectively). Different values of beta parameter (β_s), which dictates the strength of density-dependent mortality, did not vary the observed pattern (Supplementary material, Supporting Information Appendix S3, Figure C7).

3.3 | Resource provisioning effectiveness (RPE)

Landscape properties affected the effectiveness of the simulated seed dispersal mutualism by affecting the energy assimilation and nutrient balance of frugivores. Landscapes with high spatial autocorrelation of plant species hampered the ability of frugivores to locally

balance their diet. As a result, when focal species were rare (abundance 0.05) and nutrient imbalance was high (0.8–1), birds needed to explore larger areas to balance their diet but nutritional status was poorer (Figure 5a).

On average, movement costs were 3.75 times higher in the spatially autocorrelated landscapes (135.66 kJ/day) than in well-mixed ones (36.12 kJ/day). Consequently, in autocorrelated landscapes, energy investment in food searching represented 37.5% of daily energy expenditure (instead of a 13.3% of well-mixed landscapes). Daily energy expenditure (DEE) varied significantly among landscape types despite that all values fell within the ranges of a sustainable energy budget for simulated birds (<456.3 kJ/day). When fruiting resources were well mixed at local scales, DEE values were close to field metabolic rates expected according to simulated bird body size (271.03 vs. FMR = 246.25 kJ/day), but in spatially autocorrelated landscapes, the additional energy investment in fruit searching lead to a 16% increment in DEE (313 kJ/day). Increased energetic costs due to food searching resulted in a decrease of 19.8% in the effectiveness of resource provisioning (Figure 5b). Lmg metrics showed that 33% of the variance explained by the model ($R^2 = 0.84$) depended on spatial autocorrelation of fruiting species.

4 | DISCUSSION

Overall, our simulations support the diet complementation hypothesis (DCH). By mixing different fruit resources to balance their diets, frugivores promoted rare species overrepresentation in the seed rain. Furthermore, our findings provide a theoretical foundation to empirical studies showing that frugivory can play a central role in diversity maintenance of plant communities where plant–frugivore mutualisms are common (Carballo-Ortiz, González-Castro, Yang, de-Pamphilis, & Carlo, 2017; Carlo & Morales, 2016; Herrera, 2002), and where diet complementation is a component of frugivore foraging

(Murphy, 1994). Results also show that resource provisioning effectiveness (RPE) depends to a great extent on the spatial configuration of fruiting resources, which in turn dictates the energetic costs that frugivores will have to pay to balance their diet.

Two conditions needed to be met to favour the overrepresentation of plant species in the seed rain. First, plant species needed to be rare at the landscape scale (i.e., <5% of individuals), and second, the nutrient imbalance in fruits needed to be high. In such scenarios, fruits from rare plants became more limiting to frugivores' diets because they were necessary to balance diets—a complementary effect—but difficult to obtain. This caused rare fruits to be consumed and dispersed at higher proportions than expected by their relative abundances. Interestingly, rarity on its own had little impact on species representation in the seed rain. Rare-biased dispersal depended to a great extent on the nutritional composition of the fruiting assemblage. Thus, our results support the idea that fruit selection by frugivores is less dependent on specific fruit traits than on the relative value of a particular trait with respect to the fruiting environment (Blendinger, Martin, Acosta, Ruggera, & Araoz, 2016).

Our simulations in a simplified system of two plant species demonstrate that diet complementation can confer quantitative dispersal advantages to the rare species even when there is no a priori preference for such rare fruits. Whenever fruits of different species complement each other and frugivores consume them jointly, diet complementation will result in rare-biased dispersal. This would apply to richer plant communities with more diverse and complex nutrient environments (Supporting Information Appendix S4, Figure D1). Rare-biased dispersal will be even stronger in cases were (a) rare plants are the only source of limiting complementary nutrients (e.g., vitamins, electrolytes) or (b) rare plants bear more nutritious or attractive fruits than common species. But how common is fruit-mixing in frugivore diets and nutrient complementarity among fruits in natural frugivore–plant communities?

In general, fruit-eating birds consume multiple fruiting species over short periods of time instead of sticking to just one preferred or abundant species (Levey & Del Rio, 2001). The underlying causes of such behaviour remain poorly understood, but similarly to what occur with other taxa (Raubenheimer et al., 2015), birds may mix different fruit resources to maintain macronutrients balance. In general, fruits in plant communities show large interspecific variation in lipid content (cv > 75%) and a complementary negative co-variation with carbohydrates (Herrera, 1987; Jordano, 1995; Galetti et al., 2011; see Supporting Information Table C1 in Appendix S3). Broadly speaking, fruits are either lipid-rich and carbohydrate poor or vice versa. Bird preferences for lipid or carbohydrate-rich fruits are mostly dictated by their digestive traits (i.e., gut retention times, Levey & Del Rio, 2001), but they may switch among both kinds of foods to obtain adequate quantities of both nutrients without the need of overingesting one of them (Raubenheimer & Simpson, 1999).

Microconstituents including minerals (i.e., electrolytes) and secondary metabolites can also influence fruit choices by frugivores (Levey & Del Rio, 2001). Like macronutrients, electrolytes of fleshy fruits are highly variable among plant species (Herrera, 1987).

Moreover, it seems that in general, fruit pulp is electrolyte poor (Jordano, 2000) and plants like figs (*Ficus* spp.) take advantage of this deficiency and attract frugivores with essential but uncommon minerals (e.g., calcium, O'brien et al., 1998). In the case of secondary metabolites, birds may avoid ingesting large amounts of a specific toxic compound by consuming multiple fruiting species (Levey & Del Rio, 2001). In sum, regardless of the dietary element in question, we predict that rare fruits with distinct pulp composition will be preferentially consumed by frugivores.

Diet complementation also depends on the capacity of frugivores to track nutrients. Although studies evaluating the regulatory effects of nutrients on frugivore movements are lacking, abundance of certain frugivorous species has been found to be more strongly associated with fruit nutrient qualities than by overall fruit availability (Blendinger et al., 2015). Moreover, animal movement patterns driven by their nutritional demands are commonplace in nature (e.g., Johnson et al., 2017; Nie et al., 2015). In our simulations, fruit-tracking behaviour emerged from the necessity of frugivores to search alternative food resources to meet their nutritional demands. This had two important consequences: Fruit-tracking promoted rare-biased dispersal irrespectively of plant spatial configuration, but it increased foraging costs for frugivores. For example, when plant species were found in monospecific patches, birds had to move longer distances across patches to balance diets. This extra energy expenditure led to a decline of almost 20% of the resource provisioning effectiveness. Finally, when considering the seed-to-seedling transition, our results show that diet complementation can have long-standing consequences in the composition of the community of recruits. Despite that the advantages of rare species conferred by density-dependent mortality disappeared in homogeneous landscapes (see Morán-López, Carlo, & Morales, 2018 for similar results), rare plants continued to show the highest seed dispersal effectiveness thanks to their overrepresentation in the seed rain.

4.1 | Model simplifications

To understand the general principles of diet complementation as a frequency-dependent mechanism, we simplified our plant community by considering only two species bearing fruits that were equally nutritious but complementary for birds. First, it is unlikely that different fruiting species are equally nutritious. Second, real plant communities are more complex by having more species and by differing in a larger multidimensional trait space of fruit nutrients (i.e., Galetti et al., 2011). Our results were, however, robust to such complexities. When simulating richer plant communities where multiple nutrients affected fruit choice and fruits differed in their nutritional value, our result showed the same core principle—rare-biased dispersal emerged when rare plants offered fruits with a distinct pulp composition (Supporting Information Appendix S4, Figure D1-2). Furthermore, rare-biased dispersal occurred when common fruits were up to fifty per cent more balanced than rare ones. However, it decreased as common fruits became more nutritionally

balanced (Supporting Information Appendix S4, Figure D3). Future work evaluating DCH in nutritional milieus with increased attractiveness of common fruits will provide valuable information about the vulnerability of this coexistence mechanism to changing fruiting environments.

Last, we simulated dispersal by strictly frugivorous animals in spite that the vast majority of bird frugivores have mixed diets that include protein-rich insects and other animals (Levey & Del Rio, 2001). We expect that such behaviour will have a minor effect—if any at all—on fruit-mixing. As fruits are notoriously deficient in protein (Jordano, 2000), animal matter should complement equally all fruiting species. Nevertheless, in the case that it modifies fruit complementation, other food resources than fruits can be easily incorporated in our model.

5 | CONCLUSIONS

Our work shows that diet complementation can act as a strong frequency-dependent mechanism conferring advantages to rare plant species during the dispersal and recruitment stages. This provides a behavioural mechanism by which frugivores can promote diversity maintenance in plant communities (Carlo & Morales, 2016). Future progress, however, will depend on the testing and exploration of the DCH in real frugivore–plant communities. For example, indirect support for DCH could be obtained by comparing the rates of frugivory (and dispersal) for two kinds of rare fruits: those that nutritionally complement common ones and those that do not. If DCH occurs, then frugivory rates will be higher for the nutritionally distinct fruiting species. Another promising albeit challenging approach is to test model predictions about frugivory rates. This can be attained when data on frugivores' nutritional demands (inferred from diets, *see* Raubenheimer et al., 2015), fruit nutrients and fruit relative abundances are available in a given community. We hope that our theoretical approach stimulates more studies addressing the generality of diet complementation as a frequency-dependent mechanism and its role on structuring plant communities.

AUTHORS' CONTRIBUTIONS

T.M.-L. designed diet complementation submodels and resource provisioning assessment, analysed data and wrote the manuscript; T.A.C. conceived the idea that fruit choices by frugivores can act as frequency-dependent mechanism conferring advantages to rare plants and helped write the manuscript; G.A. helped at evaluating which behavioural mechanisms can provide rare-biased dispersal and revised the manuscript; J.M.M. conceived the idea that diet complementation can act as a frequency-dependent mechanism, helped at improving design concepts of the model and revised the manuscript. He served as a led for this work; All authors approved the final version of the article.

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