

LETTER

Reciprocity and interaction effectiveness in generalised mutualisms among free-living species

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Abstract

Mutualistic interactions among free-living species generally involve low-frequency interactions and highly asymmetric dependence among partners, yet our understanding of factors behind their emergence is still limited. Using individual-based interactions of a super-generalist fleshy-fruited plant with its frugivore assemblage, we estimated the Resource Provisioning Effectiveness (RPE) and Seed Dispersal Effectiveness (SDE) to assess the balance in the exchange of resources. Plants were highly dependent on a few frugivore species, while frugivores interacted with most individual plants, resulting in strong asymmetries of mutual dependence. Interaction effectiveness was mainly driven by interaction frequency. Despite highly asymmetric dependences, the strong reliance on quantity of fruit consumed determined high reciprocity in rewards between partners (i.e. higher energy provided by the plant, more seedlings recruited), which was not obscured by minor variations in the quality of animal or plant service. We anticipate reciprocity will emerge in low-intimacy mutualisms where the mutualistic outcome largely relies upon interaction frequency.

KEYWORDS

asymmetry, Bayesian, ecological networks, frugivory, Mediterranean, plant–animal interactions, reciprocity, resource provisioning effectiveness, seed dispersal, seed dispersal effectiveness

INTRODUCTION

Mutualisms are ecological interactions entailing beneficial outcomes for the interacting partners. These benefits broadly emerge from interspecific encounters where there is an exchange of resources (Kiers et al., 2011). Despite recent interest in interspecific exchanges, especially focusing on strict and intimate interactions (Guimarães et al., 2007), much of the reciprocal effect between generalised, free-living, mutualistic partners remains unexplored (Thompson, 2009).

Species-level analyses of complex interaction networks have revealed highly heterogeneous structures (i.e. high variance in number of interactions per species), weak levels of mutual dependence, and high asymmetry in interaction strength (Bascompte & Jordano, 2014; Johnstone

& Bshary, 2008; Wootton & Stouffer, 2016). Interaction asymmetry in complex networks of free-living species (Bascompte et al., 2006), as well as energy flow asymmetry in food webs (Rooney et al., 2006), appear as quintessential characteristics of these complex systems, closely associated with their stability (Berlow, 1999). Yet, our understanding of the factors behind the emergence of asymmetric interactions is very limited; for example, if generalised mutualistic interactions between free-living species entail exchanges of services, is there a “fair two-way transfer” of resources (Chomicki et al., 2020; Kiers et al., 2011), that is, is there reciprocity?

Reciprocity, as defined herein, is the existence of a positive association in the rewards provided between mutualistic partners. We consider a mutualistic system to be reciprocal if the reward provided by one organism

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(e.g. pollen grains or fruits offered by plants) matches the reward from its mutualistic partner (e.g. fertilised ovules or dispersed seeds). If an increase or decrease in reward does not return proportional changes in the reward by the other partner, so that both rewards keep balanced, those interactions would be less, or not reciprocal at all. Without an external reference, it is not possible to determine if the exchange in resources between partners is equal or fair. A population or community perspective will allow us to understand whether specific pairwise interactions are exchanging their resources at 'fair' cost, or at least at the cost set by the population or community. Aside from previous work on mycorrhizal symbioses, the reciprocity of less intimate and 'lagged' mutualisms (i.e. with delayed responses beyond the interaction) has been rarely addressed. However, previous studies explore other definitions of reciprocity using different approximations that are related to the degree of partner's dependence and not to the balance in rewards exchanges (e.g. Burns, 2003; Guerra & Pizo, 2014; Herrera, 1984; Reid, 1990).

Partner dependence, that is how much a partner relies upon another partner for its services, is a better-explored aspect of mutualistic interactions. Dependence can be estimated as the proportion of service obtained from a specific partner relative to the total service obtained from all partners. Dependence differs from reciprocity in that it examines the reliance from the perspective of the partner, and not the whole population. Estimating dependence also allows the calculation of interactions asymmetry by comparing the mutual dependence of both partners. Asymmetry emerges when a species/organism depends a lot on one partner but, in turn, the partner does not rely as much on that particular pairwise interaction (Bascompte et al., 2006; Jordano, 1987; Vázquez et al., 2007).

A generalised property of free-living species networks is the high frequency of weak interactions (Jordano, 1987) so that when other interactions are strong, their dependence becomes highly asymmetric. This pattern in the mode of interaction between organisms is known as disassortativity, whereby organisms that establish many interactions tend to interact with less connected organisms (Barabási, 2016), and is often found in biological networks (Newman, 2003). Weak links appear as a characteristic feature of complex systems which are made up of highly diversified components (Csérmely, 2009; Granovetter, 1973). Weak links also provide support for network stability (McCann et al., 1998). Most previous analyses of network patterns in real-world ecosystems have considered species-level interactions. However, interaction asymmetries at the individual-level remain largely unexplored, despite likely being the most appropriate level to address interaction outcomes (Clark et al., 2011). Actual ecological interactions that we can observe, sample and document, occur from interspecific encounters between individuals (Dupont et al., 2014;

Jordano, 2016). One might therefore wonder if, when looking at a more refined level (e.g. from species to individuals), we could still expect asymmetry in mutual dependence.

Few studies so far have analysed interaction asymmetry beyond variation in just interaction frequency or strength, further examining differences in interaction quality (González-Castro et al., 2022; Guerra & Pizo, 2014; Herrera, 1984; Jordano, 1987). Interaction outcomes may yield different results from those expected solely on the basis of interaction frequency (Janzen 1983; González-Castro et al., 2022), and so it is possible that infrequent interactions result in higher fitness than frequent interactions, affecting the reciprocity balance. A useful tool to measure the functional outcome (fitness) of mutualisms in terms of both interaction quantity and quality at the individual level is the effectiveness framework (Schupp, 1993; Figure 1a). Consideration of individual variation and interaction outcomes expands our understanding of the potential consequences, for example, demographic or evolutionary, of ecological interactions.

In this study, we calculate the two-sided rewards for seed dispersal mutualistic interactions between plants and animal frugivores by means of the Resource Provisioning Effectiveness (RPE) and Seed Dispersal Effectiveness (SDE) frameworks (Schupp et al., 2017). We look at mutual reciprocity (i.e. the balance in the exchange of resources) from an individual perspective in a plant population using SDE and RPE as estimates for the reward obtained in the relationship (Figure 1d). We explore whether mutualistic dependencies are still asymmetrical when looking from a plant individual perspective and when incorporating both interaction frequency and quality (Figure 1e). We use as study organism the plant *Pistacia lentiscus*, a species defined as super-generalist species because it interacts with a large part of the local diversity of partner species, being heavily connected to the rest of the community (García, 2016; Jordano et al., 2002; Parejo-Farnés et al., 2020). Super-generalists play a fundamental role in ecological networks because they provide great cohesion (Guimarães et al., 2011). A two-sided study of such mutualism at the plant individual level informs about the diversity of individual rewards, the diversity of mutualistic partners and their effects, and the consequences on resource exchange between them.

Here, we address three specific objectives: (1) characterise the effectiveness of the mutual beneficial service between individual plants and their frugivorous species, (2) test if the service provided between partners in terms of the amount of reward is reciprocal and (3) explore if there exists asymmetry in the mutual dependencies when looking at a plant individual level and considering interaction outcomes; that is, accounting for interaction quality beyond interaction frequency.

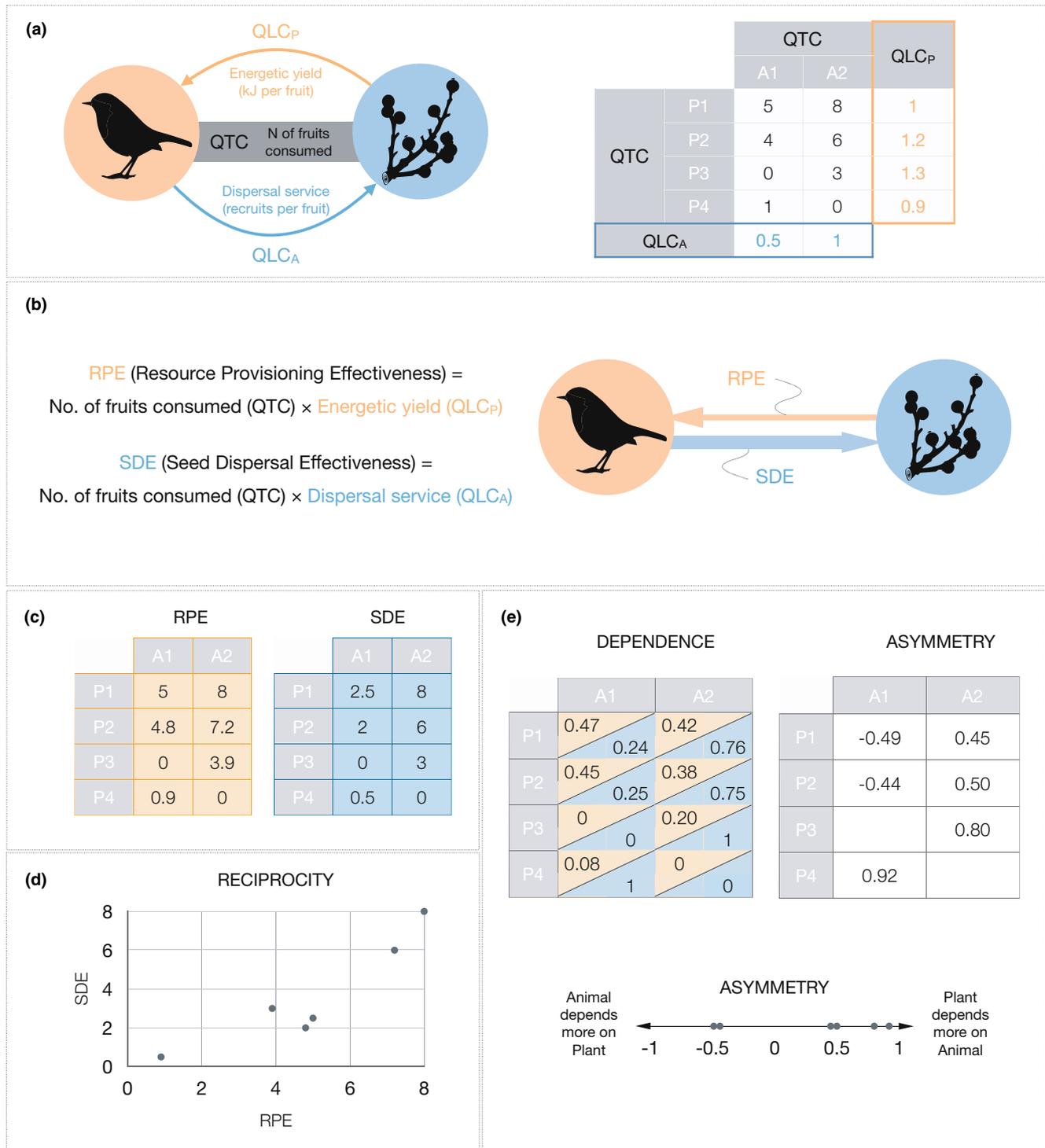


FIGURE 1 Schematic representation of this study approach to characterise plant-frugivore seed dispersal mutualisms, showing: (A) the three main subcomponents present in the mutualism between any two nodes in the network: the interaction frequency or quantity component (QTC) and the two-sided quality (QLC) of the service provided by the partners. For this example we present the animal frugivore in orange, and the plant individual in blue; plant's quality is the energetic yield per fruit (QLC_P) and bird's quality is the probability of seedling recruitment per consumed fruit (QLC_A). On the right we provide an example adjacency matrix with simulated numbers of quantity and quality data, with two animals (A1 and A2), and four plants (P1–P4). (B) The two subcomponents (quantity and quality) are combined to calculate the effectiveness of the interaction from the bird (Resource Provisioning Effectiveness, RPE) and the plant's perspective (Seed Dispersal Effectiveness, SDE). (C) Resulting calculations of RPE and SDE using the example matrix in (A). (D) Reciprocity (i.e. the balance in rewards exchange between partners) is assessed by the correlation between RPE and SDE values of all pairwise interactions. (E) Derivation of mutual dependence estimates and interaction asymmetry for plant and animal partners. Dependence values for animals (i.e. how much the animal depends on each particular plant, orange upper-left cells) are calculated based on RPE values, while dependence values for plants (blue lower-right cells) are based on SDE values. The asymmetry of each pairwise interaction is calculated as the standardised difference between the two dependence values in each interaction, and ranges between -1 and +1 (see Box 1).

METHODS

Species and study site

Pistacia lentiscus (Anacardiaceae) is a dioecious, wind-pollinated, animal seed-dispersed shrub that can be considered as a ‘foundation species’ (Whitham et al., 2006) in lowland Mediterranean scrublands. Numerous resident and migrant frugivorous birds rely on *P. lentiscus* fruits as a nutritional resource (González-Varo et al., 2019) and act as its seed dispersers, with infrequent consumption by mammals (Perea et al., 2013).

Fieldwork was conducted between the years 2019–2020 at two study sites in Doñana National Park (Huelva, SW Spain): La Mancha del Rabicano in El Puntal site (EP) and Laguna de las Madroñas (LM). Both areas consist of Mediterranean sclerophyllous scrubland dominated by *P. lentiscus* coexisting with a total of 28 fleshy-fruited species recorded in the area. We monitored 40 individual *P. lentiscus* plants per study site (Suppl. Mat. A). This sampling included all the female fruiting plants found in LM population. In EP site, we chose a representative sample of female plants scattered across the site and covering the full-size gradient in the population.

Interaction frequency: Quantity component (QTC)

The interaction frequency of *Pistacia lentiscus* plants with avian frugivore species was assessed through DNA-barcoding and continuous-monitoring cameras (Quintero et al. 2021) during the complete fruiting season, between September 2019 and March 2020.

We placed seed traps beneath individual plants at both populations, where we collected a total of 2691 faecal and regurgitated seed samples (1913 for EP and 778 for LM). Visiting avian species were identified with DNA-barcoding analysis of collected samples. Animal-origin DNA present in the surface of the samples was extracted, amplified and then sequenced following protocols in González-Varo et al. (2014) with minor modifications (Suppl. Mat. B.1). Retrieved sequences were identified using BOLD Systems database or BLAST from the NCBI. More than 90% of the collected samples were analysed ($n = 2510$) and the identification success was 94%.

Using monitoring cameras, we recorded animal visitation and feeding events at focal plants in one of the sites (EP). All individual plants were monitored every fortnight along the fruiting season for a total of nine times, accumulating *c.*19h observation per plant. Recordings lasted *c.* 2.2h and started in the early morning (Suppl. Mat. B.2). We analysed the video recordings with the help of DeepMeerkat software (Weinstein, 2018). We obtained the feeding frequency of animals (i.e. fraction of visits with actual fruit consumption) and the number

of fruits consumed per visit. Avian species identification was possible for 91.5% of the $n = 3970$ visits recorded by cameras and 24% of the interaction events included feeding records.

The total number of frugivorous bird species recorded was 27; 26 were recorded with cameras and 22 with DNA barcoding. Interaction accumulation curves (IAC) were used to determine sampling completeness (see Suppl. Mat. B.3; Colwell & Coddington, 1994; Jordano, 2016). Overall, sampling completeness (sensu Chacoff et al., 2012) was 93% for both methods; 95% for cameras and 96% for DNA-barcoding.

To estimate the total number of fruits consumed by each bird species at each individual plant, we multiplied four sequential steps: (1) the total number of visits at each site, (2) the probability that a given bird species visited a particular plant, (3) the probability that a visit included a feeding event and (4) the number of fruits consumed per visit by each bird species. We estimated these quantities using Bayesian models fitted with Stan (Stan Development Team, 2022) and brms package (Bürkner, 2017) in R 4.1.2 (R Core Team, 2021). The Bayesian approach allowed us to combine information on bird visitation rates coming from DNA-barcoding and monitoring cameras, to estimate a few unobserved quantities, such as missing feeding rates for some species, by sharing information across taxa, and to obtain and propagate uncertainties along multiple effectiveness components (see Suppl. Mat. E.1 for details on each model). Since posterior distributions were often right-skewed, we report their median throughout.

Interaction outcome for the animal: Quality Component (QLC—RPE)

Plant quality was defined as the energetic reward provided per fruit consumed. Feeding behaviour was different among the avian species recorded: some birds consume the whole fruit regurgitating or defecating the seed intact (legitimate seed dispersers), others consume part of its pulp discarding the seed (pulp thieves); while other birds peel the fruit, break the seed coat and consume the embryo inside the seed (seed-predators or granivores). Because avian species consume different parts of the fruit, the energy obtained refers to the pulp for swallowers and pulp consumers, and to the seeds in the case of predators (see Table S.A.1 for frugivory type categories).

We collected fruits from each plant (mean = 31 fruits, range = 17–63, Suppl. Mat. C) and measured both pulp and seed fresh mass. Fresh mass was converted to dry mass using *P. lentiscus* % water content (Jordano, 1984). To obtain the energy contained per fruit, we then multiplied the pulp and seed dry mass by their estimated energy yields: 25.25 kJ/g for pulp and 28.14 kJ/g for seed (see Suppl. Mat. E.2).

BOX 1 Reward, reciprocity and asymmetry calculations

Reward estimation using the Effectiveness framework

We estimated the rewards exchanged between mutualistic partners using the Resource Provisioning Effectiveness and Seed Dispersal Effectiveness framework (RPE and SDE; Schupp et al., 2017, Quintero et al., 2020). The effectiveness of the mutualistic interaction is estimated as the product of a quantity and quality component. The quantity component (QTC) was common for both RPE and SDE, that is, the total number of fruits consumed by a specific bird species on a given plant. Quality from the animal's perspective was the energy acquired per fruit consumed (referred to pulp or seed energy depending on bird's feeding behaviour). From plants' perspective, the quality component represents the probability that a consumed fruit becomes a seedling surviving its first summer. RPE therefore estimates the total energy provided by an individual plant to a bird species across the fruiting season, and SDE estimates the potential number of seedlings recruited coming from an individual plant by interacting with a bird species. Below we define the components for the rewards calculation:

RPE_{ij} : Total energy that bird species j obtained by feeding in plant i

$$RPE_{ij} = QTC_{ij} \times QLC_RPE_i$$

SDE_{ij} : Number of plant i seedlings recruited through consumption by bird species j

$$SDE_{ij} = QTC_{ij} \times QLC_SDE_j$$

QTC_{ij} : Number of fruits consumed by bird species j in plant i along the fruiting season

$$\begin{aligned} QTC_{ij} = & \text{Total no. of visits in population} \\ & \times \text{Prob. that bird species } j \text{ visits plant } i \\ & \times \text{Prob. bird species } j \text{ consumes fruit during visit} \\ & \times \text{No. fruits bird species } j \text{ consumes per visit} \end{aligned}$$

QLC_RPE_i : Energy contained per fruit pulp or seed of plant i

$$\begin{aligned} QLC_RPE_i = & \text{Fresh pulp or seed mass of plant } i \text{ (g)} \times \text{non-water\% in pulp or seed} \\ & \times \text{energetic yield per gram of dry pulp or seed} \end{aligned}$$

QLC_SDE_j : Probability that a fruit consumed by bird species j becomes a seedling surviving its 1st summer

$$\begin{aligned} QLC_SDE_j = & \text{Prob. seed escaping predation when manipulated by bird species } j \\ & \times \sum_{m=1}^{m=5} [\text{Prob. bird species } j \text{ deposits a seed at microhabitat } m \\ & \times \text{Prob. seed escaping post dispersal predation in microhabitat } m \\ & \times \text{Prob. seedling emerging and surviving its 1st summer in microhabitat } m] \end{aligned}$$

Reciprocity

To estimate reciprocity between partners we used Pearson correlation coefficients between the log-transformed RPE and SDE values. We aggregated the RPE and SDE values for each individual plant, that is adding up the values for all bird species with which it interacted, resulting in the total energy provided by the plant and the number of seedlings recruited through interactions with its bird assemblage. We used 1000 samples from the posterior distribution of RPE and SDE calculated for each plant, to consider uncertainties in the estimation of reciprocity (Suppl. Mat. F.1). A high positive correlation indicates high reciprocity, meaning that plants providing more energy (RPE) also obtain a higher number of seedlings recruited (SDE).

Calculating dependence and asymmetry between bird species and individual plants.

We calculated two mutual dependence (d) values for each pairwise interaction, one for the plant ($d_{P_i \rightarrow A_j}$) and one for the animal species ($d_{A_j \rightarrow P_i}$; Suppl. Mat. F.2).

$$\begin{aligned} d_{P_i \rightarrow A_j} &= \frac{SDE_{ij}}{\sum_{A=1}^n SDE_i}, \text{ for the dependence of } P. \textit{lentiscus} \text{ plant } i \text{ on animal species } j; \text{ and,} \\ d_{A_j \rightarrow P_i} &= \frac{RPE_{ij}}{\sum_{P=1}^m RPE_j}, \text{ for the dependence of animal species } j \text{ on plant } i, \end{aligned}$$

where d is the dependence of plant i on animal species j , or vice versa; SDE_{ij} is the estimated number of seedlings recruited coming from plant i via frugivore species j ; RPE_{ij} is the amount of kilojoules plant i provided to frugivore species j ; and n and m represent the total number of animal species and individual plants, respectively.

Interaction asymmetry (AS) is defined as:

$$AS_{P_i, A_j} = \frac{d_{P_i \rightarrow A_j} - d_{A_j \rightarrow P_i}}{\max(d)}$$

AS values can range from -1 to 1 , where 0 indicates total symmetry (both partners depend on each other with the same intensity), values approaching $+1$ indicate that the plant is more dependent on the animal than vice versa, and negative values indicate that the animal is more dependent on the plant than the plant on the animal.

Interaction outcome for the plant: Quality Component (QLC—SDE)

We estimated the quality of animals as seed dispersers according to the: (1) probability of seeds escaping predation by granivorous birds, (2) microhabitat use by each bird species, (3) probability of seeds escaping post-dispersal predation and (4) probability of seedling emergence and early survival (past their first summer) in each microhabitat. We estimated these probabilities using Bayesian models as above (see Suppl. Mat. E.3 for details). The product of these four steps determined the probability of seedling recruitment resulting from the consumption of one fruit by a specific avian consumer.

We found a few undamaged, depulped seeds ($n = 36$) in the seed traps beneath plants that were attributed to seed predators through DNA-barcoding. Seeds dropped during fruit handling indicated sporadic dispersal events by seed predators, whose probability was estimated using the total number of preyed-upon seeds (open seed endocarp halves) and the number of undamaged seeds found in seed traps attributed to granivores (Suppl. Mat. D.1 and E.3).

The intensity of microhabitat use by the different bird species was inferred from the seed rain of *P. lentiscus* seeds collected at five microhabitats: under *Pistacia lentiscus* conspecifics (PL), under other fleshy fruited species (FR), under non-fleshy fruited species (NF), under pine trees (*Pinus pinea*; PP) and open ground areas (OA). At each microhabitat, we collected *P. lentiscus* dispersed seeds and identified the bird species through DNA-barcoding. For the PL microhabitat, we used the seed traps located beneath the focal individual plants (see above). To sample microhabitats FR, NF and PP we placed additional seed traps at 15 replicated points per microhabitat. For open areas (OA) we scanned 17, 1-m wide, transects during the season. The number of dispersed seeds collected at each microhabitat allowed us to estimate the probability of dispersal to each specific microhabitat by each bird species (Suppl. Mat. D.2 and E.3).

Finally, we measured post-dispersal seed predation, seedling emergence and survival at each microhabitat. To study post-dispersal predation, we placed 10 seeds

on a petri dish (six replicates per microhabitat) and monitored the rate at which seeds experienced predation (mainly by rodents, see Suppl. Mat. D.3 and E.3). We also installed germination stations (13 replicates per microhabitat, each containing 16 sown seeds) to estimate seedling emergence and survival (see Suppl. Mat. D.4).

Effectiveness, reciprocity and asymmetry calculations

We calculated RPE and SDE as the product of quantity and their respective quality components (i.e. the interaction frequency multiplied by its functional outcome; Figure 1 and Figure S.E.1). We estimated the reciprocity in reward exchange between partners, their mutual dependence and asymmetry following the procedure presented in Box 1.

To assess the robustness of the observed asymmetry values to variations in our sampling design, we repeated the asymmetry calculations using replicated random subsets of 20, 40 and 60 plants, to examine potential effects of the number of focal plants on the distribution of asymmetry values. We also calculated the asymmetry in a randomised network of the same size (i.e. 80 focal plants) following Patefield and Vázquez null models to test if the observed and randomly expected asymmetry values differed (Suppl. Mat. H).

RESULTS

Plant individual-based interactions

We estimated that birds consumed a total of 2.2×10^5 fruits from the 80 marked plants at both *P. lentiscus* populations (90% credibility interval: 1.5×10^5 – 6.6×10^5). This consumption represents c. 20% of the total number of fruits produced by focal plants in the 2019–2020 season (Suppl. Mat. G.1). We detected 27 bird species consuming *P. lentiscus* fruits, of which 12 are considered

residents, 9 summer or trans-Saharan, migrants and 6 winter migrants (Suppl. Mat. A). More than 85% of the consumed fruits were eaten by just three species: *Curruca melanocephala*, *Erithacus rubecula* and the seed predator *Chloris chloris*. These species behaved as super-generalists, interacting with the majority of individual plants (Figure 2). The next most significant consumers were *Turdus merula* and the winter migrant *Sylvia atricapilla*.

Resource provisioning and seed dispersal effectiveness

Pistacia lentiscus plants were highly variable in Resource Provisioning Effectiveness (RPE) provided to avian species (Figure 3). On a per-interaction basis a frugivore species consumed a median of 101 fruits on each plant (90% CI: 2–2680). We estimated that *Curruca melanocephala* and *Erithacus rubecula* ate more than 4000 fruits, and *Chloris chloris* predated more than 5500 seeds, at certain individual plants. This intensity of consumption represents, however, just a small proportion of the available crop offered: 90% of the plants had less than half their crop size removed by birds (Suppl. Mat. G.1). The quantity component accounted for almost all (93%) of the variation in RPE (Suppl. Mat. E.5). Regarding quality, we found up to sevenfold differences in the energetic content of fruits from individual plants. Birds exploited the full gradient of fruit sizes (Suppl. Mat. G.2), but in general, avian consumption was higher in plants with larger crops, canopy area and pulp content (Suppl. Mat. G.3).

Seed Dispersal Effectiveness (SDE, Figure 3) was also determined more by the quantity than the quality component, the latter varied little among bird species (variance partitioning: quantity = 69%, quality = 31%; Suppl. Mat. E.5). Except for seed predators, which had negligible contributions to recruitment (because they destroyed 99.9% of the seeds consumed), the probability of recruiting a seedling per consumed fruit was similar for all bird species (median = 1.1×10^{-4} ; 90% CI = 1.0×10^{-5} – 9.6×10^{-4}), with *Curruca melanocephala* emerging as the highest quality disperser, followed by other members of the Sylviidae family (Figure 3; Figures E.3.4). Recruitment probabilities at the final stage were low; even the most effective pairwise interaction (involving *C. melanocephala* and plant '314'), would have resulted in SDE = 0.53 seedlings (<1 seedling) surviving the first summer.

Differences among frugivore species in dispersal quality result from their distinctive microhabitat use (Suppl. Mat. E.3.1) and existing trade-offs between recruitment stages in different microhabitats (Suppl. Mat. E.3.2; E.3.3). For example, seeds falling under pine trees had the highest probability of surviving rodent predation (median probability = 0.023), followed by those arriving to open areas (median probability = 0.013).

Seedling emergence and survival, on the other hand, was highest in open areas and lowest beneath pines (median probability = 0.038 in OA versus 0.003 in PP). Overall, Open Area was the microhabitat with highest probability of recruitment, yet very few seeds arrived there, hence this microhabitat hardly contributed to recruitment. The high quality of *C. melanocephala* (median probability = 1.2×10^{-4}) emerged from its preferential dispersal towards the most suitable microhabitats: beneath non-fleshy fruited plants and *P. pinea*. In contrast, heavy *P. lentiscus* fruit consumers like *E. rubecula* showed medium quality (median probability = 1×10^{-4}) because it frequently deposits seeds under *P. lentiscus* plants, a microhabitat where the probability of escaping post-dispersal seed predation and seedling survival were medium to low.

Reciprocity

We found a high correlation between RPE and SDE (mean Pearson r on log–log values = 0.93; Suppl. Mat. F.1). High correlation indicated high reciprocity in the interactions between individual *P. lentiscus* plants and their bird consumers: more seedlings were recruited from plants supplying more energy (Figure 4). In other words, the larger the reward provided by one interaction partner, the larger the reward contributed by the other partner. This high reciprocity stems from both RPE and SDE being mainly driven by the quantity component (intensity of consumption) rather than by differences in plant and frugivores quality. As a result, more seedlings were recruited from plants which had more fruits consumed (mean slope of $\log \text{SDE} \sim \log \text{RPE} = 0.83$, SD = 0.06; Figure 4), regardless of differences in the composition of their frugivore assemblages. Deviation from a slope of 1 indicates a 'diminishing return' effect, so that the number of seedlings recruited did not increase in the same proportion as the total energy provided by plants. This diminishing return was not caused by interactions with seed predators (mean slope of $\log \text{SDE} \sim \log \text{RPE}$ excluding seed predators = 0.85, SD = 0.04); who damaged all plants in similar proportions. Additionally, plants presenting greater rewards had larger crop sizes and were consumed by a higher number of bird species (Figure 4).

Dependence and asymmetry

Mutual dependencies on the partner were in general low (Figure 5). Most pairwise interactions (96% from birds' perspective, and 76% from plants') showed dependencies below 0.25, indicating that most interactions contributed to the partner only a small fraction of the total reward obtained (i.e. energy income for birds or seedlings recruited for plants). There were, however, some strong, highly dependent interactions, namely

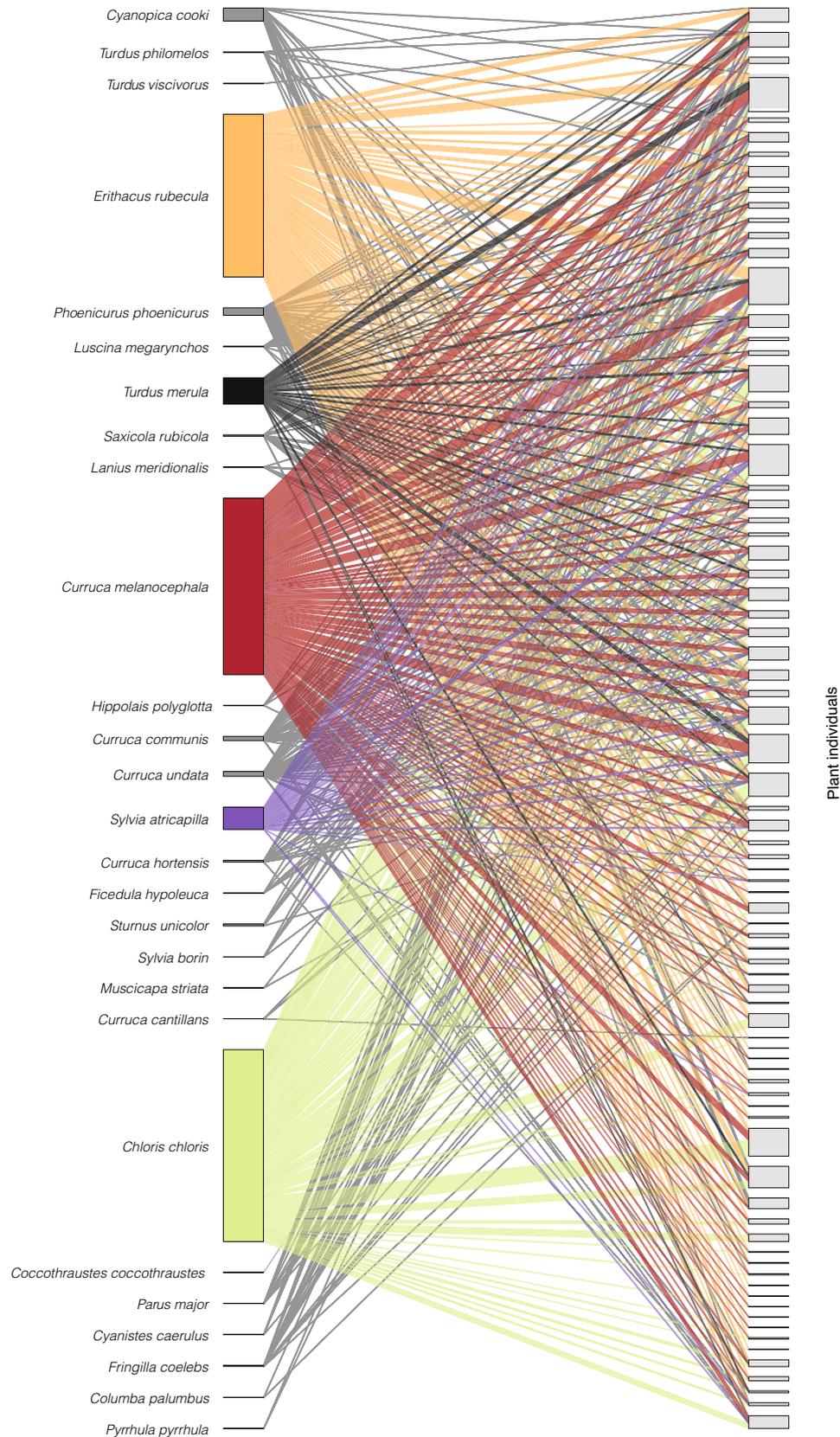


FIGURE 2 Interaction network between avian consumer species and individual *Pistacia lentiscus* plants, where the node and link width is proportional to the total number of fruits consumed on each plant. Non-legitimate dispersers (n = 7) are grouped at the end of the network.

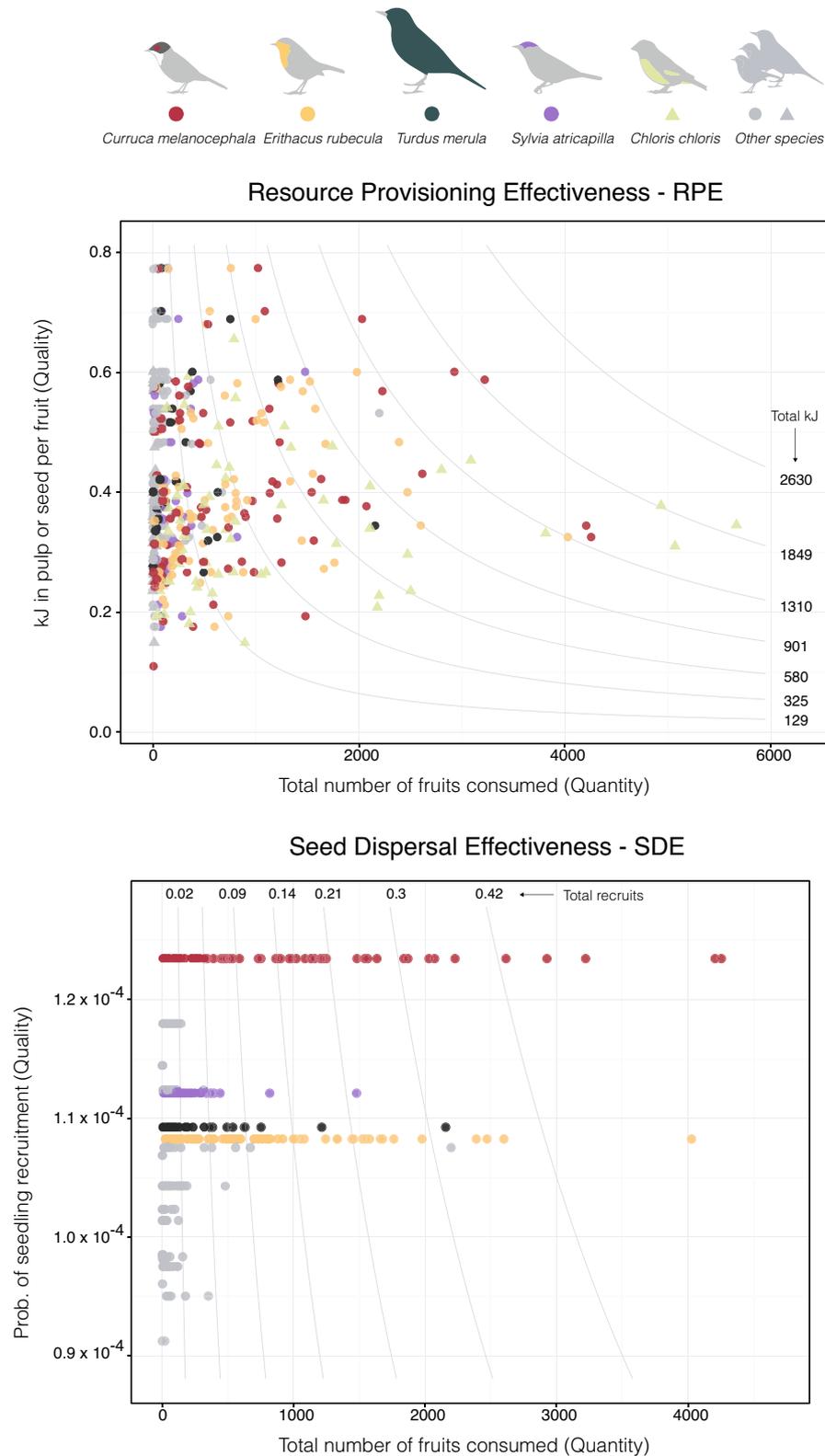


FIGURE 3 Landscapes for Resource Provisioning Effectiveness (RPE) and Seed Dispersal Effectiveness (SDE). Each point represents an individual pairwise interaction between an individual plant and a frugivorous avian species. In both landscapes, the horizontal axis depicts the total number of fruits consumed by each bird species in each individual plant. Symbols represent feeding behaviour (circles for legitimate dispersers, and triangles for non-legitimate dispersers). In the RPE landscape, the vertical axis represents the median energy (kJ) obtained from the pulp or seed from each individual plant. In the SDE plot, the vertical axis represents the posterior median probability of recruiting a seedling from a fruit ingested by each bird species. Hence, the product of the horizontal (Quantity) and vertical (Quality) axis gives the effectiveness of each bird-plant pairwise interaction: the total energy (kJ) in the case of RPE, and total number of plant recruits for SDE. Different combinations of quantity and quality can produce equal effectiveness values, as shown by isolines. Note seed predators are not shown in the SDE landscape visualisation, because their dispersal quality is zero or close to zero and their inclusion distorts the graph (see Supp Mat E.4 for complete SDE landscape).

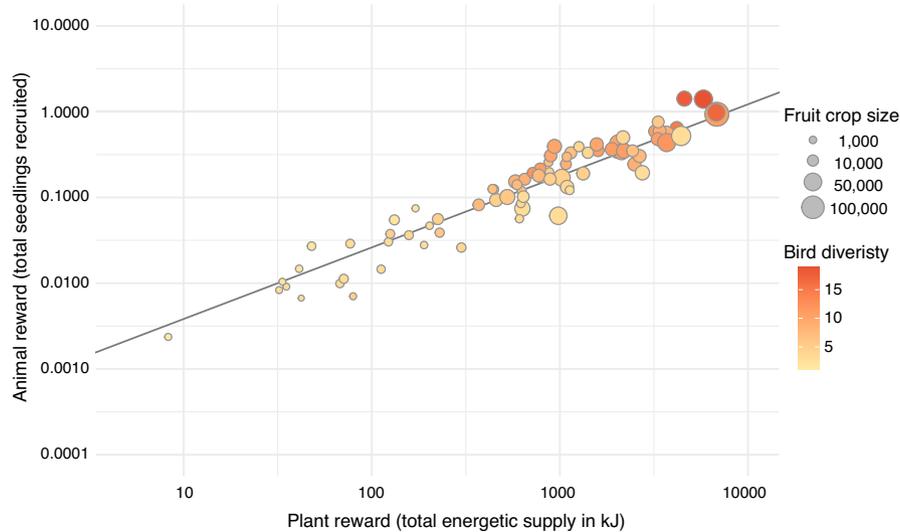


FIGURE 4 Relationship between the total energetic supply provided by individual plants (aggregating all its consumer bird species) and the number of seedlings recruited by each plant ($n = 79$ plants). The positive relationship indicates highly reciprocal interactions: the higher the reward offered by the plant, the higher the reward received from its bird consumers. Point size represents plants' initial fruit crop size, and colour intensity indicates the number of animal species partners, so that plants involved in larger rewards had larger crop sizes and larger number of frugivore partners. Note both axes are in logarithmic scale.

those involving the two main dispersers *E. rubecula* and *C. melanocephala*: plants strongly depended on both bird species for effectively dispersing their seeds and recruiting (Figure 5, left). In contrast, avian species were less dependent on individual plants. Only a few rare bird species showed high dependency on specific plants (Figure 5, centre).

When comparing the corresponding dependencies of each partner, we found that most bird-plant interactions were highly asymmetric (Figure 5, right); 71% of interactions had absolute asymmetry values over 0.75. These asymmetry values did not deviate significantly from those obtained using null models (Suppl. Mat. H). Two major processes caused asymmetry to emerge. First, plants depended strongly on the main avian consumers (*C. melanocephala*, *E. rubecula*), while these birds had low dependencies on individual plants (asymmetry values towards 1) because they were feeding and obtaining energy from many plants, hardly depending on any particular one. Second, when the animals had high dependency on a particular plant (asymmetry values towards -1), the plants in turn hardly depended on that particular bird. These interactions were dominated by seed predators (mainly *C. chloris*), pulp consumers and locally uncommon bird species, which provided no or very limited seedling recruitment. Symmetric interactions (where both partners had similar dependency values) were scarce: only 16% of interactions had asymmetry values between -0.5 and 0.5 and were represented by strongly frugivorous and moderately abundant birds such as *T. merula*, *S. atricapilla* and *Cyanopica cooki*. In these cases of symmetric interactions, the importance of individual plants for energy provisioning was balanced with the importance of these birds as effective seed dispersers.

DISCUSSION

We report interaction patterns for a super-generalist plant species, with the aim of documenting variation in mutual dependence with animal seed dispersers at the plant individual level and degree of interaction reciprocity at the population scale. Our results allowed us to link the structure of individual-based interaction networks and the fitness consequences in local plant population recruitment.

Interaction intensity dominates partner effectiveness

Most previous studies have focused on effectiveness from a species-level, community perspective (although see Guerra et al., 2017; Palacio, 2019; Jácome-Flores et al., 2020). The individual focus in *P. lentiscus* revealed ample variation in fruit consumption by animal frugivores at individual plants, while showing smaller variation in the quality of partner's reward. Both RPE and SDE variation were driven by the quantity component, rather than quality, indicating that interaction frequency per se is acting as a good surrogate of effectiveness, as found in previous studies (Vázquez et al., 2005). However, accounting for interaction quality may change interpretations of partner effectiveness in other systems (e.g. rank reversals in González-Castro et al., 2022).

The resource provisioning effectiveness landscape (Figure 3) did not reflect clear preferences of bird species for plants with energy-rich fruits. However, when aggregating the consumption data of non-granivorous birds by individual plants, we found that large plants, with larger

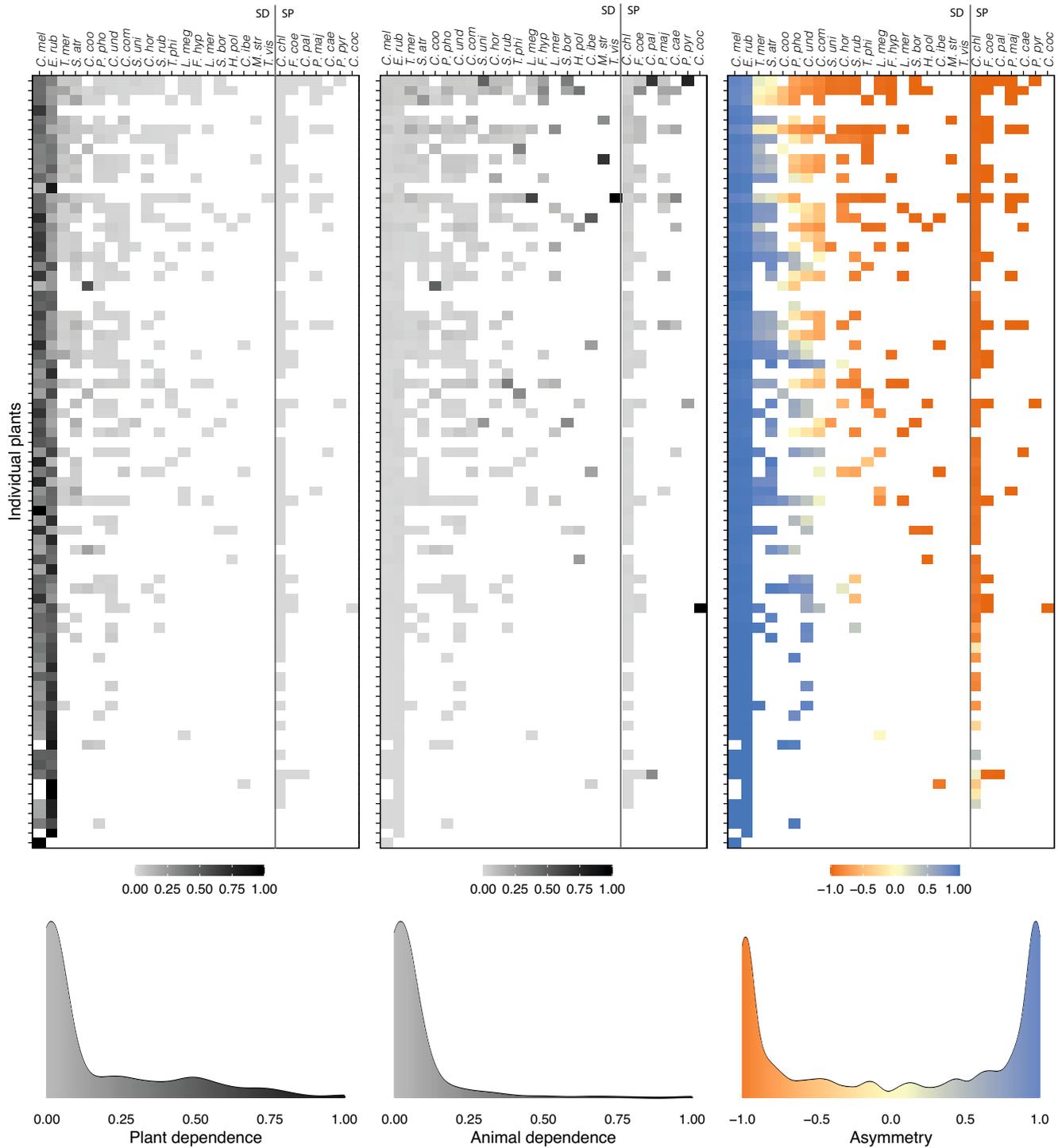


FIGURE 5 Interaction matrices between individual *Pistacia lentiscus* plants and their avian consumers. The first matrix (left) depicts how much each plant's seed dispersal effectiveness (number of seedlings recruited) depends on each bird species, whereas the second matrix (centre) shows how much the resource provisioning effectiveness (energy obtained) of each bird species depends on each particular plant. Both matrices range from 0 (no dependence at all) to 1 (total dependence on that particular partner). The third matrix (right) shows the asymmetry in dependence for each unique bird-plant pairwise interaction. Colours gradually veering towards blue (asymmetry values approaching 1) indicate interactions where the plant is more dependent on the animal than vice versa, whereas colours veering towards orange (i.e. asymmetry approaching -1) indicate interactions where the animal is more dependent on the plant. Symmetrical interactions, where the dependence of both partners is similar, are represented by yellow tones (asymmetry values close to 0). The lower graphs represent the frequency distribution of the above matrix values. Animal species codes in alphabetical order: *C.cae* = *Cyanistes caeruleus*, *C.chl* = *Chloris chloris*, *C.coc* = *Coccothraustes coccothraustes*, *C.com* = *Curruca communis*, *C.coo* = *Cyanopica cooki*, *C.hor* = *Curruca hortensis*, *C.ibe* = *Curruca iberiae*, *C.mel* = *Curruca melanocephala*, *C.pal* = *Columba palumbus*, *C.und* = *Curruca undata*, *E.rub* = *Erithacus rubecula*, *F.coe* = *Fringilla coelebs*, *F.hyp* = *Ficedula hypoleuca*, *H.pol* = *Hippolais polyglotta*, *L.meg* = *Luscinia megarhynchos*, *L.mer* = *Lanius meridionalis*, *M.str* = *Muscicapa striata*, *P.maj* = *Parus major*, *P.pho* = *Phoenicurus phoenicurus*, *P.pyr* = *Pyrrhula pyrrhula*, *S.atr* = *Sylvia atricapilla*, *S.bor* = *Sylvia borin*, *S.rub* = *Saxicola rubicola*, *S.uni* = *Sturnus unicolor*, *T.mer* = *Turdus merula*, *T.phi* = *Turdus philomelos*, *T.vis* = *Turdus viscivorus*.

fruit crops, producing heavier (more energetic) fruits, received a larger number of seeds dispersed (Suppl. Mat. G.3). Plant size and crop are well known to affect frugivory (Ortiz-Pulido et al., 2007; Sallabanks, 1993; Schupp et al., 2019) and are both related to the ontogeny, growth and size hierarchies in plant populations (Weiner & Solbrig, 1984). Other factors not analysed here, such as secondary compounds, fruit accessibility or fruiting neighbourhood can also be affecting consumption patterns (Moermond & Denslow 1985; Carlo et al., 2007; Cipollini & Levey 1997).

Legitimate seed dispersers also exhibited limited variation in the quality component of seed dispersal effectiveness (Figure 3). The resulting probability of recruitment per consumed fruit was surprisingly similar between frugivore species, indicating a broad functional redundancy in their dispersal service (González-Castro et al., 2015). However, when considering the final seed dispersal effectiveness, two bird species (*C. melanocephala* and *E. rubecula*) emerged as the main contributors to seedling recruitment due to their high consumption. The redundancy encountered in the quality component could make the dispersal of *P. lentiscus* less susceptible to the loss of bird species or fluctuations in bird populations (Zamora, 2000); however, marked changes in bird abundance, particularly of the dispersers that consume the most fruit, could compromise plant recruitment.

Reciprocity in partner rewards as a feature of mutualistic systems

Although the exchange of rewards between bird species and individual plants varied over several orders of magnitude, there was a high correlation between the rewards obtained by each partner in the interaction. High correlation between rewards points to a stable and fair two-way transfer in the exchange of mutualistic services. In the case of *P. lentiscus*, the reciprocity in the rewards stems from the strong dominance of the quantity component (intensity of consumption), common to both resource provisioning and seed dispersal effectiveness. Such high reciprocity appears characteristic of many seed dispersal systems and other generalised, resource-based mutualisms (Ollerton, 2006; Wheelwright & Orians, 1982). However, reciprocity in a mutualistic system could be compromised whenever there are large differences between partners quality, as occurs for example in systems with highly heterogeneous frugivore assemblages (García-Rodríguez et al., 2021; González-Castro et al., 2015). Reciprocity can also be broken when antagonists disrupt, to a variable extent, mutualistic interactions of plants with legitimate seed dispersers (Jácome-Flores et al., 2020); however, mutualism breakdown scenarios have been largely examined for intimate interactions, not for free-living species (Chomicki & Renner, 2017; Sachs & Simms, 2006).

The deviation of reciprocity from strict proportionality (log slope = 1) could be caused by: (i) plants that produce heavier fruits have fewer seeds dispersed and get fewer seedlings recruited per amount of energy offered than small-fruited plants, (ii) highly fecund individuals (that disperse many fruits) attract both highly effective and less effective frugivores and (iii) the fact that our analysis did not account for likely increasing seedling recruitment probabilities with increasing fruit and seed size. If bigger and more energetic fruits with larger seeds implies higher survival probability at the seedling stage (Piper 1986; Leishman et al., 2000), then our analysis could be underestimating the number of seedlings recruited for those plants.

Our results are consistent with previous reports showing that extremely high seed production and consumption are required to ensure recruitment, given sharp decreases in survival probability as seeds move along dissemination and establishment stages (García-Fayos & Verdú, 1998; Gómez-Aparicio, 2008; Herrera et al., 1994). Following our estimates, individual *P. lentiscus* plants would have to disperse >8000 seeds to have just a single recruit surviving their first summer. Thus, successful plant recruitment requires huge reproductive effort from plants, even in well-functioning dispersal mutualisms with high reciprocity.

Highly asymmetric dependencies between mutualistic partners

The majority of interactions between bird species and *P. lentiscus* individual plants were highly asymmetric: when one partner depended strongly on the other, the latter depended much less on the former. The highly skewed distribution of dependence values was likely generated by the combination of varying bird abundances (Vázquez et al., 2007), differences in the degree of frugivory, and varying fruit production and attractiveness to frugivores from the plant individual side. Assessing individual variation in long-lived plants and the outcomes of their interactions with shorter-lived frugivores provide insights into the delayed consequences for both partners.

A widely recognised constraint for coevolution between interacting species is asymmetry in generation time (and thus, evolutionary rates), violating one of the assumptions early stated by Janzen (1980) in his definition of coevolution: simultaneity. This is especially evident in interactions between short-generation, small frugivorous passerines and long-lived woody plants. Lack of simultaneity in evolutionary response has been implied, for example, to explain how megafauna-dispersed plants survived (through, e.g. vegetative propagation) to the Pleistocene–Holocene extinction of large mammals acting as their seed dispersers (Guimarães et al., 2008). Our results show that plant individuals differ in the way their mutualistic interaction assemblages

are built and this results in extremely skewed contributions to population-level seedling recruitment, a delayed response to the interaction itself.

The high asymmetry between mutualistic partners' interdependence at the individual level is consistent with previous findings at the species level (Bascompte et al., 2006; Guerra & Pizo, 2014; Guimarães et al., 2006; Jordano, 1987). In Herrera (1984), most observed dependencies between frugivores and plant species were also weak or highly asymmetric. Interestingly, at the species level, *P. lentiscus* showed quite symmetric dependencies with its main seed dispersers. Our analysis revealed that, while bird species consumed *P. lentiscus* fruits heavily, they did not depend on particular plants, but rather spread their dependencies, generating highly asymmetric interactions. If individual birds could have been identified, rather than aggregated to species level, many of those plants' strong dependencies on the main consumers might in turn transform into weak links, with just a few strong interactions (e.g. territorial birds strongly depending on a specific patch of *P. lentiscus*). Hence, zooming in to the individual level seems important because it may enrich our perceptions of the embedded dependencies in mutualistic networks (Tonos et al., 2021) and address the proper scale in order to understand emerging properties at the species-level (Clark et al., 2011).

The available evidence suggests that symmetric dependencies are rare in mutualistic systems (Bascompte et al., 2006). So far, symmetric interactions have been reported only in very specific local communities, such as honeyeater-mistletoe facultative interactions (Reid, 1990) or impoverished island systems (González-Castro et al. 2022). The disassortativity in the way species interact seems to promote asymmetry in partners' dependence. The absence of symmetry in the dependence between species agrees with previous work arguing that reciprocal specialisations are rare (Joppa et al., 2009).

Concluding remarks

Interactions between the individuals of a super-generalist plant with its fruit consumers have shown to be reciprocal in terms of rewards exchange, despite partners being highly asymmetric in their mutualistic dependence. These aspects appear quite general to less intimate mutualisms among free-living species (e.g. pollination and seed dispersal) that are largely dependent upon interaction frequency for the harvesting of food resources by animals. A key feature for the success of super-generalist organisms appears to be related to abundance parameters that define their interaction frequency (Fort et al., 2016) and, ultimately, their fitness. In contrast, highly specialised interactions most likely depend on the ability to maintain reciprocity by means of a fine-tuned quality service between interacting species, where dependencies between partners would

likely be more symmetric and intimate (Guimarães et al., 2007; Kiers et al., 2011). We might expect the emergence of high-reciprocity, high-asymmetry patterns when mutualisms among free-living species rely on encounter frequencies, whose variance among species is so large as to obscure variation in the quality of outcome. Exceptions may include some mutualisms in specific environmental settings (e.g. oceanic islands) or characterised by high specificity of the interaction. Further studies on the reward reciprocity of generalised mutualistic interactions will help to evidence the diversity of engagement forms between animals and plants and the mechanisms behind the perpetuation of mutually beneficial relationships.

AUTHOR CONTRIBUTIONS

EQ: Conceptualisation, Methodology, Field and Laboratory work, Data curation, Analysis, Writing-Reviewing and Editing, Visualisation, Project administration. FRS: Conceptualisation, Methodology, Data curation, Analysis, Validation, Supervision, Visualisation, Writing-Reviewing and Editing. PJ: Conceptualisation, Methodology, Data curation, Supervision, Project administration, Funding acquisition, Visualisation, Writing-Reviewing and Editing.

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OPEN RESEARCH BADGES



This article has earned Open Data and Open Materials badges. Data and materials are available at: https://github.com/PJordano-Lab/MS_effectiveness.

DATA AVAILABILITY STATEMENT

The data and code generated for this study are available at https://github.com/PJordano-Lab/MS_effectiveness and archived in the dryad repository (doi:10.5061/dryad.02v6wwq6n).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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