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PERSPECTIVE

The ecological and evolutionary significance of effectiveness landscapes in mutualistic interactions

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Abstract

Mutualism effectiveness, the contribution of an interacting organism to its partner's fitness, is defined as the number of immediate outcomes of the interactions (quantity component) multiplied by the probability that an immediate outcome results in a new individual (quality component). These components form a two-dimensional effectiveness landscape with each species' location determined by its values of quantity (x-axis) and quality (y-axis). We propose that the evolutionary history of mutualistic interactions leaves a footprint that can be identified by three properties of the spatial structure of effectiveness values: dispersion of effectiveness values, relative contribution of each component to the effectiveness values and correlation between effectiveness components. We illustrate this approach using a large dataset on synzoochory, seed dispersal by seed-caching animals. The synzoochory landscape was clumped, with effectiveness determined primarily by the quality component, and with quantity and quality positively correlated. We suggest this type of landscape structure is common in generalised coevolved mutualisms, where multiple functionally equivalent, high-quality partners exert similarly strong selection. Presumably, only those organisms located in high-quality regions will impact the evolution of their partner. Exploring properties of effectiveness landscapes in other mutualisms will provide new insight into the evolutionary and ecological consequences of mutualisms.

KEYWORDS
effectiveness landscape, mutualistic interactions, seed dispersal, synzoochory

INTRODUCTION

Mutualistic interactions are extremely diverse and widespread and play critical roles in ecosystem function, population dynamics and community structure (Bronstein, 2015). The effectiveness of a mutualistic interaction for the interacting species has long been considered to be key to understanding the evolution of mutualistic interactions and the ecological consequences of those interactions (e.g. Stebbins, 1970). While it is generally accepted that the effectiveness of a mutualistic interaction is a function of some measure of quantity, representing the frequency of the interaction, and some measure of quality, representing the outcome of the interaction, there are many views of what metrics best represent effectiveness, quantity and quality. Here, we follow a framework founded on the seed dispersal effectiveness framework (Schupp, 1993; Schupp et al., 2010) that has been recently generalised to all mutualistic interactions (Schupp et al., 2017). In this framework, effectiveness is ideally viewed as the contribution of one partner to the interacting partner's fitness or, in alternative formulations, demography. Furthermore, effectiveness is quantified as a quantity component (QTC) multiplied times a quality component (QLC): Effectiveness = QTC × QLC. In this framework QTC is not simply the number of interactions (e.g. the number of visits a seed disperser makes to a fruiting plant), but rather is the number of immediate outcomes of the interaction (e.g. the number of seeds dispersed by species *i*). QLC, then, is a measure of the probability that an immediate outcome results in the production of a new reproductive adult (e.g. the probability that a seed dispersed by animal *i* produces a new reproductive plant or the probability that a fruit eaten by an animal *j* produces a new reproductive animal). QTC multiplied by QLC, then, yields an effectiveness value quantified by a fitness estimate resulting from the interaction (e.g. the number of new reproductive adults resulting from the seed dispersal services of species *i*). In reality, due to multiple constraints few empirical studies have been able to follow the consequences of an interaction through to the production of new reproductive adults. Instead, in most cases some earlier life stage is quantified and used as a proxy of fitness outcome (e.g. the number of established 2-year-old seedlings resulting from the seed dispersal services of species *i*).

The effectiveness of mutualistic interactions is central to understanding the ecological and evolutionary roles played by the interacting organisms (Schupp et al., 2017). Highly effective interacting species will contribute strongly to the fitness and population dynamics of their partners (Godinez-Álvarez et al., 2002; Ruggera et al., 2016; Schupp, 1993; Schupp et al., 2010). They will exert strong selection pressures on the suite of traits mediating that interaction as well, potentially shaping phenotypic evolution and coevolution in a significant way (Gómez et al., 2019; Jordano, 1995; Palacio & Ordano, 2018; Reid, 1991; Traveset et al., 2019; Valverde et al., 2019). Natural selection is expected to favour the evolution of mutualistic traits that simultaneously increase the quantity and the quality of interactions, since both contribute to overall effectiveness. When a given species interacts with multiple species, the pattern of variation in effectiveness will influence that species' ability to discriminate among them and to increase the quantity of interactions with those partners providing the highest quality interactions (Blendinger, 2017; Calviño-Cancela & Martín-Herrero, 2009; Castro et al., 2013; Li et al., 2016; McConkey et al., 2018; Rother et al., 2016; Spiegel & Nathan, 2007). Understanding the effectiveness of individual interactions contributes to a deeper understanding of the drivers of population recruitment and demography and of the evolution of interaction systems (Schupp et al., 2010, 2017).

The patterns of effectiveness values can be visualised using a mutualism effectiveness landscape (Figure 1), which has QTC on the x-axis and QLC on the y-axis (Schupp et al., 2010, 2017). Because these axes are multiplicative, all combinations of quantity and quality yielding the same effectiveness value are connected by isoclines, which increase in value from lower left to upper right; this facilitates visual interpretation of the landscape (Figure 1). Effectiveness landscapes have proven very useful to evaluate the contributions of different interacting organisms to the recruitment of many plants and identifying which processes, whether quantity or quality related, mediate this function (Castro et al., 2017; Kato & Koike, 2018; McConkey et al., 2018). From this perspective, the effectiveness landscape has stimulated intensive research on the nature and identity of the most important interacting organisms for many plant species, mostly considering seed dispersal mutualisms (e.g. Camargo et al., 2016; McConkey et al., 2018; Mokotjomela et al., 2016; Nogales et al., 2017; Quintero et al., 2020; Rodríguez-Pérez & Traveset, 2010), but more recently increasingly with pollination mutualisms (e.g. Fontúrbel et al., 2017; Valverde et al., 2019).

PROPERTIES OF EFFECTIVENESS LANDSCAPES

We suggest that the effectiveness landscape, aside from the descriptive, visual function that it has played during the last decade, can also serve as a conceptual tool to help elaborate hypotheses about how different mutualistic interaction systems may have evolved. We propose that the 'spatial' arrangement (defined here as the scatter of effectiveness values across the landscape defined by the QTC and QLC axes) of the effectiveness values within an effectiveness landscape provides important insight into the ecology and evolution of mutualistic interactions. In particular, three non-exclusive properties of this spatial arrangement can be useful to evaluate how mutualistic interactions have evolved:

1. The *dispersion of effectiveness values*. This property describes the spatial distribution of the effectiveness values across the landscape, and gives insight into how similar or, alternatively, how different the interacting organisms are in terms of their effects on fitness (i.e. how multiple pollinators or dispersers affect the fitness of the plant they are interacting with). Dispersion can vary from a null random dispersion (Figure 1a), to a uniform (regular, even, over-dispersed) dispersion, where effectiveness values are separated from each other on the landscape more than expected by random processes (Figure 1b), and a clumped (aggregated, patchy) dispersion, where the effectiveness values cluster in statistically distinct groups having similar values of effectiveness (Figure 1c). Clumped spatial patterns indicate that there are distinct groups of species that have similar effects on the fitness of their partner, revealing the occurrence of functional equivalence within clustered groups of interacting organisms (Calviño-Cancela & Martín-Herrero, 2009; González-Castro et al., 2015; Palacio, 2019). In contrast, over-dispersed effectiveness landscapes indicate that different interacting organisms have very distinct effects on the fitness

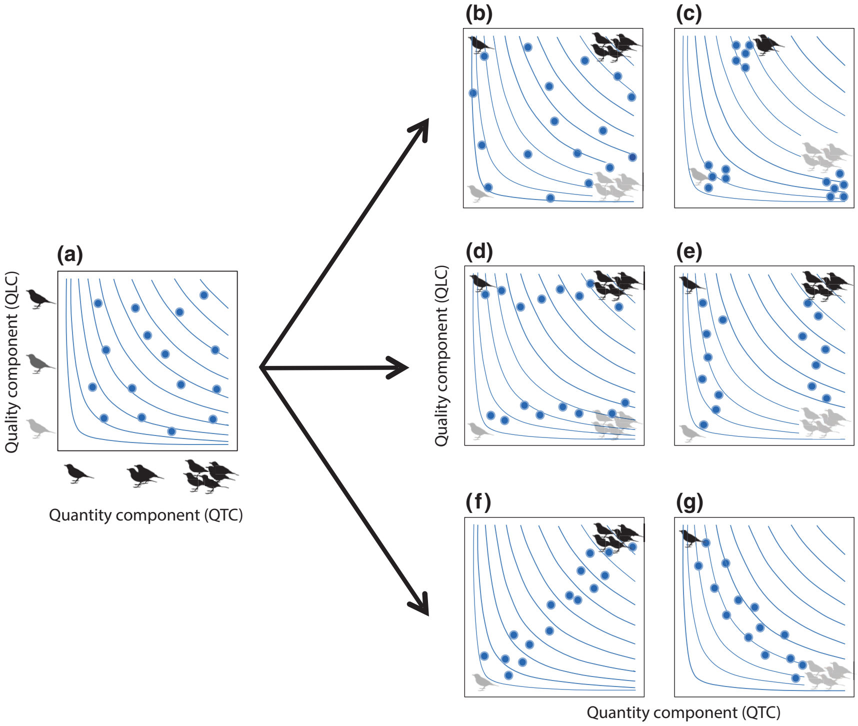

FIGURE 1 Spatial structure of effectiveness landscapes highlighting the proposed properties (see text for details). (a) Null scenario where effectiveness values are randomly distributed across the landscape, isotropic, and with no correlation between components. (b) Scenario where the dispersion of effectiveness values is uniform. (c) Scenario where the dispersion of effectiveness values is clumped. (d) Scenario where the pattern of effectiveness values is influenced mostly by the quality component. (e) Scenario where the pattern of effectiveness values is influenced mostly by the quantity component. (f) Scenario with positive correlation between components. (g) Scenario with negative correlation between components. Silhouettes illustrate the range variation in QTC and QLC components: for QTC, more silhouettes indicate more interaction events and larger QTC values (not just more abundance of interacting organisms); for QLC, darker silhouettes illustrate larger QLC values. In panel (a) the silhouettes highlight the axes, while in panels (b–g) they identify positions on the landscape relevant to the illustrated property

of their partner, and consequently they are not interchangeable. Phylogenetically diverse assemblages of interacting organisms can produce this pattern (Escribano-Avila et al., 2014; Nogales et al., 2017). Whereas in over-dispersed landscapes there is a possibility to respond to the selection exerted by those individual species having the highest fitness effects, in clumped landscapes natural selection will favour those groups of functionally equivalent species that have altogether as a group the highest effect on fitness (Gómez & Zamora, 1996; Zamora, 2000). We suggest that over-dispersed landscapes stimulate the evolution of specialised systems and clumped landscapes promote the evolution of generalised mutualistic systems.

2. The *component relative contribution*. This property describes which of the two effectiveness components, QTC and QLC, if either, has the greatest impact on the structure of effectiveness values. Three possibilities exist. First, the two components may be equivalent in their impact on effectiveness values (Figure 1a). Second, the landscape may have quality-driven effectiveness, where the QLC component axis has the greatest impact on the structure of effectiveness values (Figure 1d). Lastly, the landscape may have quantity-driven effectiveness, where the QTC component axis has the greatest impact on the structure of effectiveness values (Figure 1e). Quantity-driven effectiveness tends to be common in non-adaptive generalised systems where effectiveness is largely driven by ample variation in local partner abundance (Blüthgen et al., 2006; Brodie et al., 2009; Vázquez et al., 2005; Zamora, 2000). In contrast, quality-driven effectiveness is associated with systems where one or a few mutualists vary greatly in per-visit efficiency. Variation in per-visit efficiency (QLC) is a precondition for specialisation (Schemske & Horvitz, 1984).
3. The *component correlation*. This property describes the statistical association between the values of quantity and quality. It can vary from the null pattern of no correlation (Figure 1a), to a positive component correlation, when those interacting organisms with higher values of the quality component are also those with higher values of the quantity component (Figure 1f), and a negative component correlation where those interacting organisms with higher values of the quality component have lower values of the quantity component and vice-versa (Figure 1g). Interaction specialisation is expected to cause effectiveness landscapes to exhibit significant positive component correlation

(González-Castro et al., 2015), a feature resulting from natural selection having shaped those traits that preferentially attract the highest quality interacting species (similar to Stebbins (1970)'s 'most effective pollinator principle'). In contrast, a negative component correlation is likely associated with generalised interactions (Calviño-Cancela & Martín-Herrero, 2009; González-Castro et al., 2015; Palacio, 2019).

We presume that these three properties, when evaluated together, give information on how coevolved and specialised are diversified mutualistic interactions among free-living species. Methods to assess and quantify coevolution among free-living species are under research (Week & Nuismer, 2019), and we lack generally applicable statistical methods that yield numerical estimates for coevolution's strength and significance in the wild. We propose that specialised coevolved interactions will result in quality-driven, positively correlated and overdispersed landscapes, whereas generalised coevolved interactions will result in quality-driven, positively correlated yet clumped landscapes around several distinct functional groups. In contrast, highly generalised, low-specificity interactions will produce quantity-driven and negatively correlated landscapes. In this type of interaction, the landscape will be clumped if the target species is interacting with functionally redundant or phylogenetically related partners. Otherwise, the landscape will be evenly dispersed or overdispersed, suggesting coevolution is not a major driver.

SYNZOOCHORY: A CASE STUDY

The three structural properties described in the previous section and the effectiveness landscapes they occupy are informative at different taxonomic scales. They can be assessed for a population of a single target species interacting with an assemblage of mutualists (one plant species dispersed or pollinated by several animals, or interacting with several species of mycorrhizal fungi or nitrogen-fixing bacteria). This is the most common way that effectiveness landscapes have been constructed in the literature. However, they can be also assessed for different populations of a target species to assess geographical variation or, scaling down, they can be assessed for different individuals of a given interacting species to study interindividual variation in effectiveness. At the largest, grossest scale, the properties can be calculated for a given type of interaction using higher order taxonomic units in order to assess more general patterns (e.g. the general effectiveness of a family of dispersers on the suite of plant species dispersed by that family) in order to infer larger-scale evolutionary patterns. This is the approach we take here, using data at the level of disperser families.

We illustrate the value of assessing these landscape properties of mutualistic interactions using a large dataset on synzoochory, the deliberate transportation of seeds externally by granivorous animals, and their subsequent survival (Gómez et al., 2019). In the following we first give a brief overview of synzoochory and of the dataset. Second, we describe the general patterns in the synzoochorous effectiveness landscape. Third, we present a thorough exploration of the three landscape structural properties we suggest are informative. Fourth, in order to better understand what traits of dispersers affect the effectiveness landscape structure we conclude with an analysis of the effects of six disperser traits on effectiveness values. Synzoochorous systems include many aspects shared with plant–animal mutualisms and are thus a good model or case study to discuss drivers of effectiveness variation.

Overview of synzoochory and the dataset

Synzoochory is a widespread phenomenon across both plant and animal phylogenies, being observed in at least 1339 plant species differing in life forms from annual and short-lived herbs to long-lived trees (Gómez et al., 2019). Because the animals involved in synzoochorous seed dispersal systems act as both seed dispersers and seed predators, there is an inherent conflict for the plant (Bogdziewicz et al., 2019), and specific animal–plant interactions have been shown to span a broad range on a mutualism (dispersal and caching)—antagonism (consumption) continuum (Gómez et al., 2019). The occurrence of this continuum is expected to have large implications for the structure of the synzoochorous effectiveness landscape, since both effectiveness components will be influenced by the dual role of the dispersers. From the animal's perspective, seeds are a very attractive nutrient- and energy-rich food resource that can be stored for the long term (Vander Wall, 2001). From the plant's perspective, the dispersed seeds may be stored some distance from the parent plant, frequently in favourable microsites, and some escape being eaten if the animal forgets them, stores more than can be consumed, or dies before recovering them, resulting in successful plant recruitment (Iluz, 2011; Vander Wall, 2001).

We have compiled a comprehensive dataset including information on QTC, QLC and effectiveness for 1192 studies × plant species combinations, comprising 647 plant species and 24 animal families belonging to five main groups: rodents (Cricetidae, Cuniculidae, Dasyproctidae, Echimyidae, Heteromyidae, Hystricidae, Muridae, Nesomyidae, Octodontidae, Platacanthomyidae and Sciuridae), marsupials (Potoroidae), birds (Corvidae, Paridae, Picidae and Sittidae), insects (Carabidae, Formicidae, Gryllidae and Scarabaeidae) and land crabs (Gecarcinidae, Gecarcinucidae, Coenobitidae and Ocypodidae). (Dataset S1).

Our dataset contains information on studies performed on disparate systems in different localities, habitats and continents, during different time periods, and with different experimental methods and sample sizes. This heterogeneity will in and of itself result in large differences among studies in the number of seeds dispersed, making comparisons and detection of real patterns difficult. Consequently, in order to make QTC values comparable across studies and to avoid spurious effects, we quantified QTC as the proportion of seeds dispersed by a given type of disperser during a given dispersal period (Gómez et al., 2019; McConkey et al., 2018). Specifically, QTC was estimated as the proportion of the experimentally offered seeds that was harvested and dispersed by each species of hoarding animal, irrespective of the seed's final fate (whether cached, forgotten and recruited as a new plant, or whether consumed and killed either before or after caching). Under this definition, the proportion of seeds consumed *in situ* (at the parent plant or in experimental seed stations) is not included in the computation of QTC, because no dispersal service was provided. Thus, QTC varied between 0 and 1 for all studies in our dataset.

As noted in the introduction, QLC is ideally defined as the probability that a dispersed seed produces a new adult (Schupp et al., 2010). However, given the diversity of studies included in this review, ranging from annual plants to long-lived trees, information on this full demographic loop from adult to new adult is nearly absent. Thus, we used the post-dispersal outcome that was quantified most frequently in our original dataset (Gómez et al., 2019) as representing QLC: the proportion of dispersed seeds that were cached, either by scatter hoarding or larder hoarding. We acknowledge that the final magnitude of QLC will be substantially lower than that obtained from primary caches. Many hoarders retrieve their own caches or pilfer others' caches and subsequently eat some to many of the seeds from primary caches while recaching others in a new location, scatter-hoarded seeds and larder-hoarded seeds generally differ substantially in the likelihood of recruitment, and the location of caching (e.g. distance from a conspecific, microhabitat) can affect the probability of a seed successfully producing a new adult (Dittel et al., 2017; Longland & Vander Wall, 2019; Vander Wall, 2001). Thus, the proportion of seeds buried in primary caches offers only an incomplete, very early picture of QLC. Nonetheless, it does have strengths for our study. First, it provides a standard metric at a standard stage in the chain of post-dispersal processes that strengthens comparisons across dispersal systems. Second, using this early measure of QLC maximises sample sizes in order to make more robust comparisons; extending QLC to later stages, such as survival to germination, rapidly and substantially reduces the sample sizes. As with QTC, QLC varied between 0 and 1. Seed dispersal effectiveness (SDE) was calculated as the product of QTC and QLC (Schupp et al., 2010).

General patterns of the synzoochorous effectiveness landscape

The mean magnitude (±1 standard error) of QTC, when pooling all studies, was 0.52 ± 0.01, ranging from as low as nearly 0.0 to as high as 0.70 (Figure 2), indicating that on average more than 50% of the seeds are moved away from the source by these synzoochorous dispersers. These values of the QTC component are similar to those reported for other dispersal modes. The proportion of fruit removed by assemblages of endozoochorous frugivorous birds ranges between about 46 and 100% (Davidar & Morton, 1986; Herrera, 1984; Jordano, 1995, 2013; Jordano & Schupp, 2000), whereas ants disperse up to 50% of the seeds of myrmecochorous plants in some parts of Australia (Hughes & Westoby 1990, 1992; Parr et al., 2007). It is true that the quantity values may be somewhat overestimated because the proportion of seeds removed by synzoochorous animals was in many cases estimates not from direct observations of parent plants but rather from seed stations where seeds were generally concentrated at high densities, and there is ample evidence showing that granivores tend to consume more seeds when offered in high densities (Dudenhöffer et al., 2016; Hulme & Borelli, 1999; Sarabi, 2019). Nonetheless, our results do not suggest that the QTC of synzoochorous seed dispersers differs dramatically from that of other dispersal systems.

In contrast, the values of the QLC component were overall quite low, despite the fact that we calculated the quality of dispersal at its very earliest stage (seed caching, irrespective of ultimate seed fate). The mean magnitude of QLC was 0.16 ± 0.01, indicating that on average only 16% of the dispersed seeds are placed in primary caches (Figure 2). The distribution along the quality axis (with most values clustered at 0.0–0.05 and 0.1–0.25) is more restricted than along the quantity axis (values spanning 0.0–0.70); while there are many very low values of quality, there are few moderately high values, with only two greater than 0.3. Given that hoarding animals tend to revisit their caches and pilfer the caches of others (Muñoz & Bonal, 2011; Vander Wall et al., 2005), the proportion of seeds remaining intact and emerging from these caches is presumably much lower. Consequently, quality likely would be much lower if using some later stage of the plant recruitment process, such as survival until germination or establishment. In fact, the proportion of initial seeds surviving and producing a seedling is quite low in most synzoochorously dispersed plants, usually close to 0% (Campbell, 1971; Cao et al., 2017; Gómez et al., 2008; Jansen et al., 2004; McConkey et al., 2003; Minkey & Spafford, 2016). We believe that this outcome reflects the dual nature of synzoochorous dispersal systems where the animals are both seed dispersers and seed predators, consuming some to many of the dispersed seeds even as they cache others (Gómez et al., 2019). That is, most synzoochorous dispersers, even the most effective, tend

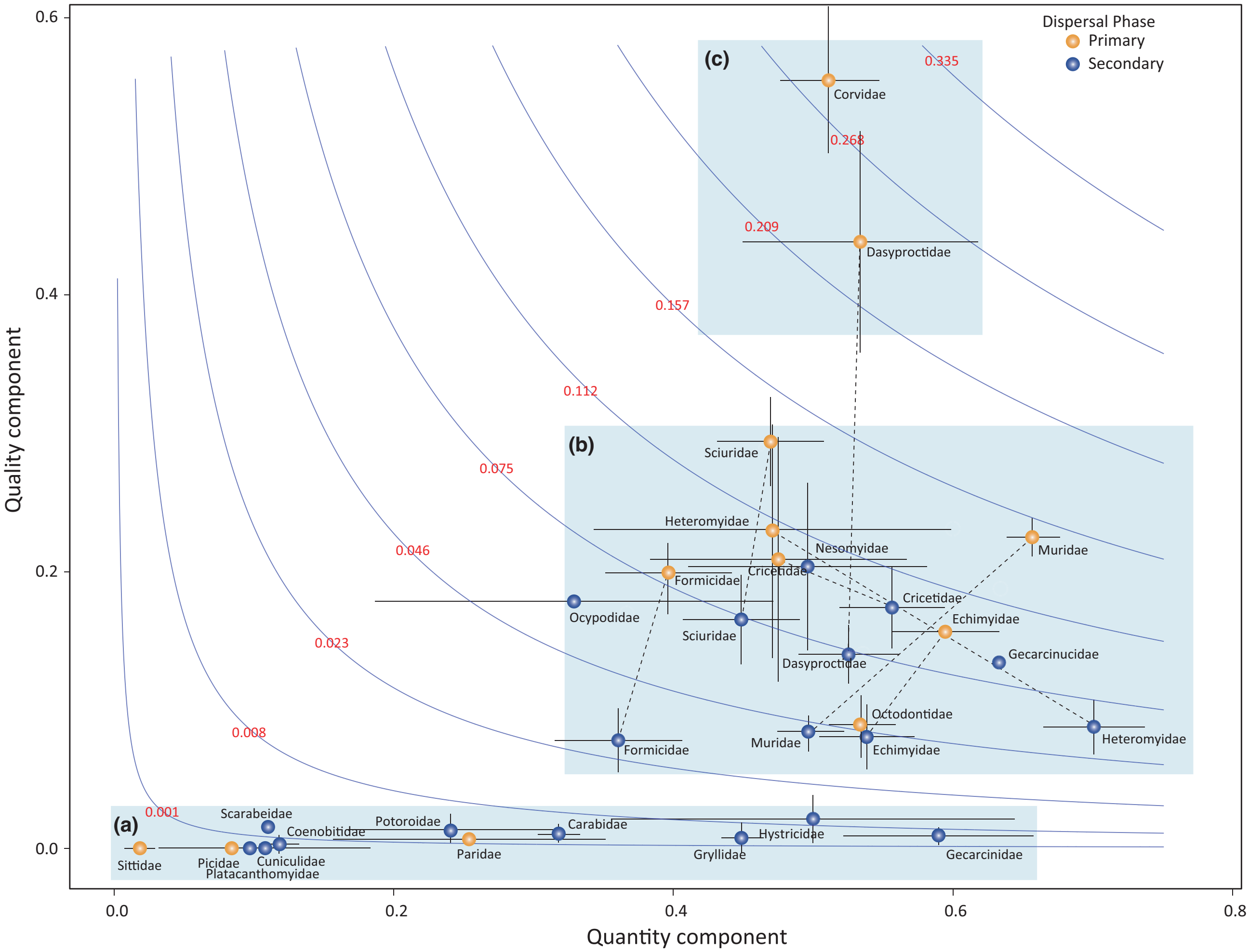

FIGURE 2 Seed dispersal effectiveness landscape of synzoochory. The dispersers belonging to each of the three clusters obtained after applying the 30 validation indices are highlighted. Variance along QLC was almost zero and negligible for some species. Effectiveness landscape isoclines were plotted using the R package effect.lndscp (Jordano, 2014)

to move a considerable amount of seeds away from the parent plants just to eat them in other places rather than cache them (Blackham & Corlett, 2015; Gómez et al., 2008; Li & Zhang, 2003; Wenny, 2005). Synzoochory is in many cases merely delayed post-dispersal seed predation, because the animals transport the seeds to distant places to consume them there rather than to hoard them (Andersen et al., 2000; Blank & Bell, 1982; Capistra-Barradas & Moreno-Casasola, 2006; Cole, 2009; Fleury et al., 2014; Gross et al., 1991; Wenny, 2000; Youngerman et al., 2019).

Structural properties of the synzoochorous effectiveness landscape

Dispersion of effectiveness values

The synzoochorous effectiveness landscape was significantly clumped (Figure 2; $R = 0.55$, $A = 0.04$, $p < 0.001$ in all cases, 1000 bootstrapping iterations, aggregation tested using the Clark–Evans R test (Wiegand & Moloney, 2014) with Donnelly edge correction (Baddeley et al., 2015) and the Hopkins–Skellam *A* index (Baddeley et al., 2015) to control for spatial inhomogeneity). Dispersers formed three clusters (according to a hierarchical cluster analysis using the function NBClust from the R package NbClust that determines the optimal number of clusters by choosing the most frequent partition obtained from 30 validation indices (Charrad et al., 2014), see Table S1, Figure 2), each one comprising dispersers with contrasting size, morphology, behaviour and/or ecology. One cluster was quite taxonomically diverse and composed of 12 very diverse families across birds, rodents, insects and land crabs. This group occupied a broad range on the QTC axis, ranging from barely more than 0.0 to nearly 0.6, but all families had very low values of QLC and thus of SDE. It has long been known that members of this cluster such as species of Carabidae, Paridae and Sittidae cache seeds (e.g. Hutchins et al., 1996; Kirk, 1972; Moreno et al., 1981). However, families in this cluster are mostly generalist consumers that do not depend heavily on stored seeds. For example, the gecarcinid land crabs consume fresh and decomposing litter and whatever living plant material they can reach from the ground (Greenaway & Raghaven, 1998). Although nuthatches (Sittidae) cache seeds, their diets are dominated by insects (e.g. Mohammadi et al., 2016) and they immediately consume many transported seeds (Hutchins et al., 1996). Paca (Cuniculidae) are highly frugivorous generalist herbivores that destroy many seeds (Beck-King et al., 1999) while discarding others intact and apparently seldom caching seeds (Pimentel & Tabarelli, 2004). Similarly, ground beetles (Carabidae) and crickets (Gryllidae) are polyphagous with diverse diets including substantial quantities of seeds (Blank & Bell, 1982; Frei et al., 2019). A second group was composed of many families of rodents and ants with intermediate values of effectiveness moderately to highly dependent on seeds (Arnon et al., 2010; Beck & Vander Wall, 2010; Gómez et al., 2008; Hirsch et al., 2012; Hollander & Vander Wall, 2004; Longland et al., 2001; Mull, 2003; Pizo, 2008; Russo, 2005; Steele et al., 2015; Vander Wall, 1994). Although these families have high to very high values of QTC, they all share relatively low values of QLC (Figure 2). The third and by far smallest cluster was composed of two primary disperser families, Corvidae (jays, magpies, etc.) and Dasyproctidae (agoutis and acouchis), and was the cluster exhibiting highest effectiveness because they combined relatively high values of QTC with the highest values of QLC (Figure 2). This is not surprising, given the large number of studies documenting the importance of corvids (Gómez, 2003; Lanner, 1996; Pesendorfer et al., 2016; Vander Wall, 1990) and agouties (Forget & Vander Wall, 2001; Jansen et al., 2002, 2004) as seed cachers.

This clumped structure indicates that many synzoochorous dispersers, although differing in morphology, ecology and behaviour, have significant functional similarity with respect to their quality of dispersal, and ultimately effectiveness as dispersers at this early stage (Blendinger, 2017). This suggests they may to some extent be ecologically indistinguishable to plants. It remains to be seen whether this equivalence remains if other quality metrics closer to total fitness, such as number of seeds surviving or emerging in caches and number of seedlings surviving to sapling, are considered. For example, corvids (e.g. Gómez, 2003) tend to disperse seeds much greater distances than dasyproctids (e.g. Forget, 1992), which might affect the quality of dispersal post-caching.

Component relative contribution

We found two lines of evidence suggesting that the synzoochorous effectiveness landscape was quality-driven. First, the quality component explained much more variance (76%) in effectiveness than did the quantity component (17%; calculated using the function aov from the R package stats; R Core Team, 2014), despite the range of QTC values being much greater. Second, by using bearing correlograms to test how spatial autocorrelation varies along the two component axes (Rosenberg, 2000), we found that spatial autocorrelation of both SDE and cluster membership was significant along the QLC component but not along the QTC component (Table 1). This indicates that variation along the quality component was more abrupt than variation along the quantity component. In fact, the distribution of SDE values for synzoochorous families was extensive and gradually scattered across the QTC axis but discontinuous and clumped along the QLC axis (see above). Lastly, there was an absence of disperser families occupying the region with low QTC and high QLC values; that is, all families that were quantitatively unimportant were also qualitatively unimportant (Figure 2). We presume that QLC explains more of the variation in effectiveness than does QTC as a consequence of the dual nature of synzoochorous seed dispersal, where, unlike in other dispersal modes, many seeds are sacrificed to consumption for the successful dispersal of others (Bogdziewicz et al., 2019). Consequently, species differing substantially in dispersal quantity exhibited magnitudes of dispersal quality similar to those of other species belonging to the same cluster. In fact, the three disperser clusters described above were clearly separated along the quality component axis but overlapped extensively along the quantity component axis (Figure 2). As a consequence, in the synzoochorous landscape the quality component contributed most to the total variance observed in effectiveness, and the differences among dispersers in effectiveness are much

TABLE 1 Analysis of the relative contribution of each component, determined by testing the component-dependent change in spatial autocorrelation of effectiveness using bearing correlograms (Rosenberg, 2000)

Spatial autocorrelation	Mantel *r*	*p*-value
Seed dispersal effectiveness		
Total	0.464	0.001
Along QTC	−0.328	0.988
Along QLC	0.591	0.001
Cluster identity		
Total	0.578	0.001
Along QTC	−0.006	0.548
Along QLC	0.404	0.001

Note: This analysis detects directionally in spatial autocorrelation structures and thereby tests how spatial autocorrelations vary along the two components directions (Rosenberg, 2000). The change in spatial autocorrelation occurs along the axis where spatial autocorrelation is significant. We tested both the values of seed dispersal effectiveness as well as the cluster identity. For each of the two components, the transformed distance matrix is obtained by first calculating the natural logarithm of the original distance matrix, followed by weighting its values by the squared cosine of the clockwise bearing angle depicted by each pair of individuals and the fixed spatial direction. The angles used were those corresponding to the axis defined by the quantity component and the axis defined by the quality component. The significances of the spatial autocorrelations were obtained using a permutation test (999 permutations) using a script provided by Valverde et al. (2016).

more strongly affected by their relative positions along the quality axis than by their positions along the quantity axis. However, considerations of the relative contributions of the two components of effectiveness have not given consistent results in mutualism studies. Rodríguez-Rodríguez et al. (2013) found that the two components contributed similarly to the variance in pollination effectiveness of *Isoplexis canariensis*. On the other hand, Calviño-Cancela and Martín-Herrero (2009) found that the quality component explained most of the variance in endozoochorous seed dispersal of *Corema album*, similar to our results with synzoochory. By contrast, the effectiveness of *Virola surinamensis* (*nobilis*) seed dispersal was more strongly related to the quantity than the quality of dispersal (Schupp, 1993).

Component correlation

There was a significant positive between-component family-wise correlation ($r = 0.49$, $p = 0.005$, df = 29, Pearson correlation, calculated using the function cor in the R package stats; R Core Team, 2014). Some families had relatively high values of both QTC and QLC (e.g. Corvidae and primary dispersal by Dasyproctidae), while other families had intermediate values of both components (e.g. primary dispersal by Sciuridae and Formicidae), and still other families had quite low values of both components (Figure 2). A proximate consequence of this positive correlation is the absence of interactions in the quadrant corresponding to high QLC and low QTC values. That is, although there are many low-quality but high-quantity synzoochorous dispersers, it is very unlikely to find high-quality but low-quantity ones. This contrasts with what has been found in endozoochorous dispersal, where high quality is many times exhibited by species with low quantity (Blendinger, 2017, McConkey et al., 2018, Schupp et al., 2010, Pizo & Camargo, 2018; but see González-Castro et al., 2015). Specialisation to effective dispersers is intraspecifically favoured by the observed QTC–QLC correlation (Gómez et al., 2019; Gómez & Zamora, 1999, 2006; González-Castro et al., 2015; Jordano & Schupp, 2000; Mayfield et al., 2001; Sahli & Conner, 2006). This may have important consequences to predict the occurrence of synzoochory-mediated plant selection. Adapting Stebbins' (1970) 'most effective pollinator principle' to synzoochory, seed traits will be presumably shaped mostly by those dispersers combining high quantity with high quality (González-Castro et al., 2015). If this is true, the most important agents of selection for synzoochory-mediated seed traits will be corvids and dasyproctids. Those plant species interacting with these dispersers will presumably have more opportunity to evolve traits promoting effective dispersal. In agreement with this idea, it is widely acknowledged that synzoochorous pines and oaks have coevolved with nutcrackers, jays and other corvids (Bossema, 1979; Lanner, 1996; Smallwood et al., 2001; Steele et al., 2001; Vander Wall & Beck, 2012). Curiously, it is assumed that agoutis disperse mostly seeds that were consumed in the past by currently extinct megafauna (Jansen et al., 2012), so, despite its relatively high effectiveness, the role of these rodents as selective agents of seed traits is less clear.

Overall, we found that the synzoochorous SDE landscape has a very distinctive structure defined by its clumped and quality-driven effectiveness with significant positive correlation between quality and quantity components. We presume that synzoochory-mediated evolution is much more likely in systems situated in those regions of the landscape where both components are high, and the path to reach this privileged location is favoured primarily by among-disperser differences in quality rather than in quantity.

Factors affecting the synzoochorous effectiveness landscape

We explored which factors could putatively affect the observed structure in the synzoochorous effectiveness landscape. For this, we recorded for each case study six variables that have been previously demonstrated to shape the interaction between plants and their synzoochorous dispersers (Gómez et al., 2019): (1) *Disperser functional group*, considering five main functional groups (rodents, marsupials, birds, insects and land crabs) (2) *Dispersal phase*, distinguishing between primary (Phase I) and secondary (Phase II) dispersal. We considered dispersal to be primary when the animal took the seeds directly from the canopy or from the ground beneath the mother plant's canopy, whereas we considered dispersal to be secondary when the animals moved seeds that had previously been dispersed biotically by another organism or abiotically, or experimentally mimicked this (Gómez et al., 2019). Note that in our dataset secondary dispersal does not include any examples of seed caches being re-dispersed by other individuals of the same or different species, although this is a frequent form of secondary dispersal. (3) *Seed mass*, in mg (Dataset S1) using the Seed Information Database of Kew Gardens (data.kew.org/sid), the TRY Plant Trait Database (https://www.try-db.org/TryWeb/Home.php), and from original sources. (4) *Disperser behaviour*, distinguishing between larder hoarders, scatter hoarders and mixed caching behaviour. Larder hoarders take the seeds to their burrows and nests, storing them in large quantities before consuming them (Hartke et al., 1998; Honek et al., 2003; Steinberger et al., 1991). In contrast, scatter hoarders bury the seeds in small, scattered caches beneath moss, litter, or in shallow soil layers (Bossema, 1979; Gómez, 2003; Pesendorfer et al., 2016). We categorised behaviour using the information provided in the individual studies. We are well aware that some disperser species may act in other ways when interacting with other plants, but we preferred to be conservative and have considered only the behaviour indicated in the individual studies included in our dataset to avoid any bias towards well-studied species. (5) *Disperser mass*, in mg using information from Elton Traits database (Wilman et al., 2014), the Animal Diversity Web (http://animaldiversity.org/) and from original sources. (6) *Disperser pouch*, distinguishing between presence and absence, or dispersers with both types. The presence of pouches can modulate the pattern and outcome of the interaction between granivores and plants, because species with pouches tend to disperse more seeds and to longer distances (Vander Wall, 1990). We recorded the presence of cheek pouches in rodents and gular (= throat) pouches in birds. Four rodent families (Cricetidae, Heteromyidae, Nesomyidae and Sciuridae) in our database have species with cheek pouches to collect and store seeds (Ryan, 1986). In birds, only Corvidae have species with pouches or pouch-like structures (Vander Wall, 1990). No other disperser group has any kind of pouch, as far as we know.

To test which variables affected SDE we performed phylogenetic generalised least squares models (PGLS) including as unit the plant species and considering their phylogenetic relationship (Freckleton et al., 2002). Four variables significantly affected the effectiveness values (Table 2). First, SDE was significantly associated with seed mass (Table 2). This relationship was positive (ß = 0.013 ± 0.003, phylogenetically controlled slope ±1 SE), indicating that plant species producing large seeds were dispersed more effectively than those species producing small seeds. Interestingly enough, this relationship was due to the observed positive effect of seed mass on QLC (0.190 ± 0.005). In contrast, QTC was higher in plant species producing smaller seeds (−0.028 ± 0.025) although this effect was weaker than the QLC effect. We believe that this across-species pattern is caused, at least partially, by the differential effectiveness and behaviour of different hoarders. Most studies finding an intraspecific benefit of larger seeds have been conducted on nut-bearing trees primarily dispersed by two relatively highly effective types of dispersers, jays and large rodents (Gómez et al., 2008; Jansen et al., 2002; Jansen et al., 2004; Muñoz & Bonal 2008; Vander Wall, 2003; Xiao et al., 2005). These vertebrates tend to hoard larger seeds in comparison to other less effective dispersers such as ants, crabs or small rodents, which move smaller seeds of grasses and annual herbs (Gómez et al., 2019; Kaspari, 1996; Lai et al., 2018; McMurray et al., 1997; Sivy et al., 2011). It is interesting to note that, despite the net benefit of producing larger seeds, there was a conflict between quantity and quality components. Small seeds were dispersed more frequently but were buried with less probability than large seeds. Under these circumstances, synzoochory may be a factor selecting macroevolutionarily for larger seeds (Galetti et al., 2010).

Disperser behaviour also significantly affected SDE (Table 2). Scatter hoarders were more effective than larder hoarders (Figure 3a). However, the cluster of highly effective dispersers was composed of two scatter hoarders, the cluster of dispersers with low effectiveness was composed exclusively of larder hoarders and the intermediate cluster was composed of a set of disperser groups with mixed behaviour (Detrain & Tasse, 2000; Honek et al., 2003; Kirk, 1972; Koenig et al., 2008; Luna et al., 2018; McConkey et al., 2003; Pesendorfer & Koenig, 2016; Vander Wall, 1990; Vander Wall et al., 2005). Again, this pattern was mediated by QLC (Table 2). Extending the analysis of quality into later plant life history stages is expected to make these differences in effectiveness even greater as it is generally thought that the likelihood of successful seedling establishment from larder hoards is much less than from scatter hoards (Vander Wall, 1990).

Effectiveness was also affected positively by the presence of pouches in the dispersers (Table 2, Figure 3B). It is interesting to note in the cluster of highly effective

TABLE 2 Results of the PGLS exploring the effects of plant and disperser traits in the synzoochory effectiveness ($N = 455$ plant species)

		QTC		QLC		SDE	
	df	***F***	***p***	***F***	***p***	***F***	***p***
Seed mass (mg)	1	0.71	0.400	**4.835**	**0.029**	**7.228**	**0.008**
Dispersal phase	2	4.251	0.015	**10.332**	**0.000**	**4.251**	**0.015**
Disperser group	7	1.57	0.143	**3.501**	**0.001**	1.808	0.085
Disperser mass (mg)	1	0.107	0.744	0.004	0.953	0.236	0.628
Disperser behaviour	2	0.211	0.810	1.481	0.229	**4.246**	**0.015**
Disperser pouch presence	1	**9.701**	**0.000**	2.54	0.080	**6.581**	**0.002**

Note: All traits were averaged per plant species. There were eight disperser groups (rodent, bird, crab, insect, marsupial, rodent+bird, rodent+crab and rodent+insect), three dispersal phases (primary, secondary and both) and three dispersal behaviour groups (scatter, larder and both). The pgls was performed using the function pgls in the R package caper (Orme, 2013) and the function anova.pgls.fixed provided by William Gearty (https://bitbucket.org/wgearty/profile/repositories); *F, F statistic*; *P, associated probability*. The phylogeny of the plant species included in our dataset was generated using the function 'S. Phylomaker' provided by Qian and Jin (2016) running in the R package phytools (Revell, 2012). This function builds a phylogeny matching the list of species provided by the user with the PhytoPhylo megaphylogeny, a backbone phylogeny available in the PhyloMaker repository (https://github.com/jinyizju/S. PhyloMaker) (see Qian and Jin (2016) for details). Significance value appears in Bold.

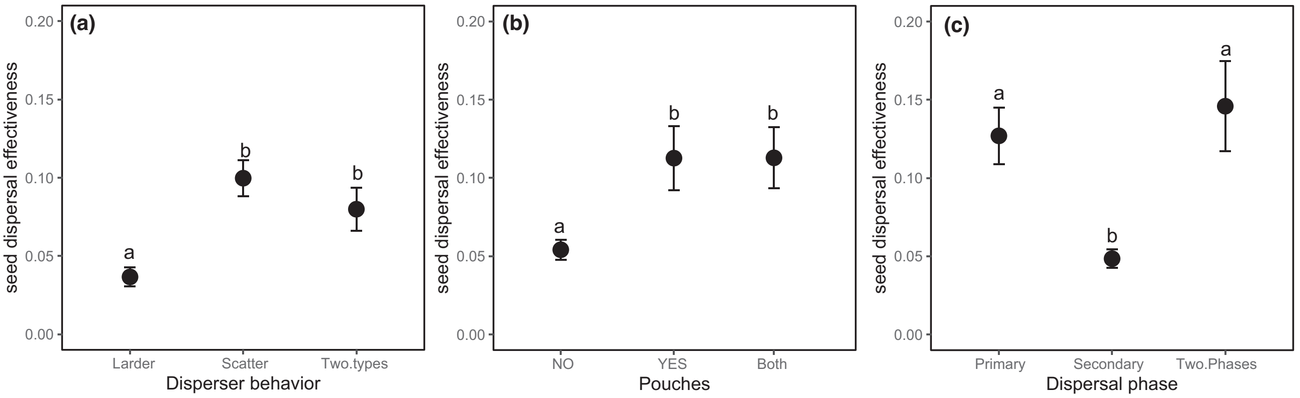

FIGURE 3 Differences in synzoochory effectiveness depending on (a) the behaviour of the disperser, (b) presence of pouches and (c) the phase of the dispersal

dispersers only corvids had anatomical structures analogous to pouches (Vander Wall, 1990). In fact, the relationship between pouches and effectiveness was mediated by QTC rather than by QLC (Table 2), meaning that pouched dispersers dispersed more seeds than pouchless dispersers. This could be related with the ability of pouched dispersers to move a considerable amount of small seeds at the same time (Gómez et al., 2019).

Finally, the location of most dispersers on the landscape also depended on the phase in which they were involved. In general, primary dispersers were more effective than secondary dispersers. (Figure 3c). This was not just because the most effective groups of dispersers, such as corvids, were primary dispersers, since all dispersers participating in both phases (Formicidae and the rodents Cricetidae, Dasyproctidae, Echymidae, Heteromyidae, Muridae and Sciuridae) were more effective when acting as primary than when acting as secondary dispersers (Figure 2). In fact, Dasyproctidae shifted from the cluster with highest effectiveness, when acting as primary dispersers, down to the cluster with intermediate effectiveness, when acting as secondary dispersers (Figure 2). Few studies have compared the effectiveness of primary versus secondary dispersal for the same plant species. Roth and Vander Wall (2005) found that secondary caches contributed less to chinquapin (*Castanopsis sempervirens*) seedling recruitment than did primary caches. In some cases, the quality of dispersal by secondary dispersal differed from the quality of dispersal by primary dispersal depending on the habitat in which the secondarily dispersed acorns were encountered (Gómez et al., 2008). Overall, observing the effectiveness landscape and taking into account the dual nature of synzoochory, it seems that secondary-dispersing synzoochorous species are more likely to act as post-dispersal seed predators. The greater effectiveness of primary dispersers was mostly due to a greater quality component (Table 2, Figure 2). So, primary dispersers generally transport similar number of seeds as secondary dispersers, but tend to cache a higher proportion of them. Nevertheless, we believe that the higher effectiveness of primary dispersal may be at least partially due to the larger size of the primarily dispersed seeds in our database (median weight = 1591 mg) than that of the secondarily dispersed seeds (504 mg; Figure S1). It is widely known that dispersers tend to hoard larger seeds more often than smaller seeds (e.g. Jansen et al., 2002, 2004), and we have documented this at the entire landscape level (see above). Secondary dispersal may have evolved in spite of its lower effectiveness because when combined with primary dispersal it can increase the net benefits of seed dispersal (Vander Wall & Longland, 2004).

CONCLUSION

We propose in this study that the three properties of the effectiveness landscape, namely the dispersion of the effectiveness values, the relative contribution of each component to the overall value of effectiveness and the correlation between components, can give insight into how mutualistic interactions may have evolved. As an example, we have investigated these properties in a mutualistic facultative interaction, synzoochorous seed dispersal. We found that the effectiveness landscape describing this interaction is clumped, quality-driven and shows positive QLC–QTC correlation. We believe that this structure is the consequence of synzoochorous plants coevolving mostly with some disperser functional groups. In particular, we presume that synzoochory-mediated evolution is much more likely in plants situated in those regions of the landscape where both components are high, and the path to reach this privileged location is favoured by among-disperser differences in quality more than in quantity.

The degree to which these three structural properties can explain how other types of mutualism have evolved is presently unknown. However, we believe that clumped, quality-driven and positively correlated landscapes will be commonly found in generalised coevolved mutualisms, where multiple functionally equivalent high-quality partners will exert similarly strong selective pressures. In contrast, we speculate that non-coevolved mutualisms could be characterised by negatively correlated landscapes where a conflict between QTC- and QLC-mediated selective pressures will arise, whereas random landscape will be evidence of mutualisms where partners exert weak selection upon each other. We suggest that applying this approach to a broader range of mutualisms will give new insight into the evolutionary and ecological consequences of mutualisms.

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AUTHORS CONTRIBUTIONS

The study was conceived, performed and written by all authors.

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DATA AVAILABILITY STATEMENT

All data are available in the supplementary materials and, should the manuscript be accepted, they will be archived in Dryad repository (https://doi.org/10.5061/dryad.5tb2rbp59).

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