

# Synzoochory: the ecological and evolutionary relevance of a dual interaction

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## ABSTRACT

Synzoochory is the dispersal of seeds by seed-caching animals. The animal partner in this interaction plays a dual role, acting both as seed disperser and seed predator. We propose that this duality gives to synzoochory two distinctive features that have crucial ecological and evolutionary consequences. First, because plants attract animals that have not only positive (seed dispersal) but also negative (seed predation) impacts on their fitness, the evolution of adaptations to synzoochory is strongly constrained. Consequently, it is not easy to identify traits that define a synzoochorous dispersal syndrome. The absence of clear adaptations entails the extra difficulty of identifying synzoochorous plants by relying on dispersal traits, limiting our ability to explore the full geographic, taxonomic and phylogenetic extent of synzoochory. Second, the positive and negative outcomes of interactions with synzoochorous animals are expressed simultaneously. Consequently, synzoochorous interactions are not exclusively mutualistic or antagonistic, but are located at some point along a mutualism–antagonism continuum. What makes synzoochory interesting and unique is that the position of each partner along the continuum can be evaluated for every plant–animal interaction, and thus the continuum can be precisely described by assessing the relative frequency of positive and negative interaction events in each pairwise interaction. Herein we explore these two main features of synzoochory with a comprehensive quantitative survey of published studies on synzoochory. Synzoochory has been recorded for at least 1339 plant species differing in life forms, from annual and short-lived herbs to long-lived trees, belonging to 641 genera and 157 families widely distributed across the globe and across the seed plant phylogeny. Over 30 animal families belonging to five disparate taxonomic groups (rodents, marsupials, birds, insects, and land crabs) potentially act as synzoochorous dispersers. Although synzoochory appears to be fundamentally a secondary dispersal mode, many abundant and dominant trees are primarily synzoochorous. In addition, we found evidence of the existence of diplosynzoochory (caching animals acting both as primary and secondary dispersers of the same individual seed), mostly in nut-bearing trees. Finally, we found that synzoochorous interactions are widely spread across the mutualism–antagonism continuum. Nevertheless, there were some differences among disperser species and functional groups. Corvids and some rodents (cricetids, nesomyids, sciurids) were located in the positive-effects region of the continuum and presumably behave mostly as dispersers, whereas land crabs and insects were located in the negative-effects extreme and behave mostly as seed predators. Our review demonstrates that synzoochory is not an anecdotal ecological interaction. Rather, it is pivotal to the functioning of many ecosystems where the natural regeneration of keystone plant species depends on the activity of granivorous animals that play a dual role. This distinctive interaction should not be ignored if we wish to have an accurate understanding of the functioning of natural systems.

**Key words:** conditional mutualism, dual effects, hoarding, interaction intensity, mutualism–antagonism continuum, seed-dispersal adaptation, seed-dispersal effectiveness, zoochory.

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## I. INTRODUCTION

Plants can disperse their seeds through multiple mechanisms, many of which involve the action of animals. Seeds can be transported incidentally on the outside of animals, attached to their skin, fur, or feathers, a dispersal mode called ectozoochory or epizoochory (Couvreur *et al.*, 2008). Alternatively, seeds can be transported inside animals, a dispersal mode called endozoochory (van der Pijl, 1982; Jordano, 2000). Animals providing this service are mostly frugivorous vertebrates (Fleming & Kress, 2011; Jordano, 2013), although some frugivorous invertebrates (de Vega *et al.*, 2011; Blattmann *et al.*, 2013; Boch *et al.*, 2013), mammalian herbivores (Janzen, 1984; Malo & Suárez, 1995; Pakeman *et al.*, 2002; Mouissie *et al.*, 2005) and granivorous birds (Heleno *et al.*, 2011; Tella *et al.*, 2015; Blanco *et al.*, 2016) can also disperse seeds by endozoochory. In addition, many plants are dispersed by ants in myrmecochory (Beattie, 1985; Rico-Gray & Oliveira, 2007). A common feature of these, otherwise diverse, animal-mediated dispersal modes is that there are specific plant structures that have apparently evolved to promote dispersal either by attracting the dispersers or by facilitating the attachment and/or movement of the seeds by the disperser (Sorensen, 1986; Willson & Traveset, 2000; Herrera, 2002; Lengyel *et al.*, 2010). Thus, animal-mediated seed dispersal strategies in higher plants are based on a myriad of adaptations, both on the plant side in order to secure effective seed dispersal (*sensu* Schupp, Jordano & Gómez, 2010), and on the animal disperser side in order to use plant resources efficiently (Jordano, 2000). For example, epizoochorous seeds display barbs, recurved bract tips, hooked prickles and hairs, curved spines, viscid mucilage or other adhesive structures (Sorensen, 1986; Yang *et al.*, 2012). These morphological structures favour adhesion to the external parts of the disperser's bodies (Fahn & Werker, 1972). Endozoochorous plants, on the other hand, produce fleshy fruits to attract frugivorous dispersers (Jordano, 2013). A fascinating variety

of fleshy fruit displays involving sophisticated infructescences, ancillary rewards and diversified colours, odours, and pulp nutrient contents has evolved among plants to attract endozoochorous dispersers (van der Pijl, 1982; Willson & Whelan, 1990; Cipollini & Levey, 1997; Jordano, 2000; Herrera, 2002; Valido, Schaeffer & Jordano, 2011). Finally, myrmecochorous ants are attracted to the seeds by attached lipid-rich elaiosomes (Beattie, 1985; Rico-Gray & Oliveira, 2007). In these latter two cases, the animal feeds on these secondary structures rather than feeding directly on the seeds, which are dispersed.

Contrasting with these dispersal modes, synzoochory is a dispersal mode where the dispersers, rather than being attracted to a secondary trait, are directly attracted to the 'seed' (defined broadly as the dispersal unit, independently of its anatomical structure or embryological origin) – the seed is the reward. Specifically, synzoochory is defined as the deliberate transportation of seeds externally, generally in the mouth, by a granivorous animal, followed by the hoarding of at least a fraction of those seeds (Dixon, 1933; van der Pijl, 1982). Thus, synzoochory involves the dispersal of seeds, an attractive long-term, storable food for animals, by species directly seeking resources within the seed such as endosperm or embryos (Vander Wall, 1990; Hulme, 2002). Seeds not consumed immediately may be stored some distance away from the parent plant, and some may escape being eaten if the animal forgets them, stores more than can be consumed, or dies before recovering them (Iluz, 2011). Relying on granivores to disperse seeds may represent a 'window of opportunity' given that many of them handle fruits and seeds in unique ways that may eventually favour successful establishment. In particular, many granivores do not process seeds *in situ* nor ingest them or destroy them immediately after visiting a fruiting plant, but take the seeds away from the vicinity of the parent and frequently cache them for later use in sites suitable for seedling establishment (Vander Wall, 2001).

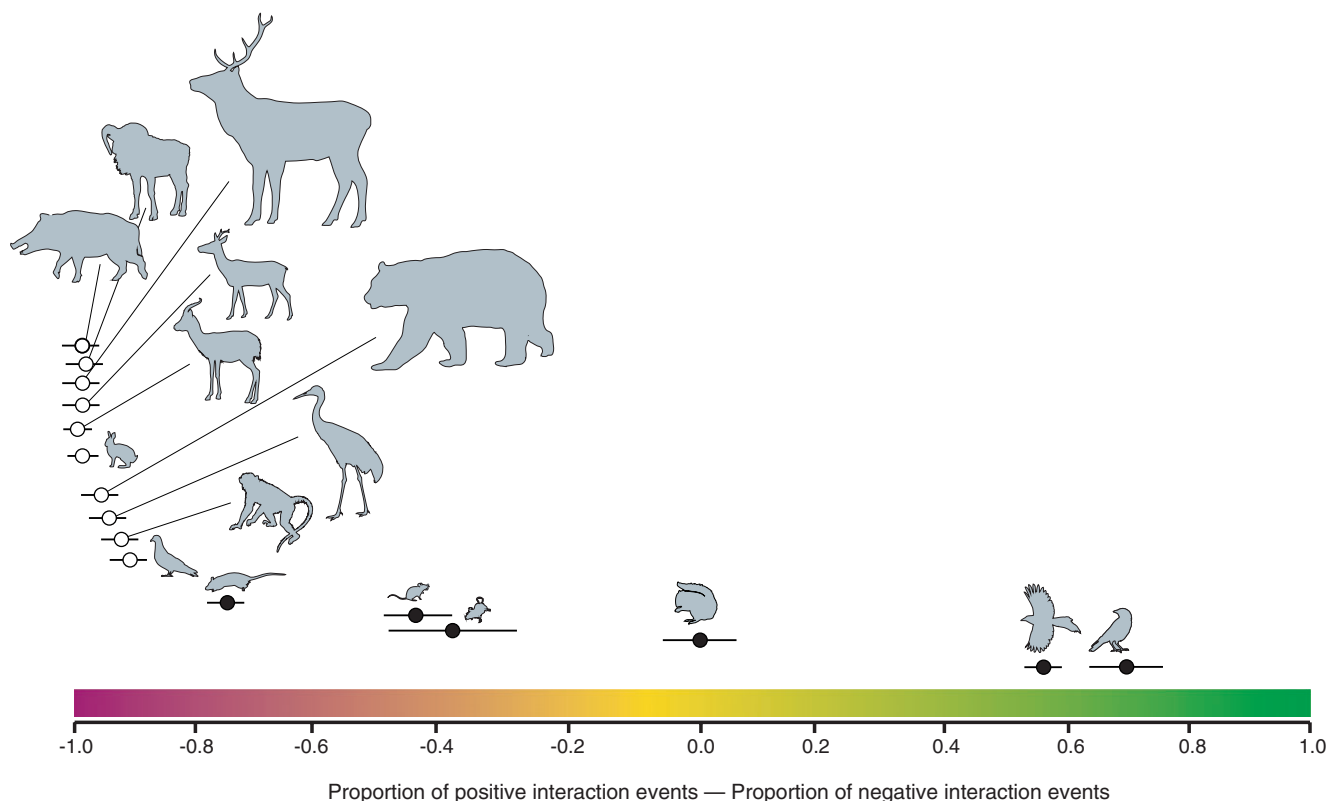
Etymologically, synzoochory means ‘dispersal together with animals’ (*syn-* from Greek ‘together’), and refers to the act of moving the seeds not inside or outside the animal but along with it. Although the term synzoochory was introduced in the scientific literature long ago (Dixon, 1933), it has not been used as frequently as other seed-dispersal terms despite this type of dispersal being widely studied during the last five decades. In most of these studies, this type of dispersal was referred to as dispersal by hoarding or caching. We propose nevertheless that the term ‘synzoochory’ is more consistent with the general terminology in seed-dispersal studies.

Synzoochory was originally considered similar to myrmecochory (Fahn & Werker, 1972), although the general opinion today is that these two types are different. In addition, synzoochory has been related to dyszoochory (*dys-* meaning ‘ill’ or ‘bad’), the dispersal of seeds by granivores that accidentally lose them during transport, and stomatochory (*stomato-* meaning ‘mouth’), the transport of seeds in the bill or mouth (van der Pijl, 1982; Iluz, 2011). These two dispersal modes have been observed in ants (Wolff & Debussche, 1999; Rico-Gray & Oliveira, 2007), granivorous birds like pigeons and parrots (Böhning-Gaese, Gaese & Rabemanantsoa, 1999; Blanco *et al.*, 2015; Tella *et al.*, 2015; Baños-Villalba *et al.*, 2017) and some granivorous mammals, such as bats and primates, which drop seeds while feeding (Kevan & Gaskell, 1986; Barnett *et al.*, 2012). Although they share some common characteristics, synzoochory is unique because it is a dispersal mode provided by animals that intentionally move and cache seeds, albeit unintentionally losing some of them. In brief, under our conception, synzoochory is the dispersal of seeds by seed-caching seed predators.

Because synzoochory is carried out by seed-eating animals, a major feature that distinguishes this type of dispersal from other animal-mediated dispersal modes is the animal partner of this plant–animal interaction plays a dual role, acting simultaneously as an effective seed disperser and as a seed predator (Hulme, 2002; Retana, Picó & Rodrigo, 2004; Theimer, 2005; Vander Wall & Beck, 2012). The dual role played by synzoochorous dispersers has two main consequences for the dynamics and evolution of synzoochory. A first consequence is that the positive (effective seed dispersal) and negative (seed predation) outcomes of the interactions are expressed simultaneously (Hulme, 2002; Aliyu *et al.*, 2018). Even the removal of several seeds by a single animal can result in a fraction of them being successfully dispersed while others are directly preyed upon. For this reason this interaction is considered to be a conditional mutualism (Jorge & Howe, 2009; Aliyu *et al.*, 2018), becoming mutualistic when the benefit of effective seed dispersal exceeds the cost of seed predation (Theimer, 2005). It is widely acknowledged that mutualistic organisms can confer benefits to their partners while also imposing fitness costs (Bronstein, 2001). For example, mycorrhizal fungi benefit their partners by providing increased uptake of limiting soil resources such as phosphorous, but at the same time harm them by consuming carbon from photosynthesis. Thus, although mycorrhizal fungi are usually mutualistic,

they can be parasitic under some environmental conditions or when they colonize certain hosts (Johnson, Graham & Smith, 1997; Hoeksema *et al.*, 2010). A mutualism–antagonism continuum has been considered a useful framework to study the functioning of interspecific interactions where interacting organisms have both positive and negative effects on their partner, including symbiotic interactions such as legume–rhizobium symbioses (Regus *et al.*, 2015), endophytes (Saikkonen *et al.*, 1998; Mandyam & Jumpponen, 2015) and mycorrhizae (Karst *et al.*, 2008; Johnson & Graham, 2012), and non-symbiotic interactions such as endozoochory (Perea *et al.*, 2013; Montesinos-Navarro *et al.*, 2017), ant–plant defence mutualisms (Cushman & Whitham, 1989; Cushman & Addicott, 1991), brood parasitism (Canestrari *et al.*, 2014), pollination (Rodríguez-Rodríguez, Jordano & Valido, 2017) or synzoochory (Theimer, 2005; Zwolak & Crone, 2012; Sawaya *et al.*, 2018).

Thus, synzoochorous interactions are located somewhere along a continuum running between pure mutualism and pure parasitism (Johnson & Graham, 2012; Johnson *et al.*, 1997). For example, multiple granivorous animals consume the acorns of Holm Oak (*Quercus ilex*) in the Western Mediterranean. Many of these species of ungulates (wild boar *Sus scrofa*, red deer *Cervus elaphus*, fallow deer *Dama dama*, mouflon *Ovis orientalis*, Spanish ibex *Capra pyrenaica*, roe deer *Capreolus capreolus* and Cuvier’s gazelle *Gazella cuvieri*), lagomorphs (European rabbit *Oryctolagus cuniculus* and Iberian hare *Lepus granatensis*), and rodents (crested porcupine *Hystrix cristata* and garden dormouse *Eliomys quercinus*) consume and destroy nearly all of the acorns they find, thus acting mostly as seed predators (Díaz *et al.*, 1993; Santos & Tellería, 1997; Leiva & Fernández-Alés, 2003; Gómez, 2004; Beudels-Jamar, Lafontaine & Devillers, 2005; Bonal & Muñoz, 2007; Muñoz & Bonal, 2007; Gómez & Hódar, 2008; Smit, Díaz & Jansen, 2009; Mori, Bozzi & Laurenzi, 2017). Holm-oak acorns are also consumed by several species of vertebrates which occasionally successfully disperse them endozoochorously or dyszoochorously, such as common crane *Grus grus* (Avilés, Sánchez & Parejo, 2002), woodpigeon *Columba palumbus* (Smit *et al.*, 2009), Barbary macaque *Macaca sylvana* (Deag, 1983; Ménard, 2002) and brown bear *Ursus arctos* (Wiegand *et al.*, 1998; Rodríguez *et al.*, 2007; Lalleroni *et al.*, 2017). In addition, Holm-oak acorns are consumed by larder- and scatter-hoarding rodents, such as black rat *Rattus rattus*, woodmouse *Apodemus sylvaticus*, Algerian mouse *Mus spretus* and red squirrel *Sciurus vulgaris*, which may disperse and cache some of the acorns they encounter (Bonal & Muñoz, 2007; Muñoz & Bonal, 2007; Pons & Pausas 2007a; Gómez, Puerta-Piñero & Schupp, 2008). Finally, acorns are consumed by scatter-hoarding corvids, such as hooded crow *Corvus cornix*, Eurasian jay *Garrulus glandarius* and magpie *Pica pica*, which disperse and cache a large proportion of the acorns they harvest (Santos & Tellería, 1997; Gómez, 2003; Pulido & Díaz, 2005; Pons & Pausas, 2007b; Melletti & Mirabile, 2010; Morán-López, Alonso & Díaz, 2015a; Martínez-Baroja *et al.*, 2017). Thus, the animals consuming Holm-oak acorns occupy different



**Fig. 1.** A hypothetical representation of the mutualism–antagonism continuum for the Holm oak *Quercus ilex* and the granivorous species feeding and potentially dispersing the acorns. The  $x$ -axis represents the range of outcomes of the pairwise oak–granivore interactions between extremes of only positive interaction effects (green) and only negative interaction effects (purple). The location of each granivorous species along the  $x$ -axis is calculated as the proportion of acorns that were dispersed alive and either cached (synzoochorous seed dispersers) or deposited intact (others) minus the proportion of acorns that were eaten *in situ* or immediately after being dispersed. Because accurate information on these values does not exist for all species, the positions as well as the intraspecific variations of each granivorous species have to be taken only as approximate values intended to show in which part of the gradient each species is more likely to lie based on the published literature and our own observations. Synzoochorous seed dispersers are represented as filled dots, and non-caching species as white dots. Species represented, from right to left: *Garrulus glandarius*, *Pica pica*, *Sciurus vulgaris*, *Apodemus sylvaticus*, *Mus spretus*, *Rattus rattus*, *Columba palumbus*, *Macaca sylvanus*, *Grus grus*, *Ursus arctos*, *Oryctolagus cuniculus*, *Gazella cuvieri*, *Capreolus capreolus*, *Cervus elaphus*, *Ovis orientalis*, *Sus scrofa*. Note that there is no meaning to the vertical spread of species, which is imposed to separate the species spatially so that the patterns can be clearly visualized. The silhouettes of the granivores were downloaded from [www.phylopic.org](http://www.phylopic.org). They have a Public Domain license without copyright, except the silhouettes of *G. cuvieri* (R. Groom), *O. cuniculus* (S. Werning), and *R. rattus* (R. Groom) that have a Creative Commons license (<http://creativecommons.org/licenses/by/3.0>).

positions on the continuum running between full antagonism and full mutualism, and in fact together occupy much of the gradient (Fig. 1). This continuum can be operationally defined as the proportion of seeds receiving positive effects (dispersed and either cached or deposited intact) minus the proportion of seeds receiving negative effects (eaten *in situ* without being dispersed or eaten immediately after being dispersed), variables typically recorded in observational and experimental studies of synzoochorous interactions (Forget & Vander Wall, 2001; Hulme, 2002; Forget & Wenny, 2005).

A second consequence of the occurrence of this duality is that it may limit the options of plants to evolve adaptations to dispersers. Since adaptations for attracting dispersers will simultaneously attract predators, there will be

conflicting selection pressures on fruit and seed traits (Smith, 1975). Because the same organisms tend to exert complex regimes of conflicting selection when acting simultaneously as dispersers and predators (Smith, 1975; Vander Wall, 2001; Gómez, 2004), synzoochorous dispersers exert weak selective pressures most of the time. Consequently, there is not a clear suite of adaptive traits associated with synzoochory (Smith, 1975; Howe & Smallwood, 1982; van der Pijl, 1982), and defining a synzoochorous dispersal syndrome based solely on plant traits is thus difficult (Howe & Smallwood, 1982; Iluz, 2011). The absence of apparent adaptations means that we cannot reliably identify synzoochorous plants by means of specific dispersal traits (but see Vander Wall & Moore, 2016; Vander Wall, Barga & Seaman, 2017), a practice frequently employed to identify epizoochorous, endozoochorous and



myrmecochorous plants (Tiffney & Mazer, 1995; Rico-Gray & Oliveira, 2007). This lack of traits universally associated with synzoochory has important practical consequences for determining its importance and frequency (but see Vander Wall & Moore 2016; Vander Wall *et al.*, 2017). Consequently, there is not yet a general overview of the radiation and extent of synzoochory among higher plants. This is surprising given that Theophrastus of Eressus observed synzoochorous dispersal of oaks by jays about 2300 years ago, making this dispersal mode probably one of the first to be described scientifically (Thanos, 2005).

Herein we propose a framework to study synzoochory based on its defining characteristics. However, rather than picking a few, arbitrarily selected illustrative case studies of synzoochory to obtain general patterns, we conducted a quantitative survey, as comprehensive as possible, and extracted from it the main features of this unique plant–animal interaction. Specifically, we first explore the geographic, taxonomic and phylogenetic extent of synzoochory among seed plants, both empirically describing the diversity of plants receiving the dispersal service as well as the variety of animals engaged in this mode of dispersal. We also discuss the dispersal phase when hoarding animals act and the intensity of interaction of this dispersal mode. Finally, we highlight the consequences of the most remarkable feature of this dispersal mode, the dual role as predators and dispersers played by the animal partners. Our goal is to depict the ecological and evolutionary relevance of this critical dispersal mode.

## II. THE EXTENT OF SYNZOOCHORY

### (1) The database

No quantitative review summarizing the number and identity of plant species that are dispersed by synzoochory has been performed since Vander Wall (1990). To obtain an updated database including published information on seed dispersal by synzoochory, we conducted computer searches including the terms (alone or in combination) ‘seed dispersal’, ‘seed predation’, ‘synzoochory’, ‘scatter-hoarding’, ‘seed burial’, ‘seed removal’, ‘seed caching’ and ‘hoarding’. We considered only those animals feeding directly on seeds, disregarding species consuming other parts of the reproductive structures of the plants, such as frugivores, elaiosome-eating ants, floral herbivores, etc. That is, other types of dispersal, such as endozoochory and myrmecochory, were not included in the database. In addition, to distinguish granivorous species acting as potential seed dispersers from those acting solely as seed predators, we follow the definition of dispersal in Schupp *et al.* (2010). In this view a seed is dispersed when it is moved horizontally from the location where it was encountered, irrespective of its final fate. Thus we omitted studies where the authors explicitly stated that the animals do not move any seed but consume all of the handled seeds *in situ* (strict-sense granivory, as in seed-eating birds). Furthermore, to distinguish synzoochorous dispersers from

dyszoochorous and stomatochorous dispersers, and exclusive seed predators that disperse seeds before consuming them, we only included in our database information on those animals reported to cache seeds. By doing this, we were conservative and only retrieved those studies where it was explicitly indicated that the plants were interacting with animals that remove, transport and cache some fraction of the seeds they encounter, irrespective of the final fate of the transported seed. That is, where animals both dispersed seeds and contributed to the first critical step of effective dispersal by caching some seeds rather than simply consuming them all. Nevertheless, assuming that dispersal occurs when there is horizontal movement of seeds (Schupp *et al.*, 2010), once a given granivorous animal disperser was identified as a seed hoarder in at least one study, we considered all cases involving dispersal by that species as being synzoochorous dispersal even in the absence of evidence of caching in a particular study.

From each source, we retrieved the plant and animal taxonomic identities, the country and date of the study, and the main biome where the interaction took place. Olson *et al.* (2001) distinguished 14 main biomes, but we grouped these into three main categories in order to ensure enough samples in each type of habitat to make reliable inferences. We grouped those studies made in tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, tropical and subtropical grasslands, savannas, and shrublands, tropical and subtropical coniferous forests, mangrove, and flooded grasslands and savannas into a Tropical category. Likewise, we grouped all the studies made in temperate broadleaf and mixed forests, temperate coniferous forests, boreal forests/taiga, temperate grasslands, savannas, and shrublands, montane grasslands and shrublands, and tundra into a Temperate category. Finally, those studies made in Mediterranean forests, woodlands, and scrub or sclerophyll forests, deserts and xeric shrublands were grouped into an Arid category. In addition, to the fullest extent possible we compiled the seed mass (in mg) of the species included in the data set. We obtained this information from the Seed Information Database of the Kew Garden ([data.kew.org/sid](http://data.kew.org/sid)), the TRY Plant Trait Database (<https://www.try-db.org/TryWeb/Home.php>) and from original sources. Our final database is provided electronically (see online Supporting information, Appendix S1).

### (2) Number and identity of synzoochorous plants

Our review indicates that synzoochory is not an anecdotal phenomenon. Rather, synzoochory has been observed in at least 1339 plant species differing in life forms from annual and short-lived herbs to long-lived trees ( $N = 2223$  case studies, Appendix S1) and belonging to 641 genera and 157 families widely distributed across seed plants (Table 1). That is, synzoochory has been observed in about 35% of the plant families accepted by the Plant List v.1.1 (<http://www.plantlist.org>). There are reports of synzoochory in species from each of the four gymnosperm groups (Cycadophyta,

Table 1. Number of seed plant species per plant family where synzoochory has been observed

| Family             | Spp. | Family           | Spp. | Family          | Spp. | Family           | Spp. |
|--------------------|------|------------------|------|-----------------|------|------------------|------|
| <b>Gymnosperms</b> |      |                  |      |                 |      |                  |      |
| Araucariaceae      | 2    | Ephedraceae      | 5    | Pinaceae        | 55   | Zamiaceae        | 1    |
| Cupressaceae       | 4    | Ginkgoaceae      | 1    | Podocarpaceae   | 1    |                  |      |
| Cycadaceae         | 1    | Gnetaceae        | 2    | Taxaceae        | 2    |                  |      |
| <b>Angiosperms</b> |      |                  |      |                 |      |                  |      |
| Acanthaceae        | 3    | Casuarinaceae    | 1    | Juncaceae       | 5    | Plumbaginaceae   | 1    |
| Achariaceae        | 1    | Celastraceae     | 3    | Lamiaceae       | 6    | Poaceae          | 147  |
| Adoxaceae          | 3    | Cervantesiaceae  | 1    | Lauraceae       | 34   | Polygonaceae     | 13   |
| Aextoxicaceae      | 1    | Chrysobalanaceae | 8    | Lecythidaceae   | 7    | Portulacaceae    | 1    |
| Aizoaceae          | 3    | Cistaceae        | 9    | Liliaceae       | 2    | Primulaceae      | 7    |
| Amaranthaceae      | 9    | Cleomaceae       | 1    | Linaceae        | 4    | Proteaceae       | 8    |
| Amaryllidaceae     | 1    | Clusiaceae       | 11   | Loganiaceae     | 3    | Putranjivaceae   | 1    |
| Anacardiaceae      | 20   | Colchicaceae     | 1    | Magnoliaceae    | 3    | Ranunculaceae    | 3    |
| Anisophylleaceae   | 1    | Combretaceae     | 6    | Malpighiaceae   | 2    | Resedaceae       | 2    |
| Annonaceae         | 5    | Connaraceae      | 2    | Malvaceae       | 18   | Restionaceae     | 3    |
| Apiaceae           | 8    | Convolvulaceae   | 4    | Melastomataceae | 17   | Rhamnaceae       | 8    |
| Apocynaceae        | 9    | Cornaceae        | 2    | Meliaceae       | 17   | Rhizophoraceae   | 2    |
| Apodanthaceae      | 1    | Corynocarpaceae  | 1    | Menispermaceae  | 2    | Rosaceae         | 27   |
| Aquifoliaceae      | 1    | Coulaceae        | 2    | Moraceae        | 26   | Rubiaceae        | 15   |
| Araceae            | 1    | Crassulaceae     | 1    | Muntingiaceae   | 1    | Rutaceae         | 2    |
| Araliaceae         | 5    | Cucurbitaceae    | 2    | Myricaceae      | 1    | Sabiaceae        | 1    |
| Arecaceae          | 74   | Cyperaceae       | 7    | Myristicaceae   | 13   | Salicaceae       | 1    |
| Asparagaceae       | 7    | Dilleniaceae     | 1    | Myrtaceae       | 19   | Santalaceae      | 2    |
| Asteraceae         | 65   | Dipterocarpaceae | 3    | Neuradaceae     | 1    | Sapindaceae      | 19   |
| Austrobaileyaceae  | 1    | Ebenaceae        | 6    | Nitrariaceae    | 1    | Sapotaceae       | 20   |
| Balsaminaceae      | 1    | Elaeagnaceae     | 1    | Nothofagaceae   | 1    | Saxifragaceae    | 1    |
| Berberidaceae      | 1    | Elaeocarpaceae   | 6    | Nyctaginaceae   | 2    | Schisandraceae   | 2    |
| Betulaceae         | 7    | Ericaceae        | 3    | Ochnaceae       | 1    | Scrophulariaceae | 3    |
| Bignoniaceae       | 6    | Erythropalaceae  | 1    | Oleaceae        | 3    | Simaroubaceae    | 1    |
| Bixaceae           | 1    | Erythroxylaceae  | 2    | Orobanchaceae   | 1    | Solanaceae       | 4    |
| Boraginaceae       | 11   | Euphorbiaceae    | 29   | Oxalidaceae     | 2    | Staphyleaceae    | 2    |
| Brassicaceae       | 28   | Fabaceae         | 150  | Paeoniaceae     | 1    | Styracaceae      | 1    |
| Burseraceae        | 10   | Fagaceae         | 123  | Pandaceae       | 1    | Surianaceae      | 1    |
| Cactaceae          | 3    | Geraniaceae      | 7    | Pandanaceae     | 3    | Tamaricaceae     | 1    |
| Calophyllaceae     | 3    | Gentianaceae     | 1    | Papaveraceae    | 1    | Theaceae         | 2    |
| Campanulaceae      | 2    | Goodeniaceae     | 1    | Passifloraceae  | 1    | Ulmaceae         | 2    |
| Cannabaceae        | 3    | Grossulariaceae  | 1    | Phyllanthaceae  | 1    | Urticaceae       | 5    |
| Capparaceae        | 1    | Haemodoraceae    | 1    | Phytolaccaceae  | 1    | Verbenaceae      | 4    |
| Caprifoliaceae     | 3    | Hernandiaceae    | 2    | Piperaceae      | 1    | Violaceae        | 1    |
| Caricaceae         | 1    | Humiriaceae      | 2    | Pittosporaceae  | 3    | Xanthorrhoeaceae | 2    |
| Caryocaraceae      | 4    | Icacinaeae       | 1    | Plantaginaceae  | 13   | Zygophyllaceae   | 3    |
| Caryophyllaceae    | 14   | Juglandaceae     | 11   |                 |      |                  |      |

Ginkgophyta, Gnetophyta and Pinophyta) and from most angiosperm groups (Table 1). Because we have included in the data set only those species from which we found published evidence of synzoochory, we are likely to be lacking many species belonging to families typically dispersed by synzoochory (e.g. Fagaceae, Arecaceae, Juglandaceae, etc.) but that have not been studied; thus the true extent of synzoochory will be more widespread than we document here. We fully support the claim by Vander Wall, Kuhn & Beck (2005b) that many times where seed predation has been reported, at least some of the seeds were likely cached instead and therefore dispersed synzoochorously rather than simply being preyed upon.

Even with the limited attention that synzoochory has attracted among ecologists, its ample taxonomical

distribution and high frequency of occurrence are striking. In fact, the taxonomic distribution of synzoochory is comparable to the frequency of other more systematically studied dispersal mechanisms. For example, according to Rico-Gray & Oliveira (2007), myrmecochory occurs in about 3000 species, whereas Lengyel *et al.* (2010) report evidence of myrmecochory in more than 11500 species from 334 genera and 77 families. Although myrmecochory has been reported in far more species than synzoochory, this latter dispersal mechanism is much more widely spread over the phylogeny of the land plants, occurring in nearly twice as many genera and families as myrmecochory. A similar case occurs with endozoochory mediated by frugivores. Herrera (1989) reported about 151 families, including both gymnosperms and angiosperms, bearing fleshy fruits and thereby being

totally or partially dispersed by means of endozoochory. Given the high proportion of woody species with fleshy fruits found in many vegetation types (Howe & Smallwood, 1982; Jordano, 2013) the number of endozoochorous species perhaps exceeds that of synzoochorous species; nonetheless, the number of families represented in these two dispersal modes is equivalent. It is interesting to note that Tiffney & Mazer (1995) inferred biotic dispersal, pooling all biotic dispersal modes, for 123944 species from 6501 genera and 202 families. Although the number of species and genera exhibiting synzoochory make up only a fraction of the species and genera that are biotically dispersed, a remarkable 72% of families having biotic dispersal of some kind appear to include species with synzoochory. It is worth noting that in most of these reviews the form of biotic dispersal was inferred when a given plant species displayed specific structures to attract specific dispersal vectors (elaiosome, fleshy pulp, etc.). In our case, rather than inferring a synzoochorous plant species based on the presence of a given trait, we included in our review only those species where synzoochory was definitively observed. This approach is very conservative. If we had inferred synzoochory from the presence of certain traits, such as large seeds, hard testa, dehiscent fruits, etc. (Vander Wall *et al.*, 2017), the number of recorded synzoochorous species would be substantially greater. For example, Galetti *et al.* (2010) proposed that plant species with seeds larger than 0.9 g can be dispersed by scatter-hoarding agoutis in the Neotropics. If we used this criterion, the number of species potentially dispersed through synzoochory in tropical and subtropical areas as well as in many temperate forests would have been substantially larger. However, at the same time we would have missed a large number of synzoochorous species that do not express such traits. In brief, we presume that synzoochory is much more frequent than reported to date, and with the data at hand it has been demonstrated that synzoochory occurs in many ecologically and morphologically disparate lineages of plants.

### (3) Number and identity of synzoochorous dispersers

Food hoarding has been reported in many different types of animals, both vertebrates and invertebrates (Vander Wall, 1990). However, only a subset of these species hoards seeds and thereby potentially contributes to effective seed dispersal. In our database, 33 animal families belonging to five main taxonomic groups (rodents, marsupials, birds, insects, and land crabs) have been documented dispersing and caching seeds and thus acting as synzoochorous dispersers (Table 2). The most frequent synzoochorous dispersers were by far rodents, which dispersed about 66% of the plant species in our database. Rodents were not only the most frequent but also the most diverse group of dispersers, with 15 families represented in our database (Table 2). Of these families, the most frequent rodent dispersers were sciurids, dasyproctids, murids, and heteromyids (Table 2). Insects were also important caching animals, dispersing 19% of the plant species included in

Table 2. Number of plant species reported as being synzoochorously dispersed by members of each animal family and group

| Family              | Number of plant species dispersed |
|---------------------|-----------------------------------|
| <b>Insects</b>      | <b>487</b>                        |
| Formicidae          | 461                               |
| Scarabaeidae        | 3                                 |
| Carabidae           | 12                                |
| Gryllidae           | 17                                |
| <b>Land crabs</b>   | <b>62</b>                         |
| Gecarcinidae        | 55                                |
| Gecarcinucidae      | 1                                 |
| Grapsidae           | 1                                 |
| Ocypodidae          | 3                                 |
| Potamidae           | 2                                 |
| <b>Birds</b>        | <b>132</b>                        |
| Corvidae            | 100                               |
| Ptilonorhynchidae   | 1                                 |
| Emberizidae         | 1                                 |
| Fringillidae        | 2                                 |
| Paridae             | 18                                |
| Picidae             | 21                                |
| Sittidae            | 6                                 |
| <b>Marsupials</b>   | <b>17</b>                         |
| Hypsiprymnodontidae | 13                                |
| Potoroidae          | 4                                 |
| <b>Rodents</b>      | <b>733</b>                        |
| Caviidae            | 1                                 |
| Cricetidae          | 84                                |
| Ctenomyidae         | 1                                 |
| Cuniculidae         | 15                                |
| Dasyproctidae       | 136                               |
| Echimyidae          | 66                                |
| Gliridae            | 1                                 |
| Heteromyidae        | 116                               |
| Hystriidae          | 9                                 |
| Muridae             | 180                               |
| Nesomyidae          | 44                                |
| Octodontidae        | 1                                 |
| Platacanthomyidae   | 2                                 |
| Sciuridae           | 214                               |
| Spalacidae          | 1                                 |

the database. Synzoochorous insects were principally ants (Table 2). Note that we are only considering granivorous ants that disperse non-myrmecochorous seeds (seeds without elaiosomes). It is important to note that plants dispersed by harvester ants are probably dispersed both through synzoochory and dyszoochory simultaneously. Ants were not the only insects that dispersed seeds synzoochorously; beetles and crickets are also active caching animals (Table 2). The larvae of some species of carabids accumulate grass seeds in their burrow (Kirk, 1972), while some crickets have been observed caching seeds of trees and grasses (Blank & Bell, 1982; Sidhu & Datta, 2015). Birds, mostly corvids, were the third most important group of synzoochorous dispersers, moving seeds of 12% of plant species. Land crabs, mostly from the family Gecarcinidae, also hoard

Table 3. Number of plant species dispersed by each group of hoarding animal during each phase of the dispersal process. Primary dispersal is when the animal moves seeds directly from the plant or from the ground directly beneath the mother plant. Secondary dispersal is when the animal moves seeds that were primarily dispersed biotically or abiotically. Diplosynzoochory occurs when a seed is moved sequentially by more than one synzoochorous disperser. The number of plant species in which more than one type of disperser provided either primary or secondary dispersal is also included

|                    | Primary dispersal | Secondary dispersal | Diplosynzoochory |
|--------------------|-------------------|---------------------|------------------|
| Land crab          | 0                 | 45                  | 0                |
| Insect             | 259               | 192                 | 19               |
| Bird               | 46                | 25                  | 0                |
| Marsupial          | 2                 | 14                  | 0                |
| Rodent             | 142               | 484                 | 17               |
| Rodent + Land crab | 0                 | 16                  | 0                |
| Rodent + Insect    | 0                 | 6                   | 4                |
| Rodent + Bird      | 22                | 3                   | 41               |

seeds and may contribute to effective seed dispersal. Finally, we found evidence of synzoochory by marsupials, although this evidence was very scarce. In fact, as far as we know, only one species of rat-kangaroo, *Hypsiprymnodon moschatus*, has been observed hoarding 13 species of seeds (Dennis, 2003), and two species of bettongs, *Bettongia penicillata* and *B. lesueur*, have been observed in the wild caching seeds of four plant species, *Santalum spicatum*, *S. acuminatum*, *Acacia acuminata* and *Gastrolobium microcarpum* (Murphy *et al.*, 2015; Chapman, 2015). Furthermore, it is known that the mountain pygmy possum *Burramys parvus* caches seeds in captivity (Kerle, 1984), but no information exists about this behaviour in the wild (Smith & Broome, 1992).

The caching behaviour, and its implications for the effectiveness of seed dispersal, varies among the different groups of dispersers. Ants, granivorous carabids and land crabs are mostly larder hoarders that take the seeds to their burrows and nests, storing them in large quantities before consuming them (Hartke, Drummond & Liebman, 1998; Steinberger, Leschner & Shmida, 1991; Whittaker, Partomihardjo & Riswan, 1995; Honek, Martinkova & Jarosik, 2003; Fall, Drezner & Franklin, 2007; Bulot, Provost & Dutoit, 2016). Some seeds are forgotten within nests or in the middens surrounding them and can germinate and recruit new individuals. Some rodents are also larder hoarders. Rats of the genus *Rattus* carry many (up to thousands) seeds and other food to sheltered husking stations to eat them there (Campbell *et al.*, 1984; McConkey *et al.*, 2003; Dennis *et al.*, 2005). Other rodents, such as the Indian giant squirrel *Ratufa indica*, make larder hoards in arboreal nests (Somanathan, Mali & Borges, 2007). Among birds, the acorn woodpecker *Melanerpes formicivorus* stores a large number of acorns in granaries in tree trunks (Koenig & Mumme, 1987). In all of these cases, although it is likely rare to extremely rare, there is the potential for some seeds

to survive, germinate, and emerge as seedlings. By contrast, corvids and many rodents are scatter hoarders, burying the seeds in small, scattered caches (Bossemma, 1979; Gómez, 2003; Pesendorfer *et al.*, 2016; Lichti, Steele & Swihart, 2017). It is widely acknowledged that scatter-hoarding species are much more effective as dispersers than larder-hoarding species (Vander Wall, 1990; Vander Wall & Beck, 2012; Pesendorfer *et al.*, 2016).

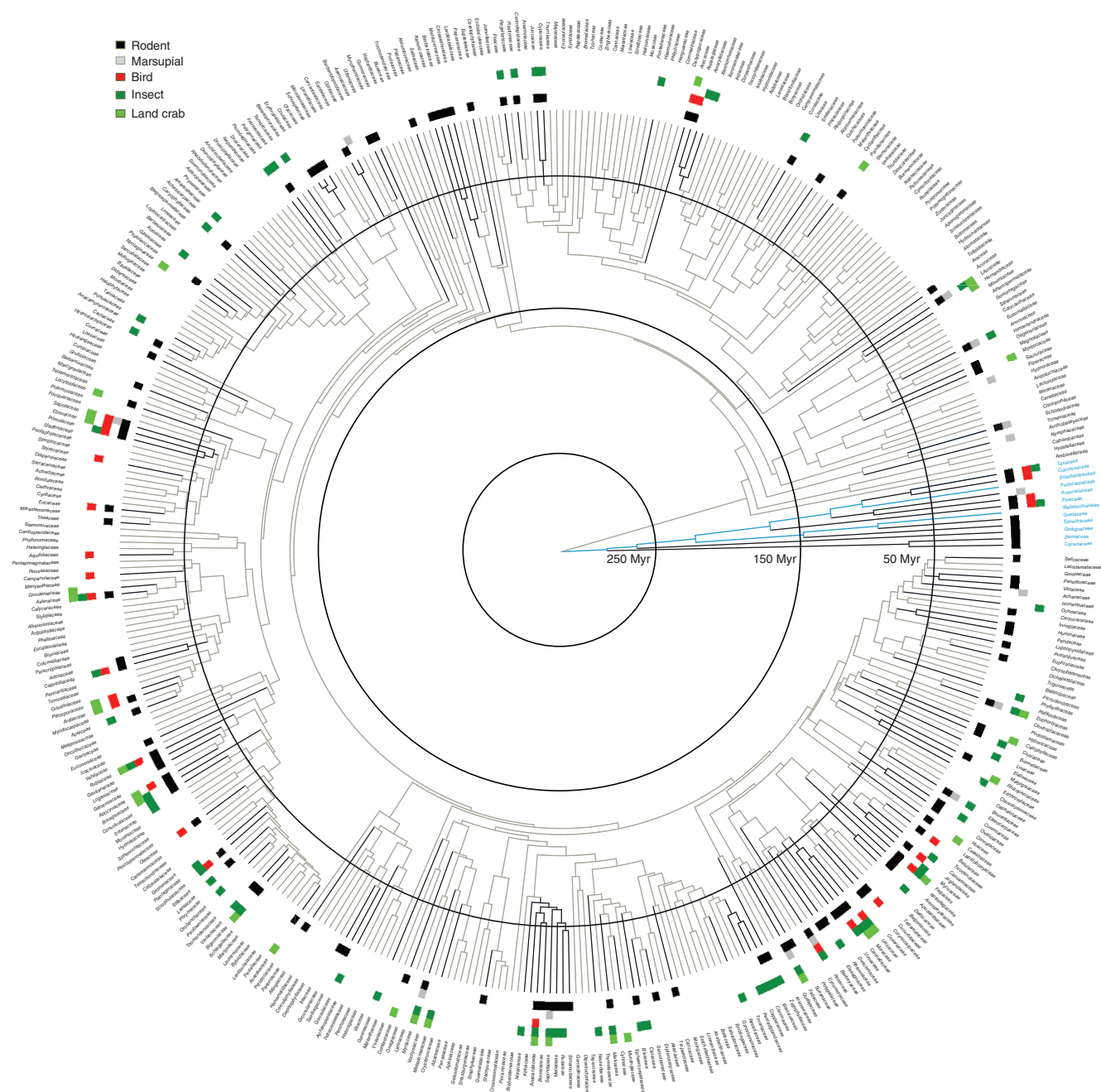
In general, plants with records of synzoochorous dispersal were dispersed almost exclusively by a single group of dispersers (Table 3), although the prevalence of this pattern may be due in part to incomplete data. In addition, when more than one disperser group dispersed a plant species, the combinations of groups were not randomly assembled. In all cases when two different dispersers interacted with the same plant species, one was a rodent (Table 3). Remarkably, rodents also dispersed about 50% of the plants dispersed by birds. We suspect that with more complete data this proportion would be even larger.

#### (4) Phylogenetic distribution of synzoochory

A further feature that makes synzoochory a potentially important process in natural systems is its phylogenetic spread. When mapping the presence of synzoochory onto a fossil-calibrated phylogeny of seed plant families (Harris & Davies, 2016), this dispersal mode, rather than being circumscribed to a distinct part of the land plant phylogeny, is widely scattered and present in most plant lineages (Fig. 2). It seems that synzoochory has evolved multiple times during the evolution of land plants, a pattern shared with other dispersal modes such as myrmecochory (Lengyel *et al.*, 2010). An indirect way to explore this idea is to look for the phylogenetic signal of synzoochory, a way of testing whether a given trait is randomly distributed across the phylogeny, supporting the idea of multiple origins, or evolved following a Brownian distribution, suggesting that the trait is perfectly phylogenetically conserved and supporting the idea of just a few origins followed by subsequent diversification. We found an intermediate situation. There was some phylogenetic structure because the phylogenetic signal of all disperser groups except insects departed significantly from that expected under a random distribution (i.e. from  $D = 1$ ; Table 4). At the same time, the distribution of synzoochorous dispersal was not totally phylogenetically conserved for any of the disperser groups (Table 4). Thus, it appears that the evolution of synzoochory has been labile; although having some phylogenetic structure, it has appeared multiple times and among clades of variable ages throughout the evolutionary history of land plants.

The evolutionary history of synzoochory has been discussed previously. For example, Vander Wall (2001) suggests that synzoochorous nuts evolved both from wind-dispersed and frugivore-dispersed plants. Our phylogenetic analysis suggests that, irrespective of the type of dispersal transition underlying the evolution of synzoochory, this dispersal mode is potentially very ancient, since some lineages in which synzoochory occurs are very old, more than 250 million





**Fig. 2.** Phylogenetic relationships of the plant families where synzoochory has been reported at least in one species ( $N = 1339$  plant species, 157 plant families). Tree calibration according to Harris & Davies (2016). Green = angiosperms; Blue = gymnosperms. Myr, million years.

years (Fig. 2). Interestingly, the synzoochorous animal dispersers are much younger than this. Rodents appear to have originated during the Paleocene, approximately 92 million years ago (Mya) (Asher *et al.*, 2005; Bininda-Emonds *et al.*, 2007), much more recently than the appearance of their host plants. The oscine passerines, the group to which the corvids belong, originated about 53 Mya (Ericson *et al.*, 2002, 2005; Ericson & Johansson, 2003), although Fernando, Peterson & Shou-Hsien (2017) show that Corvidae likely originated

more recently in the late Miocene, 8.0–5.9 Mya. These are all much more recent than the likely origin of synzoochory according to our phylogeny. The situation is different for hoarding invertebrates. Ants likely originated in the Late Jurassic or Early Cretaceous, about 100 Mya, whereas the subfamily Myrmecinae, to which most synzoochorous ants belong, probably appeared during the Late Cretaceous, 90 Mya (Barden, 2017). In fact, there are fossils of *Messor*, a ant genus with many hoarding species, from deposits dating

Table 4. Phylogenetic signal of each disperser group. The phylogenetic signal was tested using the parameter  $D$  (Fritz & Purvis, 2010) performed in the R package ‘caper’ v.0.5.2 (Orme, 2018).  $D = 0$  indicates a phylogenetically conserved trait;  $D = 1$  indicates that the trait is randomly distributed across the phylogeny. The R script used to perform this analysis, written in R v.3.1.0, is provided as Appendix S2

|           | $D$ values | $P$ values departing from |         |
|-----------|------------|---------------------------|---------|
|           |            | $D = 1$                   | $D = 0$ |
| Rodent    | 0.737      | 0.002                     | 0.000   |
| Bird      | 0.525      | 0.001                     | 0.069   |
| Insect    | 0.868      | 0.124                     | 0.000   |
| Land crab | 0.667      | 0.020                     | 0.011   |

to 34 Mya (Barden, 2017). Likewise, carabid beetles belonging to the granivorous tribe Harpalinae appeared during the Cretaceous between 92 and 153 Mya (Ober & Heider, 2010). A similar situation is seen for land crabs; Gecarcinidae, the most frequently synzoochorous crab family, appeared during the middle Eocene or even earlier during the Late Cretaceous (Brösing, 2008; Tsang *et al.*, 2014). This palaeontological evidence suggests three possibilities: (i) synzoochory was carried out exclusively by invertebrates during early geological periods; (ii) other now-extinct vertebrates, perhaps including the multituberculates (Vander Wall, 2001), cached seeds before the origin of present-day caching rodents and birds; or (iii) synzoochory has appeared more recently in old lineages. This latter possibility suggests that perhaps synzoochory did not evolve *per se*, but rather arose as accidental interactions that occurred spontaneously when the right animal traits met the right plant traits. Nonetheless, once synzoochory arose, it appears that in at least some of these interactions both the animals and the plants have evolved traits to increase the benefits and decrease the drawbacks of the interaction (Vander Wall, 2001).

#### (5) Geographical and ecological distribution of synzoochory

Synzoochory has been reported in all terrestrial biogeographic realms except Antarctica (Fig. 3). It has been reported in most parts of the planet, from South and North America to Europe, South Africa and tropical Africa, the Far East, Australia and many oceanic islands (Fig. 3). Clearly, synzoochory occurs all over the world rather than being restricted to or dominant in only one or a few regions. In this respect, it is similar to endozoochory, which also occurs in most biomes (Jordano, 2013), but it is more widely distributed than myrmecochory, a dispersal mode with about 90% of the plant participants found in Australia and South Africa (Rico-Gray & Oliveira, 2007). Nevertheless, from Fig. 3 some potential gaps are clear. For example, there is a dearth of information on synzoochory in most of the African continent and Central Asia. This could be due to true rarity of synzoochory in these regions or more likely to a lack of research effort (see Yadok *et al.*, 2018).

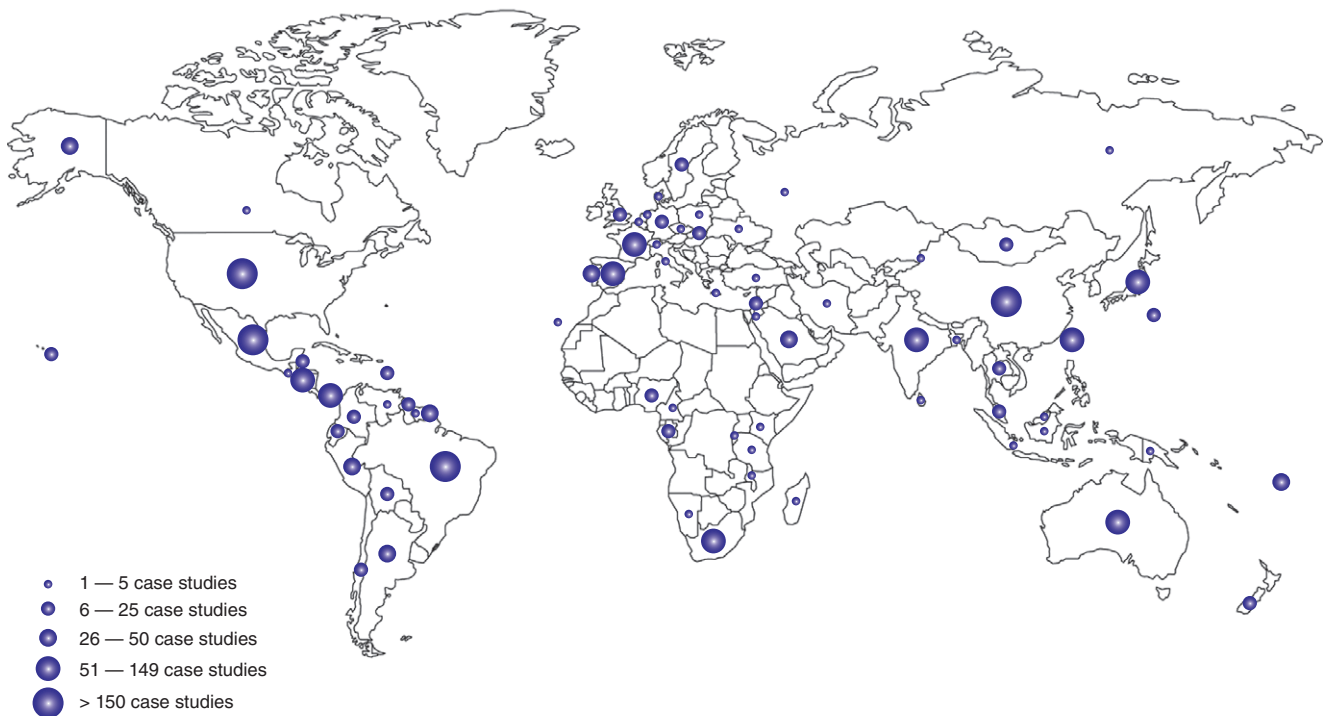
Likewise, synzoochory seems to be present in a wide variety of habitats. For example, synzoochory is frequently observed in tropical habitats, where agoutis, giant rats and similar rodents disperse many tree species (Forget, Milleron & Feer, 1998; Forget & Vander Wall, 2001). In fact, about 50% of the synzoochorous plants included in our database inhabit tropical environments, mostly species of palms and fabaceous trees and shrubs. This does not necessarily mean that synzoochory is the major dispersal type in the tropics. To determine this, it will be necessary to calculate the proportion of plant species actually dispersed by synzoochory in different tropical communities, something that is beyond the scope of the present study. Synzoochory has been also extensively reported in oaks, beeches, and walnut trees in temperate and mediterranean forests from Europe, North America, Central Asia, and the Far East (Den Ouden, Jansen & Smit, 2005; Purves *et al.*, 2007; Lei, Shen & Yi, 2012; Pesendorfer *et al.*, 2016). In many of these forests, nut-bearing trees are a major component of the plant community, and consequently synzoochory is probably the most important dispersal mechanisms in the dynamics and structure of these communities. Dispersal by hoarding animals is also common in arid and semi-arid systems. In these environments, the plants most frequently dispersed by synzoochory are small-seeded shrubs and grasses, and the main synzoochorous dispersers seem to be rodents and ants (Giannoni *et al.*, 2001; Beck & Vander Wall, 2010; Arnan *et al.*, 2012; Vander Wall & Beck, 2012).

### III. THE ECOLOGICAL RELEVANCE OF SYNZOOCHORY

#### (1) Synzoochory as primary or secondary dispersal

Seed dispersal is a multi-step process; in many cases seeds are moved repeatedly and sequentially from the mother plant to the final position where they germinate and recruit (Chambers & MacMahon, 1994). Seed dispersal may sometimes comprise two neatly differentiated phases: primary dispersal and secondary dispersal (Vander Wall & Longland, 2004). Primary dispersal is when the animal moves seeds directly from the plant or from the ground directly beneath the mother plant. Secondary dispersal is when the animal moves seeds that were primarily dispersed biotically (endozoochorously, epizoochorously, etc.) or abiotically (by wind, water, etc.).

Synzoochory appears to be primarily a secondary dispersal mode. In fact, almost 65% of the plant species included in our database were secondarily dispersed through synzoochory (Table 3). Thus, synzoochory is widely considered a mechanism contributing to the redistribution of seeds that were primarily dispersed by other biotic agents or by abiotic processes (Vander Wall *et al.*, 2005b; Beck & Vander Wall, 2011; Arnan *et al.*, 2012; Jansen *et al.*, 2012). Secondary dispersal is the most important service provided by land crabs and rodents (Table 3). These



**Fig. 3.** Geographic distribution of reported cases of synzoochory ( $N = 2223$  case studies).

animals tend to harvest seeds from the soil, in faeces, in regurgitated pellets or even underground (Enders & Vander Wall, 2012). In addition, these two types of dispersers act frequently as secondary dispersers of the same plant species (Table 3).

Nonetheless, synzoochory is also a relevant mode of primary dispersal. We found that more than 550 species of plants in our database (about 40% of the plants) were primarily dispersed by synzoochory. In most cases of primary dispersal, caching animals tend to harvest the seeds directly from the plant. This behaviour is very common in well-known caching animals such as corvids (Bossemma, 1979; Lanner, 1996), tree squirrels (Moller, 1983; Viljoen, 1983) and, to a lesser extent, harvester ants (Bulot, Provost & Dutoit, 2016). We presume that many plant species dispersed by harvester ants are both primarily and secondarily dispersed by these insects. More information on these synzoochorous dispersers is required before we can comment on the importance of primary *versus* secondary dispersal in these systems. However, primary dispersal also occurs after the seeds have detached from the parent plant. In these cases animals move seeds that have fallen directly beneath the canopies of the parent plants that otherwise would remain undispersed (Schupp *et al.*, 2010). This behaviour has been documented in several rodents, such as woodmice (Gómez *et al.*, 2008) and agouties (Jansen *et al.*, 2002), as well as in some tropical ants (Lima, Oliveira & Silveira, 2013), and it is probably more common than previously thought. Interestingly, although the diversity of plant species primarily dispersed by synzoochory may be lower than the diversity of secondarily dispersed species, their abundance and geographic distribution can be similar

or even higher. For example, Vander Wall & Moore (2016) and Vander Wall *et al.* (2017) found that, in North America, the abundance of plants primarily dispersed by synzoochory was twofold the abundance of plants secondarily dispersed by synzoochory. This was mostly because the main components of many North-American plant communities are oaks and other nut-bearing trees, such as pinyon pines, beeches and walnuts. We presume that a similar situation occurs in Europe and temperate Asia, where nut-bearing trees dominate most forests. Thus the synzoochorous seed-dispersal mode will be central to the life histories and natural regeneration of tree species that dominate some biomes (e.g. temperate and boreal forests, some tropical rainforests), with a potential role as foundation species (Ellison *et al.*, 2005) that have a central functional effect at the ecosystem level.

Sometimes the same hoarding animal species act as both the primary and secondary disperser. This phenomenon occurs for example when jays or tree squirrels pilfer and redistribute primary caches made by conspecifics (Vander Wall, 2000, 2002b; Emery & Clayton, 2001). In fact, intraspecific cache pilfering is not rare among scatter-hoarding rodents and corvids (Vander Wall, 2000, 2002b; Gerhardt, 2005), and may have influenced the foraging and caching behaviour of the dispersers and the spatial pattern and dispersal distance of cached seeds (Moore *et al.*, 2007; Sunyer *et al.*, 2013). Consequently, we presume that many nut-bearing trees are frequently dispersed both primarily and secondarily by the same species of rodents and birds.



## (2) Diplosynzoochory

Diplochory, or two-phase dispersal, occurs when a seed is moved sequentially by more than one dispersal mechanism or vector (Vander Wall & Longland, 2004). Six main types of diplochory have been identified: anemocory followed by synzoochory, ballochory followed by myrmecochory, and endozoochory followed by either dispersal by dung beetles, synzoochory, myrmecochory or endozoochory (Vander Wall & Longland, 2004; Nogales *et al.*, 2007; Padilla, González-Castro & Nogales, 2011; Hämäläinen *et al.*, 2017). However, diplochory can also emerge when two hoarding animals act as both primary and secondary dispersers of the same seed. That is, synzoochory by one species of disperser followed by synzoochory by a second disperser species. There is ample evidence of the existence of such diplosynzoochory in nature, although no formal description of this phenomenon has been proposed. In agreement with this empirical evidence, we found many species to be dispersed both primarily and secondarily by different types of synzoochorous animals (Table 3). Most of these species were oaks (32 spp.) and pines (9 spp.). These two genera are primarily dispersed either by jays or by tree squirrels and secondarily by ground-dwelling rodents such as heteromyids, murids or cricetids (Quintana-Ascencio, González-Espinosa & Ramírez-Marcial, 1992; Vander Wall, 2002b; Gómez, 2003; Hollander & Vander Wall, 2004; Gómez *et al.*, 2008). Diplosynzoochory will be frequent in plant species that are dispersed by different hoarding animals. Based on our current knowledge, we presume that diplosynzoochory will be the rule in most nut-bearing trees.

## (3) The quantity component of effectiveness in synzoochorous dispersal systems

An accurate understanding of the relevance of any ecological interaction requires estimation of the intensity of interaction among the interacting partners (Wootton & Emmerson, 2005). There are multiple, somewhat contrasting definitions and metrics of interaction intensity or strength (Paine, 1980; Wootton, 1997; Wootton & Emmerson, 2005; Bascompte, Melián & Sala, 2005; Bascompte, Jordano & Olesen, 2006; Schleuning *et al.*, 2011). In plant–disperser interactions, the intensity of interaction is usually quantified as the quantity component of seed-dispersal effectiveness, estimated as the proportion of the fruit crop removed by a given disperser (Schupp, 1993; Schupp, Jordano & Gómez, 2010, 2017). This metric denotes the relative frequency of interaction events maintained with that disperser and it is analogous to some *per capita* interaction strength metrics widely used in food-web studies (Wootton, 1997; Laska & Wootton, 1998). Because synzoochorous dispersers act as both seed predator and seed disperser, the most reliable estimate of the quantity component of synzoochory effectiveness will be the proportion of the seed yield that is harvested and dispersed by each species of hoarding animal, irrespective of its 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* (in the parent plant or in experimental seed stations) is not included in the computation of the interaction intensity, because no dispersal service has been provided.

We found information on the quantity component in 893 case studies. Pooling these studies, synzoochorous dispersers dispersed on average 52% of the seed crop. This magnitude was similar irrespective of the phase where synzoochory happened (primary = 50%; secondary = 52%), suggesting that in many species synzoochory is not a supplementary mechanism of moving seeds but is likely the main route by which plants disperse their seeds (Vander Wall & Beck, 2012). Nevertheless, caution is needed because often the proportion of seed removed was not estimated from direct observations of parent plants but rather from seed stations where seeds were generally concentrated at high densities, resulting in potential overestimation of removal rates. In addition, because secondary dispersal occurs once the seeds have been subject to primary dispersal, the interaction intensity at this phase is probably also overestimated. Nevertheless, we need to take into account that these estimates are derived from pairwise interactions (one plant – one disperser). In fact, these magnitudes are similar to the interaction intensity reported for other dispersal modes for the entire assemblage of dispersers. In endozoochorous systems, the proportion of fruit removed by assemblages of 5–25 frugivorous birds ranges between 46 and 100% depending on fruit traits (seed size, fruit size, pulp composition, etc.) (Herrera, 1984; Davidar & Morton, 1986; Jordano, 1995, 2013; Jordano & Schupp, 2000). A similar magnitude of interaction intensity (up to 50%) was found in myrmecochorous dispersal by ants removing elaiosome-bearing seeds in some sites in Australia (Hughes & Westoby 1990, 1992; Parr *et al.*, 2007). Thus, the intensity of interaction between synzoochorous plants and dispersers is similar to that found in other widely studied dispersal systems. Nevertheless, in synzoochory, the interaction intensity varies across dispersers (Table 5). The proportion of the seed crop dispersed by some taxa, such as nuthatches (Sittidae), woodpeckers (Picidae), tuco-tucos (Ctenomyidae), dung beetles (Scarabaeidae), and pacas (Cuniculidae), is relatively low, while the proportion of seeds dispersed by other animals, such as ants (Formicidae), ground beetles (Carabidae), land crabs, corvids, heteromyids, squirrels (Sciuridae), murids, agouties (Dasyproctidae) and bettongs (Potoroidae), is high (Table 5). These latter taxa are thus likely to have stronger ecological and evolutionary impacts on their interacting plant partners (Lanner, 1996; Wolff & Debussche, 1999; Hulme, 2002; Hulme & Kollmann, 2005).

## IV. THE CONSEQUENCES OF THE DUAL ROLE OF SYNZOOCHOROUS DISPERSERS

### (1) The absence of a specific synzoochory syndrome

Seed-dispersal syndromes are suites of traits adapted to specific dispersal modes and that have evolved in



Table 5. Quantity component (the proportion of seeds that is harvested and dispersed but not necessarily cached) of the interaction between synzoochorous plants and dispersers.

| Disperser         | <i>N</i>   | Quantity component $\pm 1$ S.E.   |
|-------------------|------------|-----------------------------------|
| <b>Insect</b>     | <b>111</b> | <b>0.41 <math>\pm</math> 0.03</b> |
| Carabidae         | 4          | 0.60 $\pm$ 0.04                   |
| Formicidae        | 89         | 0.38 $\pm$ 0.03                   |
| Gryllidae         | 16         | 0.58 $\pm$ 0.08                   |
| Scarabaeidae      | 2          | 0.11 $\pm$ 0                      |
| <b>Land crab</b>  | <b>33</b>  | <b>0.57 <math>\pm</math> 0.06</b> |
| Gecarcinidae      | 28         | 0.59 $\pm$ 0.07                   |
| Gecarcinucidae    | 1          | 0.63                              |
| Grapsidae         | 1          | 0.67                              |
| Ocypodidae        | 3          | 0.37 $\pm$ 0.14                   |
| <b>Bird</b>       | <b>53</b>  | <b>0.43 <math>\pm</math> 0.05</b> |
| Corvidae          | 39         | 0.48 $\pm$ 0.05                   |
| Paridae           | 7          | 0.24 $\pm$ 0.13                   |
| Picidae           | 1          | 0.08                              |
| Sittidae          | 3          | 0.02 $\pm$ 0.01                   |
| <b>Rodent</b>     | <b>694</b> | <b>0.53 <math>\pm</math> 0.01</b> |
| Caviidae          | 3          | 0.13 $\pm$ 0.03                   |
| Cricetidae        | 82         | 0.55 $\pm$ 0.04                   |
| Ctenomyidae       | 1          | 0.04                              |
| Cuniculidae       | 4          | 0.08 $\pm$ 0.07                   |
| Dasyproctidae     | 97         | 0.52 $\pm$ 0.03                   |
| Echimyidae        | 58         | 0.54 $\pm$ 0.03                   |
| Heteromyidae      | 60         | 0.71 $\pm$ 0.04                   |
| Hystriidae        | 8          | 0.50 $\pm$ 0.14                   |
| Muridae           | 189        | 0.56 $\pm$ 0.03                   |
| Nesomyidae        | 18         | 0.49 $\pm$ 0.08                   |
| Octodontidae      | 1          | 0.60                              |
| Platacanthomyidae | 1          | 0.10                              |
| Sciuridae         | 168        | 0.46 $\pm$ 0.03                   |
| <b>Marsupial</b>  | <b>2</b>   | <b>0.63 <math>\pm</math> 0.12</b> |
| Potoroidae        | 2          | 0.63 $\pm$ 0.12                   |

response to selection imposed by the dispersers (van der Pijl, 1982). In some cases, identifying the seed-dispersal syndrome is easy. For example, the myrmecochorous syndrome can be identified by the presence and chemical composition of elaiosomes (Gorb & Gorb, 2003), whereas the endozoochorous syndrome is traditionally identified by the presence of fleshy fruits (van der Pijl, 1982). However, the evidence supporting the existence of a genuine synzoochory syndrome based on one or several main adaptations is weak (Vander Wall & Beck, 2012). For example, although the presence of wingless seeds is widely associated with dispersal by synzoochory in pines (Lanner, 2000), synzoochorous dispersers also disperse winged pine nuts (Thayer & Vander Wall, 2005; Vander Wall, 2008). Similarly, seed coat and/or endocarp thickness has been claimed to be an adaptation to synzoochory. Although some synzoochorous dispersers do exert positive selection on this trait (Benkman, Balda & Smith, 1984; Siepielski & Benkman, 2008; Zhang & Zhang, 2008), others exert negative selection (Siepielski & Benkman, 2007, 2008), causing the emergence of conflicting selection. We presume that there is no clear synzoochory syndrome because the functional diversity of synzoochorous

dispersers is high and the selection regimes exerted by them vary in sign and are even conflicting in some systems (Howe & Smallwood, 1982). The fact that synzoochory is primarily a secondary dispersal mode (see Section III.1) means that other selective pressures, related to primary dispersal and probably pre-dating the selective pressures imposed by extant synzoochorous dispersers, may have played a more prominent role shaping plant traits for many synzoochorously dispersed species.

The trait most often considered in terms of synzoochory is seed size (Vander Wall & Moore, 2016; Vander Wall *et al.*, 2017). Many studies have explored the relationship between seed mass and interaction with caching animals (Brewer, 2001; Jansen *et al.*, 2002; Jansen, Bongers & Hemerik, 2004; Vander Wall, 2003; Gómez, 2004; Xiao, Zhang & Wang, 2005a; Forget *et al.*, 2007; Gómez *et al.*, 2008; Muñoz & Bonal 2008; Wang & Chen, 2009), generally finding that larger seeds are more frequently or more effectively dispersed than smaller ones (but see Yadok *et al.*, 2018), and hence suggesting that synzoochory may select for larger seeds (Galetti *et al.*, 2010). However, most of these studies were conducted on nut-bearing trees primarily dispersed by jays or large rodents, which represent only a restricted subset of synzoochorous seed dispersers. Vertebrates tend to move large seeds: the mean ( $\pm$  S.D.) seed mass in our database dispersed by birds and rodents was  $1580.1 \pm 312.7$  mg ( $N = 204$  species) and  $4464.5 \pm 381.7$  mg ( $N = 577$  species), respectively. However, given the high functional diversity of synzoochorous dispersers, many of which act as secondary dispersers, we should expect more than one optimum in seed size. For example, ants and other insects tend to disperse very small seeds (Kaspari, 1996; Lai *et al.*, 2018); the average size of seeds dispersed by insects in our database was  $3.6 \pm 0.4$  mg ( $N = 311$  species). Similarly, many rodents inhabiting arid environments hoard seeds of grasses (McAdoo *et al.*, 1983; McMurray, Jenkins & Longland, 1997; Borchert 2004; Sivy *et al.*, 2011). Large seed size has previously been attributed to selection by extinct endozoochorous megafauna (Janzen & Martin, 1982; Jansen *et al.*, 2012; Galetti *et al.*, 2018), suggesting that large seed size in some synzoochorously dispersed species could be an exaptation.

Lastly, a trait that might affect the size of synzoochorously dispersed seeds is the presence of cheek pouches in rodents or gular (= throat) pouches in birds. The presence of gular pouches was not related to the size of dispersed seeds in the sample of birds included in our data set ( $F = 0.51$ , d.f. = 2,120,  $P = 0.601$ ,  $N = 123$  plant species, one-way ANOVA), but corvids were the only group that included pouched birds. However, four rodent families (Cricetidae, Heteromyidae, Nesomyidae, Sciuridae) in our database have cheek pouches to collect and store seeds (Ryan, 1986). In addition, within Sciuridae, pouches are present only in ground squirrels (e.g. *Tamias*, *Eutamias*, *Ammospermophilus*, *Spermophilus* and *Sciurotamias*; Ryan, 1986). A comparison of seed sizes dispersed by rodent species with pouches against those dispersed by rodent species without pouches identified a significant difference ( $F = 15.88$ , d.f. = 2,628,  $P = 0.0001$ ,

$N = 631$  plant species, one-way ANOVA), with larger seeds being dispersed by pouchless rodents ( $4659 \pm 412$  mg) or by a combination of rodents with and without pouches ( $3903 \pm 733$  mg) than those dispersed exclusively by rodents with pouches ( $1229 \pm 300$  mg). To check that this was not due to differences in body mass across rodent groups, we repeated this analysis only for Sciuridae and controlled for body mass, but found the same pattern (data not shown). Whereas pouched rodents tend to move many small seeds of grasses and forbs, pouchless rodents often move individual large seeds such as acorns. Thus, it appears that the presence of cheek pouches allow rodents to forage energetically efficiently on small seeds.

In sum, there is no strong support for the suggestion that synzoochory is restricted to a narrow seed size range. Rather, the empirical evidence suggests that synzoochorous dispersal occurs for a wide range of seed sizes. It would be interesting to determine whether the diversity of seed sizes observed in synzoochorously dispersed plants is the result of multiple adaptive optima to synzoochory, i.e. that seed size is adapted not to a synzoochory syndrome but to specific synzoochorous dispersers. Thus, there could be separate syndromes of dispersal by corvids, by agouties, by squirrels, etc. However, the evolution of seed size will have been shaped in many synzoochorously dispersed plants not by their dispersers but by other biotic and abiotic agents, such as drought, shade, predispersal and postdispersal seed predators, seedling–seedling competition, and seed dormancy and germination timing (Westoby, Jurado & Leishman, 1992; Leishman & Westoby, 1994; Saverimuttu & Westoby, 1996; Bond, Honig & Maze, 1999; Gómez, 2004).

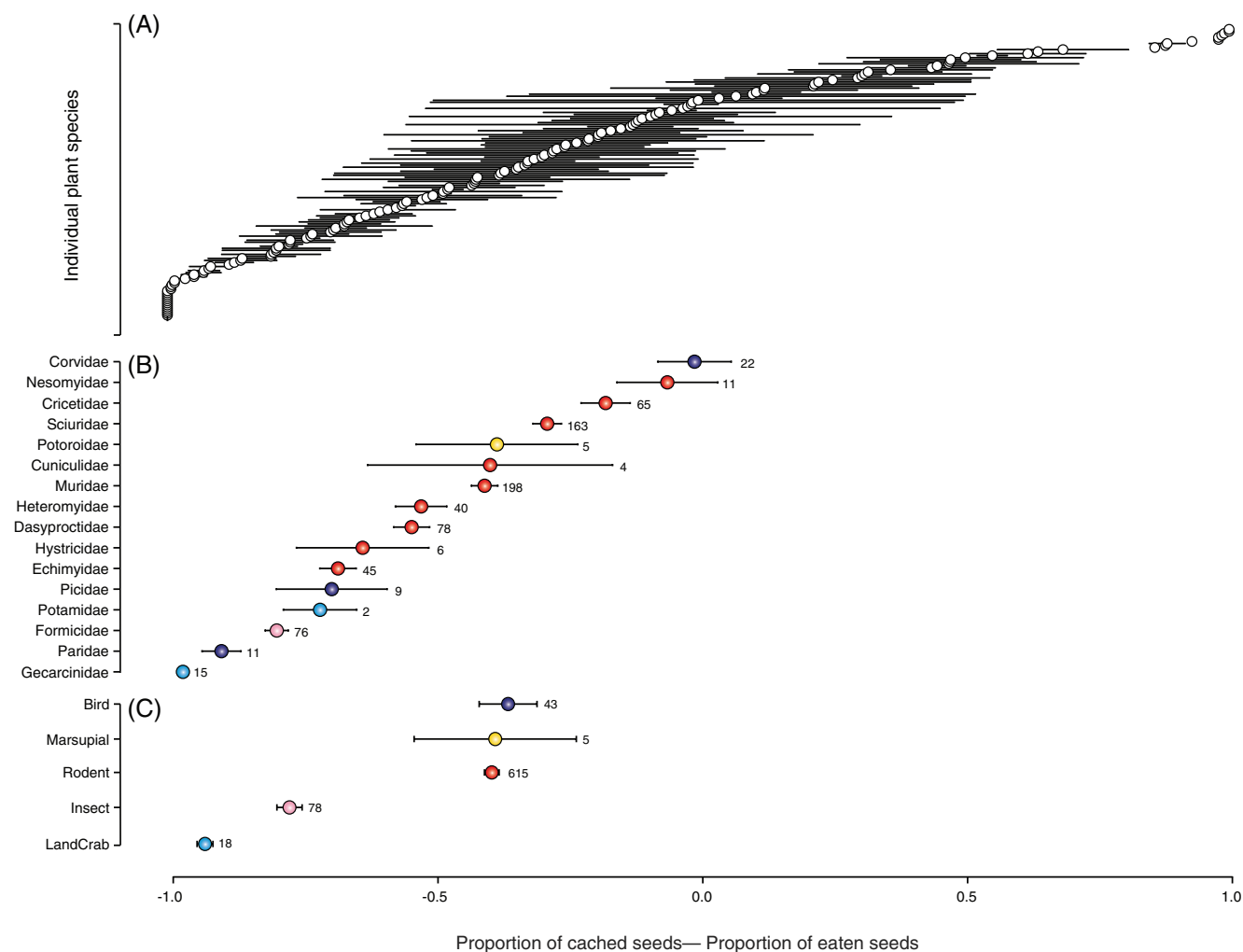
## (2) The mutualism–antagonism continuum in synzoochory

A distinctive feature of synzoochory is that the interacting animals have two direct and contrasting effects on the plant, one positive in terms of effective seed dispersal and the other negative in terms of seed predation (Hulme, 2002; Retana *et al.*, 2004; Theimer, 2005; Vander Wall & Beck, 2012). Thus, synzoochorous interactions are located along a mutualism–antagonism continuum. Unfortunately, there is no unified quantitative method available to establish the position that a given pairwise interaction occupies on that continuum [but see Zwolak & Crone (2012) and Sawaya *et al.* (2018)]. We propose that one way to identify this position is to calculate the proportion of interaction events with negative effects for the fitness of the plant relative to the proportion of events with positive effects. In the case of synzoochory, this is the proportion of seeds consumed either *in situ* or after dispersal but before caching (negative fitness effect) *versus* the proportion of seeds that are dispersed and cached (positive fitness effect).

Following this approach, we can plot the position of each pairwise interaction along a line representing the normalized difference in the proportion of interaction events with positive fitness effects (dispersal and caching of seeds) minus the

proportion of interaction events with negative fitness effects (seed predation). For example, Fig. 1 shows where each potential Holm oak disperser species is located on this  $-1.0$  to  $+1.0$  gradient. Figure 4 presents results for all studies in our database that included appropriate information. It is notable that few pairwise interactions appear near either the positive or negative extremes, with most values being intermediate along the continuum (Fig. 4A). When grouping by different types of caching animals, interaction events tend to be more negative in invertebrates than in vertebrates (Fig. 4C). Within rodents, there is also extensive variation in the proportion of positive *versus* negative interaction events. For cricetids, nesomyids and sciurids interactions tended to have relatively higher (less negative) values, whereas values for Neotropical spiny rats (echimyids) and porcupines (hystricids) were more negative (Fig. 4B). Thus the former group of rodents perhaps function more effectively as seed dispersers, whereas the latter group behaves mostly as seed predators. It is important to acknowledge that the net effect of any hoarding animal on its host plant can be beneficial or detrimental not only as a consequence of its position along this continuum but also as a function of the difference in population recruitment of that plant with and without the animal (Jansen & Forget, 2001; Zwolak & Crone, 2012; Elwood *et al.*, 2018). Consequently, any synzoochorous interaction will be located along a positive–negative continuum irrespective of its net outcome on the host–plant population.

Exactly where different pairwise interactions are located on this continuum will depend on variations in particular intrinsic and extrinsic factors characterizing the pair of interacting organisms (Hurly & Lourie, 1997; Theimer, 2005; Chang & Zhang, 2014). For example, the difference in size between seeds and granivores is one intrinsic factor determining the proportion of seeds cached *versus* consumed (Jansen *et al.*, 2002, 2004; Vander Wall, 2003; Gómez, 2004; Xiao, Zhang & Wang, 2005a; Forget *et al.*, 2007; Wang & Chen, 2009). Another important factor is related to the caching behaviour of granivores (Dally, Clayton & Emery, 2006). Seed chemistry may also affect the proportion eaten *versus* cached (Fleck & Woolfenden, 1997; Smallwood, Steele & Faeth, 2001; Wang & Chen, 2008). For example, high-tannin acorns are cached more often than low-tannin acorns (Xiao, Chang & Zhang, 2008; Xiao *et al.*, 2009) or survive partial consumption by granivores better (Steele *et al.*, 1993). Among extrinsic factors, the presence of competitors, potentially pilfering caches, influences the probability of a seed of being cached or eaten (Vander Wall, Hager & Kuhn, 2005a; Dally *et al.*, 2006; Dittel, Perea & Vander Wall, 2017). The presence of non-caching granivores may also influence the behaviour of hoarding granivores (Price & Mittler, 2006; Puerta-Piñero, Gómez & Schupp, 2010). For example, the proportion of *Quercus ilex* acorns cached by rodents is influenced by the presence of red deer *Cervus elaphus* (Muñoz & Bonal, 2007; Muñoz, Bonal & Díaz, 2009). The spatial structure of vegetation, both at local and landscape scales, may also determine the proportion of seeds cached *versus* eaten (Puerta-Piñero *et al.*, 2010; Yang & Yi, 2011;



**Fig. 4.** Locations of synzoochorous interactions on the mutualism–antagonism continuum as defined by the proportion of seeds that were dispersed and cached minus the proportion of seeds that were eaten *in situ* or after dispersal but before caching for (A) individual plant species ( $N = 142$  plant species, 442 case studies), (B) disperser families, and (C) major disperser taxonomic groups. Dots indicate mean values; lines indicate variation among dispersers interacting with the same plant species (A), or among plant species interacting with the same disperser family (B) or major taxonomic group (C). Numbers beside dots indicate the number of plant species interacting with each type of disperser.

Puerta-Piñero, Pino & Gómez, 2012b; Castro *et al.*, 2012; Morán-López *et al.*, 2015a,b; Aliyu *et al.*, 2018). For example, the proportion of seed effectively dispersed by Eurasian jays is significantly influenced by the presence of pine woodlands and afforestation (Rolando, 1998; Gómez, 2003; Pons & Pausas, 2007b; Sheffer *et al.*, 2013; Pesendorfer *et al.*, 2016). In summary, the variable effect of granivores on plant fitness is not only context-dependent but also depends on intrinsic features of the interacting organisms.

## V. PROSPECTS

Synzoochory is an abundant and widespread dispersal mode that should be included when studying the relationships between animals and seeds. Due to the dual nature of

this interaction, synzoochory should be considered not only by ecologists interested in mutualistic interactions and ecological networks but also by those working on antagonistic interactions and food-web dynamics. Considering synzoochorous interactions between granivorous animals and plants will provide a more accurate perspective on the functioning of natural systems (Elwood *et al.*, 2018).

To understand fully the importance of synzoochory in nature, it is necessary to determine accurately the net outcome of synzoochorous interactions. This requires the conceptual and methodological unification of two separate ecological subdisciplines: dispersal ecology and seed-predation ecology. Future experiments designed to quantify seed loss to seed predators should take into consideration the possibility that some removed seeds are actually effectively dispersed rather than eaten (O'Rourke

*et al.*, 2006; Alignier *et al.*, 2008; van Blerk, West & Midgely, 2017). It is convenient to assume, as most studies on seed predation do, that all seeds removed are consumed (Westerman *et al.*, 2006), but this may not be true. Taking this into account will require changes to the way ecological experiments are performed and analysed. For example, when offering seeds at feeding stations to granivores, seed fate should be tracked beyond removal from the station, to establish that the seed is actually consumed rather than being cached or dropped (Forget & Wenny, 2005; Xiao, Jansen & Zhang, 2006a; Hirsch, Kays & Jansen, 2012; Sidhu & Datta, 2015; van Blerk *et al.*, 2017). Although this will undoubtedly make experiments more laborious, it will provide precious information on the real nature of seed–animal interactions.

An important gap in the study of synzoochory is related to our ignorance about how effective this dispersal mode is. Although a practical framework for evaluating seed-dispersal effectiveness has been developed (Schupp, 1993; Schupp *et al.*, 2010, 2017), it is applied only infrequently to synzoochory studies (but see, for example, Hollander & Vander Wall, 2004). In addition, very few studies collect data on seed fate past the seed-caching stage, a very early stage in recruitment for evaluating the true effectiveness of dispersal. Consequently, we know little about the impact of synzoochory relative to other dispersal modes (endozoochory, myrmecochory, anemochory, etc.) on plant fitness and population dynamics (Hulme, 1998, 2002; Jansen & Forget, 2001; Vander Wall & Longland, 2004; Pesendorfer *et al.*, 2016; Elwood *et al.*, 2018), as well as on community structure and mutualistic network topology and architecture (Donatti *et al.*, 2011). Filling this gap will not only improve our understanding of natural systems but will also have enormous value for developing appropriate conservation and restoration strategies (Pons & Pausas, 2008; Puerta-Piñero *et al.*, 2012a; Pesendorfer *et al.*, 2016).

A sizeable number of the pairwise interactions considered herein involved large-seeded plant species and large-bodied mammal and bird species. Recent empirical evidence shows that these large-seeded plants and megafauna are being particularly affected by drivers of global change such as deforestation, defaunation, forest fragmentation, overhunting, etc. (Barnosky *et al.*, 2012; Dirzo *et al.*, 2014), leading to ecosystems with reduced ecological function (e.g. significantly reduced C-storage potential of defaunated forests due to lack of recruitment of large-seeded hardwood species) (Bello *et al.*, 2015). Several tree taxa with synzoochorous adaptations are dominant foundation species in their ecosystems, and their dispersers are megafauna with unique ecological roles. Losing these synzoochorous interactions would thus represent a serious threat to the persistence of temperate and tropical forest ecosystems.

## VI. CONCLUSIONS

(1) Synzoochorous dispersal is carried out by seed-caching seed predators. This type of dispersal differs from most other

animal-mediated dispersal modes because the animal partner in this plant–animal interaction plays a dual role, acting as both seed disperser and seed predator. In contrast to other dispersal modes, synzoochory is a dispersal mode in which the dispersers, rather than being attracted to a secondary trait, are directly attracted to the seed itself: the seed is the reward.

(2) The ecology of synzoochory has been studied mostly in systems involving large-seeded plants and scatter-hoarding rodents and corvids. However, synzoochory occurs in most types of plants, from trees to herbs bearing both large and small seeds, and among angiosperm and gymnosperm lineages (Fig. 2). It is likely that this mode of dispersal has evolved multiple times and that in some plant lineages might be a very ancient way of dispersing seeds. Synzoochory is probably far more common than we have been able to document. Many studies on seed predation have probably overlooked the occurrence of synzoochorous dispersal.

(3) Synzoochory is performed by a variety of granivorous animals, from vertebrates such as rodents and birds to invertebrates such as insects and land crabs. All share a common feature – they cache a proportion of the seeds that they harvest. However, they differ in the intensity with which they interact with the plant. Some animals, such as squirrels and corvids, disperse a relatively high proportion of the seeds that they find, whereas others, such as nuthatches and rats, disperse only a small fraction of seeds and tend to eat most seeds *in situ* (Table 5).

(4) The high frequency of synzoochory probably reflects the opportunistic nature of this interaction and the absence of specialized structures associated with the dispersal event. While myrmecochory requires the presence of elaisomes, endozoochory by frugivores generally requires the presence of fleshy pulps and epizoochory is greatly facilitated by external structures such as hooks or sticky substances, synzoochory occurs without any apparent specialized adaptation. In this type of dispersal, the seed itself is the dispersal structure, and any seed can potentially be transported and cached by caching granivores given appropriate ecological conditions.

(5) Synzoochory may be both a primary and a secondary dispersal mode. Primary synzoochorous dispersers are mostly corvids, some types of rodents and ants, whereas other types of rodents, land crabs and some insects are the main secondary dispersers (Table 3). Synzoochory sometimes occurs during both phases of the dispersal process. This diplosynzoochory is especially likely when the primary disperser is a corvid or a squirrel and the secondary disperser is a ground-dwelling rodent.

(6) Perhaps the most distinctive feature of synzoochory is the dual role that most hoarders play as seed predator and effective seed disperser. These pairwise interactions can be located along a mutualism–antagonism continuum. Pairwise synzoochorous interactions are widely spread along this continuum.



(7) Synzoochory is not an anecdotal ecological interaction; it is pivotal to the functioning of many forest ecosystems where the natural regeneration of keystone large-seeded plant species crucially depends on the persistence of animal species that are under serious threat due to forest loss, overhunting and other human activities. Conservation efforts should aim to preserve not only the participant species, but also the conditions supporting their functional interactions.

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## IX. SUPPORTING INFORMATION

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

**Appendix S1.** Supplementary data set.

**Appendix S2.** R script for phylogenetic signal.

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