

## Meta-analysis

### Ants as diaspore removers of non-myrmecochorous plants: a meta-analysis



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Diaspore (e.g. seeds, fruits) dispersal is pivotal for plant communities and often involves several steps and different dispersing agents. Most studies focusing on diaspore dispersal by animals have highlighted the role of vertebrates, neglecting the role of ants in the diaspore dispersal of non-myrmecochorous plants. Diaspore dispersal by ants is especially relevant in the current scenario of declining of vertebrate populations and, consequently, collapse of the dispersal system of large-seeded plants. Although ants can never compensate for the dispersal service provided by vertebrates, they can mitigate the impact of vertebrate decline via removal of diaspores deposited on the ground. We have used a meta-analytical approach to investigate the contribution of ants in the removal of non-myrmecochorous diaspores (through vertebrate exclusion experiments). We considered the number of diaspore removal as effect size and factors such as plant growth forms, diaspore and ant size, habitat type as moderators. In addition, we investigated the role of such factors on the diaspore removal distance by ants. Ants played complementary role to non-myrmecochorous diaspore removal services provided by vertebrates (mean *Hedges' g* of  $-0.30$ ). The ant diaspore removal was 69% higher for diaspores from shrubs than that of tree diaspores and removal of small-sized diaspores were 69% and 70% higher in comparison to medium- and large-sized diaspores, respectively. Regarding the diaspore removal distance by ants, those of tree species were removed 32% farther than those of shrub species, and diaspores were removed three- times farther in the savanna than in rainforest ecosystems. Our results highlight the shrubs and small-sized diaspores. Regarding the diaspore removal distance, the ants can be crucial for the dispersal of tree diaspores and in the savanna ecosystems. Finally, considering the biodiversity crisis, the ants may play an even more important role than appreciated in diaspores dispersal.

Keywords: ant–plant interactions, defaunation, diplocory, mutualism, seed dispersal, effectiveness

Our study is the first review (meta-analysis) to describe the global role of ants on removal of non-myrmecochorous seeds. Overall, we have found at least 13 ant genera removing 48 plant species across 12 countries. Our results highlight the ability of ants to remove more shrubs and small-sized diaspores. Regarding the diaspore removal distance, the ants can be crucial for the dispersal of tree diaspores and in the savanna ecosystems. Finally, considering the biodiversity crisis, the ants may play an even more important role than appreciated in diaspores dispersal.



## Introduction

Diaspore (e.g. seeds, fruits) dispersal is an important and advantageous ecological service for plant communities that often involves several steps and disperser agents: abiotic (e.g. water, wind, ballistic) and biotic (e.g. vertebrates and invertebrates) (Fenner and Thompson 2005). Most of seeds and fruits of angiosperms are dispersed primarily by vertebrates (Howe and Smallwood 1982, Jordano 2000). Human activities have had particularly negative direct and indirect effects on the population of large frugivorous vertebrates (Dirzo et al. 2014, Ripple et al. 2015, Rey et al. 2017). Such negative influences have culminated in the local extinction of many vertebrate dispersers that may lead to the collapse of some specific dispersal systems, especially those involving plant species with large diaspores (Galetti et al. 2006, 2015, Pérez-Méndez et al. 2016). However, the consequences of the vertebrate dispersers decline to the small-diaspore species remain unknown. This group of plant species represents most angiosperms (Moles et al. 2005) and, although diaspores can be primarily dispersed by vertebrates, most of diaspore dispersal outcome rely on the secondary dispersal services provided by non-vertebrate dispersers, mainly ants (Pizo and Oliveira 2001, Christianini and Oliveira 2009, 2010, Magalhães et al. 2018). These invertebrates are highly resilient to habitat disturbance (Anjos et al. 2017, Oliveira et al. 2017, Andersen 2018) and, because of it, can exert disproportional effect on the demography of plant species occurring in vertebrate-free habitats. Therefore, understanding more about the role of invertebrates as secondary disperser in vertebrate-free conditions seems to be an important step to improve our knowledge about the functioning of seed dispersal in human-depauperated habitats.

In plants that are dispersed primarily by vertebrates (non-myrmecochorous plants), the diaspores can be dispersed in two main stages (i.e. diplocory). The first is promoted by vertebrate dispersers (e.g. mammals and birds) and often results in density-dependent diaspore escape and decreased seedling mortality away from the parental plant (Vander Wall and Longland 2005). The second stage of dispersal is promoted by other dispersers including ants, dung beetles, crickets or even vertebrates (Santana et al. 2016, Braga et al. 2017, Griffiths et al. 2017, Carvalho et al. 2020), and occurs after diaspores have fallen to the ground as a result of fruit manipulation by vertebrate dispersers or simply by natural fall (Christianini and Oliveira 2010). The second stage usually results in subtle movement that beget in diaspore escape from predation and the direct deposition of diaspores in microsites favorable for germination and establishment (Vander Wall and Longland 2005).

Ants have been pointed as the main group of invertebrates secondarily removing diaspores in several ecosystems (Christianini and Oliveira 2009, 2010, Griffiths et al. 2017, Magalhães et al. 2018). Despite the great importance of ants on diaspore removal, most studies have neglected their contribution to diaspore dispersal in comparison to vertebrates (Fenner and Thompson 2005). In addition, most of

focus has been devoted to the role of ants on the dispersal of myrmecochorous species (i.e. plants with seed bearing lipid-rich appendages called elaiosome, adapted for seed dispersal by ants; see Beattie, 1985) (Rico-Gray and Oliveira 2007). Someone can argue that such neglecting can come from the recognized ant's potential of acting as predator of non-myrmecochorous diaspores (MacMahon et al. 2000). However, studies focusing on the post-dispersal diaspore fate have shown that seed survival is more frequent than seed predation following secondary diaspore removal (Vander Wall et al. 2005). Additionally, there are many evidences indicating that a considerable percentage (largely variable among plant species) of non-myrmecochorous diaspores removed by ants tend to find a favorable microsite, with low mortality rates and high germination rates (Levey and Byrne 1993, Vander Wall and Longland 2005, Christianini et al. 2007, Christianini and Oliveira 2009). Therefore, secondary diaspore dispersal by ants can be so important as the primary dispersal in patterning plant communities.

Overall, the ants can benefit plants on diaspore dispersal in many ways such as by the number of diaspores removed, diaspore removal distance and diaspore fate (Giladi 2006, Leal et al. 2015, Griffiths et al. 2017, Fernandes et al. 2019). However, the magnitude of these benefits is conditioned by several factors, both biotic and abiotic (Manzaneda et al. 2009, Gallegos et al. 2014, Guerra et al. 2018, Magalhães et al. 2018). We can highlight four main factors that can directly affect the number of diaspores removed by ants, which include ant body size, diaspore size, plant growth form and habitat features. In tropical environments, small-bodied ants are the ones responsible by the largest number of diaspores removed, while large-bodied ants remove a lower quantity of diaspores (Leal et al. 2014b, Pizo and Oliveira 2001). Therefore, it is expected that ants are responsible for larger quantity of diaspores removed in locations in which small-bodied ants are the main disperser species (Pizo and Oliveira 2001, Anjos et al. 2018). Regarding the diaspore size, our expectation is the opposite. In general, due to morphological limitations, small diaspores are more likely to be removed by ants than medium- and large-sized diaspores (Pizo and Oliveira 2001, Anjos et al. 2018). Aside from diaspore size, other plant traits such as plant growth forms also influence the quantity of diaspores removed by ants. Shrub diaspores, for instance, should be more frequently removed by ants than tree diaspores, since shrub diaspores tend to be smaller than the those of trees and can be more easily manipulated and, therefore, removed (Pizo and Oliveira 2001, Anjos et al. 2018). Finally, it is expected that ants remove larger numbers of diaspores in drier ecosystems (e.g. savanna and Mediterranean) than in wetter ones (e.g. rainforests), due to the greater activity of the ants in the former ecosystems related to a greater ease of locomotion on the ground (e.g. less litter) (Leal et al. 2007, Leal et al. 2014b, Christianini and Oliveira 2009).

Aside from the number of diaspores removed, the distance of diaspore removal is one of the main factors modulating seed dispersal effectiveness (Schupp et al. 2010). Farther diaspores

are removed by ants, can result in increased probability that they will germinate and establish successfully (Andersen 1988, Fernandes et al. 2019), increasing an ant's contribution to plant colonization dynamics, subpopulation persistence and spreading (Gallegos et al. 2014, Pascov et al. 2015). The main factors affecting distance of diaspore removal by ants seems to be the same affecting the quantity of diaspores removed, but with slightly different magnitude and direction. Large-bodied ants are expected to remove diaspores for longer distances than small-bodied ones (Pizo and Oliveira 2001, Leal et al. 2014b). Similarly, small diaspores, or most of the diaspores of shrubs, also tend to be removed farther than large or tree's diaspores (Gómez and Espadaler 2013). In addition, due to the higher activity of ant species and to the habitat conditions (e.g. amount of litter), diaspores tend to be removed to greater distances in drier rather than wet ecosystems (Gómez and Espadaler 2013). Finally, the diaspore removal distance transported by ant workers is influenced by the density and distribution of ant nests (Andersen 1988). In the rainforest, for instance, where the ant nest density is higher than dry ecosystems, fallen diaspores are more likely to be near to an ant nest and then can be displaced for shorter distances than in dry ecosystems (Gómez and Espadaler 1998).

Here, we investigate the relative role of ants on diaspore removal of non-myrmecochorous plants and postulate some factors that can modulate the contribution of ants to this process in scenarios in which vertebrate contribution to seed removal is compromised. Therefore, we used a meta-analytical approach comprised of gathering information from

published papers evaluating secondary diaspore removal of non-myrmecochorous plants using exclusion experiments in which the vertebrate's access to the diaspores was not allowed (Fig. 1a). In addition to the evaluation of the general effect of vertebrate exclusion on the number of diaspores removed, we also evaluated whether the diaspore removal services provided by ants in the absence of vertebrates is modulated by 1) plant growth form, 2) diaspore size, 3) ant body size and 4) ecosystem type. We hypothesized that the complementary effect of ants is stronger 1) for shrub than tree diaspores, 2) for smaller diaspores than for the bigger ones, 3) for diaspores removed by small ants than for the larger ants and 4) in drier (e.g. savanna and Mediterranean) than in wetter ecosystems (e.g. rainforest). Finally, we also evaluated some factors expected to modulate the effectiveness of diaspore removal by ants using diaspore removal distance as a component of seed dispersal effectiveness. We hypothesized that 5) tree diaspores would be removed over shorter distances in comparison to shrub diaspores and that 6) the diaspores in rainforest (wetter ecosystems) would be removed over shorter distances than those of the savanna (drier ecosystems).

## Material and methods

### Data collection and inclusion criteria

We searched for papers in ISI Web of Knowledge (<www.isiknowledge.com>), Scopus (<www.scopus.com>), subject

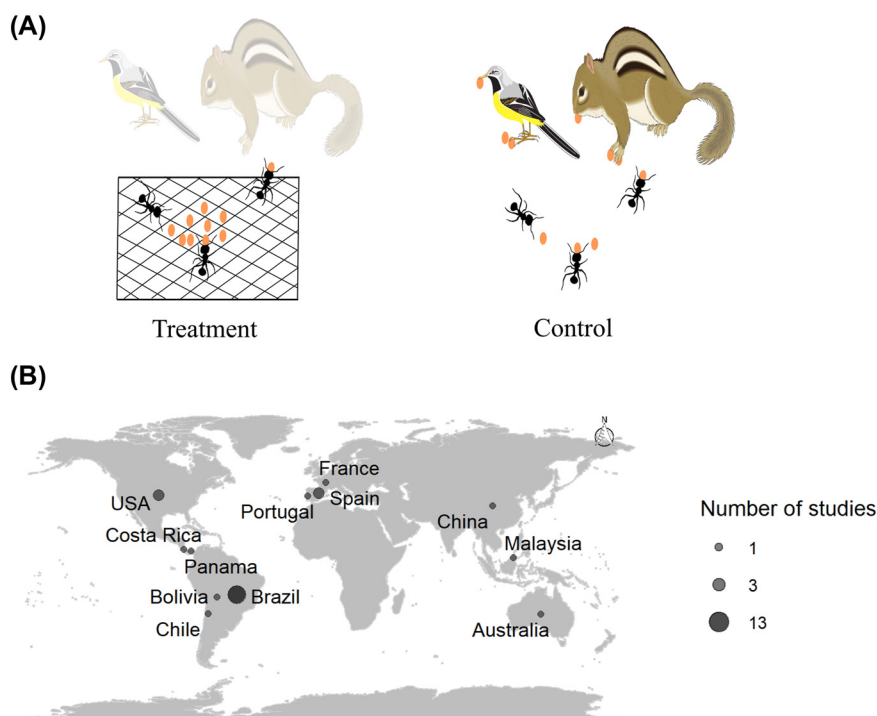


Figure 1. (A) Experimental design included in the analysis evaluating diaspore removal rates. On the left, the treatment group (ants only) is shown, with vertebrate exclusion that was accomplished through the use of experimental cages. On the right, the control group (vertebrates + ants) is shown without cages. (B) Global distribution of the number of studies per country included in the analysis.

area: Life Sciences) and Google Scholar (<www.scholar.google.com>) databases using all available years up to January 2020. We used the following key terms in our search: 'ant seed remov\*' or 'ant secondary dispers\*'. Our initial search identified 180 studies that were potentially appropriate for our meta-analysis.

We screened the abstract and methods sections of the 180 identified studies for information meeting our inclusion criteria. We selected studies according to three criteria. Studies must have: 1) investigated ant and vertebrate removal using the intact and natural diaspores (seeds or fruits) of non-myrmecochorous plants; 2) experimentally evaluated the influence of ant diaspore removal by contrasting control groups (ants and vertebrates) with treatment groups in which the access of diaspores to vertebrates had been avoided through the use of an exclusion cage (only ants); 3) been conducted under field conditions. After applying our inclusion criteria, 28 studies from our initial search remained in our data set. These studies were performed in 26 different locations (12 countries) (Fig. 1b), used 48 plant species belonging to 32 botanical families and yielded 104 estimates of effect size for our analysis (Supplementary material Appendix 1 Fig. A1). Even though the number of studies is relatively low for meta-analysis purposes, the performance of our analysis was adequate, since we had more than 10 effect sizes for each moderator included in our models, as recommended by Harrell (2001) and Nakagawa et al. (2017). In addition, our analysis presented low level of heterogeneity (as reported in the Results section), which makes our results robust despite the relatively low number of effect sizes (Nakagawa et al. 2017). We used this data set for all analysis described below (see Supplementary material Appendix 1 Table A1 for a more detailed description of information in this data set).

### Data extraction and effect sizes

From each selected paper, we recorded the mean number of removed diaspores, the variance and the sample size of treatments in which diaspores were available to vertebrate and ants (control, hereafter) and in which vertebrates were experimentally excluded (treatment, hereafter). For studies in which authors used different densities of diaspores to estimate diaspore removal rates (Hulme 1997), we considered each value of diaspore removal rate as a different effect size in our analysis, since diaspore density can influence removal rate (Wandrag et al. 2013). We classified each study according to ecosystem type as savanna, Mediterranean or rainforest, following the individual criteria used by the authors to define the studied ecosystem. We also extracted from papers information about the mean diaspore size (length) of the model species used in each study. We used a diaspore size classification scheme adapted from Pizo and Oliveira (2001), considering more parsimonious classification system, in which ants can remove large diaspores, for instance. Moreover, Pizo and Oliveira (2001) based their diaspore size classes on only six plant species of the Brazilian Atlantic forest (Pizo and Oliveira 2000, Passos and Oliveira 2002). Therefore, we

classify diaspores as small when they were < 5 mm, medium if they were 5.1–9 mm and large when they were > 9.1 mm. In addition, we classified the plant species used in each study according to growth form (shrub or tree) following the individual criteria used by the authors of each study. When information about mean diaspore size and/or plant growth form was not available within original studies, we searched for such information in the available literature using the plant species name as keyword (57 effect sizes).

We used *Hedges' g* (J-corrected *Hedges' d*) as the metric of effect size for all analysis due to our small sample size (Borenstein et al. 2009). To calculate the *Hedges' g*, we used the treatment as a reference (only ants had access to diaspores), subtracting from it the mean values of the control group (vertebrates and ants had access to the diaspores). As small vertebrates (e.g. mice and birds) and ants are the major groups of secondary dispersers of diaspores (Griffiths et al. 2017), treatments in which vertebrates were excluded provide information regarding the service of diaspore removal offered by ants in situation in which vertebrates are absent. Therefore, positive values of *Hedges' g* occur when means from treatments in which vertebrates were excluded were higher than the ones from treatments in which vertebrates were allowed. It indicates a positive effect of vertebrate exclusion on the quantity of diaspores removed and, consequently, a higher level of contribution of ants to the total quantity of diaspores removed in the habitat. The opposite was true for negative values of *Hedges' g*. Negative values of *Hedges' g* indicate that the mean values from treatments in which vertebrates were excluded were lower than the means from treatments in which vertebrates were allowed. Consequently, it means that the contribution of ants to diaspore removal in the habitat is low. Finally, effect sizes near zero can be a result of two different situations in the original studies (Supplementary material Appendix 1 Table A2). The first situation is when both vertebrates and ants barely remove any diaspores offered in the studies. In these cases, mean values from the treatment (vertebrates excluded) and control groups would be similarly low, causing *Hedges' g* values to be close to zero. The second situation is when ants were the main responsible for the removal of diaspores on the ground regardless of vertebrate removal.

### Statistical analysis

We built meta-analytic random-effects models using the 'metafor' package (Viechtbauer 2010) on R software (<www.r-project.org>). We considered the *Hedges' g* as the response variable, the inverse of the variance associated with the *Hedges' g* as the weight. We also used the study identity and the plant family as random factors to control for pseudoreplication associated with more than one data gathered in the same study and potential plant phylogenetic effects on diaspore removal patterns, respectively. We considered that the overall effect size of vertebrate exclusion on diaspore removal (without moderators) was significantly different from zero if 95% confidential intervals (CI) did not include zero (Borenstein et al. 2009). Finally, we performed

three separate mixed effect meta-analysis with ecosystem type (savanna, Mediterranean or rainforest), plant growth form (shrub or trees) and diaspore size (small, medium or large) as moderators to investigate how these factors can modulate the effect size of ants on non-myrmecochorous diaspore removal. Because higher rates of the removal of shrub diaspores by ants can be related to the tendency of shrubs to produce smaller diaspores than trees (Leal et al. 2015), we tested whether shrub and tree plant species included in our data do indeed have diaspores of different sizes. When evaluating the effect of diaspore size on non-myrmecochorous diaspore removal, we did not consider the influence of ecosystem type, since we did not have sufficient numbers of effect sizes of large diaspores in Mediterranean ecosystems, for instance. However, we additionally tested whether diaspores from different ecosystem types were of different size. For the latter two analysis, we built generalized linear models (GLM) using a quasi-Poisson distribution on 'lme4' package (Bates et al. 2015) on R software (<www.r-project.org>).

Large-bodied ants are considered high-quality dispersers because they are able to remove diaspores for larger distances, increasing the chances of seed survival compared to the removal distance of the small-bodied ones (low-quality dispersers) (Christianini and Oliveira 2010, Gómez and Espadaler 2013, Leal et al. 2014b). Therefore, we used ant body size as a proxy for ant species quality as diaspore disperser. In each study, we considered the ant species removing diaspores at the highest frequency as the main disperser ant. Information regarding the frequency of diaspore removal by different ant species was only available in a subset of the studies used in the previous analysis (n=18 studies). We classified the main disperser ant in each study of this subset as large-bodied when they were > 5 mm and small-bodied when they were < 5 mm (Leal et al. 2014a). Since the studies considered did not report the body size of the disperser ants (body length), we gathered such information from original descriptions of ant species (or congeneric species) from descriptions within the taxonomic literature, or from regional taxonomic keys, if available. Thus, Myrmicinae ants (except *Aphaenogaster*, *Pogonomyrmex* and *Atta* genus) were classified as small-bodied ants and Ponerinae, Ectatomminae and Formicinae (*Cataglyphis velox*) (plus *Aphaenogaster*, *Pogonomyrmex* and *Atta* genus) were classified as large-bodied ants (Supplementary material Appendix 1 Table A1). Despite the huge variation in size among individuals in *Atta* species, the largest individuals are often the ones that remove diaspores in tropical environments (Kaspari 1996). Consequently, we classified *Atta* species as large-bodied ants. To evaluate how the effect of vertebrate exclusion on diaspore removal by ants can be modulated by the quality of the main disperser ant, we performed a mixed effect meta-analysis using ant size (small or large bodied) as a moderator, *Hedges' g* as a response variable and study identity and plant family as random factors.

We explored the possibility of publication bias graphically using funnel plots and statistically using Egger's regression test (Egger et al. 1997), modified according to Habel and Schultz (2015). In this test, we maintained the same structure

of the model evaluating the effect of vertebrate exclusion on the number of diaspores removed, but included the variances of *Hedges' g* as a moderator. If the intercept of the regression test significantly deviated from zero, the overall relationship between the effect size and its respective variance in each study is considered asymmetrical, and therefore, biased (Sterne and Egger 2005). Due to the recommendation of Egger et al. (2007), we based our evidence of publication asymmetries in  $p < 0.1$  since our dataset consists of a relatively small number of studies. Additionally, we estimated the effect size heterogeneity into the models using  $I^2$ . The  $I^2$  statistic describes the percentage of variation across studies due to data heterogeneity rather than chance (Higgins et al. 2003).

## Distance of diaspore removal

To describe the general characteristics of diaspore removal services provided by ants, we searched for the mean distance of the removal of diaspores by ants in the studies included in our dataset. In addition, we performed an additional search in the online databases using all available years up to and including January 2020, using 'distance AND diaspore AND ant' as the key terms. We selected studies that have 1) investigated diaspore removal by ants using intact and natural non-myrmecochorous diaspores; 2) measured the distance of diaspore removal by ants and that have 3) been conducted under field conditions. After searching the online databases, only two additional studies were included in the previous database and we were able to get 67 effect sizes regarding the mean removal distance of diaspores by ants in 13 studies. We classified the ecosystem type, plant growth form and the diaspore size from the model plant species used in each additional study following the same criteria described above. To evaluate the effect of ecosystem type and plant growth form on mean removal distance of diaspores, we built GLMM models with Gaussian distributions, using ecosystem type or plant growth form as fixed factors and study identity, diaspore size and plant family as random factors ('lme4' package: Bates et al. 2015). We included diaspore size (small, medium or large) as a random factors to control effects that diaspore traits may have on the mean removal distance of diaspores (Pizo and Oliveira 2001).

## Results

### Publication bias and heterogeneity

We found evidences for a publication bias in our dataset supported by both the funnel plot (Supplementary material Appendix 1 Fig. A2a) and the intercept of Egger's regression (intercept = -2.11; CI = -2.55 to -1.67;  $p < 0.01$ ). We observed a moderate level of heterogeneity in our model ( $I^2 = 64\%$ ) (Koricheva et al. 2013). We removed 11 potential outliers until we get an unbiased dataset according to Egger's regression model (intercept = -0.72; CI = -1.80 to 0.36;  $p = 0.19$ ; Supplementary material Appendix 1 Fig. A2b). After outlier's removal, we had 93 effect sizes from 25

different studies. Model heterogeneity was markedly reduced ( $I^2 = 32\%$ ) in this unbiased dataset, which produced a model with low level of heterogeneity (Koricheva et al. 2013). Below, we present all results regarding our unbiased dataset (93 effect sizes) that produced models with lower level of heterogeneity.

### Diaspore removal rate

Forty-three plant species from 29 families (6.3% of living angiosperm families) (APG 2003) had diaspores removed by ants within the selected studies. Melastomataceae was the most common plant family in the studies (eight *Miconia* species). Twenty-three effect sizes came from studies conducted in rainforest, 13 in Mediterranean and 55 in savanna ecosystems. For 40 effect sizes, plants were classified as shrubs and for 53 effect sizes, they were classified as trees. The number of effect sizes evaluating the removal of diaspores considered small, medium and large were 40, 36 and 16, respectively. Four effect sizes were conducted in ecosystems different than the ones we were focusing (e.g. temperate forest, subalpine forest). Also, we were not able to find information regarding the diaspore size of the plant species used in one study (e.g. *Solanum lycocarpum*). Therefore, we removed these effect sizes from the analysis regarding the ecosystem type and diaspore size, respectively (Supplementary material Appendix 1 Table A1). Overall, the studies considered here reported at least 13 ant genera acting as main dispersers. Ants of the genus *Pheidole*, *Cyphomyrmex*, *Atta* and *Aphaenogaster* were the most frequently observed ant species acting as main diaspore removers in the studies.

We found a mean Hedges'  $g$  value of  $-0.30$  ( $\pm 0.51$ , SD) which represents an intermediate negative effect of vertebrate exclusion on the quantity of diaspores removed ( $Z = -3.94$ ,  $p < 0.01$ , CI =  $-0.40$  to  $-0.13$ ; Fig. 2). The effect size of vertebrate exclusion on diaspore removal was 69% higher for shrub than tree diaspores (QM = 8.60, df = 1,  $p < 0.01$ ,  $n = 93$ ; Fig. 3a). Surprisingly, shrub and tree species had diaspores of similar size ( $F = 2.67$ ; df = 90;  $p = 0.10$ ; Supplementary material Appendix 1 Fig. A3) and diaspores from plants occurring in different ecosystems did not differ in size ( $F = 0.10$ ; df = 87;  $p = 0.89$ ; Supplementary material Appendix 1 Fig. A4). However, the effect size of vertebrate exclusion on the removal of small-sized diaspores was 69% and 70% higher in comparison to medium and large-sized diaspores, respectively (QM = 7.20, df = 2,  $p = 0.02$ ,  $n = 92$ ; Fig. 3b). The effect size of vertebrate exclusion on the quantity of diaspores removed was similar among the three types of ecosystems (QM = 0.06, df = 2,  $p = 0.96$ ,  $n = 89$ ). Finally, the effect size of vertebrate exclusion on the quantity of diaspores removed was not affected by the body size of the main ant species removing diaspores in each study (QM = 0.61, df = 1,  $p = 0.43$ ,  $n = 61$ ).

### Distance of diaspore removal

Regarding the distance of diaspore removal, we considered the savanna and rainforest ecosystem types. Since only one study was performed within the Mediterranean ecosystem, the study

was excluded from the analysis. Therefore, our analysis was focused on the Neotropical region. Ants removed diaspores, an average of 2.39 m ( $\pm 4.44$ , SD), with most of the removal events being shorter than 5 m (Fig. 4). Diaspores from tree species ( $n = 34$ ) were removed 32% farther than diaspores from shrub species ( $n = 32$ ) (analysis with  $\log + 1$  transformed data to improve model fit:  $\chi^2 = 5.80$ , df = 1,  $p = 0.01$ ; Fig. 5a). Likewise, diaspores in savanna ecosystems ( $n = 54$ ) were removed three-fold farther than diaspores removed in rainforest ecosystems ( $n = 12$ ) (analysis with  $\log + 1$  transformed data to improve model fit:  $\chi^2 = 5.29$ , df = 1,  $p = 0.02$ ; Fig. 5b).

### Discussion

Our results showed that exclusion of vertebrate dispersers had a negative impact on the quantity of diaspores removed. It means that ants have an intermediate contribution regarding the quantity of diaspores secondarily removed. Therefore, ants can only partially mitigate the impact of vertebrate exclusion on secondary diaspore removal in the habitats in which vertebrate populations are declining. This is in accordance with other studies suggesting that ants exert a complementary role in the removal of non-myrmecochorous diaspores in relation to diaspore removal services provided by vertebrates (Christianini and Oliveira 2010, Camargo et al. 2016). This complementary role seems to be more important with respect to the removal of shrub and of small-sized diaspores. Finally, ants removed diaspores from tree species and diaspores located in Neotropical savanna ecosystems at longer distances than shrubs diaspores and those of rainforest ecosystems, respectively, meaning that ants also seem to offer a relatively better dispersal service in such circumstances.

Although ants are considered one of the main secondary disperser agents, especially among invertebrates (Vander Wall and Longland 2005, Griffiths et al. 2017), our results show that their overall contribution as dispersers of non-myrmecochorous diaspores in quantitative terms is still lower than the contribution of vertebrate agents. Indeed, scatter-hoarding rodents and birds are known for removing large quantities of diaspores on the forest floor (Vander Wall and Longland 2005). For instance, in the Panama rainforest, agoutis buried more than half of all *Virola nobilis* (Myristicaceae) diaspores found in the fecal deposits of primary dispersers (Forget and Milleron 1991). Despite the relatively lower contribution of ants on dispersal of non-myrmecochorous diaspores than vertebrates, it is important to highlight that the quantity of diaspores removed by different disperser agents (quantitative term) is just one of the components used to access seed dispersal effectiveness (Schupp et al. 2010). The outcome of diaspore dispersal for the plants also depends on the quality of dispersal service provided by different disperser species (Vander Wall and Longland 2005, Schupp et al. 2010). If the most common diaspore removers are also granivore species, the quantity of diaspores removed in this habitat is far from being a faithful guide to assess the outcome of diaspore dispersal for the plants considered.

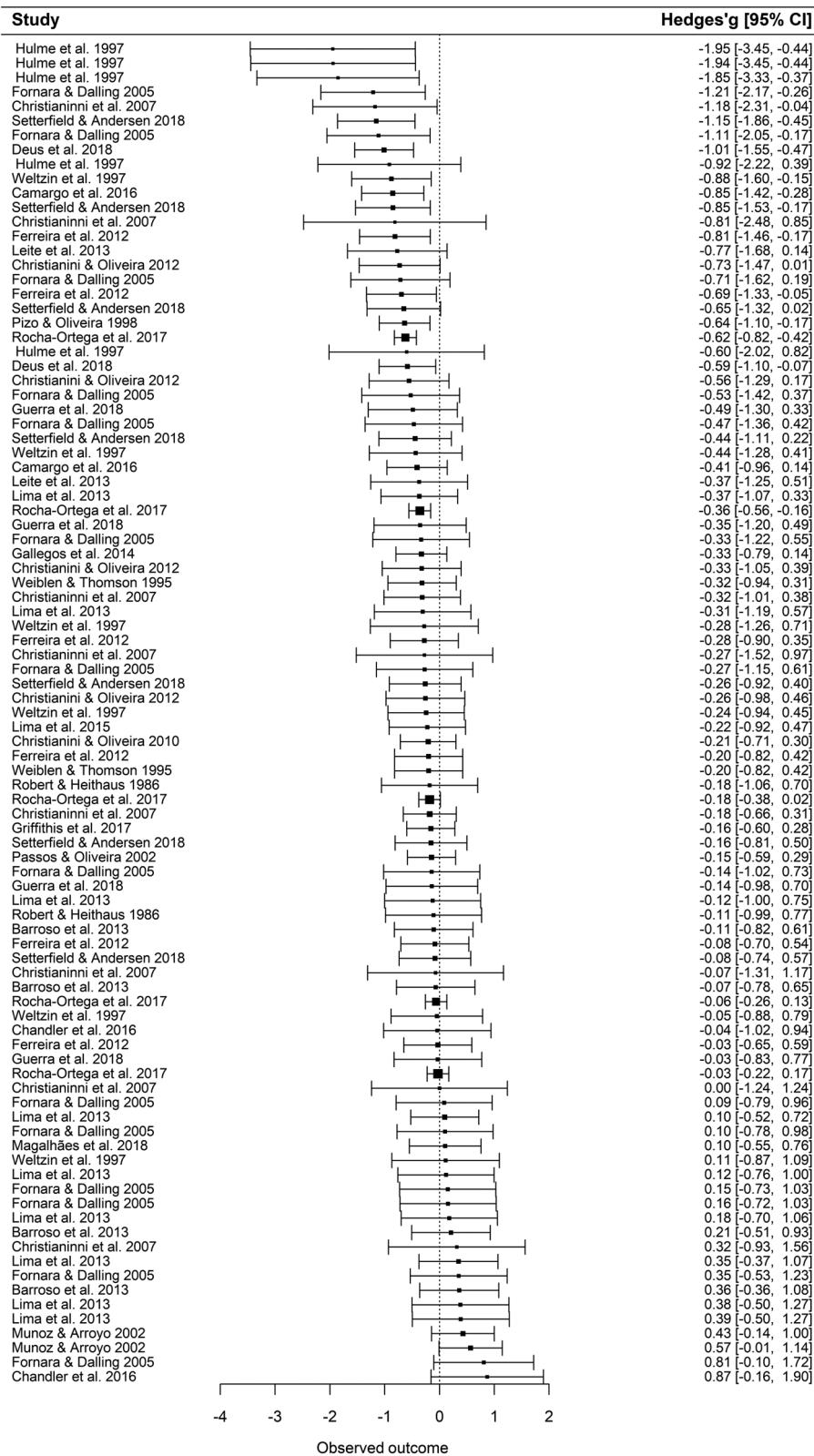


Figure 2. Effect of diaspore removal by ants through vertebrate exclusion experiments. Weighted-mean effect size (observed outcome) and 95% CI for diaspore removal by ants.

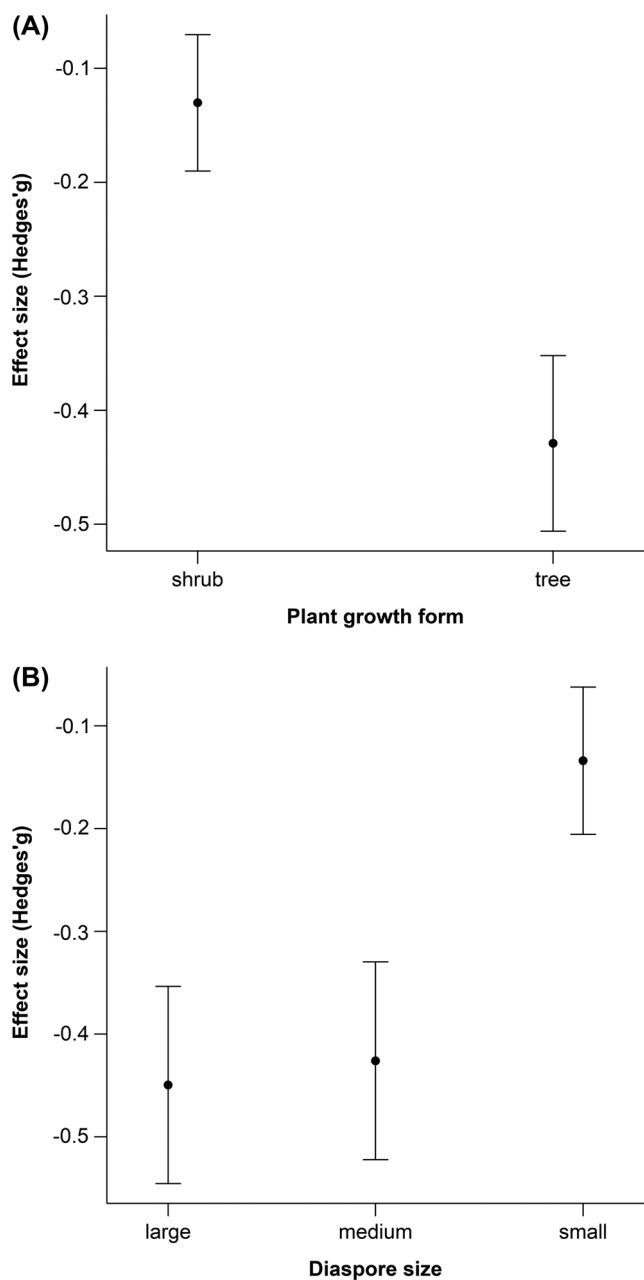


Figure 3. (A) Effect size of vertebrate exclusion in the diaspore removal by ants in relation to plant growth form ( $QM = 8.60$ ,  $df = 1$ ,  $p < 0.01$ ,  $n = 93$ ) and (B) diaspore size ( $QM = 7.20$ ,  $df = 2$ ,  $p = 0.02$ ,  $n = 92$ ). We classified the diaspores into three size classes adapted from Pizo and Oliveira (2001), which included small ( $< 5$  mm); medium (between 5.1 mm and 9 mm) and large ( $> 9.1$  mm). The filled circle shows the mean and bars represent the standard error.

Some ant groups, such as granivorous species, are more likely than others to prey on diaspores and ant predators are more effective dispersers (Pizo and Oliveira 2000, Christianini et al. 2007). Considering birds, corvids (Corvidae) are the main diaspore predators and the tit birds (Paridae) are the most important diaspore dispersers (Gómez et al. 2018). Likewise, regarding rodents, species of the family Nesomyidae and the

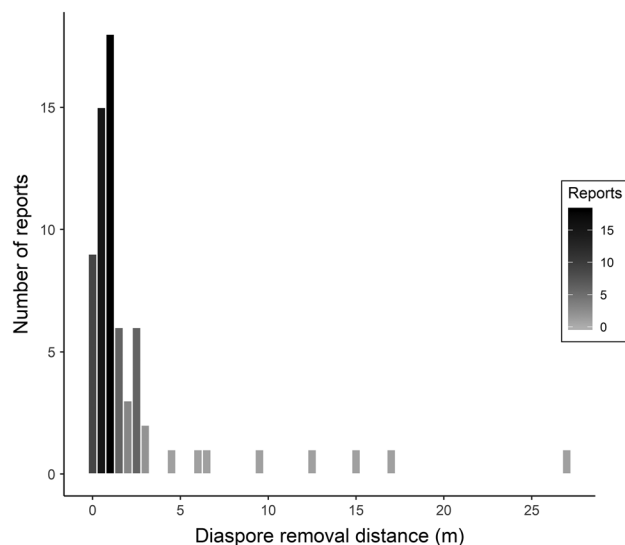


Figure 4. Diaspore removal curve generated by plotting the distance diaspores were displaced by ants in different effect sizes ( $n = 67$ ). The values along the x-axis represent the mean distance diaspores were removed.

spiny rats (Echimyidae) are the main predators and diaspore dispersers, respectively (Gómez et al. 2018). Among the ants, the species belonging to the genus *Messor* and *Pogonomyrmex* are mainly granivores, consuming most of the diaspores they remove (MacMahon et al. 2000). It is important to note that such ants represented were the main removing species in only 6.45% of our data set, not appearing in our dataset of seed removal distance. Although studies focusing on seed fate after secondary removal have shown that seed survival is more common than seed predation after removal (Vander Wall and Longland 2005), it seems important that future studies investigate the real fate of diaspores after the removal by different disperser agents in habitats in which vertebrates are endangered. If ants have an intermediate impact on the number of diaspore removal, but disproportionally benefit seed survival in relation to vertebrates, it means that plants can be actually benefiting from the decline of vertebrates in the anthropized habitats. This would be especially true for small and shrub diaspores, as effect size of vertebrate exclusion were higher for such plant groups. In the other hand, if ants predate a higher proportion of removed diaspores than vertebrate dispersers, plants are not only being prejudiced by reduction in the number of diaspores removed in vertebrate-free conditions, but also suffering with increasing rates of seed predation.

For disperser agents (e.g. monkeys, birds, rodents, ants, other invertebrates), diaspore size is an important factor influencing the outcome of interactions between plants and dispersers (Jordano 2000, Pizo and Oliveira 2001, Cramer et al. 2007, Braga et al. 2017, Anjos et al. 2018). Several studies have shown that small diaspores are more frequently removed by ants than large ones in tropical forests (Kaspari 1996, Pizo and Oliveira 2001, Marthews et al. 2008) and in savanna ecosystems (Anjos et al. 2018). Here, in a broader perspective (that also include Mediterranean ecosystems), we have found



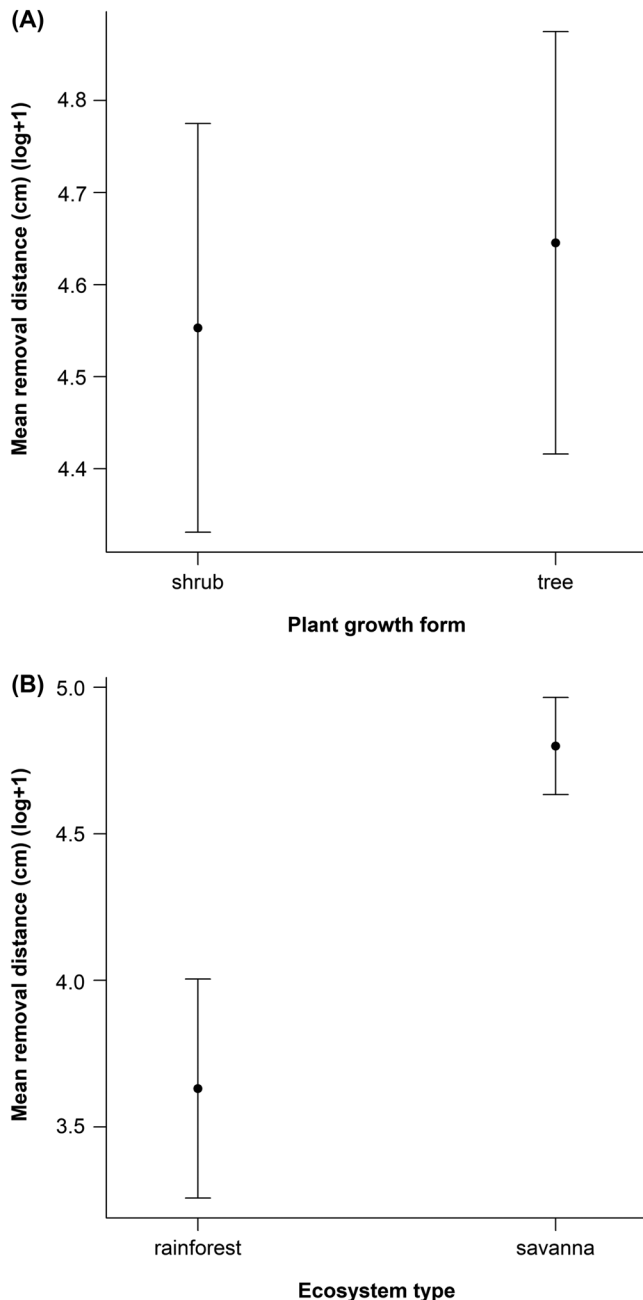


Figure 5. (A) Mean distance of diaspore (cm) by ants depending on the plant growth form and (B) ecosystem type. Data from our analysis has been shown as a log + 1 transformed to improve model fit. The filled circle represents the mean distance and the bars represent standard error.

that this pattern is consistent at a global scale. Nevertheless, small diaspores can contain lower energy rewards for ants compared to larger diaspores, but the ease of handling smaller resource favors the removal of larger amounts of smaller diaspores in relation to the larger ones (Hughes and Westoby 1992, Edwards et al. 2006). The removal of smaller diaspores may be crucial for habitat regeneration, since seedlings of small diaspores are more sensitive to the stresses associated

with seedling establishment (Leishman et al. 2000). Hence, it is possible that the secondary dispersal service provided by ants has higher relative values in disturbed habitats or in habitats under regeneration (Gallegos et al. 2014). In addition, diaspore size tends to be influenced by several factors such as plant growth form and the ecosystem type in which the plant species grown. For instance, it is expected that tree diaspores should be larger than the diaspores of shrubs (Salisbury 1974). Further, rainforest plants also tend to have larger diaspores than plants from drier ecosystems (Foster and Janson 1985). However, as we considered a subset of non-myrmecochorous plants, which have ‘small’ diaspores that can be removed by ants, differences in diaspore size were not influenced by these factors.

Shrub diaspores were more frequently removed by ants than tree diaspores. At least 57% of the evaluated shrub species are pioneer plants (e.g. *Miconia* and *Erythroxylum* genera) (Turner 1990, Dalling and Wirth 1998) that are likely to produce larger quantities of diaspores than tree species. Therefore, it is possible that such large quantities of diaspores deposited on the ground would attract more ants, resulting in higher rates of diaspore removal by ant species. Regardless the mechanism behind it, this pattern also seems to occur among myrmecochorous plants (even when diaspore size is controlled), which have a closer evolutionary relationship with ants (Leal et al. 2015). Therefore, ants can play a more important role in the dispersal of the diaspores of shrubs and small-diaspore plant species in general, than in the dispersal of tree and large-diaspore species, independently of whether plants are myrmecochorous or non-myrmecochorous. In addition, small-diaspore and those from shrubs have been favored in environments subject land use change (Castro et al. 2010), which may imply an increase in the importance of ants in diaspores dispersal and consequently in the recovery of this type of habitat.

Regarding the diaspore removal distance provided by ants, we found that the mean removal distance of non-myrmecochorous diaspores in ecosystems belonging to Neotropical region ( $2.39 \pm 4.44$  m, mean  $\pm$  SD) is similar to the global mean observed for myrmecochorous diaspores ( $2.24 \pm 7.19$  m; mean  $\pm$  SD) (Gómez and Espadaler 2013). However, contrary to our expectation, diaspores of tree species were removed at mean distances 32% larger than the mean distance shrub diaspores were removed. This result clearly contrasts with the patterns regarding distance of diaspore removal of myrmecochorous plants (Leal et al. 2015). Indeed, myrmecochorous dispersal has been seldom observed in tree species and such patterns have previously been explained by the decreased ability of ants in removing tree diaspores over distances long enough to reduce parental–offspring conflict for tree species (Leal et al. 2015). However, an important factor that needs to be considered when comparing myrmecochorous and non-myrmecochorous patterns of dispersal is the ant response to energetic rewards offered by non-myrmecochorous diaspores. In both plant groups, ant attraction to diaspores had been related to the lipid content of the attractive tissue attached to the diaspores (e.g. elaiosome, aril or pulp) (Christianini et al.

2007, Fischer et al. 2008, Reifenrath et al. 2012). Since shrub and tree species produced diaspores of similar size, it is possible that the removal of tree diaspores over longer distances than those of shrubs is not related to the size of the diaspores, but with variation in the quantity or quality of the energetic rewards for ants. If true, as higher the amount or quality of the energetic reward provided by the diaspores, farther the diaspores should be removed by the ants. Further research examining the chemical composition of diaspores will be necessary to evaluate this hypothesis.

Mean removal distance was also higher in the savanna than in rainforest Neotropical ecosystems. Importantly, these results can be biased by the methodological difficulty of estimating diaspore removal distance by ants in studies from wet ecosystems. In such ecosystems, soil is covered by a thick layer of litter that constrains researcher's ability to track diaspores removed by ants. However, it is also possible that such differences are biologically meaningful, especially because records of diaspores removal by ants over impressive distances in drier environments are not rare. For instance, Whitney (2002) studying *Acacia ligulata* (myrmecochorous plant), reported that diaspores were able to be removed by ants over 180 m in the Australian arid zone. Ants in these arid ecosystems (e.g. Australian savanna) have removed diaspores for longer distances than estimated elsewhere, being pivotal for diaspore dispersal of many myrmecochorous plant species (Pascov et al. 2015). Moreover, the mean removal distance by ants of non-myrmecochorous diaspores from Brazilian savanna 'Cerrado' (72% of the studies conducted in the savanna ecosystems in our dataset) is higher than mean global estimate for myrmecochorous plants (Gómez and Espadaler 2013). Likewise, in this recent global review, the mean removal distance in sclerophyllous habitats was almost two-fold higher than the removal by ants in mesophyllous habitats (Gómez and Espadaler 2013). It is possible that one of the mechanisms behind such a disproportional distance of diaspores removal in savanna ecosystems is due to the variation in the density of ant nests between different habitats (Gómez and Espadaler 1998) such as savanna and rainforest ecosystems. In savanna ecosystems, the density of ant nests is lower than in wetter ecosystems. This allows ants to explore larger foraging areas and carry diaspores longer distances back to their nests (Hölldobler and Wilson 1990).

Finally, our study is the first meta-analysis investigating the overall effect of ants on the functioning of the dispersal of non-myrmecochorous diaspores. Our results allow us to propose three general conclusions. The first is one regarding the functioning of ant-plant interactions. The second regards the functioning of dispersal systems in general and, the third one, regarding the role played by ants in patterns of secondary seed dispersal in vertebrate-free conditions. First, mechanisms acting behind the diaspore dispersal for myrmecochorous and non-myrmecochorous plants seem to be similar. Much of the quantitative and qualitative patterns of diaspore removal that we described here matched to the ones already described in revisions about myrmecochorous dispersal. Therefore, we believe that our understanding about the role of ants in the

dispersal of non-myrmecochorous diaspores can benefit more from these comparisons with myrmecochorous diaspore dispersal. Second, although we focused only on the role of ants as diaspore removers, our results can shed a new light on the functioning of diaspore dispersal in many ecosystems and the role of different disperser agents on it. Even with ants being pointed as the one of the most important diaspore removers in tropical environments (Griffiths et al. 2017), we showed that they are not able to quantitatively compensate for diaspore removal services provided by other animals in non-myrmecochorous plants. Taken together, these results suggest that, although different dispersal agents can benefit the dispersed diaspores locally, they can play different roles on the diaspore dispersal process that cannot be compensated by other agents. This led us to our third conclusion: ants are not alternative dispersers in anthropized habitats in which vertebrate populations are declining. However, small-sized diaspores and shrubs species can still benefit relatively more from ant services than large-diaspores and trees plant species. The magnitude of vertebrate exclusion on secondary dispersal, although, might depend on the ant effects on seed survival after the removal. Therefore, understanding more about the quality of dispersal services provided by different animals and its impact on diaspore fate after removal is a fruitful venue of investigation if we want to understand more about the future of anthropized habitats.

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Supplementary material (available online as Appendix oik-06940 at <[www.oikosjournal.org/appendix/oik-06940](http://www.oikosjournal.org/appendix/oik-06940)>). Appendix 1.