Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal

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Abstract

Anthropogenic habitat disturbance is a strong biodiversity change driver that compromises not only the species persistence but also the ecological interactions in which they are involved. Even though seed dispersal is a key interaction involved in the recruitment of many tree species and in consequence critical for biodiversity maintenance, studies assessing the effect of different anthropogenic disturbance drivers on this interaction have not been performed under a meta-analytical framework. We assessed the way habitat fragmentation and degradation processes affect species diversity (abundance and species richness) and interaction rates (i.e., fruit removal and visitation rates) of different groups of seed-disperser species at a global scale. We obtained 163 case studies from 37 articles. Results indicate that habitat degradation had a negative effect on seed-disperser animal diversity, whereas habitat fragmentation had a negative effect on interaction rates. Birds and insects were more sensitive in terms of their diversity, whereas mammals showed a negative effect on interaction rates. Regarding habitat, both fragmentation and degradation had a negative effect on seed-disperser animal diversity only in temperate habitats, and negative effects on interaction rates in tropical and temperate habitats. Our results indicate that the impact of human disturbance on seed-disperser species and interactions is not homogeneous. On the contrary, the magnitude of effects seems to be dependent on the type of disturbance, taxonomic group under assessment, and geographical region where the human impact occurs.

Keywords: bats, birds, habitat degradation, habitat fragmentation, insects, regeneration

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Introduction

Human-related habitat disturbance is one of the most important biodiversity change drivers worldwide (Chapin et al., 2000). Anthropogenic activities often involve habitat loss, fragmentation, degradation, and transformation processes that create heterogeneous human-dominated landscapes (McIntyre & Hobbs, 1999). While the consequences of habitat fragmentation (defined as the process that modifies habitat area, connectivity, and spatial arrangement, involving habitat loss) on biodiversity components are relatively well studied and attributable to area, edge, and isolation factors (Ewers & Didham, 2006; Didham et al., 2012; Magrach et al., 2014), the effects of habitat degradation (defined as the process that modifies habitat quality, making it less suitable or accessible to the resident species) are by far less studied (McIntyre & Hobbs, 1999; Fischer & Lindenmayer, 2007). Habitat degradation effects are less evident, especially when degradation interacts with habitat loss processes (e.g., Fontúrbel, 2012).

Habitat fragmentation and degradation processes coexist in many systems. On the one hand, habitat fragmentation is related to area reduction (usually related to habitat loss), edge effects, and increase in the isolation degree of the remaining habitat patches (McIntyre & Hobbs, 1999), which affect community composition and interactions, leading to simplified communities usually dominated by generalist and disturbance-tolerant species. On the other hand, habitat degradation is related to structural changes that may lead to simplified habitat textures (Fischer et al., 2008), which are usually related to changes in microhabitat conditions that are known to affect ecological interactions (Galetti et al., 2003).

Plant-animal interactions have a key role in the maintenance of biodiversity (Valiente-Banuet et al., 2014). In particular, frugivory and seed dispersal are important interactions as they are involved in seed establishment and plant recruitment (Gomes et al., 2008). At least 78% of the woody species in tropical and temperate forests depend on animal vectors for primary or secondary seed dispersal (Howe & Smallwood, 1982; Ollerton et al., 2007). However, habitat disturbance may disrupt disperser populations and seed
dispersal interactions, leading to reduced plant recruitment, small population size and increased risk of local extinction (Rodriguez-Cabal et al., 2007). There is abundant literature reporting the effects of habitat fragmentation on individual species (e.g., Lindenmayer et al., 1999; Rodriguez-Cabal et al., 2007; Lancaster et al., 2011; Boyle et al., 2012). A recent review examined the consequences of fragmentation and selective logging on seed dispersal, concluding that habitat fragmentation had weaker effects on animal-mediated seed dispersal than selective logging (Markl et al., 2012). Previously, Gray et al. (2007) reached a similar conclusion after examining the effects of habitat disturbance on bird foraging guilds. Even though these studies contributed substantially to our knowledge on this subject, extrapolating species-level effects to broad taxonomic categories and geographical regions is still a challenging task as many species may respond idiosyncratically depending on the type of disturbance and habitat (Vargas et al., 2012). To the best of our knowledge, no study has assessed the effects of habitat degradation (as defined above) on seed dispersal. In consequence, whether different seed-disperser animal groups differ in their response to habitat fragmentation and degradation remain largely unknown.

The aim of this study was to summarize, in a meta-analytic framework, the effects of habitat fragmentation and degradation on species diversity and interaction rates of birds, mammals (frugivores acting as primary dispersers), and insects (ants and dung beetles, acting as secondary dispersers), in an attempt to identify sensitive taxonomic groups, as well as potential regional (tropical or temperate) effects. More specifically, we aimed to answer the following questions: (i) Do seed-disperser animal diversity and interaction rates differ in their response to habitat fragmentation and habitat degradation? (ii) Do responses of seed-disperser animal diversity and interaction rates to habitat fragmentation and degradation differ between tropical and temperate regions?

Materials and methods

Literature survey and data inclusion criteria

We searched the available literature by topic, using the ISI Web of Science, Scopus, and Science Direct databases (January 1988–October 2014) using eight search terms: ‘frugivor* AND habitat fragm*’, ‘frugivor* AND habitat degrad*’, ‘frugivor* AND habitat transform*’, ‘frugivor* AND habitat disturbance’, ‘seed dispers* AND habitat fragm*’, ‘seed dispers* AND habitat degrad*’, ‘seed dispers* AND habitat transform*’, and ‘seed dispers* AND habitat disturbance’. Those eight search terms were selected to include both frugivory and seed-dispersal processes, as well as habitat disturbance and particularly habitat fragmentation, degradation, and transformation. We limited our search to peer-reviewed articles in English, excluding reviews and gray literature.

An initial search resulted in 1777 articles, which were reduced to 547 after filtering search results by research area (we included the following areas: ecology, biodiversity conservation, environmental sciences, zoology, ornithology, plant sciences, evolutionary biology, and forestry) and document type (articles only). From those 547 articles, we removed duplicate records resulting in a total of 421 articles (Fig. 1a); from those 17 were related to habitat degradation, 56 related to habitat disturbance (reporting fragmentation or degradation), two regarding habitat transformation (excluded from the analysis due to the low sample size), and 346 related to habitat fragmentation. We were able to access the full text of the 421 articles, which were read in full to determine their suitability for the analysis, from those, we excluded 202 articles for being not relevant or making no comparisons (Fig. 1b).

Then, we examined these articles looking for studies that met the following four criteria: (i) describing either habitat fragmentation (defined as those studies focused on habitat remnants where the observed effects could be mainly attributed to area, edge, or isolation effects) or habitat degradation (defined as those studies focused on habitats with contrasting quality, structure, fire regime, or logging, where area, edge, or isolation effects were negligible); (ii) reporting the effects of either habitat fragmentation or degradation on seed-disperser diversity (species abundance and richness) and interaction rates (fruit removal and visitation rates); (iii) having at least two contrasting situations, a control (undisturbed) and disturbed (fragmented or degraded) conditions. For habitat fragmentation studies, we considered as fragments those remnants <120 ha, and as continuous forest those stands >600 ha (Markl et al., 2012), or at least 10 times larger than the smallest fragment when the previous condition was not met; and (iv) reporting the mean, sample size, and a dispersion measure of the dependent variables (standard error, standard deviation, or any other measure from which a standard error may be calculated upon). Inclusion criteria assessment was performed by one person (FEF) to avoid a potential inter-reviewer bias. As result of this second screening process, we excluded 181 articles that have not met our inclusion criteria (mostly, not reporting sample sizes of standard deviations), resulting in 38 usable articles (Fig. 1c). From those 38 articles, we excluded one article that reported responses in terms of genetic diversity, despite being interesting, this was the only article reporting this kind of measurement and therefore had no comparison possibilities with the remaining cases. Therefore, 37 articles were included in the analyses (Fig. 1d). Literature search and report followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) statement (Moher et al., 2009).

From the 37 articles that fulfilled the four inclusion criteria, we gathered 163 case studies. As some papers presented more than one case study, we considered as independent cases those reporting different species or different locations (Aguilar et al., 2006; Morales & Traveset, 2009). When more than one
fragment size was evaluated in the same study, we contrasted the smallest fragment with the largest continuous stand; likewise, we compared those situations reporting the most and the least degraded habitats (Markl et al., 2012); intermediate situations were not compared to avoid multiple comparison problems. When data were presented only in graphical form, we used GRAPHCLICK 3.0 (Arizona Software, Switzerland) to extract the mean and dispersion values. In the case of multiple measurements across time (i.e., two or more years of data sampling), we considered each sampling year as a separate case study.

Effect size calculation and moderators

To measure the effect size of each study case, we used Hedges’ unbiased standardized mean difference (Hedges’ d, Hedges & Olkin, 1985), which is calculated as follows:

\[ d = \frac{X_E - X_C}{s_{EC}} \]

where \( X_E \) is the mean value of the disturbed (fragmented or degraded) measure, \( X_C \) is the mean value of the control measure, \( s_{EC} \) is the pooled standard deviation of both treatments and \( J \) is a term that corrects effect size for low sample sizes. This measurement has been largely used in ecological meta-analyses when the main goal is to estimate the magnitude of the effect of a particular treatment by comparing the results of the control and experimental group (Gurevitch et al., 2001). Negative values indicate that the response variable became reduced in disturbed habitats.

We conducted separate analyses for diversity and interaction rate responses. First we estimated the overall habitat fragmentation and degradation effects on both responses. Then, we defined three moderator variables: (i) disturbance type (habitat fragmentation or degradation), (ii) taxonomic group [birds, mammals, birds + mammals (i.e., assemblages of frugivorous vertebrates assessed as a whole, in which it was not possible to assess the effects separately for birds and mammals), and insects], and (iii) geographical region (tropical or temperate). Aiming to contrast the effects of habitat fragmentation and degradation, we assessed the fragmentation and degradation subsets separately, examining the taxonomic group (excluding mixed bird–mammal assemblages) and geographical region moderators within them. As birds are the most frequently reported group in seed-dispersal studies, we repeated this procedure comparing tropical and temperate bird species (examining the effects of habitat fragmentation and degradation separately). We also compared bats and birds from tropical habitats. To examine the heterogeneity among moderator levels, we estimated the between-group homogeneity \( Q_{between} \) statistic, which is a \( \chi^2 \) distributed metric that...
Effect model and publication bias

As we included studies reporting different response variables of a variety of species and geographic locations, a random effects model was the appropriate way to analyze our data (Borenstein et al., 2009), and consequently, we used mixed-model effects for the analysis of the moderator variables (Gurevitch & Hedges, 1999). To quantify potential publication bias due to data correlation, we calculated Kendall’s tau correlation with continuity correction to determine whether the magnitude of effects and sample size were correlated. As studies reporting null effects are unlikely to be published and hence not included in literature surveys (potentially overestimating positive or negative effects), we estimated the Rosenthal’s fail-safe number that indicates the number of unpublished case studies with null effects needed to reverse the observed effects (Hillebrand, 2008). This calculation indicates a robust result when the fail-safe number is equal or greater than SN + 10 (Rosenthal, 1979) where N is the number of case studies. Despite the criticism about Rosenthal’s fail-safe method (Jennions et al., 2013), we decided to use this classic approach instead of Rosenberg’s weighted approach (Rosenberg, 2005) as our Hedges’ d measures already consider the sample size weights by including the J term as explained above, and Rosenberg’s approach is known to perform poorly on random effect models (Jennions et al., 2013). We also examined the relationship between effect and sample size using the funnel plot approach (Hedges & Vevea, 1996) and then conducted a ‘trim-and-fill’ procedure (Duval & Tweedie, 2000a,b) to account for potential bias due to the asymmetry of the distribution of positive and negative cases, recalculating the mean effect, and confidence intervals to verify the robustness of our results (Jennions & Moller, 2002). In addition, as we had many cases in which more than one case was obtained from the same paper (i.e., articles examining more than one species, location, seed-dispersal component, or study year), we ran an additional analysis using the article ID as a moderator variable to determine a potential bias toward negative or positive effects. Then, we calculated the Spearman rank correlation coefficient and its bias-corrected and accelerated (BCa) confidence intervals (based on 1000 bootstrap permutations) to determine whether the number of cases and the magnitude of the effect were correlated. We expected an unbiased sample to be heterogeneous (i.e., the effects are variable across articles) and the number of cases per article to be not correlated with the effect magnitude. All analyses were conducted using Comprehensive Meta-Analysis software (Borenstein et al., 2005).

Results

We identified 163 case studies from 37 articles (Fig. 1; see details on Table S1, Supporting Information), as many publications reported more than one species or sampling location. Twenty-seven of 37 articles provided more than one case study; 46% reported more than one species, 33% reported more than one location, 13% reported more than one component (e.g., frugivory rates measured for small and large seeds separately), and 8% reported measures across time. From those, 89 case studies were referred to species diversity (abundance and richness) and 74 to interaction rates (visitation and removal rates). From the 89 diversity cases, 58 came from South America, 14 from Africa, 7 from Europe, 7 from Central and North America, and 3 from Asia. From the 74 interaction rate cases, 34 came from South America, 23 from Africa, 10 from Central and North America, and 7 from Europe.

Effects on seed-disperser diversity

We found no global effect of habitat fragmentation and degradation on animal diversity when evaluated together (d = −0.20, CI = −0.44 to 0.04, P = 0.09, N = 89; Fig. 2a). Then, we examined the effects of each disturbance type (Qbetween = 2.81, df = 1, P = 0.09) and found no effect of habitat fragmentation on diversity (d = −0.08, CI = −0.41 to 0.25, P = 0.63, N = 49) but a negative effect of habitat degradation (d = −0.45, CI = −0.73 to −0.17, P < 0.01, N = 40; Fig. 2b). Regarding animal group (Qbetween = 16.63, df = 3, P < 0.01), we found a negative effect on birds (d = −0.58, CI = −1.02 to −0.14, P < 0.01, N = 35) and insects (d = −0.71, CI = −1.19 to −0.22, P < 0.01, N = 15), but no effects were detected on mammals (d = 0.24, CI = −0.07 to 0.54, P = 0.13, N = 30) or bird and mammal assemblages (d = 0.18, CI = −0.27 to 0.64, P = 0.44, N = 9; Fig. 2c). Regarding geographical regions (Qbetween = 13.60, df = 1, P < 0.01), we found no effect on tropical animal diversity (d = 0.01, CI = −0.22 to 0.22, P = 0.98, N = 75), but a negative effect on the diversity of seed-disperser animals in temperate habitats (d = −1.25, CI = −1.88 to −0.62, P < 0.01, N = 14; Fig. 2d).

Effects on interaction rates

We found a negative global effect of habitat fragmentation and degradation on interaction rates when evaluated together (d = −0.37, CI = −0.59 to −0.15, P < 0.01, N = 74; Fig. 3a). Then, we examined the effects of each disturbance type (Qbetween = 0.06, df = 1, P = 0.80) and found a negative effect of habitat fragmentation on interaction rates (d = −0.34, CI = −0.58 to −0.11, P < 0.01, N = 45), but no effect of habitat degradation (d = −0.41, CI = −0.88 to 0.06, P = 0.09, N = 29; Fig. 3b). Regarding animal groups (Qbetween = 3.81, df = 3, P = 0.28), we found a negative effect on mammals (d = −0.73, CI = −1.28 to −0.19, P < 0.01, N = 14), but no effects on birds (d = 0.21, CI = −0.46 to 0.04,
Habitat Disturbance Effects on Seed Dispersal

Effects of habitat fragmentation and degradation on animal diversity. Mean and 95% confidence intervals are shown for: (a) overall effect, (b) disturbance type, (c) animal group, and (d) geographical region. The number of case studies is given in parentheses. Asterisks indicate that confidence intervals differ significantly from zero. Qb represents the Q_between statistics that test between-group homogeneity. Significance levels: NSP ≥ 0.05, **P < 0.01, ***P < 0.001.

P = 0.13, N = 39), insects (d = −0.58, CI = −1.25 to 0.09, P = 0.09, N = 16), or bird and mammal assemblages (d = −0.04, CI = −1.02 to 0.93, P = 0.93, N = 5; Fig. 3c). Regarding geographical region (Q_between = 0.59, df = 1, P = 0.44), we found negative effects on interaction rates on both tropical (d = −0.33, CI = −0.61 to 0.04, P = 0.02, N = 58) and temperate habitats (d = −0.52, CI = −0.93 to −0.11, P = 0.01, N = 16; Fig. 3d).

Differential effects of habitat fragmentation and degradation

By examining habitat fragmentation and degradation case studies separately, we found contrasting effects between these two habitat disturbance processes. We analyzed the two other moderator variables (e.g., taxonomic group and geographical region) inside each combination of habitat fragmentation and degradation with the two selected groups of response variables. We first examined the differential effects of habitat fragmentation and degradation on seed-disperser diversity, finding a heterogeneous response to habitat fragmentation among animal groups (Q_between = 12.86, df = 2, P < 0.01; Fig. 4a) with birds affected negatively (d = −1.14, CI = −1.88 to −0.40, P < 0.01, N = 13) and mammals positively (d = 0.33, CI = 0.01–0.65, P = 0.04, N = 27), there were no cases regarding insect diversity for fragmentation. Conversely, when examining habitat degradation (Q_between = 3.98, df = 2, P = 0.14), there were no effects on birds (d = −0.12, CI = −0.49 to 0.26, P = 0.55, N = 22) and mammals (d = −0.55, CI = −1.14 to 0.03, P = 0.06, N = 3), but there was a negative effect on insects (d = −0.71, CI = −1.19 to −0.22, P < 0.01, N = 15). When examining seed-disperser diversity data by geographical region, we also found a heterogeneous effect of habitat fragmentation (Q_between = 13.79, df = 1, P < 0.01; Fig. 4b), showing no effects for tropical seed dispersers (d = 0.24, CI = −0.03 to 0.51, P = 0.08, N = 41), but negative effects for the temperate ones (d = −1.34, CI = −2.13 to −0.55, P < 0.01, N = 8). Habitat degradation (Q_between = 1.54, df = 1, P = 0.21) showed negative effects on both tropical (d = −0.39, CI = −0.69 to −0.09, P = 0.01, N = 34) and temperate (d = −0.99, CI = −1.88 to −0.10, P = 0.03, N = 6) habitats.

In a second instance, we examined the differential effects of fragmentation and degradation on interaction rates. As reported by seed-disperser diversity, we found a heterogeneous effect of habitat fragmentation on interaction rates (Q_between = 14.12, df = 2, P < 0.01; Fig. 4c) when examining data by taxonomic group, showing negative effects on birds (d = −0.31, CI = −0.54 to −0.08, P = 0.01, N = 29) and mammals (d = −1.10, CI = −1.94 to −0.25, P = 0.01, N = 9), but no effect on insects (d = 0.26, CI = −0.04 to 0.55, P = 0.09, N = 2). Regarding habitat degradation
species diversity from temperate habitats has been negatively affected by habitat fragmentation \((d = -1.79, CI = -3.05 \text{ to } -0.53, P = 0.01, N = 4)\) and degradation \((d = -0.99, CI = -1.88 \text{ to } -0.10, P = 0.03, N = 6)\), but there was no effect on those species from tropical habitats (fragmentation: \(d = -0.78, CI = -1.75 \text{ to } 0.18, P = 0.11, N = 9\); degradation: \(d = 0.07, CI = -0.34 \text{ to } 0.49, P = 0.73, N = 16\)). Regarding interaction rates (Fig. 5b), habitat fragmentation and degradation showed no heterogeneity \(Q_{\text{between}} = 0.91, df = 1, P = 0.34 \text{ and } Q_{\text{between}} = 2.68, df = 1, P = 0.10, \) respectively). Habitat fragmentation had a negative effect on tropical habitats \((d = -0.40, CI = -0.66 \text{ to } -0.14, P < 0.01, N = 22)\) but had no effect at temperate habitats \((d = -0.13, CI = -0.61 \text{ to } 0.34, P = 0.59, N = 7)\). Habitat degradation, conversely, had no effect either on tropical \((d = -1.00, CI = -2.21 \text{ to } 0.21, P = 0.10, N = 7)\) or temperate habitats \((d = 0.23, CI = -0.61 \text{ to } 1.07, P = 0.60, N = 3)\).

Finally, we compared the responses of the two major groups of tropical seed dispersers: bats and birds. For bats, we had data only for species diversity therefore no comparison on interaction rates was possible in this case. Both tropical birds and bats showed a heterogeneous response \(Q_{\text{between}} = 7.33, df = 1, P = 0.01\), whereas there was no effect on birds \((d = -0.19, CI = -0.62 \text{ to } 0.24, P = 0.38, N = 25)\), there was a

\(Q_{\text{between}} = 1.53, df = 2, P = 0.47\), there were no effects on birds \((d = -0.01, CI = -0.75 \text{ to } 0.73, P = 0.98, N = 10)\), mammals \((d = -0.28, CI = -0.86 \text{ to } 0.29, P = 0.34, N = 5)\), or insects \((d = -0.72, CI = -1.57 \text{ to } 0.13, P = 0.10, N = 14)\). When examining interaction rate data by geographical region, we found that habitat fragmentation \(Q_{\text{between}} = 0.02, df = 1, P = 0.87\) had a negative effect on those seed-disperser species from tropical habitats \((d = -0.33, CI = -0.63 \text{ to } -0.04, P = 0.03, N = 33)\) but had no effect on those from temperate habitats \((d = -0.37, CI = -0.80 \text{ to } 0.06, P = 0.09, N = 12)\). Conversely, habitat degradation had a heterogeneous effect on interaction rates \(Q_{\text{between}} = 8.10, df = 1, P < 0.01\), with no effects on interaction rates of species from tropical habitats \((d = -0.32, CI = -0.83 \text{ to } 0.19, P = 0.22, N = 25)\) but with a negative effect on those from temperate habitats \((d = -1.36, CI = -1.86 \text{ to } -0.86, P < 0.01; N = 4)\). Some moderator level combinations had sample sizes <5; therefore, those values should be interpreted with caution.

Then, we compared the differential responses of tropical and temperate bird communities. Regarding species diversity (Fig. 5a), habitat degradation \(Q_{\text{between}} = 4.48, df = 1, P = 0.03\) had a heterogeneous effect on bird diversity, but habitat fragmentation did not \(Q_{\text{between}} = 1.54, df = 1, P = 0.21\). In this case, bird
discussion

We found an overall negative effect of habitat fragmentation and degradation on interaction rates but not on seed-disperser diversity. Animal-mediated ecosystem processes are often described to respond differentially to habitat alteration due to human activities; while habitat fragmentation is often responsible for changes on interaction rates (i.e., visitation or removal rates), habitat degradation has been described to have a wide impact on diversity by the means of modifying local environmental conditions and resource distribution (Schleuning et al., 2011). Our results showed a negative effect of habitat fragmentation on interaction rates, and a negative effect of habitat degradation on species diversity, hence corroborating this assertion.

Dissecting between-group heterogeneity results indicate that, for bird, both diversity and interaction rates were negatively affected by habitat fragmentation, but they showed to be less sensitive to habitat degradation. Mammals, in turn, presented a contrasting effect between habitat fragmentation and degradation in terms of species diversity, but the interaction rates were negatively affected by habitat fragmentation only. Frugivorous birds can be indirectly affected by habitat fragmentation, because area effects related to habitat loss may compromise resource (i.e., fleshy fruits) composition and availability (Cordeiro & Howe, 2003; Gonzalez-Varo, 2010). However, many birds are able to persist in degraded habitats depending on their sensitivity to habitat change (Thiollay, 1999; Barlow et al., 2007; Cleary et al., 2007). Most frugivorous mammals reported in the case studies assessed were bats (47% of the mammals reviewed, representing 65% of the diversity cases), which showed a positive response to habitat fragmentation, but could be seriously compromised by habitat degradation, as bats depend on roosting structures for feeding (Mello et al., 2008). Unfortunately, all case studies obtained on bats were related to habitat fragmentation and disperser diversity, precluding further comparisons. This situation may also explain (at least partially) why we have not detected a significant effect on frugivore diversity due to habitat fragmentation, as bats may be more tolerant to habitat disturbance than other Neotropical mammals, resulting in a neutral effect when combined. Regarding insects, contrarily as happens with pollination where insects play a major role, only two groups of insects are involved in secondary seed dispersal: ants and dung beetles. We included 31 case studies on insects, most of them focused on dung beetles (55% of the insects reviewed) and ants (45%), as they represent important secondary dispersers in tropical forest ecosystems (Zelikova & Breed, 2008; Braga et al., 2013). The strong negative effect of habitat degradation on insect diversity may compromise secondary dispersal, in which ants and dung beetles play a major role. Diversity loss in those insects could be attributed to microhabitat changes related to habitat degradation (i.e., leaf litter loss, higher temperatures, and lower moisture) that might reduce nesting sites, compromising the recruitment of plants that depend on secondary dispersal to avoid seed predation and fungal attack (Zelikova & Breed, 2008).
Seed-disperser species may differ in their sensitivity to habitat fragmentation and degradation, some of them being highly resilient and showing similar abundances in disturbed and nondisturbed habitats. For instance, habitat disturbance is known to modify the composition of animals interacting with plants (Figueroa-Esquivel et al., 2009), leading to less diverse communities. These, in turn, are dominated by generalist and resilient species that tend to maintain – or even increase – their abundances in disturbed sites due to changes in the magnitude of antagonistic interactions such as competition and predation (Kikvidze et al., 2011). Therefore, examining interaction rates (e.g., visitation and removal rates) altogether with species diversity may be more informative than considering only species diversity. Our results showed that whereas birds and insects were negatively affected in terms of diversity, they were not affected in terms of interaction rates, but the contrary happened to frugivorous mammals. This is especially relevant if species tend to vary in their effectiveness as seed dispersers (Schupp et al., 2010), and frugivorous assemblages in disturbed habitats have few but very abundant (highly resilient) species with low seed-dispersal effectiveness.

Interaction rates were negatively affected by anthropogenic habitat disturbance, particularly by habitat fragmentation, in agreement with what was previously reported by Markl et al. (2012). However, our study goes beyond by dissecting the heterogeneity among different groups of species and major habitats, and contrasting interaction rates with species diversity. In addition, our results showed a significant negative effect of habitat fragmentation on interaction rates, which was not detected by Markl et al. (2012). Fruit removal and visitation rates may be good proxies of the quantitative component of seed-dispersal interactions, as they often relate to changes in consumption probabilities due to structural modifications (Galetti et al., 2003) and changes in the disperser assemblage composition (Figueroa-Esquivel et al., 2009; González-Varo, 2010). However, the qualitative component of seed dispersal is less common to be reported, as its assessment in field conditions is more complex and time-consuming. Effective plant recruitment (i.e., derived from both quantitative and qualitative components of seed dispersal) should be also considered in future studies to depict accurately the extended effect of habitat fragmentation or degradation on seed-disperser species, considering that recruitment may be affected not only by habitat loss (e.g., Rodríguez-Cabal et al., 2007), but also by habitat quality (e.g., González-Varo et al., 2012).

Avian frugivores from temperate habitats appear to be more sensitive in terms of species diversity. Although birds are known to be more resilient than mammals because of their high mobility (Kelt, 2001), frugivorous birds may be negatively affected by habitat needs and preferences (Hansbauer et al., 2010). Such negative effects may be related to the availability of perching structures and – more importantly – of fruit resources (Herrera & García, 2010), irrespective of birds mobility. On the other hand, many tropical avian frugivores are more resilient to habitat degradation (Peh et al., 2006; Barlow et al., 2007; Cleary et al., 2007), providing a regeneration opportunity in degraded lands by increasing the recruitment of fleshy-fruited plant species (Gomes et al., 2008), despite some frugivore birds may be more sensitive to fragmentation and therefore negatively affected.

Tropical species were negatively affected by habitat fragmentation and degradation in terms of their interaction rates, but showing contrasting responses in terms of species diversity (which might be biased by the inclusion of many bat species that appear to be more disturbance tolerant). Conversely, seed dispersers of temperate regions were negatively affected at both diversity and interaction rate level. This pattern may result from the high sensitiveness of tropical species to habitat fragmentation, probably due to the high dependence shown by many species on patchy food resources and landscape structure (Lehouck et al., 2009), which may help to explain the low interaction rates and recruitment limitations found in fragmented landscapes (Cordeiro et al., 2009). On the other hand, species of temperate regions are known to be highly dependent on the spatial and temporal variation of markedly seasonal fruit resources (Jordan, 1987, 2000), which may explain, at least in part, the reduction in diversity and interaction rates.

Concluding remarks

We found that seed-disperser animals showed a negative response to habitat fragmentation and degradation, with contrasting magnitude depending on the variable on which effects were measured (i.e., species diversity or interaction rates), animal group, or geographical region. Interestingly, birds and mammals showed differential responses in terms of diversity and interaction rates. Regarding potential biogeographical effects, disperser assemblages of temperate regions showed to be more sensitive. Despite the inherent limitation of extrapolating the responses of a subset of species to broad taxonomic and geographic categories, this study represents a first approach to have a better understanding the way human activities impact frugivorous and insect species and their role as seed dispersers.

Seed dispersal is a key interaction for maintaining biodiversity (Thompson, 1994), and it may also
represent an opportunity for recovering disturbed areas, if a minimum set of conditions relevant to the main frugivorous species persist (usually birds and bats). Managing disturbed habitats by connecting isolated remnants (Prugh et al., 2008), letting understory vegetation grow, and replacing key structural features (e.g., artificial roosts for bats) might increase frugivore activity and hence plant recruitment (Corlett, 2002). Human activities may impose exceptionally strong selection forces on natural seed-disperser populations by modifying the ecological setting where plant–animal interactions occur (Kinnison & Hairston, 2007; Galetti et al., 2013). Maintaining these key interactions in disturbed landscapes should be considered in conservation and management plans, as an opportunity for natural regeneration.

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