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A global meta-analysis of the impacts of forest fragmentation on biotic mutualisms and antagonisms

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Article Impact Statement: Forest fragmentation disrupts key ecosystem functions by negatively affecting mutualisms and strengthening parasitic interactions.

Abstract

Forest fragmentation is a grave threat to biodiversity. Forests are becoming increasingly fragmented with more than 70% now < 1 km from forest edge. Although much is known about the effects of forest fragmentation on individual species, much less is understood about its effects on species interactions (i.e., mutualisms, antagonisms, etc.). In 2014, a previous meta-analysis assessed the impacts of forest fragmentation on different species interactions, across 82 studies. We pooled the previous data with data published in the last 10 years (combined total 104 studies and 168 effect sizes). We compared the new set of publications (22 studies and 32 effect sizes) with the old set to evaluate potential changes in species interactions over time given the global increase in fragmentation rates. Mutualisms were more negatively affected by forest fragmentation than antagonisms ($p < 0.0001$). Edge effects, fragment size, and degradation negatively affected mutualisms, but not antagonisms, a different finding from the original meta-analysis. Parasitic interactions increased as fragment size decreased ($p < 0.0001$)—an intriguing result at variance with earlier studies. New publications showed a more negative mean effect size of forest fragmentation on mutualisms than old publications. Although research is still limited for some interactions, we identified an important scientific trend: current research tends to focus on antagonisms. We concluded that forest fragmentation disrupts important species interactions and that this disruption has increased over time.

KEYWORDS
antagonistic, forest fragment, meta-analytical, mutualistic, species interactions

Metaanálisis Mundial del Impacto de la Fragmentación de Bosques sobre el Mutualismo y Antagonismo Biótico

Resumen: La fragmentación del bosque es una amenaza grave para la biodiversidad. Los bosques están más fragmentados, pues más del 70% tienen < 1 km a partir del borde del bosque. Aunque hay mucha información del efecto de la fragmentación sobre las especies, hay poco conocimiento de sus efectos sobre las interacciones entre especies (mutualismo, antagonismo, etc.). Un metaanálisis realizado en 2014 por evaluó en 82 estudios el impacto de la fragmentación del bosque sobre las diferentes interacciones entre especies. Juntamos estos datos con datos publicados en los últimos diez años (total combinado de 104 estudios y 168 tamaños de efecto). Comparamos el grupo nuevo de publicaciones (22 estudios y 32 tamaños de efecto) con el grupo de para evaluar los cambios potenciales en las interacciones entre especies con el tiempo dado el incremento mundial de la tasa de fragmentación. El mutualismo fue más afectado negativamente por la fragmentación del bosque que los antagonismos ($p < 0.0001$). El efecto del borde, tamaño del fragmento y la degradación tuvieron un efecto negativo sobre el mutualismo, pero no sobre el antagonismo, un resultado diferente al del metaanálisis original. Las interacciones parasitarias incrementaron conforme se redujo el tamaño del fragmento ($p < 0.0001$)—un resultado intrigante en discrepancia con los primeros resultados. Las publicaciones recientes mostraron un tamaño promedio de efecto de la fragmentación del bosque más negativo para el mutualismo que las publicaciones antiguas. Aunque hay poca investigación sobre algunas interacciones, identificamos una tendencia científica importante: la investigación actual tiende a enfocarse en los antagonismos. Concluimos que la fragmentación del bosque altera las interacciones importantes entre especies y que este cambio ha aumentado con el tiempo.

PALABRAS CLAVE
antagonista, fragmento de bosque, interacciones entre especies, metaanálisis, mutualista

【摘要】
森林破碎化对生物多样性构成了重要威胁。森林破碎化问题已越来越严重, 目前超过 70% 的森林面积距森林边缘小于 1 公里。虽然人们对森林破碎化对单一物种的影响已有许多了解, 但对其对物种相互作用(即互利共生、拮抗等)的影响仍知之甚少。 2014 年, Magrach 等人基于 82 项研究的荟萃分析评估了森林破碎化对不同物种相互作用的影响。本研究汇总了他们的数据与过去 10 年间发表的数据(合计 104 项研究及 168 个效应量), 并将新发表的一组数据(22 项研究及 32 个效应量)与 Magrach 等人的数据进行了比较, 从而评估在全球森林破碎化率增加的背景下, 物种间相互作用随时间推移可能发生的变化。结果表明, 互利共生作用相比于拮抗作用, 受到森林破碎化的负面影响更大($p < 0.0001$)。边缘效应、森林片段大小和退化程度对互利共生关系有负面影响, 但对拮抗关系没有影响, 这与之前的荟萃分析结果不同。寄生关系的相互作用随着森林片段大小的减小而增加($p < 0.0001$), 这一有趣的结果也与之前的研究不一致。此外, 与之前的研究结果相比, 新发表的研究中森林破碎化对互利共生关系的平均效应更为负面。虽然对某些互作关系的研究仍然有限, 但我们发现了一个重要的科学趋势:目前的研究更倾向于关注拮抗作用。最后, 本研究的结论是:森林破碎化破坏了物种间重要的相互作用, 且这种破坏随时间推移正在加剧。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 拮抗, 森林片段, 荟萃分析, 互利共生, 物种相互作用

INTRODUCTION

Habitat loss and fragmentation are critical threats to Earth's biological diversity (Haddad et al., 2015; Laurance et al., 2007, 2011, 2018; Newmark et al., 2017) and ecosystem functioning (Haddad et al., 2015). Although habitat fragmentation occurs in all ecosystems, forest fragmentation is of particular concern because most of the world's terrestrial species live in forests (FAO & UNEP, 2020; Pillay et al., 2021).

Forest fragmentation increases the amount of forest edge and reduces the amount of interior forest, where most forest species reside (Laurance et al., 2011). For example, Taubert et al. (2018) identified over 130 million forest fragments across subtropical and tropical regions of the Americas, Africa, Asia, and Australia. They found that more than 70% of the world's remaining forests are < 1 km from the nearest forest edge and that 20% of remaining forests are < 100 m from the nearest edge (Haddad et al., 2015). Proximity to a forest edge creates a multitude of negative ecological effects on tropical biodiversity (Betts et al., 2017; Laurance et al., 2011, 2018).

Although the effects of forest fragmentation on species richness and community composition have been widely studied, less is understood about the broader impacts on interspecific interactions (Magrach et al., 2014). Research has previously assessed species-specific interactions in the context of fragmented forests. Some examples include research on seed dispersal (e.g., Cordeiro & Howe, 2003; Cramer et al., 2007), pollination (e.g., Aizen & Feinsinger, 1994; Hadley et al., 2014), and predation (e.g., Kareiva, 1987; Huhta et al., 2004). However, there is considerably less research that synthesizes the overall impacts of forest fragmentation on the broader categories of species interactions.

In 2014, Magrach et al. (2014) synthesized the data on interspecific interactions in fragmented forests. The authors produced a comprehensive meta-analysis in which they assessed how different components of forest fragmentation affected antagonistic and mutualistic interactions in studies published before 2012. These components included fragment size, edge effects, fragment isolation, and fragment degradation. Fragment size is used to examine the total area of a forest fragment

(Lovejoy, 1980), edge effects to assess the impacts of the artificial edge created during fragmentation (Didham et al., 1998), fragment isolation to evaluate the distance of a fragment to other similar natural habitat (Laurance et al., 2011), and fragment degradation to examine the quality of the fragment and the species in it (Tabarelli & Gascon, 2005). Magrach et al. (2014) concluded that overall mutualistic interactions are more negatively affected by forest fragmentation than antagonistic interactions and that edge effects, fragment isolation, and fragment degradation all have a negative impact on mutualistic interactions. They found that fragment size does not appreciably alter the specific types of interactions studied, including seed dispersal, pollination, mycorrhizae (a plant root−fungi interaction), predation, parasitism, and herbivory. However, they found that edge effects significantly affect seed dispersal. The authors did note the potential limitations of their findings based on the limited number of studies available for each type of interaction and the small sample sizes in each study.

Magrach et al. (2014) called for further research into the effects of forest fragmentation on species interactions to better understand how these networks and ecosystems are affected. They noted that many ecological interactions had been comparatively understudied. For example, mycorrhizae had only 3 recorded interactions, whereas seed dispersal and predation were much more extensively studied. They also noted small sample sizes were a problem that could have affected the statistical power of their meta-analysis. Now, a full decade later, there is more literature available and more research has revealed new directions in how species interactions and related ecosystem functions are affected by forest fragmentation.

We built on the research by Magrach et al. (2014) by summarizing and analyzing a decade of new data collected from 2012 to 2022. These new data should increase the statistical power of the analysis. We asked the following questions: Does forest fragmentation affect mutualistic interactions more negatively than antagonistic interactions; do the studied components of forest fragmentation affect mutualisms more than antagonisms; do these components differentially affect the 6 types of interspecific interactions previously defined by Magrach et al. (2014); are there changes in the effect sizes within each group between the studies found by Magrach et al. (2014) and the newer publications; and are there still biases based on the geographical location of research or the types of studied interactions given that Magrach et al. (2014) found most studies were conducted in Brazil?

Based on these questions, we predicted that forest fragmentation would more strongly and negatively affect mutualisms because antagonistic interactions are hypothesized to be more adaptable to environmental pressures (Brockhurst & Koskella, 2013) due to a higher connectedness of species in these networks (Baumgartner, 2020); edge effects, fragment isolation, and fragment degradation would continue to affect mutualisms more than antagonisms because habitat disturbance increases the vulnerability of specialized mutualisms (Aizen et al., 2012; Kiers et al., 2010); the 4 components of forest fragmentation previously evaluated by Magrach et al. (2014) would increase in variation with larger sample sizes as a result of the addition of new studies; and compared with the publications found by Margrach et al. (2014), newer studies would show an increase in effect size given increasing forest fragmentation worldwide (Fischer et al., 2021).

METHODS

Literature search and inclusion criteria

We replicated most of the quantitative methods for the literature review as detailed in Magrach et al. (2014). A brief overview is given here to explicate some key differences. We searched the ISI Web of Knowledge, Science Direct, and CAB Abstracts for peer-reviewed publications that assessed the impact of forest fragmentation on species interactions (search code in Magrach et al., 2014 supporting information). Magrach et al. (2014) also searched Scopus as a fourth database; however, institutional access to Scopus was unavailable to us. We limited our search period to research published from 2012 to 2022. We sought to add new data and reassess Magrach et al.'s (2014) findings; thus, we excluded all papers from their original timeline (before 2012). Because our search overlapped part of 2012, papers in their original study that appeared during our search were excluded.

We excluded papers for which the overall outcome of an ecological interaction (e.g., fruit set) was not measured, the study area was not forest fragments, and the study area was an island or island system. For unique circumstances, we applied the following criteria: if 2 different species and their interactions were analyzed in a single paper, then each interaction was measured as a separate record; if an interaction was repeatedly studied over time, we used only data from the most recent study period; if a single study analyzed 2 different outcomes for the same interaction, then only 1 outcome was used for evaluation; and if a paper used an experimental treatment, we analyzed only the control data. We excluded literature reviews because most included data already evaluated in Magrach et al. (2014). Publications that delineated small clumps of trees (< 10 individuals) as habitat patches were not considered to be within our definition of *forest fragments*. Finally, a few publications evaluated fragment shape as a component of forest fragmentation. We excluded shape as a component of forest fragmentation because it was not part of the original Magrach et al. (2014) paper and few researchers have measured it.

Data analyses

Our initial search recalled 3930 publications. After removing duplications, we had 1813 papers for review. The initial rounds of elimination based on the aforementioned search criteria resulted in 121 publications for full-text review. After reading each publication, we further excluded papers based on our criteria or the availability of data needed for our analyses (Harrison, 2011). For relevant papers that did not report the necessary data, the corresponding author was contacted to obtain the information. If authors did not respond or did not wish to share their data, the paper was not included. In our search from 2012 to 2022, we found 23 studies in which 36 interspecific interactions in fragmented forests were analyzed. However, 3 interactions were removed prior to analyses because insect galling and ant-plant mutualisms were investigated; these mutualisms did not fit into the 6 types of interactions originally analyzed in Magrach et al. (2014) or sample sizes were insufficient for analyses ($n < 2$ publications).

From each paper that fit our criteria, we extracted information on the nature of the interaction (mutualism or antagonism), the type of interaction, the type of forest where the study took place, the country where the research was conducted, the sample size, and relevant statistics. Although we recorded all interactions, we focused on 6 main types: predation, parasitism, herbivory, seed dispersal, pollination, and mycorrhizae. We also recorded the component of forest fragmentation that the author or authors assessed: fragment size, fragment isolation, forest degradation, or edge effects (Appendix S1).

In accordance with the methods outlined in Magrach et al. (2014), we calculated the effect size of each interaction with the data available in each publication to calculate Hedges' *d*, an unbiased measurement of the standardized mean difference between 2 treatments (Hedges, 1983, 1985). For these calculations, we prioritized the use of raw data over other statistical outputs, when available. If a study reported results related to a component of fragmentation as a continuous variable, we analyzed the replicates for the lowest and highest values. For articles that did not report transformable statistics but provided relevant data in graphs or figures, we used DataThief III (Tummers, 2006) or Think-Cell (Wyatt & Schödl, 2020) to extract the required information. Magrach et al. (2014) used Metawin 2.0 for their data transformations, whereas we used George Mason University's Practical Meta-Analysis Effect Size Calculator (Wilson, 2017a) to transform associated numbers and statistics into Cohen's *d*. From there, we used Hedges' *g* correction factor (Appendix S3) to transform Cohen's *d* to Hedges' *g* (Wilson, 2017b) and then transformed Hedges' *g* to Hedges' *d* using Metawin 3.0 (Rosenberg, 2022). Consistent with Magrach et al. (2014), a positive effect size indicated that increasing fragmentation escalates the strength of an ecological interaction.

After determining Hedges' *d* for each interaction, we calculated the related variance (Appendix S4) with information on the study's sample size. All the effect sizes and related variances calculated from our study were combined with the 136 effect sizes originally reported in Magrach et al. (2014). The combined data were used in the final analyses to assess the impacts of forest fragmentation on all published literature available from 1997 to 2022. Hedges' *d* and the related variance were used to generate bias-corrected 95% confidence intervals with the function resampling method with 1000 iterations in Metawin 3.0 (Rosenberg, 2022). We also calculated the mean effect size for each category of interaction. Effects were considered significant if the p value was < 0.05. If the confidence intervals overlapped zero, we still considered that the difference between the 2 means was statistically significant.

As in Magrach et al. (2014), we used random effects categorical meta-analytic models with effect sizes weighted by their variances (Vetter et al., 2013) and bootstrapped resampling procedures with 1000 iterations to assess the overall effects of forest fragmentation on mutualisms and antagonisms, to evaluate the effect of each component of fragmentation on mutualisms and antagonisms, to determine the impact of each component of fragmentation on the 6 different types of interactions, and to assess any differences between old and new publications for these groups. These models were used to determine heterogeneity in effect sizes based on Q statistics, which were tested against a chi-square distribution with $n - 1$ df, all in Metawin 3.0. To assess geographic biases, we added the number of studies per country and determined where the majority of the research was conducted.

Finally, we checked for publication bias, which often occurs in meta-analyses, because research with statistically significant results is more likely to be published than research without statistically significant results (Easterbrook et al., 1991). Publication bias is a problem in meta-analyses because it can lead to false positive results (Van Aert et al., 2019). To check for publication bias, we created funnel plots of our data and visually inspected them for asymmetry. Funnel plots are scatter plots of the treatment effects that have been estimated from each publication plotted against each effect size, in this case, Hedges' *d* (Sterne et al., 2005). Asymmetry in a funnel plot is an indicator of publication bias, and in the absence of bias, a funnel plot will appear symmetrical (Sterne & Harbord, 2004). We checked our visual observations of publication bias with the R package metafor 3.8-1 (Viechtbauer, 2010) to evaluate bias with Rosenthal's fail-safe number, which generates the number of missing studies averaging null results that would need to be added to make the combined effect sizes statistically insignificant (Orwin, 1983; Rosenthal, 1979), and Egger's regression test, which statistically measures funnel plot asymmetry (Egger et al., 1997). If both statistical tests were significant, then we assumed no publication bias and trusted that we were not missing data that would lead us to false positive results.

RESULTS

New publications and final combined data set

Magrach et al. (2014) found 82 studies published from 1997 to 2012 and an average of 5.5 studies per year, whereas we found 22 studies with an average of 2.3 studies per year for 2012–2022. Of the studies we found, 22 assessed 1 or more of the 6 categories of species interactions (32 unique interactions). In these 22 studies, 7 mutualistic interactions and 25 antagonistic interactions were examined. When we combined the studies we found with those Magrach et al. (2014) assessed, we analyzed 104 studies with 168 effect sizes. The reported numbers include the total, combined studies included in the analyses (both those included in Magrach et al.2014, hereafter old publications, and papers we

TABLE 1 Number of effect sizes for different types of species interactions after combining those previously reported by Magrach et al. (2014) with new effect sizes in publications from 2012 to 2022.

Interaction type	Old effect sizes	New effect sizes	Total effect sizes	Increase (%)*
Mutualism	58	7	65	12
Antagonism	78	25	103	32
Predation	44	13	57	30
Parasitism	16	3	19	19
Herbivory	19	9	28	47
Seed dispersal	31	3	34	3
Pollination	23	2	25	9
Mycorrhizae	3	2	5	67

*Change in the number of studies and effect sizes from the values originally reported by Magrach et al. (2014).

TABLE 2 Total number of publications and effect sizes reported for each component of forest fragmentation after combining those previous reported by Magrach et al. (2014) with data from the most recent publications from 2012 to 2022.

Component of forest fragmentation	Total publications	Increase (%)*	Total effect sizes	Increase (%)*
Fragment size	69	21	99	15
Edge effects	38	52	50	39
Fragment isolation	4	33	7	40
Fragment degradation	11	22	12	20

*Change in the number of studies and effect sizes from the values originally reported by Magrach et al. (2014).

found that were published from 2012 to 2022, hereafter new publications).

Of the total studies in our combined data set, 47 analyzed mutualisms and 69 analyzed antagonisms ($n = 116$ because some studies report both interaction types). No new studies were found that analyzed commensalisms (interaction between mutualisms and antagonisms in which one species benefits and the other species is not affected), so the category was not included.

Fragment size was the most well-studied component of forest fragmentation: 69 studies and 99 interactions were observed. Edge effect was second: 38 studies and 50 interactions were observed. Four studies evaluated the effects of isolation associated with 7 interactions. Eleven studies addressed forest degradation associated with 12 interactions.

The amount of available research increased more for antagonisms than mutualisms. We analyzed 103 effect sizes for antagonisms and only 65 for mutualisms. From the number of effect sizes originally reported in Magrach et al. (2014), the total increased by 32% for antagonisms and 12% for mutualisms. For the 6 types of interactions, the increase in sample size from the addition of new publications varied drastically from 3% for studies on seed dispersal to 67% for studies on mycorrhizae. For components of forest fragmentation, the number of interactions reported in the literature increased the most for fragment isolation (40% more effect sizes) and the least for fragment size (15% more effect sizes) (Table 1,2).

Finally, sample sizes appeared to be increasing for studies assessing the impact of forest fragmentation on species interactions. Sample sizes reported by Magrach et al. (2014) range from 4 to 1200, whereas sample sizes from the new publications ranged from 10 to 12,604 (Appendix S5).

Effects of forest fragmentation on mutualisms and antagonisms

Supporting the original findings from Magrach et al. (2014), the effects of forest fragmentation remained consistently more negative on mutualisms than antagonisms (bias-corrected bootstrapped CIs: mutualisms, −1.38 to −0.35; antagonisms −0.33 to 0.60; $Q_{between} = 15.62$, df = 1, $p = 0.0001$; antagonisms $Q_{within} = 232.34$, df = 102, $p < 0.0001$; mutualisms $Q_{within} = 116.36$, df = 64, $p = 0.0001$) (Figure 1).

Consistent with Magrach et al. (2014), no component of forest fragmentation had a significant effect on the strength of antagonisms ($Q_{between} = 0.73$, df = 3, $p = 0.87$). In addition, 3 of the 4 components of forest fragmentation had significant negative effects on the strength of mutualisms ($Q_{between} = 8.93$, df = 3, $p = 0.03$). Two of the 3 significant components of forest fragmentation remained consistent between Magrach et al. (2014) and the new combined publications: fragment degradation and edge effects. However, Magrach et al. (2014) previously found that fragment isolation had a significant effect, whereas we found that fragment size was a third significant component of forest fragmentation negatively altering the strength of mutualisms (Figure 2).

The key difference in the new findings compared with the previous findings was that in our results fragment size significantly affected mutualisms ($Q_{within} = 60.31$, df = 40, $p = 0.02$)

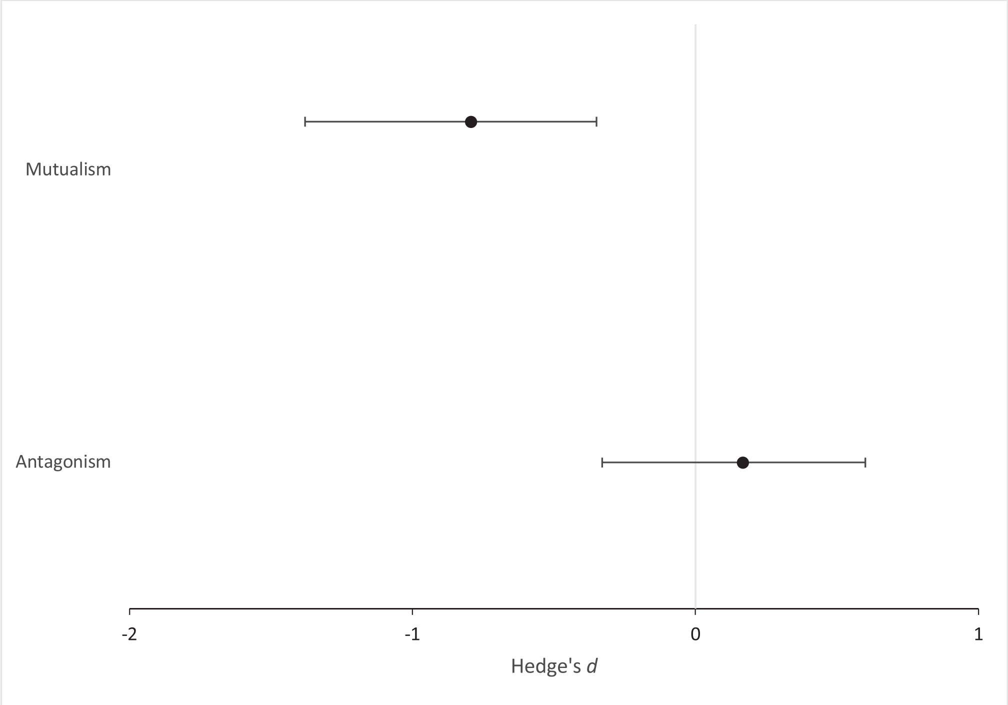

FIGURE 1 Impacts of forest fragmentation on mutualistic and antagonistic species interactions for all publications (lines, bias-corrected bootstrapped 95% confidence intervals; dots, mean effect size for each type of interaction).

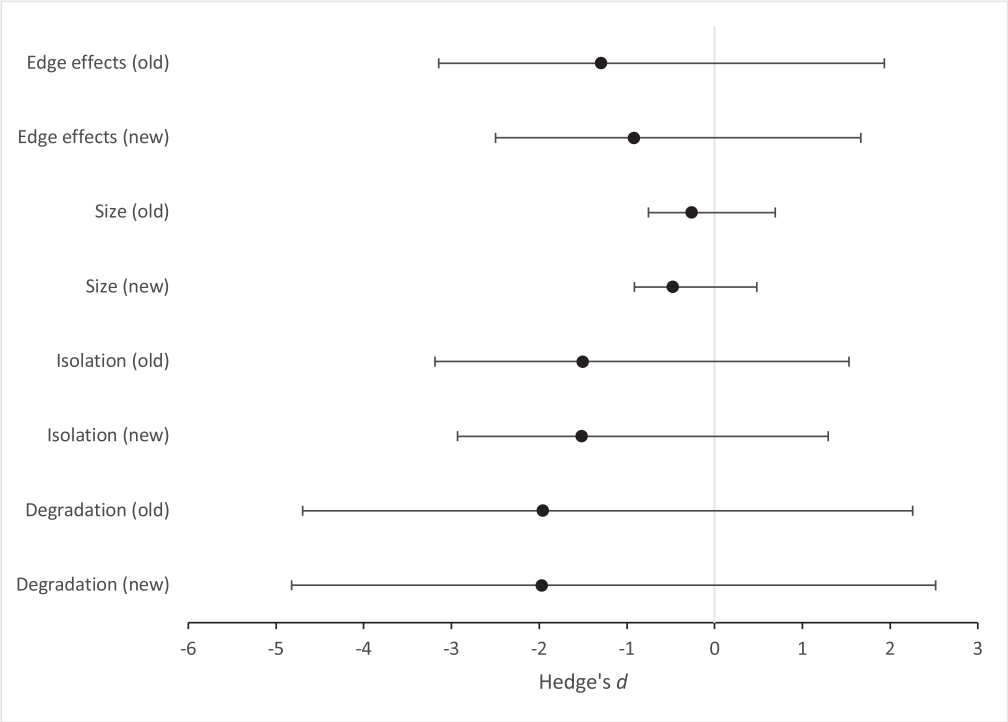

FIGURE 2 Impacts of the 4 components of forest fragmentation (edge effects, size, isolation, and degradation) on mutualistic interactions in Magrach et al. (2014) (old publications) and combined new and old publications (lines, bias-corrected bootstrapped 95% confidence intervals; dots, mean effect size for each type of interaction).

(Appendix S2), whereas fragment isolation did not have a significant effect on mutualisms ($Q_{\text{within}} = 5.30$, df = 3, $p = 0.15$). Edge effects remained a negative effect on antagonisms and mutualisms ($Q_{\text{between}} = 5.49$, df = 1, $p = 0.02$; antagonisms $Q_{\text{within}} = 97.44$, df = 36, $p < 0.0001$; mutualisms $Q_{\text{within}} = 49.33$, df = 12, $p < 0.0001$; bias-corrected CIs: antagonisms −0.67 to 0.70, mutualisms −2.63 to 0.13).

When comparing changes in the mean effect size between the old and new publications, we found a shift in the mean effect size for both antagonisms and mutualisms (Appendix S6). For antagonisms, the mean effect size of the old publications was 0.23 (bias-corrected bootstrapped CIs: −3.00 to 0.74), whereas the mean effect size of the new publications was −0.01 (bias-corrected bootstrapped CIs −0.81 to 0.75). For mutualisms, the mean effect size increased between old and new publications. Old publications assessing mutualisms had a mean effect size of −0.74 (bias-corrected bootstrapped CIs −1.29 to −0.22), whereas new publications had a mean effect size of −1.21 (bias-corrected bootstrapped CIs −2.19 to −0.10). Although these results showed an increase in the mean effect size for mutualisms and a decrease for antagonisms, the p values for these shifts between old and new publications were not significant ($p > 0.05$).

For the different components of forest fragmentation, the effect of fragment size on mutualisms was significantly different between old and new publications ($Q_{\text{between}} = 17.5$, df = 1, $p < 0.001$). Old publications had a mean effect size of 0.08 (bias-corrected bootstrapped CIs −0.44 to 0.65), whereas new publications had a mean effect size of −2.36 (bias-corrected bootstrapped CIs −3.01 to −1.83) (Appendix S7). For the effect of degradation on antagonisms, edge effects on mutualisms and antagonisms, and fragment size on antagonism, we found no significant difference between old and new publications ($p > 0.05$). Finally, isolation was incomparable because there were no new publications for mutualisms and the sample size for old publications of antagonisms was also too small for analyses ($n < 2$). There were also no new publications on the impact of edge effects and degradation on mutualisms.

Effects of forest fragmentation on the 6 types of interactions

Contrary to Magrach et al. (2014), who found that fragment size did not have a significant impact on the 6 categories of interspecific interactions, the addition of new publications caused fragment size to vary significantly between the interactions ($Q_{\text{between}} = 11.15$, df = 5, $p = 0.048$) and was notably significant for parasitism ($Q_{\text{within}} = 51.76$, df = 15, $p < 0.0001$) (Figure 3). With a mean positive effect size of 0.5, parasitism increased as forest fragmentation increased, which indicated higher amounts of parasitism in smaller forest fragments. Although Magrach et al. (2014) found that edge effects varied significantly for the different interactions, our results indicated that edge effects did not vary significantly across the 6 categories of interactions, of which only 5 were available for measurement ($Q_{\text{between}} = 6.99$, df = 4, $p = 0.14$). We were only able to analyze 19 interactions of parasitism, and this small sample size was likely the cause of confidence intervals overlapping zero.

When we compared the old publications with the new, we found a significant difference between the 2 groups for mycorrhizae ($Q_{\text{between}} = 9.68$, df = 1, $p = 0.002$). The mean effect size increased from −0.80 for old publications (bias-corrected bootstrapped CIs −1.43 to 0.17) to −2.80 for new publications (bias-corrected bootstrapped CIs −2.97 to −3.38). For the other 5 types of interactions, we found no significant differences between the new and old publications (Figure 4).

Geographic bias

Forest fragmentation research remained geographically biased. Magrach et al. (2014) originally found that 14 of their studies were conducted in Brazil, the highest number of all countries included. Of the new studies, more than one-quarter were conducted in Brazil, demonstrating a continued bias for this area. However, the research from Argentina doubled in size (increase from 4 to 8 studies).

Publication bias

We found no evidence of publication bias in our data set. There did not appear to be any funnel plot asymmetry, confirmed by Egger's test for funnel plot asymmetry (Egger's test $p = 0.76$). Rosenthal's fail-safe N calculation also confirmed a lack of publication bias ($p < 0.0001$, fail-safe $N = 9833$ publications).

DISCUSSION

We found new evidence that mutualistic interactions are more negatively affected by forest fragmentation than antagonistic interactions. Most of our findings were consistent with Magrach et al. (2014), confirming that global forest fragmentation has contrasting effects on different types of species interactions. However, these effects tended to be more negative for mutualistic interactions, which could exacerbate ecosystem decay after fragment isolation. A key difference in our combined results compared with Magrach et al.'s (2014), which is most likely caused by a larger sample size, is that fragment size negatively affected mutualistic interactions but not antagonistic interactions, such that smaller fragments had a disproportionately negative effect on mutualistic interactions compared with larger fragments or with antagonistic interactions. This negative impact of forest fragmentation on mutualisms was held when we compared old and new publications because the mean effect size was larger and more negative for new publications. We saw this with the shift for mycorrhizal interactions. When assessing the overall impacts of forest fragmentation, the mean effect size intensified from −0.80 for the old publications to −2.80 for the new publications. The sample size for this specific interaction was small, but there were still 2 key trends in the data: an increase

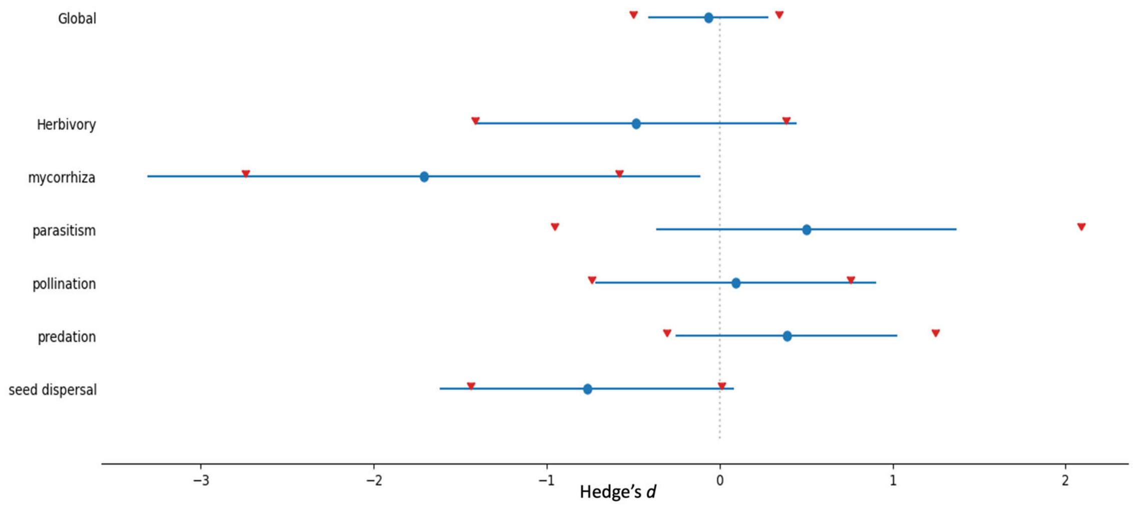

FIGURE 3 Impact of fragment size on the 6 different types of species interactions (lines, normal 95% confidence intervals; arrows, bias-corrected bootstrapped 95% confidence intervals; dots, mean effect sizes for each type of interaction).

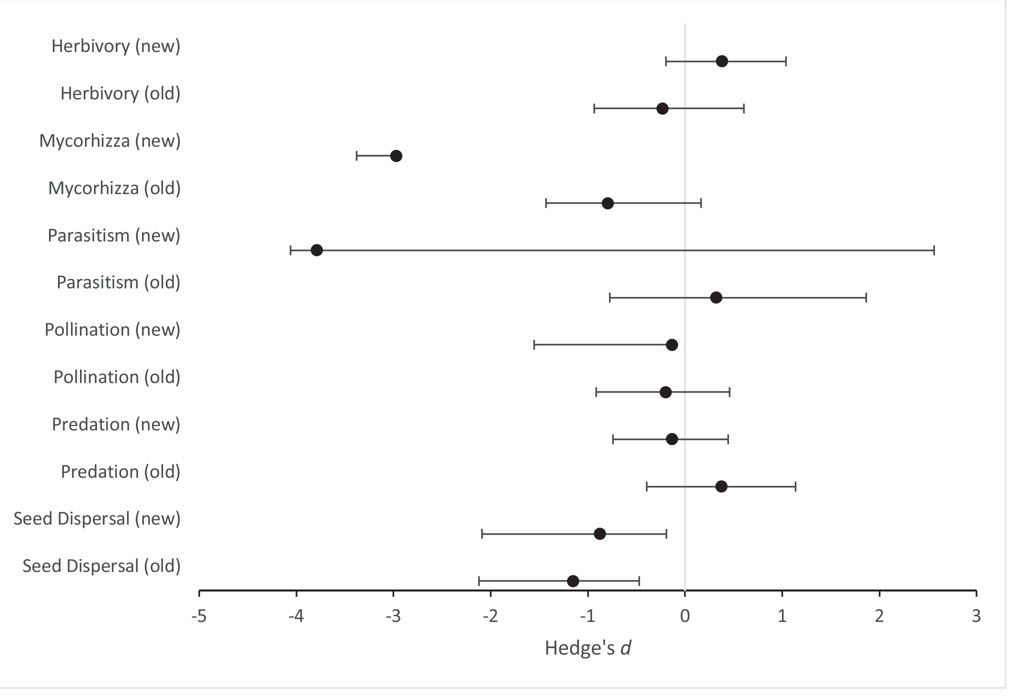

FIGURE 4 Impacts of forest fragmentation on the 6 types of species interactions grouped by Magrach et al. (2014) included publications (old) and new publications (lines, bias-corrected bootstrapped 95% confidence intervals; dots, mean effect size for each type of interaction).

in the negative effects of forest fragmentation on mutualisms and a strengthening of certain types of antagonisms.

Mutualistic interactions are hypothesized to be less adaptable to environmental pressures than antagonistic interactions (Brockhurst & Koskella, 2013). This is due to a higher connectedness of species in antagonistic networks, which has been shown via modeling to decrease the effects of disturbance and help stabilize ecological communities (Baumgartner, 2020). Conversely, mutualisms are thought to be more highly coevolved and interdependent compared with antagonisms (Kawakita et al., 2010). Habitat disturbance can increase the vulnerability of the more specialized mutualisms (Aizen et al., 2012; Kiers et al., 2010) because their coevolved counterparts might not persist in newly disturbed ecosystems (Devictor et al., 2008).

In the context of fragment size, large forest fragments can sustain more biodiversity than small fragments (Chase et al., 2020; Laurance et al., 2002, 2011; Phillips et al., 2018) and contain more habitat to buffer against abiotic stressors, such as edge effects (Gascon et al., 2000). Large amounts of biodiversity in large forest fragments increase the probability that multiple mutualistic partners are present and that their populations are stable. In degraded habitat (e.g., small forest fragments), the ecosystem decays more quickly (Chase et al., 2020), and species are more likely to be isolated or extirpated, which results in more biodiversity loss and, subsequently, the loss of the specialized partners needed to sustain mutualistic interactions (Gibson et al., 2013; Halley et al., 2016). More biodiversity in a larger fragment, or the intact forest, also ensures that one partner does not become too concentrated in an area, resulting in a shift toward antagonistic behaviors that harm the mutualism. Thus, relatively large fragments compared with small fragments are more likely to maintain mutualistic interactions.

When comparing the effects of fragment size in the old versus new publications, we found that new publications signaled a greater negative effect of fragment size on mutualistic interactions. Old publications had a mean effect size that was more than 3 times smaller than the new publications. It is well established that forests are becoming increasingly fragmented, with more than 70% of remaining forests now within 1 km of forest edge (Haddad et al., 2015). Additionally, species loss in forest fragments can take decades to manifest (Tilman et al., 1994; Gibson et al., 2013; Wearn et al., 2012). This lag has the potential to significantly delay the ultimate impacts of forest disturbance on biodiversity. As forest fragmentation continues to intensify (Fishcher et al., 2021), our results help demonstrate that mutualisms are one of the more sensitive groups facing the negative impacts of habitat disturbance.

When comparing all publications, fragment size affected the strength of parasitic interactions, such that parasitism increased in strength in small forest fragments relative to larger fragments. Habitat fragmentation alters the landscape to create improved conditions for some host–parasite interactions (Froeschke et al., 2013; Gillespie & Chapman, 2008). For example, forest fragmentation is expected to increase the occurrence of nest and brood parasitism because generalist nest predators are better able to enter the forest through the adjoining deforested land (Lloyd et al., 2005). Higher parasitism rates in small forest fragments compared with larger forest fragments have also been attributed to a large variety of hosts and food resources available in more heterogenous, fragmented landscapes (Monmany & Aide, 2009). Finally, small fragments may also indicate areas of higher human activity, which increases parasitism rates in wild species (Hussain et al., 2013; Mbora & McPeek, 2009).

Our updated meta-analysis highlights the importance of continuously pooling and assessing data on critically important ecological questions. We found a clear shift between old and new publications that showed that increasing global forest fragmentation may be altering key species interactions. New research must continue to expand on findings from previous analyses to refine prior conclusions and provide new insights (e.g., Zomer et al., 2014). Future investigations might consider a broader diversity of interaction types to capture the nuances of changes to mutualisms and antagonisms. Additional data from inaccessible studies may also help bolster these findings. Our results reaffirm that although forest fragmentation has varying effects on different types of ecological interactions; overall, those impacts are more negative for mutualisms than antagonisms. In addition, some antagonisms appear to be increasing in strength. The combined reduction in mutualistic interactions and increase in antagonistic interactions may accelerate the rate of ecosystem decay in fragmented forests over time. Such results show the importance of reassessing ecological questions previously answered with more limited data because the impacts of human disturbance can shift with time.

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SUPPORTING INFORMATION

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

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