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A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests

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Summary

1. Quantifying the impact of habitat disturbance on ecosystem function is critical for understanding and predicting the future of tropical forests. Many studies have examined post-disturbance changes in animal traits related to mutualistic interactions with plants, but the effect of disturbance on plant traits in diverse forests has received much less attention.
2. Focusing on two study regions in the eastern Brazilian Amazon, we used a trait-based approach to examine how seed dispersal functionality within tropical plant communities changes across a landscape-scale gradient of human modification, including both regenerating secondary forests and primary forests disturbed by burning and selective logging.
3. Surveys of 230 forest plots recorded 26,533 live stems from 846 tree species. Using herbarium material and literature, we compiled trait information for each tree species, focusing on dispersal mode and seed size.
4. Disturbance reduced tree diversity and increased the proportion of lower wood-density and smaller-seeded tree species in study plots. Disturbance also increased the proportion of stems with seeds that are ingested by animals and reduced those dispersed by other mechanisms (e.g. wind). Older secondary forests had functionally similar plant communities to the most heavily disturbed primary forests. Mean seed size and wood density per plot were positively correlated for plant species with seeds ingested by animals.
5. *Synthesis.* Anthropogenic disturbance has major effects on the seed traits of tree communities, with implications for mutualistic interactions with animals. The important role of animal-mediated seed dispersal in disturbed and recovering forests highlights the need to avoid defaunation or promote faunal recovery. The changes in mean seed width suggest larger vertebrates hold especially important functional roles in these human-modified forests. Monitoring fruit and seed traits can provide a valuable indicator of ecosystem condition, emphasising the importance of developing a comprehensive plant traits database for the Amazon and other biomes.

Sumário

1. Para melhor entender e prever o futuro das florestas tropicais é crítico quantificar o impacto de distúrbios antrópicos sobre as funções ecossistêmicas. Muitos estudos já avaliaram, após eventos de distúrbios, mudanças nas características funcionais da fauna relacionadas com interações mutualísticas com a flora. Porém, o efeito de distúrbios antrópicos nas características funcionais da comunidade arbórea de florestas megadiversas é ainda pouco estudado.

2. Este estudo focou em duas regiões distintas da Amazônia oriental brasileira, e utilizou um método baseado em características funcionais para entender como a dispersão de sementes, dentro de comunidades arbóreas, pode ser modificada ao longo de um gradiente de distúrbio antrópico, incluindo florestas secundárias e florestas primárias afetadas por fogo e corte seletivo.

3. Foram conduzidos inventários florestais em 230 parcelas de estudo, amostrando um total de 26.533 indivíduos vivos pertencentes a 846 espécies arbóreas. A partir de material depositado em herbários e informações da literatura, as características funcionais, para cada espécie arbórea, foram compiladas, focando no tipo de dispersão e no tamanho da semente.

4. Os distúrbios antrópicos reduziram a diversidade arbórea e aumentaram a proporção tanto de espécies com baixa densidade de madeira, como de espécies com sementes pequenas. Os distúrbios antrópicos também aumentaram a proporção de árvores com sementes que são ingeridas por animais e diminuíram àquelas dispersas por outros mecanismos, como o vento. Florestas secundárias em estágios mais avançados de sucessão apresentaram comunidades arbóreas funcionalmente semelhantes àquelas de florestas primárias com maior grau de distúrbios antrópicos. A nível de parcela, o tamanho médio das sementes e a densidade da madeira foram positivamente correlacionados para plantas com sementes dispersas por animais.

5. *Síntese*: Os distúrbios antrópicos influenciaram amplamente as características funcionais de sementes das comunidades arbóreas, com implicações diretas para as relações mutualísticas com a fauna. A elevada importância de animais na dispersão de sementes tanto em florestas primárias que sofreram distúrbios antrópicos assim como em florestas secundárias ressalta a importância de se evitar a defaunação e de promover a recuperação da fauna. As mudanças no tamanho médio da

largura da semente sugerem que grandes vertebrados tem um papel funcional especialmente importante em florestas antropizadas. O monitoramento de características funcionais de frutos e sementes pode prover um valioso indicador das condições de ecossistemas, enfatizando a importância da criação de uma base de dados compreensiva para a Amazônia e para outros biomas contendo características funcionais da vegetação.

Introduction

Tropical forests are of fundamental importance for global biodiversity (Barlow et al., 2018; Gibson et al., 2011; Slik et al., 2015), human livelihoods (Newton, Miller, Byenkya, & Agrawal, 2016), climate regulation (Silvério et al., 2015) and carbon storage (Pan et al., 2011), yet are increasingly under pressure from anthropogenic impacts (Malhi, Gardner, Goldsmith, Silman, & Zelazowski, 2014). The conversion of closed-canopy forests to agro-pastoral land-uses often makes global headlines because it results in massive loss of total forest area coupled with associated fragmentation effects (Nepstad et al., 2014). However, this loss occurs concurrently with the widespread but cryptic degradation of remaining primary forests through human-driven disturbances that do not lead to a complete removal of the canopy cover, such as selective logging, understory fires and hunting (Peres, Barlow, & Laurance, 2006; Sasaki & Putz, 2009). As a result, 80% of tropical forest landscapes currently exist in a modified state (Potapov et al., 2017), either as secondary forests in recovery following the abandonment of productive land uses (Chazdon et al., 2009), or as varyingly degraded primary forests (Bregman et al., 2016; Thompson et al., 2013).

The detrimental impacts of human modification on biodiversity and carbon stocks in tropical forests are increasingly well known (Barlow et al., 2016; Berenguer et al., 2014; Chazdon et al., 2009), but the effects on key ecological functions remain unclear (Chapin, 2003; Chazdon, 2003). Such effects are difficult to measure directly, but one indirect method involves assessing the ability of an ecosystem to retain species with functional traits (Petchey & Gaston, 2006; Violle et al., 2007). These traits can support key ecological processes even if species richness is reduced (Fonseca & Ganade, 2001; Peterson, Allen, & Holling, 1998; Tilman et al., 1997), and therefore provide important insights into ecosystem resilience (Nimmo, Mac Nally, Cunningham, Haslem, & Bennett, 2015). Plant functional traits have provided the key to understanding how hyperdiverse tropical forest communities respond to environmental change: for example, stem traits such as wood density are linked to drought and fire resilience (Brando, Oliveria-Santos, Rocha, Cury, & Coe, 2016; Phillips et al., 2009), while leaf traits such as specific leaf area are strongly related to plant growth rates and life spans (Poorter & Bongers, 2006). In contrast, plant reproductive traits (e.g. flowers, fruits and seeds) have received little attention, despite their importance to mutualistic interaction networks and tree recruitment in tropical forest systems.

Seed traits, such as seed mass and dimensions, are important determinants of the plant-animal interactions central to seed dispersal, yet are understudied compared to stem and leaf traits. Seed traits are yet to be considered in large-scale trait-based assessment of tropical forests (e.g. Gillespie Eco-evolutionary Models - GEMs; Delong & Gibert, 2016) or individual-based simulations of tropical forest plant communities (e.g. Traits-based Forest Simulator - TFS; Fyllas et al., 2014). Nonetheless, there is growing evidence that seed traits are likely to respond to human disturbance, with implications for ecological processes linked to rainforest stability and resilience (Galetti et al., 2013). For example, tropical forests can experience an increase in the number of abiotically-dispersed pioneer species and a reduction in the number of large-seeded animal-dispersed species when habitat is fragmented (Laurance et al., 2006) or key seed dispersing animals are hunted out (Terborgh et al., 2008). These changes may be mirrored in selectively logged or wildfire-affected forests (Barlow & Peres, 2008; Cochrane & Schulze, 1999; Gerwing, 2002; Slik, Verburg, & Keßler, 2002) where compositional shifts converge towards early successional communities (Berenguer et al., 2014, 2018). The negative outcomes of forest disturbance are partially reversed by succession in secondary forests, which become functionally more similar to primary forests over time (Arroyo-Rodríguez et al., 2017; Howe, 2016).

Changes in plant traits can be mediated through interactions with fauna, as many tropical forest vertebrates depend upon fruit as a food resource (e.g. Bregman, Sekercioglu, & Tobias, 2014), and the vast majority of neotropical plants rely on animals to disperse their seeds (Fleming & Kress, 2011; Howe & Smallwood, 1982). The loss of large-bodied frugivorous taxa is associated with altered composition of plant communities and an increase in abiotically dispersed species across tropical Africa, Asia and the Americas (Bovo et al., 2018; Harrison et al., 2013; Peres, 2000; Terborgh et al., 2008; Wright, 2003; Wright, Hernandéz, & Condit, 2007). Two large-scale assessments have linked this to reductions in above-ground vegetative biomass, based on the weak positive association typically found between larger seeds and higher wood density species (Bello et al., 2015; Peres, Emilio, Schietti, Desmoulière, & Levi, 2016), although this relationship varies geographically across Amazonia (ter Steege et al., 2006).

Despite clear evidence of the importance of dispersal mode and seed traits, we still lack a large-scale understanding of variation in these traits across human-modified tropical landscapes, where floral composition is a complex product of the direct effects of human-induced changes to forest structure (logging or fire-induced mortality) and landscape configuration (edge effects, reduced habitat patch size, increased isolation), and the indirect effects of defaunation and changes in seed dispersal and predation – all of which may be magnified or ameliorated by feedbacks inherent in the fruit-frugivore mutualism (Ganzhorn, 1995). As such, a large-scale assessment of dispersal mode and seed traits can provide important insights into the functional status of human-modified tropical forests, their potential resilience, and policy interventions that may enhance recovery.

We address this knowledge gap by analysing the dispersal mode and seed size of over 26,000 stems measured in 230 0.25 ha plots across two landscapes in the Brazilian Amazon. Plots were spread across forest classes that encompass disturbed and undisturbed primary forests, and a chronosequence of secondary forests that have previously been completely clear cut. First, we ask, how disturbance within primary forests and the process of succession within secondary forests affects the relative frequency of seed dispersal modes (see Table S1 for definitions). Second, we test how plot-level seed size in human-modified Amazonian forests compares to undisturbed forests. We focus on seed size in gut-dispersed species because of the importance of its relationship with gape size in frugivores (Levey, 1987; Wheelwright, 1985). Third, we examine whether any variation in dispersal mode and seed traits can be explained by our measures of disturbance history, landscape configuration, and local environment. Finally, we examine the strength of the relationship between seed size and wood density, a widely used stem trait that is strongly related to disturbance and recovery (Berenguer et al., 2018) and is of critical importance for timber stocks and carbon storage (Baker et al., 2004; Chave et al., 2006). The strength and direction of the relationship between wood density and seed size is central to simulated models of defaunation and carbon stocks (Bello et al., 2015; Peres et al., 2016; Wright et al., 2007), but these links have not been assessed in primary forests affected by either selective logging or understorey fires, nor in regenerating secondary forests that have been previously clear cut.

Materials and methods

Study sites

Forest inventories were conducted in the municipalities of Paragominas (PGM; 2°59'S, 47°21'W) and Santarém-Belterra-Mojuí dos Campos (STM; 2°26'S, 54°42'W), Pará state, in the eastern Brazilian Amazon. The availability of a gradient of varyingly-disturbed primary and varyingly-aged secondary (6-22+ years) forests at the landscape scale, coupled with the diverse range of native fruit-frugivore interactions, makes these two regions an ideal setting to investigate how human modification of forests affects plant functional traits related to seed dispersal. In each region, 18 drainage catchments (mean area ± SD = 4,667.6 ± 752.2 ha) were selected along a deforestation gradient, with forest cover ranging from 6% to 100% in each catchment (Gardner et al., 2013). Within each catchment, 0.25 ha plots (250 x 10 m) were distributed in proportion to the prevailing land uses (i.e. a catchment with more forest cover had more study plots). A total of 230 plots (57.5 ha) were surveyed across the two regions (PGM: 120, STM: 110; Table 1) in 2010 and 2011. No signs of pre-Columbian settlements, such as *terra pretas* (McMichael et al., 2012), were found in any of our plots (Berenguer et al., 2014).

All plots were located in evergreen *terra firme* forests at least 1500 m apart and at least 100 m from forest edges to reduce edge effects (M Tabarelli, Lopes, & Peres, 2008). See Gardner et al. (2013) and Berenguer et al. (2014) for a study site map and further explanation of sampling design. A combination of physical evidence and Landsat images (see Berenguer et al., 2014 for details) was used to assign each plot to one of six different forest classes along a disturbance gradient: undisturbed primary (U); disturbed primary – burned (D_B); disturbed primary – logged (D_L); disturbed primary – burned-and-logged (D_BL); secondary – old [>20 years] (S_O); and secondary – young [≤20 years] (S_Y). Within each plot, all live tree stems (including palms) ≥ 10 cm diameter at breast height (DBH) were measured, identified by experienced botanists, and, in case of doubt, samples were compared with reference material in the regional herbaria of Embrapa Amazônia Oriental and the Museu Paraense Emílio Goeldi, Belém, Brazil. A total of 26,533 stems were measured (PGM: 14,063, STM: 12,470; Table 1) and 99.4% of all stems were identified to species level. We excluded 39 Brazil nut tree stems (*Bertholletia excelsa* H. & B., Lecythidaceae) from the secondary forest plots as their very large diameters suggested they were uncut during the clear-cur process due to legal protection. Tree species were classified into families according to the APG III system (APG III, 2009). Nomenclature was verified and standardised using The Plant List (2013).

Trait measurements

We collected data on a range of fruit and seed traits of relevance to seed dispersal from a combination of herbarium collections, scientific literature and online databases. We included a total of 24,400 records (15,693 fruit; 8,707 seeds) from individually examined specimens (recording lengths and weights) at three of the most important herbaria in the Brazilian Amazon: (1) Embrapa Amazônia Oriental, Belém, (2) Museu Paraense Emílio Goeldi, Belém, and (3) Orsa Florestal, Monte Dourardo (Table S2). We also extracted fruit trait data from literature sources (see Table S3 for details), including six books and nine journal articles, in addition to literature sources contained within Frubase (Jordano, 1995). Further records were obtained for 201 species using online sources including the Kew Seed Information Database (SID; http://data.kew.org/sid/) and the New York Botanical Garden (NYBG) C. V. Starr Virtual Herbarium (http://sweetgum.nybg.org/science/vh/). Full details of fruit and seed traits compiled, as well as measurement protocols, are provided in Table S4.

Where available in each source, we recorded information on dispersal mode, fruit type, dehiscence, presence of fleshy tissue or aril, fruit colour, fruit shape, fruit dimensions, fruit mass, seed shape, seed colour, seed dimensions, seed mass, number of seeds, diaspore type, and animal dispersers (Table S3). Dispersal modes from the literature were collapsed to the following categories: (1) endozoochorous (gut-dispersed) *sensu stricto* (i.e. definite endozoochory); (2) endozoochorous (gut-dispersed) *sensu lato* (i.e. possible endozoochory); (3) eynzoochorous (scatter-hoarded); and (4) non-zoochorous

(Table S1). In cases where the dispersal mode was not stated or ambiguous (~10% of species, 5% of stems), we used functional traits to assign fruits to a predominant dispersal mechanism (Thomson et al., 2010; van der Pijl, 1982). Only 17 species (2.0%) and 489 stems (1.8%) were unclassified in terms of dispersal mode, and only 22 species (2.6%) and 466 stems (1.8%) unclassified for fruit type.

Fruit and seed dimensions (length, width and depth) and mass were treated as continuous variables. We focused on seed width (defined as the maximum distance along a plane passing through the second-longest axis) in gut-dispersed endozoochorous species (using the '*lato*' definition of possible endozoochory) as the most appropriate measure of seed size because our question regarding the effects of disturbance and recovery upon seed size is based on the association between seed size and the gape size of animal dispersal agents (Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016; Donoso, Schleuning, García, & Fründ, 2017; Mazer & Wheelwright, 1993; Wheelwright, 1985). This approach was further supported by the positive relationships between seed width and dry seed mass, and other dimensions of both seeds and fruits (i.e. length, weight) for subsets of the species where more than one dimension was available (Figure S1). Furthermore, although dry seed weights provide a good indicator of resources available for seedling establishment (Leishman & Westoby, 1994), seed width is less likely to be affected by water content. We obtained a seed width value for 771 (94.8%) of endozoochorous tree species (PGM: 596, STM: 686), and for 25,491 (96.1%) of tree stems.

In addition to data on fruit and seed traits, we extracted wood density data for tropical South America from the Global Wood Density Database (Zanne et al., 2009). For stems not identified to species level (0.6%), we used the mean seed width dimensions and wood densities for the appropriate genus or family, accordingly, and for unidentified stems (<0.2%) we used mean dimensions across all stems in the same vegetation plot (see Berenguer et al., 2014 for details).

Data analyses

To assess variation in plant traits across human-modified tropical forests, we calculated the proportion of stems in each study plot that belonged to each broad category of seed dispersal mode and fruit type (Table S1). We used a chi-squared test (Type II Wald) with Tukey comparisons to evaluate differences in the proportion of stems per plot in each seed dispersal and fruit type category across the different forest classes, and also the number of species per plot in each seed dispersal category. We used an ANOVA to similarly test differences in seed width. To assess variation in (a) the proportion of endozoochorous stems (*sensu lato*) per plot, and (b) seed width amongst endozoochorous species across forest disturbance classes, we used generalised linear mixed models (GLMMs) with binomial or Gaussian distributions for proportional and seed width data, respectively. To account for potential spatial autocorrelation and biogeographic differences, we included 'catchment' as a nested random factor and examined correlograms of Moran's I against distance. We adjusted all binomial models that showed overdispersion by adding an observation-level random effect (Bolker et al., 2009; Harrison, 2015). For species count data, we used a negative binomial distribution because there was high overdispersion with a Poisson distribution. To assess any disproportionate influence of palms, we repeated the GLMMs excluding palm stems (14 species, 409 individuals).

We used basal area as our main proxy for both primary forest disturbance and secondary forest recovery, because forest biomass (which is largely defined by stem basal area; Berenguer et al., 2015) increases over time in secondary and disturbed primary forests (Ferreira et al., 2018; Lennox et al., 2018) while basal area declines with the intensity of edge effects, selective logging and wildfires (Berenguer et al., 2014). Potential predictors were selected from a comprehensive range of environmental variables (Berenguer et al., 2014; Gardner et al., 2013) to cover both local and landscape-level conditions: basal area, soil clay content, distance to nearest primary forest edge, plot slope, surrounding area of primary forest cover, and surrounding area of undisturbed primary forest cover (Table 2). We constructed separate models for disturbed and secondary forest plots because two of the landscape level variables (edge distance and undisturbed forest cover) were not relevant for secondary forest patches and were therefore calculated only for primary forests. All combinations of first-order models were ranked using Akaike Information Criteria (AICc) values for small samples sizes, averaging all models with ΔAICc < 4.0 and calculating the relative importance of each predictor variable by summing AICc weights (Burnham & Anderson, 2002). We also present diversity results to explore whether ecosystem function tracks or precedes species loss (SI Methods). Finally, we tested for relationships between seed width and wood density (and basal area), both at the community level (using mean values per plot weighted by individual density) and species level (using mean values per species).

All analyses were conducted in R version 3.3.2 (R Core Team, 2016); models were built using the packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015), *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017), and *glmmTMB* (Brooks et al., 2017), and model selection was conducted using the package *MuMIn* (Bartoń, 2016). We standardised the continuous explanatory variables using the *sta* function from the package *vegan* (Oksanen, Blanchet, & Kindt, 2013) and checked the adjustment of all models using the package *DHARMa* (Hartig, 2019). We conducted the Moran's I tests and correlograms using the *spdep* (Bivand & Wong, 2018) and *ncf* (Bjørnstad, Ims, & Lambin, 1999) packages.

Results

Prevalence of dispersal modes and fruit types

We sampled a total of 26,533 live tree stems ≥ 10 cm DBH distributed across 230 forest plots, including 846 species from 293 genera in 72 families (Table 1). Animal-dispersal (zoochory) was the dispersal mode for the majority of both species (720; 85.1%) and stems (22,578; 85.1%; Table S5). Gut-dispersal (endozoochory) comprised the majority of these, and levels of endozoochory (*sensu lato*) were significantly higher in secondary forest plots, and primary forest plots that were both burned and logged, compared to undisturbed primary forest ($\chi^2 = 69.45$, $p<0.001$; Figure 1). The most common fruit types were berry-like, capsule-like and drupe-like, with the relative proportion of all fruit types varying significantly across forest classes (Figure S2). When compared to undisturbed forests, disturbed primary and secondary forest plots often contained elevated levels of compound fruits (e.g. Moraceae, Siparunaceae, Urticaceae) and syncarpia (e.g. Annonaceae), and reduced levels of berries and capsules. The number of gut dispersed species across forest classes (Figure S3) closely matched the pattern for overall species richness (Figures S4-5).

Seed size in endozoochorous stems

Our use of seed width as an overall indicator of seed size was supported by strong positive relationships across species between fruit weight and length, and seed weight and length, based on our measurements of carpotec specimens (Figure S1A-D), and between seed weight and seed length using measurements from literature sources (Figure S1E). The seed width of gut-dispersed tree stems was significantly lower in secondary and disturbed burned-and-logged primary forests than in undisturbed primary forests (ANOVA: $F_{5, 244} = 32.7$, $p<0.001$), and significantly lower in young secondary forests than in all disturbed forests (Figure 1). Mean seed width was significantly smaller in burned-and-logged forest than in forest that had been either logged only or burned only but old secondary forests were not significantly different from either young secondary forests or burned-and-logged forests.

Drivers of change in dispersal mode and seed size

Basal area - our main proxy for forest condition (Figures S6-7) - was the only significant variable influencing the proportion of endozoochorous-dispersed stems, with a strong negative effect in models for primary forests (Figure 2A). Basal area was also the most important variable influencing seed width, with a strong positive effect in models for disturbed primary forests (Figure 2C). Local variables, including soil clay content and slope, and landscape variables, including the proportion of primary and undisturbed forest within 1 km buffers, had weak and non-significant effects in all models. We found no significant spatial autocorrelation overall; in all models tested, the correlograms showed a few distance classes with significant spatial autocorrelation (Figure S8) but these classes were not enough to create a significant spatial bias in our mixed model frameworks (Table S6). Results were unaffected when excluding palm stems from the analyses (Figure S9), with the exception of clay becoming a significant predictor of the proportion of endozochorous-dispersed stems in secondary forests (Figure S9, panel B).

Relationships between functional traits

The mean value of wood density across forest classes was qualitatively similar to mean seed width (Figure S10) and was significantly lower in disturbed primary and secondary forests than in undisturbed primary forests. The similarity of the responses of wood density and seed width was reflected by a strong positive relationship (Pearson's: $r = 0.84$, $p<0.001$) between their plot-level mean trait values for the endozoochorous species – but this relationship was not significant for synzoochorous species and was negative for non-zoochorous species (Figure 3D-F). Species-level correlations between seed width and wood density were much weaker, and also varied according to seed dispersal mode (Figure 3A-C).

Discussion

Our results demonstrate that the effect of tropical forest disturbance extends beyond species loss to include changes in the prevalence of functional traits related to seed dispersal. In particular, through our focus on plant traits, we found that, counterintuitively, disturbance lead to tree communities in which a greater proportion of species and individuals rely on animal dispersal – but with a loss of functional breadth, and a significant shift towards small-seeded species. This complex process of community disassembly following forest degradation from e.g. fire and logging is contrasted by the reassembly observed in secondary succession. We discuss our results on the effects of disturbance and recovery on seed dispersal modes and seed size in terms of implications for both frugivores and forest resilience.

What does an altered seed dispersal network mean for disturbed forest recovery?

Our results show that human disturbance has led to a shift in both dispersal mode and seed traits in these tropical forests. There are likely to be multiple drivers of these changes. For example, hunting can reduce seed dispersal by large birds and mammals (Terborgh et al., 2008), and there may be an interaction between structural disturbance and hunting pressure. Selective logging may also influence patterns, as many of the valuable timber species such as *Manilkara* spp., *Brosimum* spp have endozoochorous fruits. However, other valuable species such as *Dinizia excelsa* are not animal dispersed (Peres & Van Roosmalen, 2002; Rosin, 2014). Isolating these disturbance-specific relationships will likely be difficult in human-modified landscapes where forests are responding to multiple drivers of change.

While there was a positive influence of secondary forest stage on seed widths, these remained far below the seed widths in primary forests even after more than 20 years of succession. There are three reasons that could explain this pattern. First, an increase in the dispersers of small-seeds could lead to an increased recruitment of small-seeded trees in forests after human disturbance. Many small-bodied frugivore taxa are common in disturbed forests (Lopes & Ferrari, 2008; Medellín, Equihua, & Amin, 2000), e.g. both bats and birds are known to be particularly important seed dispersal agents of key pioneer tree species such as *Cecropia* spp. and *Vismia* spp. (Medellin & Gaona, 1999), and small frugivorous birds have been shown to increase in abundance after a single wildfire, feeding off and helping disperse the abundant small-seeded Rubiaceae and Melastomataceae that dominated the understorey (Barlow & Peres, 2004).

Second, the lack of larger-seeded fruiting species could fail to attract the largest dispersers – preventing the immigration of zoochoric large-seeded species which are known to rely upon large-bodied frugivores as seed dispersal agents (Doughty et al., 2016; Galetti et al., 2018), and even limiting their effective dispersal if present. This introduces a possible destabilising feedback where changes in plant communities negatively impact animal communities, and those impoverished animal communities subsequently lead to further alteration of plant communities. With simultaneous losses in both plant and animal communities, future ecosystem function could appear appropriately balanced but this perspective would ignore the problem of the shifting baseline. Considering that intact baseline is crucial to more fully address the concept of resilience i.e. maximising the scope for current and future recolonization of degraded areas by primary forest species. Third, our focus on dispersal traits in stems >10cm DBH means we may have missed the presence of slow-growing large-seeded species that have not yet met the size threshold for inclusion. Indeed, the successional trajectory of forest recovery means that these smaller stems often hold wood density values closer to primary forests than larger stems (Berenguer et al. 2018), suggesting that a more detailed assessment of the dispersal traits of small stems would provide additional insights into secondary forest recovery.

Of course, we have only examined one side of the complex seed dispersal network, and have not considered other components that determine successful plant recruitment such as Janzen-Connell effects (Connell, 1971; Janzen, 1970) or edge effects (Marcelo Tabarelli, Lopes, & Peres, 2008). Spatial scale is likely to be important; faster colonisation of dispersal-limited species might be expected in secondary forest patches surrounded by primary forest. However previous land-use intensity is also key (Jakovac, Peña-Claros, Kuyper, & Bongers, 2015), and can be even more important than distance to mature forest (Fernandes Neto, Costa, Williamson, & Mesquita, 2019). The implications for seed dispersal are also complicated by potential trophic cascades and the relative effectiveness of seed dispersal agents across different plant species (Schupp, Jordano, & Gómez, 2010). This includes consideration of the importance of rodents as seed predators (Wright et al., 2000), with evidence that smaller-seeded species are less protected from rodents (Dirzo, Mendoza, & Ortíz, 2007; Fricke & Wright, 2016). The continuing challenge in interpreting the effects of disturbance on seed dispersal is to disentangle these dual, interacting effects upon plant and animal communities (Poulsen, Clark, & Palmer, 2013). Although more narrowly defined seed dispersal modes may allow more precise insights into the effect of disturbance on tropical flora, this remains very challenging due to the substantial degree of overlap in generalist fruit-frugivore networks (Bascompte & Jordano, 2007) and the continued shortage of information on what constitutes effective seed dispersal (Howe, 2016).

Will disturbed forests help conserve Amazonia's diverse frugivorous fauna?

Fruits and seeds represent a key resource for a wide range of vertebrate taxa in tropical forests, including bats (Muscarella & Fleming, 2007), birds (Kissling, Böhning-Gaese, & Jetz, 2009), fish (Goulding, 1980; Horn et al., 2011), primates (Hawes & Peres, 2014a), reptiles (Valido & Olesen, 2007) and ungulates (Bodmer, 1990), and these resources are partitioned to some degree amongst frugivore taxa (Gautier-Hion et al., 1985; Hawes & Peres, 2014b). The high proportion of smaller-seeded stems producing endozoochorous fruits in disturbed primary and secondary forests reinforces the suitability of these forests for smaller-bodied taxa such as small passerine birds and bats (Edwards, Massam, Haugaasen, & Gilroy, 2017; Medellin & Gaona, 1999; Muscarella & Fleming, 2007). However, it is not clear if these small seeded resources can sustain large-bodied frugivores specialising on large-seeded plants; although these species can naturally ingest both small and large seeds, and the relationship between animal body mass and the average size of ingested seeds may not always be positive (Chen & Moles, 2015), there may be a size threshold under which it becomes inefficient to eat small fruits. Moreover, large-bodied frugivores may face other environmental filters (such as branch connectivity and strength) that prevent them from moving through or foraging in disturbed or secondary forest.

Will changes in plant traits influence carbon storage?

Animal-plant interactions have an important but hitherto neglected influence on carbon cycling (Schmitz et al., 2018), and large-scale models have simulated the loss of carbon stocks under defaunation in undisturbed forests (Bello et al., 2015; Peres et al., 2016). Our results lend some support to this, as the relationships between seed size and the wood density at the plot level were very strong. However, these were far weaker at the species level – suggesting that while disturbed primary and regenerating secondary forests have lower values for wood density and smaller seeds, the similarity in response is driven by the relative abundance of species in plots (Chapin, 2003) rather than any clear trade-offs in these traits at the species level (e.g. Díaz et al., 2016). This is interesting because it suggests that it is not just the change in community composition, through the loss or gain of particular plant species, that drives changes in a particular trait, but rather the more complex changes in community structure. This shift in the community structure of disturbed primary forests, with a time-lagged turnover from disturbance-sensitive species to disturbance-tolerant species (Edwards et al., 2011; Moura et al., 2014), and associated changes in particular functional traits (including fruit and seed traits), means that ecosystem function can be heavily impacted, even if species richness is maintained at close to pre-disturbance levels.

The strength of this association between wood density and seed size raises the possibility that any processes that limit the dispersal of large-seeded species could negatively influence the recovery of high wood density forests. This could have longer term implications for both the carbon storage and drought sensitivity of forests: wood density is the most important predictor of carbon storage in forest after tree size (Chave et al., 2006) and a key determinant of drought sensitivity (e.g. Phillips et al., 2009). While we do not have enough data to examine these issues in detail, the potential influence of defaunation on the post-disturbance recovery trajectory of disturbed tropical forests (Bregman et al., 2016) represents a crucial research aim given very few primary forests in the eastern Amazon have escaped some degree of disturbance (Barlow et al., 2016; Tyukavina, Hansen, Potapov, Krylov, & Goetz, 2016) and the growing importance of secondary forests (Vieira, Gardner, Ferreira, Lees, & Barlow, 2014). While uncertainty remains, it is therefore prudent (from both biodiversity and carbon storage perspectives) to maintain intact forests, including extensive unlogged areas (Barlow et al., 2016; Watson et al., 2018).

Conclusions

Our results demonstrate that tropical forest disturbance has pervasive effects that extend beyond the loss of species richness, and include major implications for seed dispersal and mutualistic networks. In particular, disturbance drives a significant shift in tree communities towards small-seeded species, with an increased proportion of species and individuals relying on animal dispersal. Similar effects are observed in secondary forests recovering from clear-felling, with older secondary forests having plant communities comparable to those found in the most heavily disturbed primary forests. These findings highlight the importance of developing a more comprehensive plant traits database that goes beyond leaf and stem traits to consider seasonal or reproductive traits (flowers, fruits and seeds). They also suggest that animal-plant interactions could provide new insights into ecosystem function and resilience in human-modified tropical forests.

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Author contributions

JB and ICGV conceived this study; EB collected field data; AC, JAT, AW and ICGV collected or coordinated lab data; JEH and AW collected literature data; JEH, LFSM and JB analysed the data;

JEH and JB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.kd51c5b2g (Hawes et al., 2020). Fruit and seed measurements from herbarium collections were also contributed to the TRY Plant Trait Database (Kattge et al., 2020).

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Tables

Table 1. Number of plots (N) surveyed and numbers of stems and species of live tree ≥ 10 cm DBH per region in each forest class.

Forest class	**Paragominas**			**Santarém**		
	N plots	Stems	Species	N plots	Stems	Species
Undisturbed primary	13	1,829	271	17	1,996	363
Disturbed primary						
Burned	0	0	0	7	790	260
Logged	44	5,473	460	26	3,118	498
Burned-and-logged	44	5,167	390	24	2,799	418
Secondary						
Old (>20 years)	5	581	107	20	2,516	276
Young (≤20 years)	15	1,013	142	17	1,251	150
Total	**120**	**14,063**	**607**	**110**	**12,470**	**701**

Table 2. Summaries of the environmental variables used in this study; further details of sampling methods are described in Gardner et al. (2013) and Berenguer et al. (2014).

Code	Variable	Proxy for	Methodology	Sample scale	Models
BA	Basal area	Forest age/disturbance		Plot	Disturbance, Recovery
CC	Clay content	Soil conditions	Soil granulometry using densimeter	Plot	Disturbance, Recovery
ED	Edge distance	Local landscape context		Plot	Recovery
S	Slope	Soil conditions		Plot	Disturbance, Recovery
PF	Primary forest cover (including disturbed forests)	Forest condition	Vegetation classification based on LANDSAT imagery	1 km radius buffer around each transect	Disturbance, Recovery
UF	Undisturbed forest cover (no evidence of logging or wildfires)	Land-use history/wider landscape context	Vegetation classification based on LANDSAT imagery	1 km radius buffer around each transect	Recovery

Figures

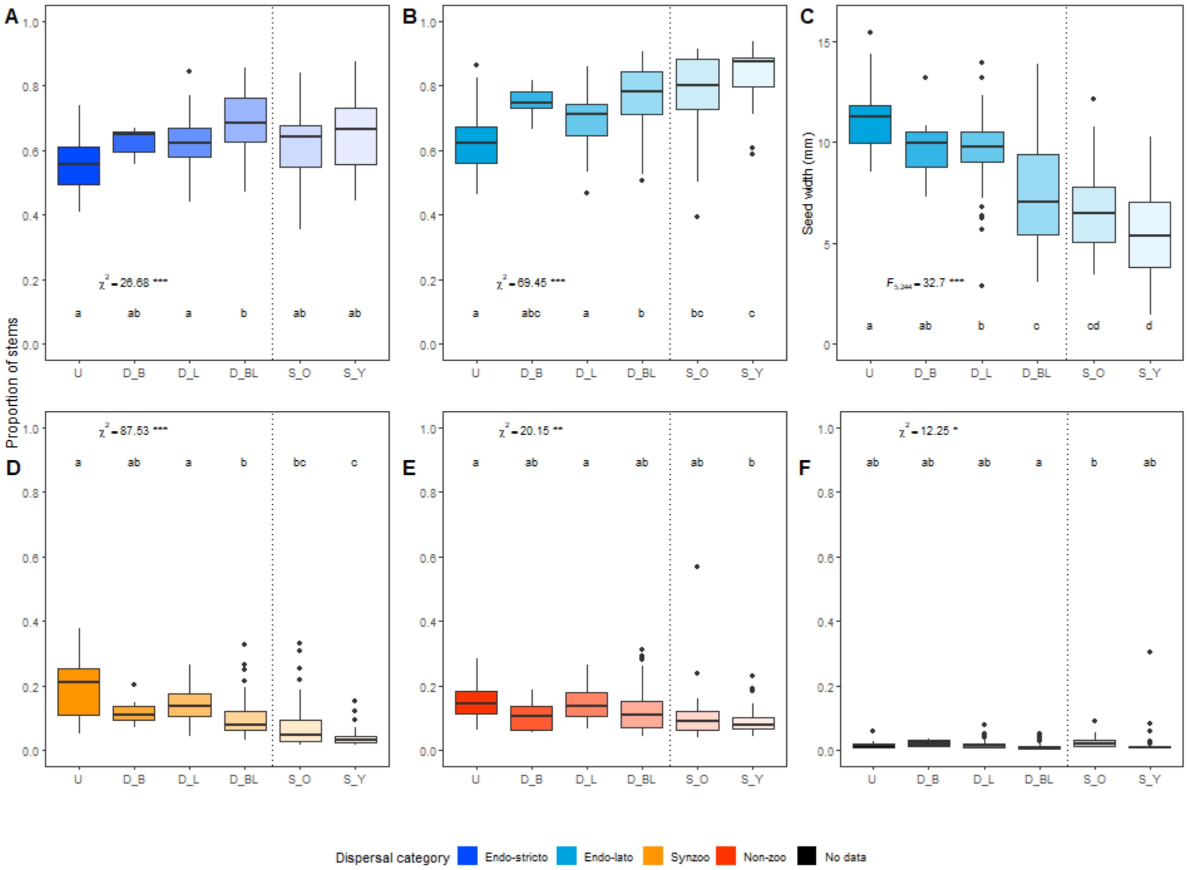

Figure 1. Proportion of tree stems (N = 26,533) per dispersal category (A-B, D-F), and mean seed width (mm) for endozoochorous (*lato*) stems (C), sampled across forest classes in both study regions (N = 230 plots). Shading represents forest classes along the disturbance gradient: U = undisturbed; D_B = disturbed – burned; D_L = disturbed – logged; D_BL = disturbed – burned-and-logged; S_O = secondary – old; and S_Y = secondary – young. Boxplots represent first and third quartiles, whiskers extend up to 1.5 times the inter-quartile range, points beyond are plotted individually, letters above represent Tukey subsets, significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

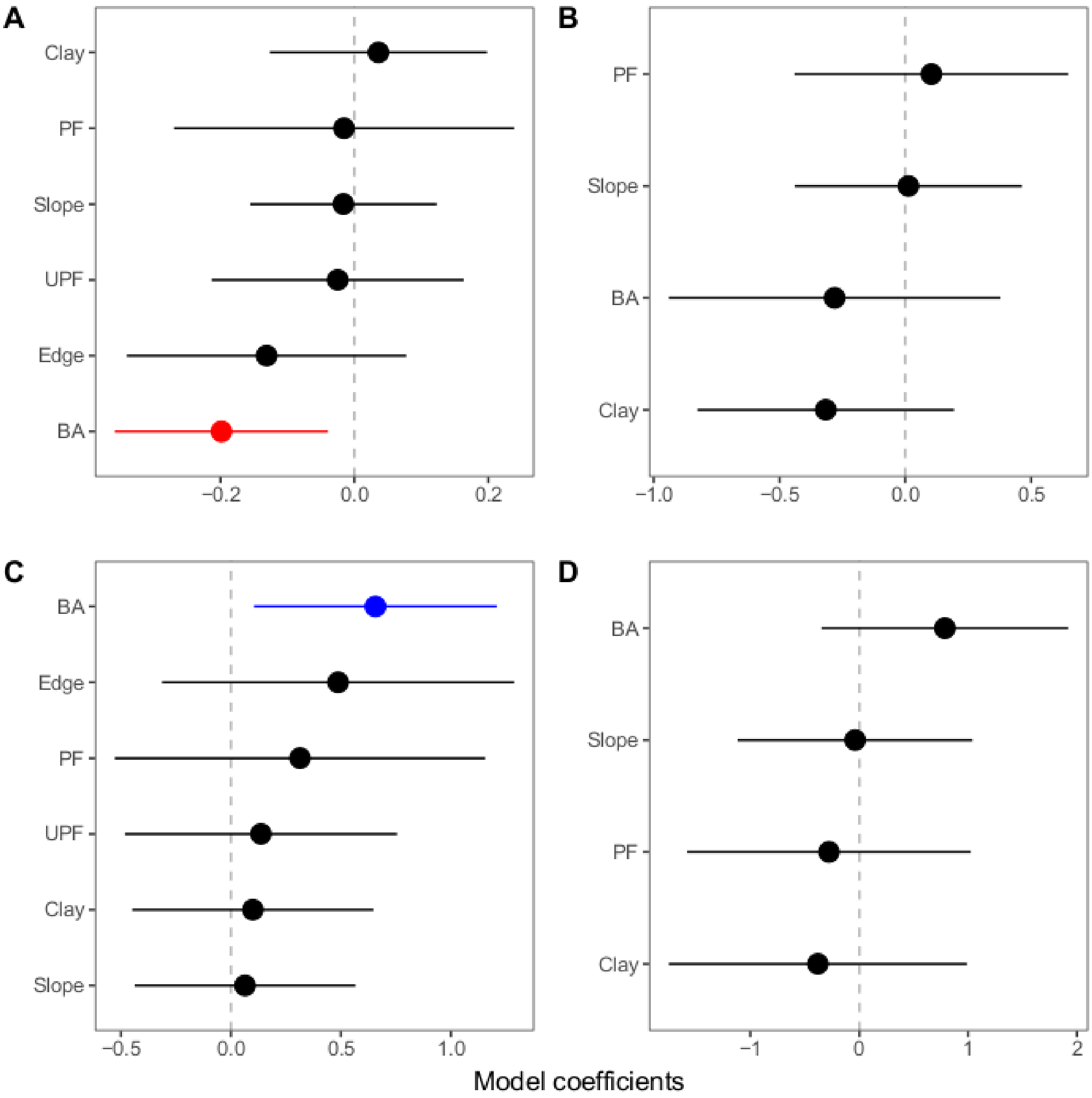

Figure 2. Coefficients (± 95% CIs) from model averaging process (all candidate models with ΔAICc < 4.0 and with standardised predictors) for the mean percentage per forest plot of all live trees ≥ 10 cm DBH that have an endozoochorous (*lato*) dispersal mode in (A) disturbed primary and (B) regenerating secondary forests, and the seed width (mm) for those endozoochorous trees ≥ 10 cm DBH in (C) disturbed primary and (D) regenerating secondary forests. BA = basal area, Clay = clay proportion of soil, Edge = distance to forest edge, PF = % primary forest within a 1 km radius, Slope = slope of terrain, UPF = % undisturbed forest within a 1 km radius.

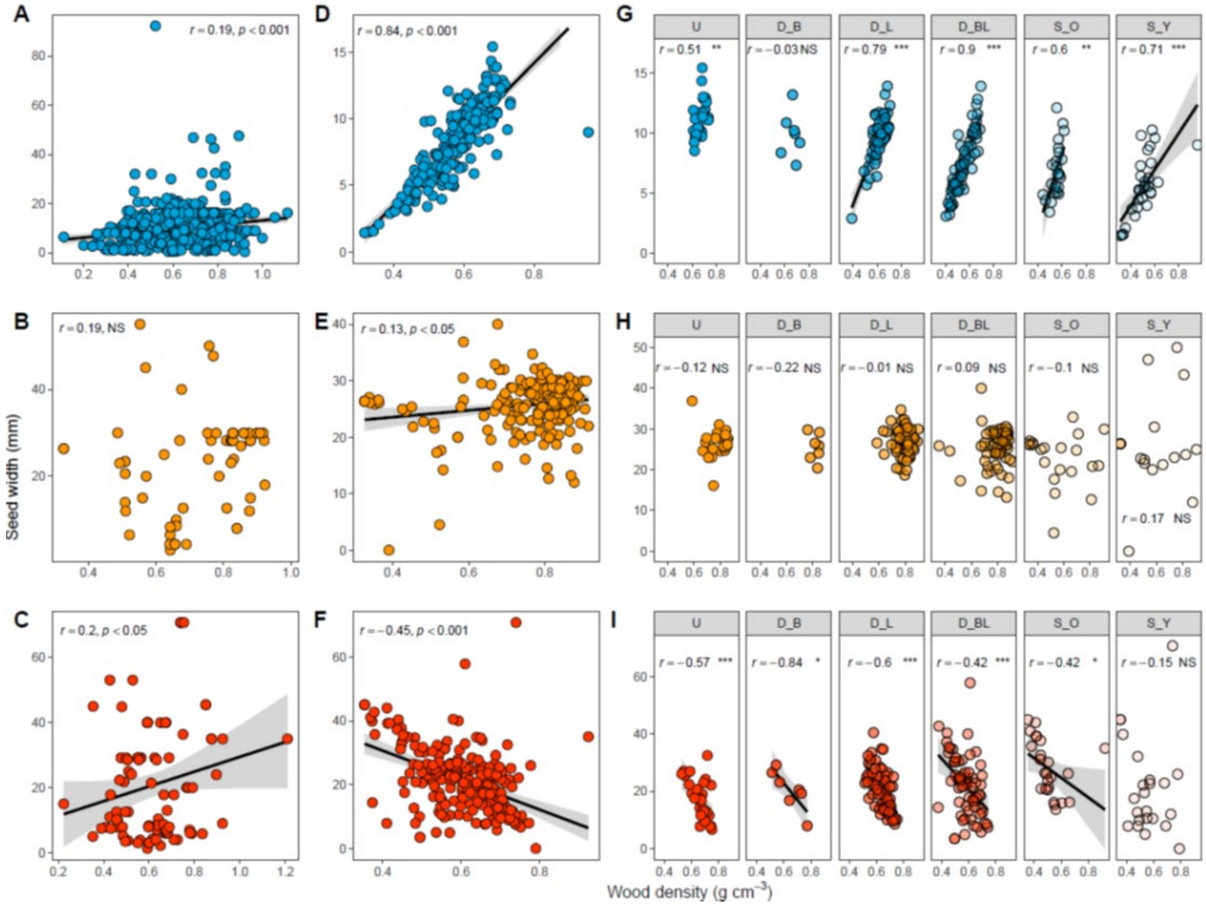

Figure 3. Relationships between seed width (mm) and wood density (g cm^{-3}) for individual tree species (A, B, C), mean values across all forest plots (D, E, F), and for plots in each forest class (G, H, I): U = undisturbed; D_B = disturbed – burned; D_L = disturbed – logged; D_BL = disturbed – burned-and-logged; S_O = secondary – old; and S_Y = secondary – young. Colours represent dispersal categories: blue = endozoochorous (*lato*), yellow = synzoochorous, and red = non-zoochorous trees ≥ 10 cm DBH. For significant correlations (Pearson's, *r*), lines and shading represent linear models with 95% confidence intervals, significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.