Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests

Authors: Tom P. Bregman[1,2*], Alexander C. Lees[3,4,5], Hannah E. A. MacGregor[1,6], Bianca Darski[7,8], Nárgila G. de Moura[4,5], Alexandre Aleixo[5], Jos Barlow[5,9], Joseph A. Tobias[1,10*]

Affiliations:

[1] Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK.

[2]Global Canopy Programme, 23 Park End Street, Oxford, OX1 1HU, UK.

[3]Division of Biology & Conservation Ecology, School of Science & the Environment, Manchester Metropolitan University, Manchester, M1 5GD, UK.

[4]Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca NY 14850, USA.

[5]Departamento de Zoologia, Museu Paraense Emílio Goeldi, Caixa Postal 399, Belém, Pará, CEP 66040‑170, Brazil.

[6]School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania, 7001, Australia.

[7]Curso de Pós-graduação de Zoologia, Universidade Federal do Pará/Museu Paraense Emílio Goeldi, Caixa Postal 399, Belém, Pará, CEP 66040-170, Brazil.

[8]Programa de Pós-graduação em Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil.

[9]Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK.

[10]Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot, Berkshire, SL5 7PY.

*To whom correspondence should be addressed. E-mail:

tpbregman@gmail.com; j.tobias@imperial.ac.uk

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Abstract

Vertebrates perform key roles in ecosystem processes via trophic interactions with plants and insects, but the response of these interactions to environmental change is difficult to quantify in complex systems, such as tropical forests. Here we use the functional trait structure of Amazonian forest bird assemblages to explore the impacts of land-cover change on two ecosystem processes: seed dispersal and insect predation. We show that trait structure in assemblages of frugivorous and insectivorous birds remained stable after primary forests were subjected to logging and fire events, but that further intensification of human land-use substantially reduced the functional diversity and dispersion of traits, and resulted in communities which occupied a different region of trait space. These effects were only partially reversed in regenerating secondary forests. Our findings suggest that local extinctions caused by the loss and degradation of tropical forest are non-random with respect to functional traits, thus disrupting the network of trophic interactions regulating seed dispersal by forest birds and herbivory by insects, with important implications for the structure and resilience of human-modified tropical forests. Furthermore, our results illustrate how quantitative functional traits for specific guilds can provide a range of metrics for estimating the contribution of biodiversity to ecosystem processes, and the response of such processes to land-cover change.

1. Introduction

Tropical forests supply a wide array of goods and services to humanity, and are integral to the long-term stability of global air quality, climate and biogeochemical cycles [1]. In turn, the health of tropical forests is underpinned by biodiversity, particularly because more than 90% of tropical woody plant species depend on animals to disperse their seeds [2], a classic case of a 'biodiversity service' vital for the long-term delivery of core ecosystem services [3]. Thus, sustainable management of tropical forests should not be solely restricted to preserving tracts of habitat, but must also target the interactions among animal and plant species that are key to ecosystem function and resilience.

The dominant threat to the world's tropical forests and their biodiversity is land-cover change [4], with negative impacts likely to escalate rapidly over the next century, driven by the projected growth of human populations and rising demand for energy, timber, food and other agricultural products [5, 6]. The resulting loss and degradation of primary forests typically reduces species richness, and increases biological homogenization, across a wide range of taxonomic groups [7-11]. However, it is becoming increasingly clear that the raw number and even heterogeneity of species surviving in communities may be poor indices of functional aspects of biodiversity [12, 13], including the trophic interactions needed to maintain recruitment and gene flow in rainforest trees [14, 15]. Consequently, the implication of land-cover change for the health and stability of tropical forest ecosystems, and their ability to recover from human-driven perturbations, is still largely unclear [16-18].

One way of addressing this problem is to focus on ecological traits associated with ecosystem processes. The standard approach uses dendrogram-based metrics,

such as functional diversity [19], to capture the range of ecological traits present in a community of species. This technique has revealed that increasing habitat disturbance may cause declines in functional diversity by eliminating species with distinct ecological traits [20-22], or else reduces functional redundancy by lowering the number of species performing similar roles within the ecosystem [23, 24].

While these findings highlight the effects of environmental change on biodiversity and the functional trait structure of ecological communities, there is currently a limit to what can be inferred about ecosystem processes. For instance, most previous studies of functional diversity pool all functional groups (e.g. dietary groups) together within total communities, making it difficult to draw conclusions about any specific process [20, 25], particularly as the impacts of land-cover change vary across such groups [26, 27]. Likewise, most previous studies are unidimensional in that they pool together multiple functional traits despite contrasting functions (e.g. diet, dispersal, etc.), making it difficult to tease apart the effects of land-cover change on different processes [28, 29]. Finally, the interpretation of previous studies is hampered by their use of functional trait categories, which are often relatively crude (e.g. broad dietary guilds) [30]. This approach potentially over-simplifies variation in function [20], largely because species within categories are not equivalent, but instead tend to perform an array of different ecological roles [31, 32]. Thus, standard methods may conceal the effects of land-cover change on ecosystem function, particularly with regard to non-linearity in underlying processes (e.g. tipping points).

To address these issues, we sampled rainforest bird communities across a gradient of land-use intensity in Amazonia and then estimated the effect of land-cover change on community structure. Specifically, we quantified structure using continuous functional traits for all members of two dietary guilds—frugivores and

insectivores—which account for (77%) of species in our sample (see the electronic supplementary material). We focused separately on these two avian guilds because they perform important but non-overlapping functional roles through their trophic interactions with plants and insects [33].

The interaction between frugivorous birds and plants has a major influence on plant dispersal and recruitment, and is critical to the long-term resilience of forests undergoing anthropogenic change [34-36]. The loss of avian frugivores from rainforest systems can alter the structure of tree communities and impede regeneration, particularly in fragmented landscapes where birds are a key vector of seed dispersal among forest patches [37-39]. Rates of forest regeneration can also be influenced by the fate of insectivorous forest birds because they regulate the top-down control of herbivory by phytophagous insects [40, 41]. Specifically, a loss of insectivores can lead to increased leaf damage, and hence both increased seedling mortality and reduced plant growth in degraded and secondary forests [42, 43].

Quantifying the full network of interactions between birds, insects and plants is a monumental—perhaps even impossible—task, even in simple ecosystems [2]. Instead, to provide an index of the type and diversity of interactions involved, we quantified biometric variables from museum specimens of all study species, and then partitioned these variables into separate niche axes, including overall size, trophic traits (beak shape), locomotory traits (tarsus:tail/wing ratio) and dispersal traits (wing shape). Although such trait axes are not direct measures of seed dispersal and insect predation, they are nonetheless informative about key aspects of the ecological niche related to such processes (see electronic supplementary material). Thus, contractions or shifts in the variety of beak shapes and locomotory traits occurring in a community reflect changes in the filling of ecological niche space across the community as a

whole, and the types, sizes or locations of the seeds and insects consumed by birds [28, 44]. Moreover, similar shifts in wing shapes are relevant to seed dispersal dynamics, particularly in patchy or human-modified landscapes [37, 45, 46]. By focusing on specific avian trophic groups, and partitioning their functional morphology into separate niche axes, we can begin to examine the influence of land-cover on multiple dimensions of biodiversity with relevance to ecosystem function and resilience [25, 29].

One advantage of quantifying multiple functional traits as continuous variables, rather than the categories adopted by many studies (e.g. [13, 18]), is that we can visualise the effects of land-cover change on the structure of communities. We plotted species in multivariate trait space (hereafter termed ‘morphospace’) to assess the volume and density of functional traits in different land-cover categories. Using the same niche axes, we then assessed changes in the structure and function of bird communities across the same gradient by applying two standard metrics: Functional Diversity, *FD* [19], and Functional Dispersion, F_{DIS} [47]. These metrics offer complementary perspectives on variation in functional diversity, with F_{DIS} being more sensitive to the overall spread of traits in morphospace and less sensitive to species richness (see electronic supplementary material).

By combining detailed datasets of species occurrence, morphological traits and land-cover, we assess the impacts of anthropogenic change on two functionally important avian guilds in Amazonian rainforests. Specifically, for each niche axis in frugivorous and insectivorous birds, we ask (1) how *FD* varies with land-cover, (2) whether this variation exceeds that predicted by purely random processes, and (3) how F_{DIS} varies across the same land-cover categories. In addition, we use linear

mixed models to ask (4) how the community mean value for each niche axis varies across a land-cover gradient, with disturbance treated as a continuous variable.

2. Materials and methods

(a) Study site and species

We collected data during intensive field surveys (July 2010–May 2011) across two study regions in eastern Amazonian Brazil as part of the Sustainable Amazon Network [48]. One area (1.9 million ha) was located in the municipality of Paragominas, another (~1 million ha) in the municipalities of Santarém, Belterra and Mojuí dos Campos (hereafter, Santarém), both in Pará state. The two regions differ in their history of human occupation, but encompass broadly similar land uses, with a mix of primary and secondary forest habitats interspersed with agricultural and silvicultural production areas. Both these mosaic landscapes are typical of recently cleared and developed regions of Amazonia, providing an ideal replicated framework for investigating the impacts of land-cover change on biodiversity and ecosystem function.

Sampling within the two regions was based on a hierarchical stratified-random design with proportional sampling of forest and non-forest areas [48]. We focused on 36 hydrological catchments, 18 per study region, each covering ~5000 ha. Within these catchments, we collected detailed environmental information in 300-m long transects (n = 377). Bird surveys consisted of two repetitions of three 15-minute point count surveys at three points evenly spaced every 150 m along each transect, with a single observer identifying species seen and heard within a fixed 75 m radius. We excluded from the analysis 47 transects in ‘rare’ habitat types (e.g. smallholder agriculture, plantations, fruticulture) that were not easily placed along a gradient of

land-use intensity, leaving a total sample of 330 transects (sites). The distribution of transects among the remaining land-cover categories is given in figure 1. In total, 472 bird species were recorded across the two regions, with an average of 154 (range = 97–208) species per catchment, and 39 (range = 2–79) species per transect. For more details of survey methods and results see the electronic supplementary material.

(b) Habitat and trophic niche

We assigned all bird species into two categories of habitat choice depending on whether they were primarily detected in (i) forest or (ii) non-forested habitats, following [49]. These categories are referred to hereafter as forest and non-forest species, respectively (see the electronic supplementary material). We ran analyses pooling forest and non-forest bird species, and then treating these groups in isolation since they are likely to show contrasting responses to forest extent and quality [50]. Moreover, non-forest species play little role in the functioning of forest ecosystems [33].

We classified species into trophic niches (dietary guilds) based on a recent assessment of diets for the world's birds [51]. Guilds were defined by the food that made up the majority (>50%) of their diet, such that species were classified as insectivores, for example, if they were largely insectivorous but also consumed smaller quantities of nectar and fruit. Species were categorized as omnivores if no primary diet was apparent (all dietary components <50% of intake). Nine major guilds were represented in our sample: Omnivore, Insectivore, Frugivore, Granivore, Nectarivore, Herbivore, Carnivore, Piscivore, and Scavengers (see electronic supplementary material). Of these, insectivores were the most frequent guild with 206 species in Santarém and 188 species in Paragominas, and frugivores were the second

most speciose guild with 67 species in Santarém and 72 species in Paragominas. We conducted all analyses separately on insectivores and frugivores because they respond differently to land-cover change and forest disturbance [49, 52]. Full species lists and classifications are provided in the electronic supplementary material (dataset S1).

(c) Environmental conditions

We used a 22-year time-series of Landsat images combined with ground-truthed vegetation mapping to classify transects into one of five land-cover classes: undisturbed primary forest, disturbed primary forest (forests affected by logging and fire events), secondary forest (6–22+ years old), arable agriculture and pasture (see electronic supplementary material). Undisturbed forests in these landscapes typically have lower mean canopy openness and higher basal area (area covered by trees and woody palms ≥ 10 cm) than forests subject to disturbance events [53]. Thus, we also used mean canopy openness and basal area to provide a continuous assessment of land-use intensity. Bird survey sampling was distributed proportionally among habitat categories by area (for a detailed breakdown of sampling see [54]). Within each land-cover class, we excluded all species with fewer than three observations across all transects within that habitat, as these are likely to be transient or low-density populations with minimal contribution to ecosystem functioning; that is, they are likely to be ‘functionally extinct’ within that land-cover class [32, 55].

(d) Trait sampling

We measured bird specimens in museum collections to generate biometric trait data for all frugivore and insectivore species (n = 365) recorded in our study. Where possible, we selected four specimens (two males; two females) from which we took

seven morphometric measurements: beak length, width and depth, wing length, Kipp's distance, tarsus length, and tail length. See electronic supplementary material for further details of data sampling and sources, methods, and rationale for selecting traits. Functional trait data are given in dataset S1.

Functional traits in birds are often strongly correlated, largely through their association with overall body size. To prevent these correlations biasing analyses towards detecting only processes associated with body size, we used ordination techniques to derive independent trait axes. Specifically, we generated three trait axes related to different ecological characteristics by applying a two-step principal component analysis (PCA) on morphological trait data, following previous studies [25, 28]. Initially, separate PCAs were undertaken on locomotory (tarsus:tail/wing ratio) and trophic traits (beak shape). In both cases, the first components correlated strongly with body size, and thus we combined them in a second PCA to produce a single size-related axis (see [28]). The second components of the locomotory and trophic PCA were both correlated with niche trait variation independent from body size. Thus, these scores were used as the locomotory and trophic trait axes, respectively (see electronic supplementary material, table S1, S2). A fourth axis (dispersal traits) consisted of the log-transformed Hand-wing index, a standard measure of flight ability computed from wing length and Kipp's distance (see electronic supplementary material).

(e) Variation in functional diversity

We calculated FD on the basis of presence-absence data for all communities (with each transect classed as a community). To test whether disturbed habitats are capable of maintaining ecosystem function, we first (Analysis 1) assessed how raw *FD* of

communities varied with land-cover. Then (Analysis 2) we assessed whether this variation deviated from random using an independent swap algorithm, which controls for underlying variation in species richness[56]; see electronic supplementary material. Specifically, the *FD* values derived for each community in the five land-cover categories were compared to a null expectation drawn from 999 random communities with species richness equal to the observed community, and the probability of presence for each particular species determined by its overall occurrence frequency across all communities [56]. Finally (Analysis 3), we assessed whether raw F_{DIS} varied across different land-cover categories. Observed values of standardised *FD* and F_{DIS} were pooled for each land-cover category.

In analyses 1–3, we used two-tailed Wilcoxon signed-rank tests to compare among categories. We completed analyses 2–3 in two different ways regarding the treatment of trait data. First, we combined all measured traits into a single PCA, and, second, we conducted the two-step PCA described above to generate derived trait axes linked to specific ecological functions. We ran null model simulations (analysis 2) separately for both regions because the two study regions lie in different biogeographical provinces and there are pre-existing differences in species composition. However, because Santarém and Paragominas were similar in their history of forest loss and disturbance and community structure [48, 54], we combined data from both regions before running Wilcoxon analyses (that is, communities were partitioned by land-cover category, but pooled across regions).

(f) Variation in the trait structure of communities

Given the high level of variation of habitat condition within land cover classes, relating to the timing, frequency and intensity of human disturbance, we also used a

Generalised Linear Mixed Model (GLMM) to examine how mean values for each trait axis varied across a continuous gradient of ecological condition (Analysis 4). Ecological condition was based on the first principal component scores from a PCA of canopy openness and basal area, which explained 92% of the variation (see the electronic supplementary material, table S3, for eigenvalues). We allowed the relationship between the environmental PC score and functional traits to be both linear and non-linear (i.e. quadratic). We accounted for potential spatial autocorrelation by including catchment number (1–36) nested within region (Santarém or Paragominas) as random effects in models. Adequate model specification was confirmed by visual inspection of the residuals. The best models were then selected using the Akaike information criterion, AIC [57], with smaller values indicating a closer fit to the observed data.

3. Results

(a) Species richness and functional traits

Species richness of frugivores and forest insectivores was high in primary forest but declines to very low levels wherever human land-use reaches the highest intensity (pastures, arable agriculture). This effect was not simply a reflection of reduced sampling in human land-uses, as confirmed by species accumulation curves [54]. The pattern was reflected in a dramatic contraction and thinning of the functional trait structure of communities across the land-cover gradient, as visualised by plotting all species in multivariate morphospace (figure 1). Both the species richness of communities, and the volume of morphospace they occupied, were intermediate in secondary forests.

(b) Functional diversity

Raw *FD* for insectivore and frugivore communities was lower in secondary forest and non-forest habitats than in primary forest (Analysis 1, figure 2, table S4). This effect was strong both when forest and non-forest species were combined, and when forest species were analysed in isolation. However, observed *FD* of non-forest insectivores remained similar across the disturbance gradient, apart from in pastures where there was a significant increase in *FD* compared to primary forest communities (figure 2). Similarly, the *FD* of non-forest frugivores remained relatively constant across the land-use gradient, except in arable agricultural habitats where the frugivore component of avian communities was removed almost entirely. We note that these patterns in raw *FD* are likely to be strongly driven by variation in species richness.

Using a null-model approach, and pooling forest and non-forest species, we found that *FD* in insectivore communities was neither more nor less than expected by chance, regardless of position across the land-use gradient (Analysis 2, figure 3a, table S5). Although observed F_{DIS} of insectivore communities changed with land-cover, the relationship was non-linear because F_{DIS} decreased from primary to secondary forest, and then increased again in pastures (Analysis 3, figure 3c, table S6). These patterns were substantially altered when we focused exclusively on forest insectivores, with *FD* significantly lower in pastures than predicted by our null model (figure 3e), and F_{DIS} significantly reduced in pastures in comparison to primary forest (figure 3g).

Regardless of whether forest and non-forest species were pooled or not, increased intensity of human land-use was associated with declining *FD* and F_{DIS} in frugivores. In secondary forests, pastures and arable land, *FD* was significantly lower

than null expectations (Analysis 2, figure 3, table S5), and F_{DIS} was lower than in primary forests (Analysis 3, figure 3, table S6).

When we focused on individual traits, we found that overall trends concealed idiosyncratic patterns (figure S1, tables S7–S9). For example, body size and locomotory traits contributed disproportionately to the low *FD* of forest insectivore and frugivore communities in pasture, while trophic traits were neither over- nor under-dispersed. In contrast, dispersal traits had higher *FD* than expected under our null expectation (figure S1). Changes in the F_{DIS} of individual traits mirrored the collapse of *FD*. Specifically, the F_{DIS} of all traits, apart from dispersal traits in insectivores, declined in secondary forests and/or pastures from highs in primary forests (figure S1, tables S10–S12). In contrast, the F_{DIS} of dispersal traits was similar in primary and secondary forest communities, and increased in pastures (figure S1l, table S10).

(c) Community structure in relation to functional traits

GLMM analyses revealed systematic shifts in mean trait values for both forest (8 models) and non-forest species (8 models) across the land-use gradient (figure S2, table S13). In some (5 of 16) cases, four of which (80%) were restricted to insectivore communities, the best fitting models included disturbance as a quadratic term (figure S2, table S13) suggesting that the rate of change in mean community traits varied across the gradient. The only model for frugivores that retained the quadratic explanatory variable was for body size in non-forest species, but in this case the linear explanatory variable was not significant, suggesting a v-shaped relationship with a minimum at intermediate levels of disturbance (figure S2e, table S13). This may reflect the presence of large toucans and terrestrial species in forested areas, and the

ability of some large frugivores (e.g. pigeons) to disperse through sparsely vegetated agricultural landscapes. However, in most (11 of 16) cases, the best fitting models included only the linear term, suggesting that the rate of change in mean community traits remained similar across the disturbance gradient (figure S2). Of these 11 cases in which a linear model was supported, 10 (91%) involved frugivores and non-forest insectivores.

4. Discussion

To assess the impact of land-cover change on key trophic interactions, we focused on discrete ecological and functional groups (forest and non-forest bird species; frugivores and insectivores), and partitioned the functional traits of each species into four dimensions of the ecological niche (size, diet, locomotion, dispersal). Our findings reveal that defaunation associated with land-cover change has different implications for insectivore and frugivore communities, and for different ecological niche axes within those communities, providing insight into the relationship between land-cover and the ecosystem processes regulated by birds.

(a) Impacts of land-cover change on functional diversity

When grouping all forest and non-forest species together, disturbed primary forests supported similar levels of *FD* relative to undisturbed primary forests. In addition, the trait structure of communities in disturbed primary forests was similarly dispersed around mean trait values (F_{DIS}). However, the impact of further increases in land-use intensity was stronger in frugivores, with significant declines in *FD* in secondary forest, and diversity dropping to almost zero in the intensively farmed agricultural

areas (figure 1). Our results suggest that the *FD* and F_{DIS} of frugivores collapses in highly disturbed habitats, presumably reflecting the removal of fruiting trees.

The impacts of land-cover change on forest-dependent insectivores were generally similar, with the total volume of trait space collapsing in agricultural habitats and only partially recovering in secondary forests (figure 1). Accordingly, the overall raw *FD* for insectivores (forest and non-forest species combined) declined with increasing habitat disturbance (figure 2a). These findings agree with previous studies concluding that rainforest insectivores are highly sensitive to land-cover change, with many species dropping out of fragmented habitat because of their poor dispersal abilities and adaptation to the forest interior [49, 58].

Nonetheless, both *FD* and F_{DIS} of insectivores were more resilient to land-cover change (figure 3), largely because non-forest insectivores occurred widely with their *FD* remaining consistent (figure 2e) and their F_{DIS} increasing in disturbed habitats (figure 3k). Focusing on forest species, and breaking functional variation down into individual traits, provides further insights. For example, both the standardised *FD* (figure S1d) and F_{DIS} (figure S1l) of dispersal traits in forest insectivores increases with land-use intensification, presumably because disturbed habitats retain some taxa with low-dispersal traits yet also receive an influx of highly dispersive taxa. In contrast, standardised *FD* for overall size and locomotory traits in forest insectivores, as well as the F_{DIS} for all other traits, showed a strong decline in disturbed landscapes (figure S1). Overall, these results reveal that the effects of land-cover change on functional diversity are (i) concealed when including non-forest species in analyses [30], and (ii) idiosyncratic across different functional groups, and ecological niche axes.

(b) Variation in trait distribution

We detected numerous shifts in the mean traits of both insectivore and frugivore communities indicating that bird communities occupied a different region of trait space after changes in human land-use (see electronic supplementary material). When plotted across a continuous gradient in land-cover, this variation in trait structure fitted both linear and quadratic models, but was best described by a quadratic fit. In all cases, and particularly in forest insectivores, the rate of change in the mean position of traits occurred most rapidly at high levels of disturbance. Such fluctuations suggest that disturbed landscapes are especially sensitive to further small increases in disturbance events (such as recurrent fires), as these have the potential to cause major changes in the position of trait diversity. This finding indicates that the turnover of species in repeatedly disturbed communities, although rapid [59], is nonetheless outpaced by changes in trait structure related to key ecosystem processes.

Focusing on individual traits, we found that large species were particularly sensitive to habitat disturbance and increasing land-use intensity, in agreement with previous studies in tropical systems [15]. Specifically, for insectivores and forest frugivores there was a decline in the overall mean size of species persisting in disturbed habitats (figure S2, table S13). We attribute these shifts to a suite of factors well known to increase the susceptibility of large species to local extinction in degraded or fragmented environments, including increased hunting [60, 61].

In general, the functional trait structure of insectivore communities shifts with increasing intensity of human land-use towards smaller tarsus to tail/wing ratio, increased dispersal, and short, wide beaks. Based on the reported link between form and function in birds [28], these findings suggest that the insectivore community is increasingly dominated by species that capture prey in flight or from canopy foliage.

The pattern also reflects the addition of mobile, opportunistic, non-forest species, in conjunction with the removal of dispersal-limited, forest-dependent species [58]. Changes in the functional trait structure of frugivore communities are less complex, and more closely related to body size. It is possible that some large frugivore species are hunted out from highly disturbed landscapes, and also that taxa persisting in these environments tend to be smaller-bodied vagile species with lower nutritional requirements.

(c) Implications for ecosystem function and landscape management

Our results suggest that 'biodiversity services' [3] supplied by birds and related to tropical forest resilience are more effectively retained in disturbed primary (i.e. logged or burnt) rainforests than in secondary forests, and that—unsurprisingly—such services collapse in agricultural land-uses. These findings are consistent with the view that disturbed (logged and burnt) primary forests are important in both maximising species richness and maintaining ecosystem function in landscape mosaics [45, 54]. Although we found that secondary forests (6–22+ years old) are significantly less complex than disturbed primary forests from a functional perspective, we note that this result is likely to be age-dependent, with the trait structure of secondary forest bird communities becoming progressively more like those of primary forests over time. Moreover, even young secondary forests may increase matrix permeability and dampen edge effects, thereby acting as an important buffer against the loss of functional diversity through land-use change, and increasing the potential for abandoned agricultural landscapes to regenerate rainforest [62].

Although the *FD* and F_{DIS} of frugivores declines precipitously in agricultural landscapes, it is worth considering whether this matters. It could be argued, for

example, that declines in *FD* with habitat disturbance are simply a response to the lower range of fruits available, in which case frugivores may continue to provide the dispersal function in full. While this is undoubtedly true to an extent, frugivore species often disappear before their food plants [32], particularly when large-bodied species are hunted to extinction [37], meaning that demand for seed dispersal outstrips supply [63]. Moreover, as many rainforest mammals, including primates, are unlikely to disperse though non-forest habitats, birds may be the main vector of dispersal for animal-dispersed trees in degraded or secondary forests [33]. From this perspective, the ability of forests to regenerate fully relies on the presence or proximity of avian seed dispersal agents, and is therefore impaired by shifts in the functional trait structure of avian communities away from the state encountered in intact forest. Once components of functional diversity in frugivores are lost, the chances of recolonisation by associated food plants are theoretically reduced.

The loss of forest insectivores in agricultural habitats is almost as extreme, but potentially offset by an influx of non-forest species. However, whether these species help to maintain the top-down control of herbivory in forest remains to be demonstrated [64], and is perhaps unlikely because non-forest insectivores tend to be generalists with different foraging strategies and a preference for more open microhabitats [65]. Thus, they may fail to capture many types of cryptic herbivorous insects in patches of forested habitat embedded in agricultural landscapes.

One drawback of our analyses is that they do not account for species abundance. Changes in abundance following disturbance often vary across species in unpredictable ways [66], potentially leading to some species becoming ‘functionally extinct’ when their abundance drops so low that they contribute little to ecological processes [32, 55]. Moreover, *FD* can be a misleading surrogate for species

contributions to ecological processes because phenotypically distinct taxa tend to be rarer and thus interact with fewer species across the network [67]. We partly address this issue by excluding species that are either transient or rare from our analyses, but—in common with most previous functional trait studies—we do not explicitly account for changes in abundance. Further work should incorporate more informative measures of abundance or interaction strength [30, 67].

Standard approaches to understanding environmental change based solely on species richness and composition may overlook important implications for ecosystem processes, leading to calls for functional diversity to be more explicitly considered in biodiversity conservation strategies [13, 68, 69]. Our results support this view, yet also highlight how treatment of functional diversity can be improved to provide greater insight. In particular, we have shown contrasting effects of land-cover change on functional traits in different avian dietary guilds, and even across different dimensions of functional trait space. Given that these idiosyncratic patterns are largely obscured by standard approaches, we propose that functional traits should, where possible, be considered in the context of specific trophic interactions or their constituent niche axes when exploring the implications of anthropogenic change on biodiversity and ecosystem resilience.

Data accessibility. All data are provided (electronic supplementary material, S2).

Authors' contributions. J.A.T., T.B. and J.B. conceived and designed the study. A.C.L. and N.G.M. designed and carried out field surveys. T.B., H.E.A.M., B.D. and A.A. collected functional trait data. T.B. carried out analyses. T.B. and J.A.T. drafted the manuscript, with all authors contributing to revisions.

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Figure 1. Functional trait distribution for forest-dependent (a) insectivorous and (b) frugivorous bird species across a land-use gradient in Amazonian forest. Sample sizes are the number of species recorded in each land-use category. Each point shows data from a single species; colours denote the density of species in a multivariate trait space ('morphospace') described by three trait axes (dispersal traits, trophic traits, and overall size); isopleths denote the areas of morphospace containing 75%, 50% and 25% of species occurring in each land-use. Arrows in (a) indicate the direction of increasing values for each principal component axes (described in electronic supplementary material, tables S3, S4). Data shown are exclusively from the Santarem landscape to avoid pooling data from different study sites, which overestimates the volume of morphospace within land-use categories.

Figure 2. Observed Functional Diversity (*FD*) for insectivores and frugivores in 330 avian communities across five land uses: primary forest (PF), disturbed primary forest (DF), secondary forest (SF), pasture (PA) and arable agriculture (AG). (a) and (b) show data for all species; (c) and (d) show data for forest species; (e) and (f) show data for non-forest species. Data from Santarém and Paragominas are pooled. Asterisks indicate that observed *FD* was significantly different from the null expectation (* <0.05, ** <0.01, *** <0.001). All statistical results are from two-tailed Wilcoxon signed-ranks tests. Full results and sample sizes in each land use category are provided in electronic supplementary material, table S5.

Figure 3. Standardized effect size of Functional Diversity (*FD*) and Functional Dispersion (F_{DIS}) for insectivores and frugivores in 330 avian communities across five land uses: primary forest (PF), disturbed primary forest (DF), secondary forest (SF), pasture (PA) and arable agriculture (AG). Data from Santarém and Paragominas are pooled. Metrics were not calculated for subsets where sample size was too low. Asterisks indicate that observed *FD* was significantly different from null expectations, or that observed F_{DIS} was significantly different from F_{DIS} in primary forest (* <0.05, ** <0.01, *** <0.001). All statistical results are from two-tailed Wilcoxon signed-ranks tests. Full results and sample sizes in each land-cover category are provided in electronic supplementary material, tables S5, S6.