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Long-term changes in avian biomass and functional diversity within disturbed and undisturbed Amazonian rainforest

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Recent long-term studies in protected areas have revealed the loss of biodiversity, yet the ramifications for ecosystem health and resilience remain unknown. Here, we investigate how the loss of understory birds, in the lowest stratum of the forest, affects avian biomass and functional diversity in the Amazon rainforest. Across approximately 30 years in the Biological Dynamics of Forest Fragments Project, we used a historical baseline of avian communities to contrast the avian communities in today's primary forest with those in modern disturbed habitat. We found that in primary rainforest, the reduced abundance of insectivorous species led to reduced functional diversity, but no reduction of biomass, indicating that species with similar functional traits are less likely to coexist in modern primary forests. Because today's forests contain fewer functionally redundant species—those with similar traits—we argue that avian communities in modern primary Amazonian rainforests are less resilient, which may ultimately disrupt the ecosystem in dynamic and unforeseen ways.

1. Introduction

Biodiversity and ecological resilience (the return to equilibrium after perturbation) are both integral components of healthy ecosystems [1–3]. The diversity–stability hypothesis states that communities with relatively high or intact species diversity are more stable and resilient [4–7]. Areas with high ecological integrity, characterized by ecological processes and species composition reminiscent of historical conditions, typically within large tracts of natural habitat, are purported to have greater ecological stability [8–12]. Unfortunately, a diminishing proportion of the natural world is described as ecologically intact, which has important implications for the future functionality of ecosystems, their resilience and the services they provide [8,11,13–16].

The loss of biodiversity has renewed a global interest in preserving relatively large tracts of intact habitat, such as wilderness areas, to blunt the ongoing biodiversity crisis [17]. However, recent long-term studies of biodiversity have revealed shifting historical baselines, even in large tracts of contiguous habitat with minimal human footprints. For example, the abundance and species composition of many

protected and relatively undisturbed deserts and forests of North and Central America have shifted over the past 100 years [18–20]. Even in the Amazon rainforest—the largest, most intact and biodiverse tropical rainforest in the world—researchers have observed changes in the avian community composition of undisturbed primary forest over the past approximately 30 years, such as declines in abundance of understory insectivore species [21]. Each long-term study adds new details that suggest biodiversity is eroding and community composition is changing, even in undisturbed and/or protected areas. Despite decades of research on the diversity–stability hypothesis ([22]; summarized in [5]), no connections have been drawn between the loss of biodiversity and the ecological resilience of these relatively undisturbed areas.

The study of functional diversity, based on morphological, ecological and behavioural traits, provides an opportunity to assess how shifting baselines might impact otherwise undisturbed ecosystems. Functional traits facilitate species' interactions with their environment, and functional diversity captures the range of ecological traits that are present within an ecological community [23,24]. Relatively high measures of functional diversity can indicate greater ecosystem resilience [23], while relatively low values of functional diversity can signal that a system is degraded, either from the extirpation or reduced abundance of species with distinct traits or a loss of multiple species with similar traits. Because species with similar traits are thought to occupy similar niches in their ecological communities, they are considered to be functionally redundant [25].

As long as functionally redundant species remain, the functional diversity of a community can sustain the loss or reduced abundance of a particular species and persist relatively unchanged. Such communities with high functional redundancy are thought to be relatively resilient to disturbance. In fact, relatively high functional redundancy is thought to be an important aspect of ecosystem integrity, especially in high diversity systems [26]. However, if declining species have distinct traits or if changes in community assemblage are too dramatic, then functional redundancy and diversity could be reduced, and with it, the ecological integrity of the system [27]. In addition to functional diversity, animal biomass indirectly reflects and impacts several ecosystem processes. For example, birds disperse fruits, pollinate plants and prey upon insect herbivores that limit primary productivity, and changes in overall avian biomass can impact these processes [28].

We know that changes in abundance have affected Amazonian bird communities in undisturbed forest, with near-ground and terrestrial insectivores showing the greatest declines and midstory frugivores the largest increases [21]. Similar shifts, albeit stronger, were observed between historical primary forests and the modern disturbed landscape (secondary forest and forest fragments), such that understory, near-ground, terrestrial and riparian insectivores as well as woodcreepers all declined in abundance across the modern disturbed landscape, whereas no avian groups increased in abundance [21]. Instead of relying on contemporary space-for-time substitutions for community composition and population trends, we use an avian baseline from 30 years prior to assess whether shifts in abundance have altered the avian biomass and functional diversity of the current communities. Finally, we also examine the biomass and functional diversity of communities in disturbed Amazonian rainforest to contrast potential changes in ecosystem function across time and forest types. Here we ask the following questions:

(i) Have shifting baselines in bird abundance led to long-term changes in avian biomass?

(ii) Has the functional diversity of avian communities in primary rainforest changed in concert with the shifting baseline?

(iii) Are temporal changes in biomass and functional diversity in modern primary forests exacerbated in the modern disturbed landscape?

(iv) If functional diversity has been lost, is the loss borne by birds with more distinct functional traits or species with similar traits (i.e. functionally redundant organisms)?

We predict that biomass and functional diversity will be greater in historical primary rainforest compared to modern primary rainforest, and that the modern disturbed landscape will have the least avian biomass and functional diversity, because more species showed mean decreases than increases in modern primary forest and because the majority of the community decreased in modern disturbed habitat [21]. We further predict that if functional diversity has been lost, it will be among the most functionally redundant species, which would be evidence of reduced functional resilience in the Amazon rainforest, as recently suggested by Boulton *et al.* [13].

2. Methods

(a) Study area and site selection

Research took place at the Biological Dynamics of Forest Fragments Project (BDFFP), about 80 km north of Manaus, Brazil, in central Amazonian rainforest. Although localized forest clearing for cattle began in the early 1980s, clearing was completed by the 1990s and the forest began to regenerate [29]. The region consists of *terra firme* rainforest and currently has greater than 90% forest cover [30].

Site selection methods follow that of Stouffer *et al.* [21] but are also summarized here. In the early 1980s (1980–1984), 34 sites were sampled for birds in continuous primary forest, spread across roughly 35 km. Each site was sampled between four and nine times and is hereafter referred to as *historical primary forest* sites. The early 1980s is an appropriate historical baseline for this study as it represents a time before any portion of the forest landscape was disturbed by deforestation and cattle ranching. In addition, there was minimal human presence in the vicinity in the decades prior to this time (T Lovejoy 2020, personal observation). Between 2008 and 2016, 21 sites were sampled 4–6 times in continuous primary forest. These *modern primary forest* sites span roughly 40 km in the same vicinity as the historical sites. However, historical and modern sites are not identical; the distance between historical sites and their nearest-neighbour modern sites ranged between 54 and 6580 m, with a mean distance of approximately 2500 m [21]. The modern disturbed landscape at the BDFFP consisted of 1 ha and 10 ha forest fragments and 25- to 35-year-old secondary forest. In our analyses, the *modern disturbed landscape* included 15 sites (four 1 ha fragments, three 10 ha fragments and eight secondary forest sites), each of which was sampled between five and 21 times between 2007 and 2016 [21].

(b) Bird sampling and data

Prior to forest clearing and the isolation of forest fragments (1980s), a standard operating procedure was implemented for studying the understory avian community with mist nets, and the same procedures have been used to collect data ever since

[31]. A site consists of a line of 16 mist nets that were sampled multiple times in the same location, except sites in 1 ha fragments, which only hosted eight nets. Each net (36 mm mesh) was 12 m long and 2.5 m tall, with the lowest trammel set on the ground. Nets were open between 06.00 and 14.00 on each day of sampling and at least one month passed between successive samples at the same site. All mist-netting occurred between June and November, which comprises the dry season at the BDFFP.

Raptors, kingfishers and species captured fewer than five times were all excluded prior to analyses. Removal of these species bypassed canopy species that rarely descend into the understory, seasonal migrants and birds too large to reliably capture with mist nets. Thus, we focused on the permanent residents of the understory community at our site [21,32].

We compiled morphological traits, both historical and modern, that described ecological strategies, such as foraging and movement, for all 79 species in our analyses (electronic supplementary material, table S1), and all species were assigned to feeding guilds based on Stouffer *et al*. [21]. When birds were captured in mist nets at the BDFFP, the bill, wing, tail and tarsus were all measured to the nearest 0.1 mm and body mass to the nearest 0.1 g. In addition to these five morphological traits, we also included hand-wing index (a measure of wing shape) [33]. For the five morphological measurements taken at the time of capture, we created species-specific averages that were relevant to each time period: historical trait measurements for the *historical primary forest* sites and modern measurements for sites in both the *modern primary forest* and the *modern disturbed landscape* sites, as Jirinec *et al*. [34] provides empirical evidence that local morphology has not remained static over time. However, if a trait was not measured at the time of capture (regardless of time period), we used the species-specific mean as reported in Johnson & Wolfe [35], which compiled trait measurements from birds captured locally at the BDFFP over its 40-year history. By focusing on measurements from local birds, we avoided the potential for unwanted variance from birds at disparate locations, which might be adapted to other ecosystems and climates. However, for one trait (hand-wing index), we did not have local measurements for each species; in this case, measurements came from a global dataset [36] and were not based on birds specific to our study site.

(c) Data analysis
(i) Biomass
When possible, body mass for each captured bird was taken directly from the capture event in each time period and habitat type. However, in cases where the mass was not collected at the time of capture, we used the average species-specific body mass from that time period as described in Jirinec *et al*. [34]. Mist-net effort was standardized by summing avian mass in each of the three forest communities by 1000 mist-net hours. The historical primary to modern primary forest comparison examined 79 species, only one of which (*Attila spadiceus*) was unique to either period (absent from the historical sample). The same process was repeated for modern disturbed sites, where only 63 species were detected, a nested subset of the same 79 species detected in primary forest. In addition, we calculated standardized biomass (per 1000 mist-net hours) separately for each foraging guild (electronic supplementary material, table S1). We used a Kruskal–Wallis by rank analysis, followed by a Dunn pairwise comparison, to test for differences in biomass between time periods, for all diets and for birds with different abundance trends (figure 2 in [21]) using the 'ggstatsplot' package [37] in R v. 4.1.0 [38].

(ii) Functional diversity
A separate principal component analysis on measured traits for all birds gave us a reduced number of uncorrelated and normalized variables in each time period (historical or modern). The first three principal components (PCs) explained 91% of the morphological trait variation for both historical and modern avian communities. PC1 explained 57% of the variation and loaded positively with size-related traits, such as mass, bill length, wing length, tarsus length and tail length. PC2 explained 23% of the variation and loaded with movement-associated traits: positively with tarsus length and negatively with hand-wing index. PC3 explained 11% of the variation and loaded positively with hand-wing index and negatively with average bill length (electronic supplementary material, table S2). Functional trait space was mapped with PCs 1, 2 and 3 and multivariate kernel densities represented by the 50%, 95% and 99% probability contours for trait space. Functional diversity metrics were scaled between 0 and 1 since morphological trait datasets differed between historical and modern forest birds.

The functional diversity of historical and modern avian communities was based on the number of capture events for each species in primary (historical and modern) and disturbed forest (modern). Similar to the biomass analysis, mist-net effort was standardized by summing avian captures in each of the three forest communities by 1000 mist-net hours. Functional richness, dispersion and evenness were calculated with the *dbFD* function in the R package 'FD' [39,40]. Functional richness for *historical primary*, *modern primary* and the *modern disturbed landscape* was estimated as the volume of multi-dimensional trait space occupied by all species captured in each community. Functional dispersion, the mean distance between each species and the centroid of trait space, was weighted by abundance. Functional evenness, the regularity of the distribution of species trait dissimilarities in functional space, was also calculated for each of the three communities. Functional evenness is highest when all pairs of nearest-neighbour distances are identical and similar in abundance, thus showing an even spread between species in trait space. To evaluate whether functional metrics differ between *historical primary forest*, *modern primary forest* and the *modern disturbed landscape*, we averaged the metrics across sites for each of the three forest communities and compared the means with *t*-tests.

To evaluate the functional distinctiveness of species that are increasing, stable or decreasing in modern primary and disturbed forests, we extracted species-specific trends from figure 2 of Stouffer *et al*. [21]. We calculated the functional distinctiveness of each species with the 'funrar' package in R [41], which measures how unusual a species' trait value is compared to that of other species in the community (ranging from 0 to 1). Lower functional distinctiveness values indicate functional redundancy while higher values indicate more functionally distinct species. We then used a Kruskal–Wallis analysis to test for differences in distinctiveness between species with increasing, stable and decreasing abundances. Finally, we used a linear regression to test if biomass was correlated with the abundance trend of nearest-neighbour species, based on distinctiveness.

To test whether functionally redundant species were decreasing more than distinctive species, we calculated community-level functional redundancy separately for *historical primary forest*, *modern primary forest* and the *modern disturbed landscape* using the 'adiv' package in R [42]. Redundancy values ranged between 0 (low community redundancy) and 1 (high redundancy; [43]). Using these redundancy values, we performed a Kruskal–Wallis analysis to test if functional redundancy changed significantly from communities in *historical primary forest* to those in *modern primary forest* and the *modern disturbed landscape*. A *post hoc* Dunn's test was used to test pairwise differences in redundancy between time periods.

3. Results

(a) Biomass

Avian biomass in *historical primary forest* (mean = 4029.54 g/1000 net hours) was not significantly different from biomass in *modern primary forest* (mean = 3918.67 g/1000 net hours) ($t = 0.08$, d.f. = 44.61, $p = 0.94$). However, compared to *historical primary forest*, the *modern disturbed landscape* showed a steep decline in avian biomass (mean = 2365.36 g/1000 net hours) ($t = 3.50$, d.f. = 19.22, $p < 0.01$; figure 1). Although the abundance of individual species did not remain static through time in primary forest [21], whether a species was increasing, stable or decreasing was not associated with a species' mass in *modern primary forest* ($\chi^2_{\mathrm{Kruskal-Wallis}} = 4.72$, $p = 0.094$) or the *modern disturbed landscape* ($\chi^2_{\mathrm{Kruskal-Wallis}} = 2.77$, $p = 0.250$). In the *modern disturbed landscape*, most species declined in abundance, regardless of a species' mass (i.e. declines were not concentrated in small or large species; electronic supplementary material, figure S1). At the guild level, there were no significant changes in biomass for frugivores ($\chi^2_{\mathrm{Kruskal-Wallis}} = 1.02$, $p = 0.6$), nectarivores ($\chi^2_{\mathrm{Kruskal-Wallis}} = 2.64$, $p = 0.27$) and omnivores ($\chi^2_{\mathrm{Kruskal-Wallis}} = 1.32$, $p = 0.52$) in *modern primary forest* or the *modern disturbed landscape* (figure 1). Similarly, for insectivores, there was no significant difference in overall biomass between *historical primary forest* and *modern primary forest*; however, insectivore biomass decreased significantly in the *modern disturbed landscape* compared to the *historical primary forest* baseline ($\chi^2_{\mathrm{Kruskal-Wallis}} = 19.99$, $p < 0.001$) (electronic supplementary material, figure S1). There were no significant differences in biomass between species described as decreasing, stable and increasing in *modern primary forest* ($\chi^2_{\mathrm{Kruskal-Wallis}} = 1.13$, $p = 0.57$) or the *modern disturbed landscape* ($\chi^2_{\mathrm{Kruskal-Wallis}} = 3.86$, $p = 0.15$). Thus, biomass was not associated with changes in a species' abundance (electronic supplementary material, figures S1 and S2).

(b) Functional diversity

Although species composition did not change, shifts in abundance caused functional trait space in *modern primary forest* to differ from historical forest communities. As expected, differences in functional trait space were even more dramatic in the *modern disturbed landscape* (figure 2), as both species composition and (largely) abundance were reduced. The majority of species that experienced declines in *modern primary forest* [21] were within the inner 50% kernel density contour, indicating similarities in morphological trait space. Declining species also tended to have smaller hand-wing indices and larger tails than species with increased abundances. By contrast, species that increased in modern primary forest showed variation along both body size and mobility axes. In addition, declining species in the *modern disturbed landscape* were evenly spread throughout trait space and showed no distinct pattern. There was no apparent pattern based on feeding guild (figure 2).

Functional richness, the volume of functional trait space, differed significantly between the historical and modern primary forest communities ($t = 2.09$, d.f. = 42.5, $p = 0.042$). Functional richness was highest in *historical primary forest* (mean = 0.46), decreased in *modern primary forest* (mean = 0.38) and was significantly lower in the *modern disturbed landscape* (mean = 0.21) ($t = 4.97$, d.f. = 22.6, $p < 0.001$). The decrease in functional richness from *modern primary forests* to the *modern*

disturbed landscapes was also significant ($t = 3.12$, d.f. = 26.3, $p = 0.004$) (figure 3). Conversely, functional evenness, the measure of global trait dissimilarities and abundance in functional space, was not significantly different between *historical primary forest* (mean = 0.74), *modern primary forest* (mean = 0.74) or the *modern disturbed landscape* (mean = 0.73). Functional dispersion ($t = 1.49$, d.f. = 33.4, $p = 0.07$; $t = 0.07$, d.f. = 18.1, $p = 0.23$) and divergence ($t = 0.43$, d.f. = 38.26, $p = 0.7$; $t = 0.59$, d.f. = 18.69, $p = 0.86$) were also not significantly different between historical primary and modern primary or disturbed forests, respectively.

The analysis of functional distinctiveness revealed no significant differences between species described as increasing, stable and decreasing in abundance in *modern primary forest* ($\chi^2_{\mathrm{Kruskal-Wallis}} = 2.77$, $p = 0.094$) or the *modern disturbed landscape* ($\chi^2_{\mathrm{Kruskal-Wallis}} = 4.72$, $p = 0.250$) (figure 4). There was also no significant relationship among body mass and abundance change for species that are nearest neighbours in functional distinctiveness ($F_{3,75} = 0.8159$, $p = 0.489$).

Functional redundancy was significantly different between the three avian communities ($\chi^2_{\mathrm{Kruskal-Wallis}} = 40.28$, $p < 0.001$), with communities in *historical primary forest* having the highest level of mean redundancy (0.96). In comparison, *modern primary forests* (mean = 0.94) had significantly less redundancy ($t = -3.85$, d.f. = 31.8, $p < 0.001$) but also significantly more redundancy than the *modern disturbed landscape* (mean = 0.91; $t = 3.59$, d.f. = 15.2, $p = 0.003$) (figure 5), indicating that communities in modern forests are comprised of species that are less likely to be functionally similar.

4. Discussion

In Amazonia, shifting baselines in avian communities [21] resulted in reduced functional diversity in modern primary forests. In particular, species with similar morphological traits—those that are functionally redundant—declined in modern primary forests, which aligns with other recent studies of reduced ecosystem resilience in today's Amazonian rainforests [13]. Avian biomass, functional diversity and functional redundancy were all reduced in the *modern disturbed landscape* compared to both *modern* and *historical primary forest*, suggesting that the *modern disturbed landscape* is likely much less resilient than primary forests. Our results from both modern primary and disturbed forests support predictions of the diversity–stability hypothesis, which state that reduced biodiversity can result in less stable communities and ecosystems.

(a) Biomass

Avian biomass remained stable in our primary forest sites across an approximately 30-year period, despite several species declining over the same timespan [21]. Avian biomass indirectly reflects birds' capacity to contribute to several ecosystem processes, as they disperse fruits, pollinate plants and prey upon herbivorous insects that limit primary productivity [28]. Our analysis did not reveal that heavier understory species were more likely to decline than lighter species in modern primary forest. Studies encompassing entire communities of tropical avifauna have indicated that larger species are more likely to decline, often due to hunting pressures in undisturbed forests [44,45], and are more likely to be extirpated from degraded or fragmented tropical forests
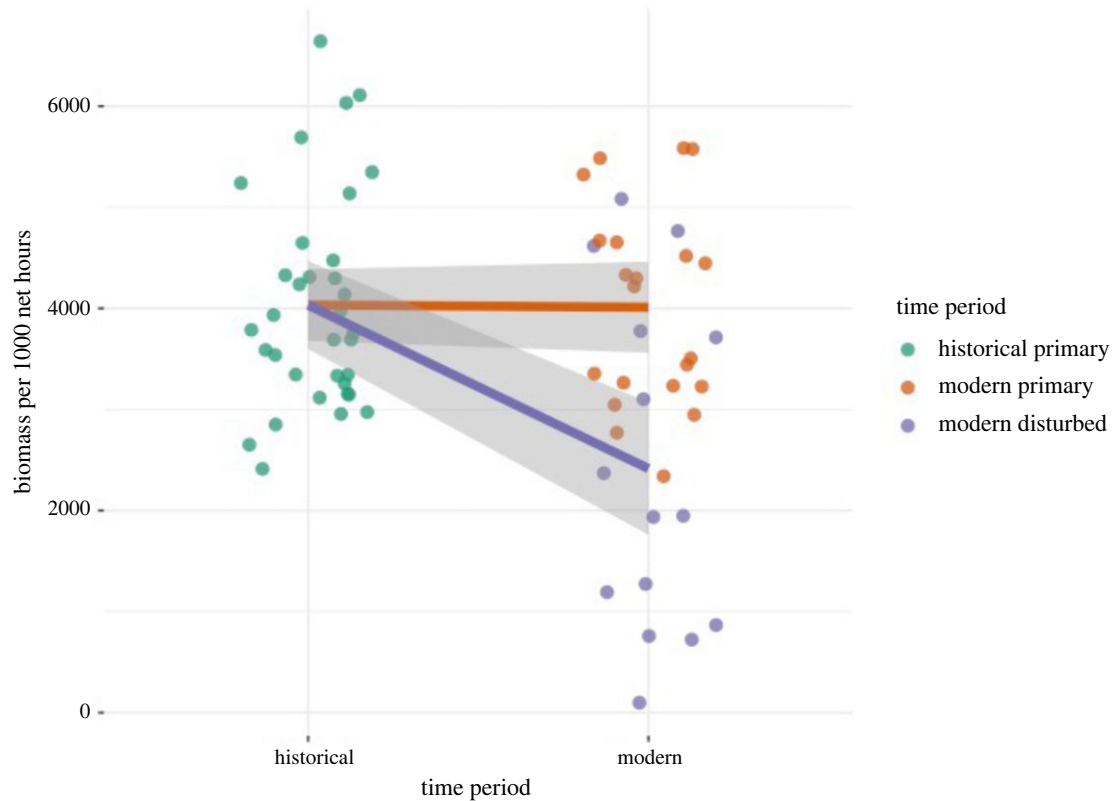
Figure 1. Avian biomass of birds captured in mist nets per 1000 mist-net hours in *historical primary forest*, *modern primary forest* and the *modern disturbed landscape*. Lines corresponding with modern habitat colours indicate fitted linear regressions from historical data, with s.e. in grey. (Online version in colour.)

[25,46,47]. However, given that our survey methods did not include the largest terrestrial species in tropical Amazonian forests, such as tinamous, curassows, trumpeters, wood-quails and wood-rails [31,48,49], our results are not generalizable to the entire avian community and should not be compared directly with whole-community studies. Due to low hunting pressure in the immediate vicinity (T Lovejoy 2020, personal observation), these larger terrestrial birds do not appear to be under direct threat from hunters at our study site, thus we do not expect that they have declined as rapidly here as has been observed elsewhere.

With only 63 of the 78 *historical primary forest* species, and no compensatory increase in species abundance, it is not surprising that avian biomass declined in the *modern disturbed landscape*. However, this reduction in biomass could also be affected by a drop in abundance. In particular, insectivore biomass was greatly reduced in the *modern disturbed landscape*, indicating that understory insectivores are slower to recover in small fragments and secondary forest than frugivores or omnivores [50]. A loss of biomass in the *modern disturbed landscape* was expected and is supported by other studies from disturbed tropical rainforest landscapes [25,51,52]. The *modern disturbed landscape* had roughly half the biomass found in *modern primary forest*, which is within the same range as other Amazonian sites with similarly aged forests [53]. If these secondary forests continue to develop, avian species richness should continue to increase, which should eventually allow biomass to converge with that of primary forest, especially because intact forest is adjacent to these secondary forest sites [53].
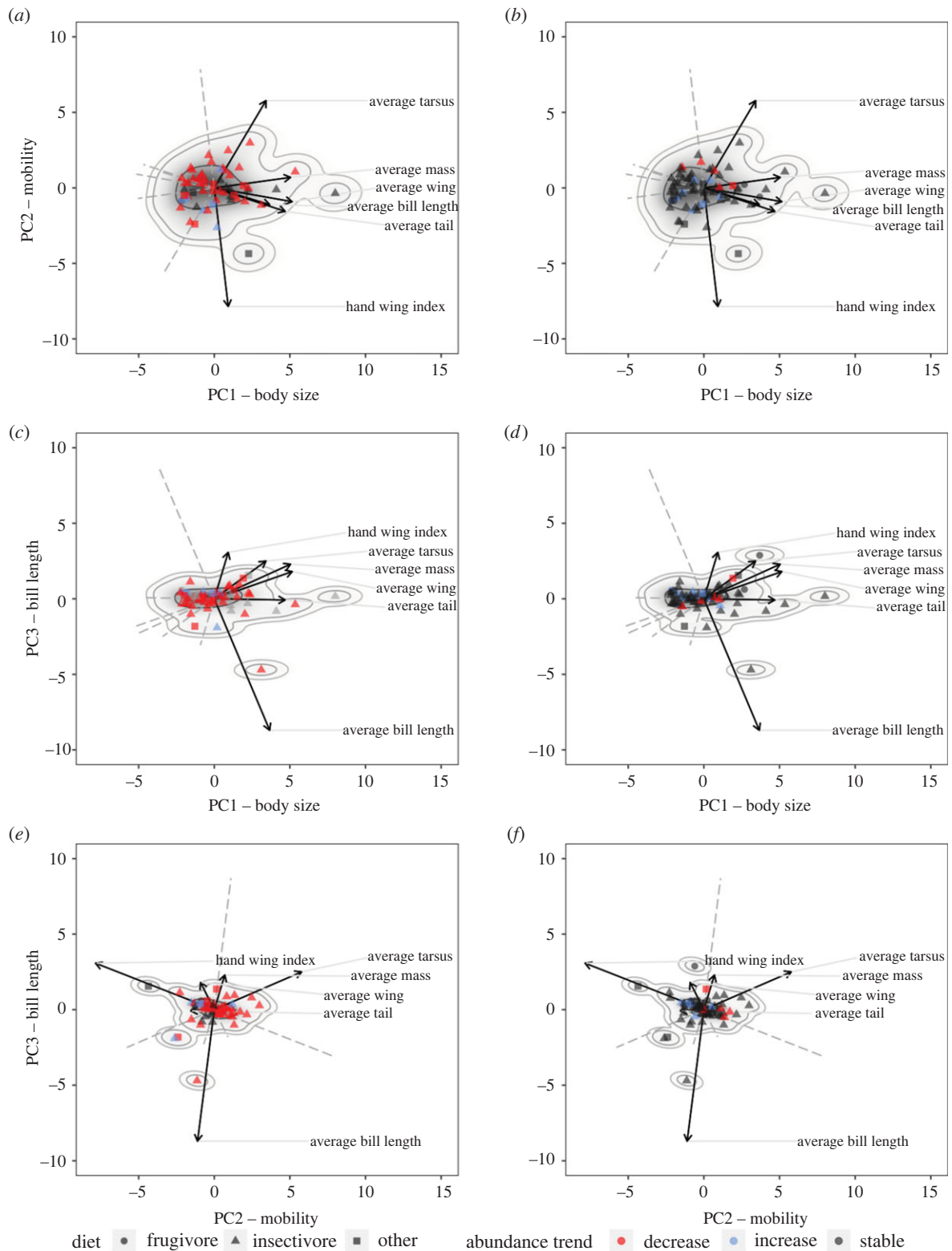
(b) Trait variation
For species in primary forest, changes in abundance (roughly along trophic guilds) correlate with the overall changes to the trait space occupied by the avian community. For example, midstory frugivores, which increased in abundance, tend to have shorter and wider bills, larger hand-wing indices, longer wings and shorter tarsus length than insectivores [54]. Using functional richness calculations, the majority of occupied trait space (85%) remained intact for avian communities in *modern primary forest*, compared to avian communities in *historical primary forest* (figure 2). In the *modern disturbed landscape*, however, only 65% of trait space was shared with *historical primary forest*. Bovo *et al.* [51] also observed an impact of habitat fragmentation on trait space, with smaller values for body mass, hand-wing index and bill width of frugivorous birds in relatively smaller forest fragments. While the full significance of reduced trait volumes remains unknown, the implications are vast in terms of fewer occupied niches [23] and overall reduced ecosystem functioning over time. In particular, the reduced functional diversity in modern avian communities, especially the *modern disturbed landscape*, may have deleterious consequences for plant species that depend on seed dispersers, pollinators and predators that regulate populations of herbivorous insects. For example, as a result of fewer seed-dispersing animals, seed dispersal is reduced in forest fragments [55]. In addition, fewer animals to pollinate flowers and disperse seeds in fragmented landscapes generates a three- to sixfold reduction in primary forest tree seeds, which is especially costly for rare and large-seeded trees in mature forest [56].

(c) Functional diversity
With no loss of species from *historical primary forest*, reduced abundances alone led to a loss of functional richness and redundancy in *modern primary forest*. The reduced functional

Figure 2. Two-dimensional functional trait space is represented by PC scores of functional traits in the *modern disturbed landscape* (*a,c,e*) and *modern primary forest* (*b,d,f*). PC1 axis reflects variation in body size, PC2 reflects variation in traits associated with mobility and PC3 reflects variation in diet and foraging traits via average bill length. Red symbols represent species that have declined, blue symbols species that have increased, and grey symbols species that have remained stable in modern forest compared to *historical primary forest* communities. Circles represent frugivores, triangles insectivores and squares represent other foraging guilds. Grey shading represents the kernel density estimates for each time period and contours show 50%, 95% and 99% probability. (Online version in colour.)

richness of understory birds in *modern primary forest* represents a smaller community niche space. This could stem from a loss of available niches, which would point to potential changes in ecosystem functioning, or something more specific to the survival and reproduction of the declining species. At the same time, species that increased in abundance did not offset the loss of functional richness in

modern primary forest communities, either because they did not show strong enough increases or because they occupy less distinct trait space.

The 15% decline in functional richness that we found in *modern primary forests* was much less than the 30–60% reduction detected in Andean cloud forest over a much longer period (100 years), although a large amount of that forested landscape
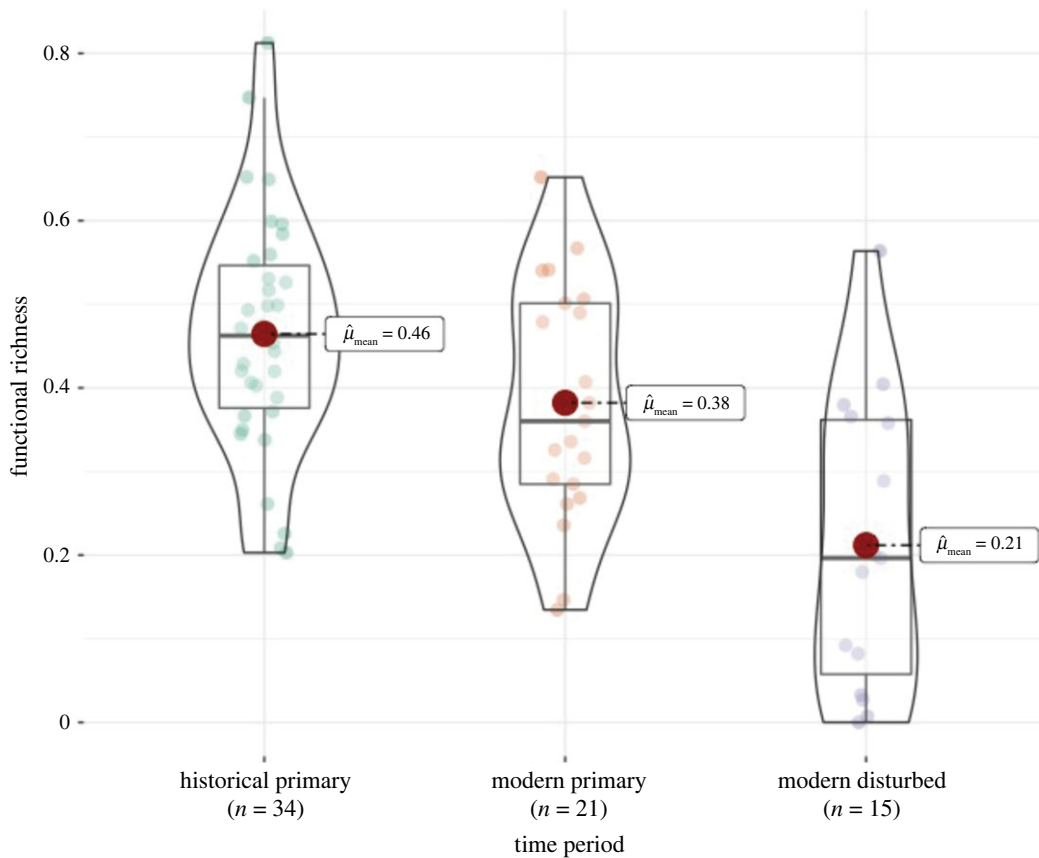
Figure 3. Violin plots of functional richness for avian understory communities in *historical primary forest*, *modern primary forest* and the *modern disturbed landscape*. All pairwise comparisons are significantly different. (Online version in colour.)

was fragmented or lost in the interim [57]. However, the 15% decline in undisturbed forest is on par with the 11–25% detected across other ecosystems [14,15,58]. In particular, degraded ecosystems such as those near urban environments displayed the greatest reduction in functional diversity [14], and species-rich coral reefs showed greater functional diversity and redundancy compared to ecosystems that were more degraded with fewer species [58]. Together, these global reductions in functional diversity are predicted to cause substantial losses to ecosystem functionality in oceanic, Mediterranean and tropical forest ecosystems [14,15,58,59].

Similar functional traits between different species lead to functional redundancy [60], and communities with greater functional redundancy exhibit greater ecological resilience [60,61], as suggested by the diversity–stability hypothesis. In both types of modern forests, *modern disturbed* and *primary forests*, functionally redundant species were more likely to decline in abundance than functionally distinct species. Decreases in functional redundancy within a community suggest a decline in ecosystem resilience, where the future loss of an individual species would have an even greater impact on ecosystem function than in communities with more redundancy. Losses and declines of species in the *modern disturbed landscape* led to a 35% reduction in functional richness compared to the 15% reduction in *modern primary forest*.

Hyperdiverse ecosystems such as the Amazon rainforest have higher levels of functional redundancy than less diverse ecosystems [24,58,62]. In hyperdiverse ecosystems, the heightened levels of functional redundancy are the result of either greater niche overlap, where species have greater niche breadth and tend to occupy a larger functional space than in less diverse systems, or tighter species packing, in which more species are

able to coexist locally. Diminished functional redundancy in hyperdiverse ecosystems could be a symptom of an overall reduction in ecological resilience, which was recently described for vegetation in the Amazon rainforest [13]. However, whether hyperdiverse ecosystems are more dependent upon functional redundancy to maintain resilience has yet to be determined. Regardless of the ecosystem or taxonomic group, habitat degradation reduces functional redundancy [62–65], which in turn compromises the resilience of the ecosystem [66].

Our findings in the *modern disturbed landscape* are similar to those from other contemporaneous studies that compared primary and disturbed tropical forests [25,51,67], indicating that more dissimilar species are likely to persist in disturbed forests. In particular, Bovo *et al.* [51] and Oliveira *et al.* [67] found that smaller forest fragments had lower functional richness than larger fragments or primary forest. Additionally, in our study, functional evenness (the equal dispersion of species in trait space) was highest in the *modern disturbed landscape*, which also had fewer species than primary forest. Higher values of functional evenness also indicate that species are less redundant in trait space and more distinct from one another compared to species in primary forest. The even distribution of species in trait space should reduce niche overlap and minimize direct competition [68,69], which can be especially important in degraded habitats likely to have fewer food resources [70,71]. In fact, a multitude of studies has observed that species with similar niches, as well as more closely related species, are less likely to coexist in degraded habitats such as forest fragments (e.g. [25,72]). Similar to our findings, the loss of species in degraded tropical forests has led to a decrease in the functional diversity of birds in other Neotropical forests [51,64,67,73,74].
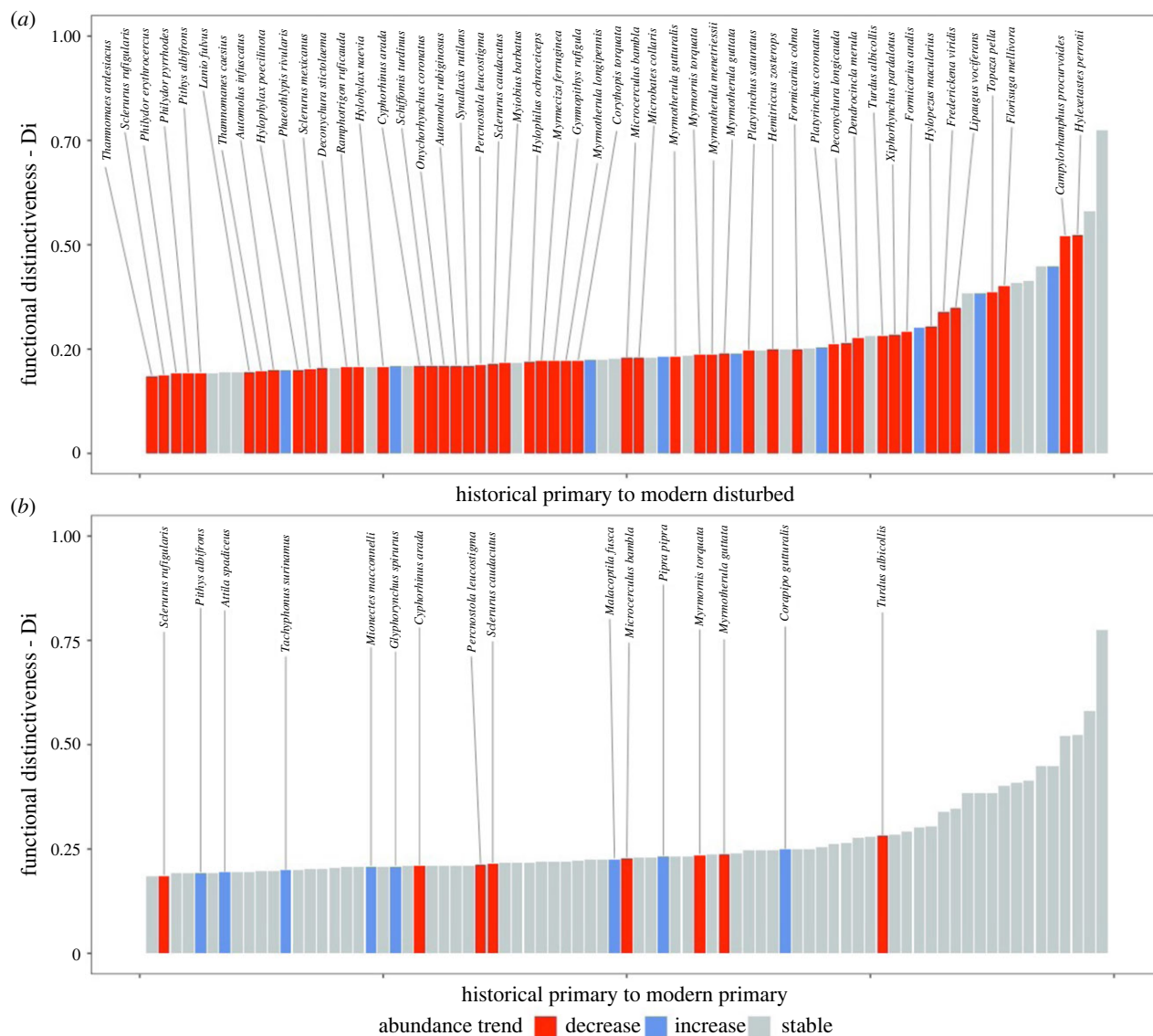
Figure 4. Functional distinctiveness of each species. Functional distinctiveness measures how uncommon a species' trait values are (from 0 to 1) compared with other species in the community. Lower values represent less distinct species and higher values represent more distinct species. Each vertical column represents a species and its functional distinctiveness relative to all other species. Red, blue and grey bars indicate species that are significantly declining, increasing and stable, respectively, in (*a*) the *modern disturbed landscape* and (*b*) *modern primary forest* when compared to *historical primary forest* communities, according to long-term population trends from Stouffer *et al.* [21]. In *modern primary forest*, Stouffer *et al.* [21] identified that near-ground and terrestrial insectivores were most likely to decline while midstory frugivores were most likely to increase in abundance, while in *modern disturbed forests*, the majority of insectivore guilds decreased (no guilds increased significantly). (Online version in colour.)

In general, results from functional diversity metrics vary depending on the number and type of traits used to calculate functional diversity [2,75]. For example, more traits and ecologically irrelevant traits can overparameterize models and give misleading results [2]. Consequently, it is critical to select the most appropriate traits to adequately assess changes to functional diversity. Although each individual functional diversity metric has its own shortcomings or biases, we attempted to minimize the limitations of any one metric by using an array of different metrics to assess the same multidimensional trait space. For example, functional richness assumes an equal distribution throughout the internal trait space and is biased by outlier points in multi-dimensional trait space [76]. However, by also assessing functional evenness and redundancy, we assess the distribution and relationship between points within that trait space. For our study system, we chose diet and morphological traits that relate to how species interact with their environment, as these two sets of

variables are linked most directly to ecosystem functions. However, if we had also selected distinct behavioural characteristics, we might have seen even more dispersion in functional diversity metrics, especially in historical primary forest, where the greatest variety of species with differing behaviours was most abundant [21], although we might have also overparameterized our models [2,75]. Thus, by not including these behavioural traits, our conclusions are likely more conservative than they would have been otherwise.

The long-term viability and resilience of tropical forests rely on the continuation of functional diversity that maintains ecosystem function, health and resilience, which is supported by a certain amount of functional redundancy in the community. Our results indicate that the observed shift from historical baselines have had tangible effects on the functional diversity, but not the overall biomass, of animal communities in otherwise pristine regions of the Amazon rainforest. The reduction and loss of species with similar traits and functional redundancy
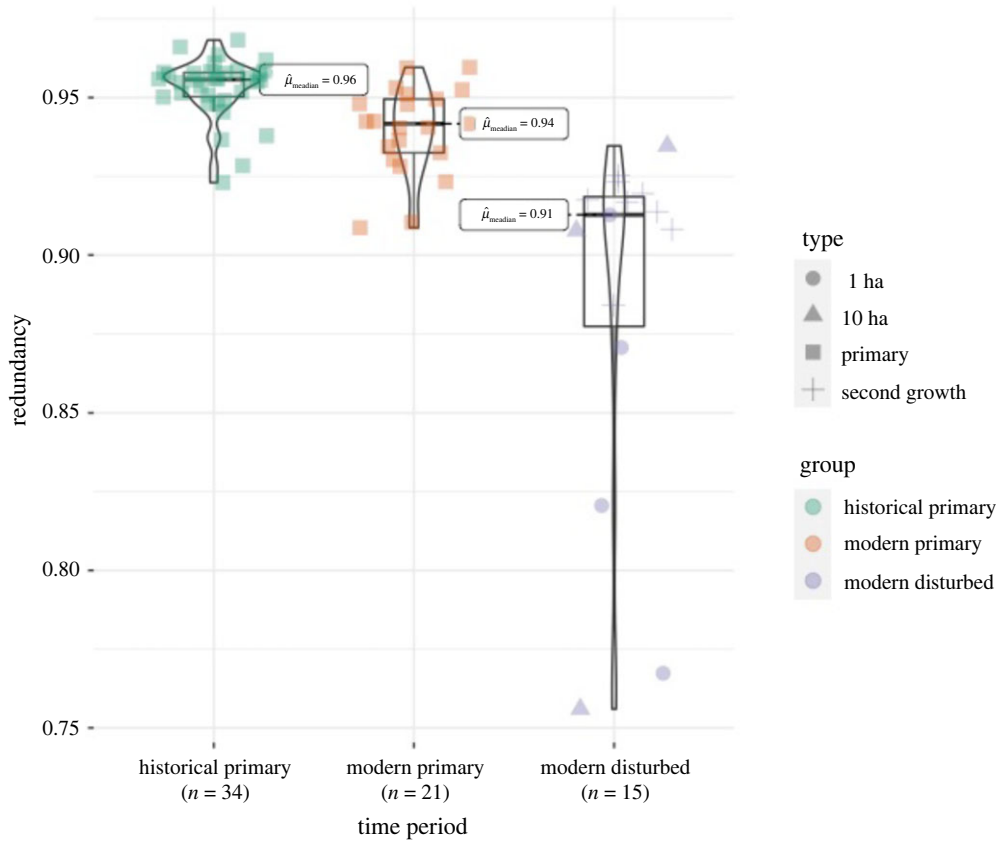
Figure 5. Comparison of functional redundancy estimates for each site during historical and modern time periods. Larger values indicate higher functional redundancy within a community, where the loss of an individual species would likely have little to no impact on ecosystem function. All pairwise comparisons are significantly different. (Online version in colour.)

support the diversity–stability hypothesis [5] and the notion that ecosystem resilience has eroded in the Amazon rainforest during recent decades [13].

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