Title

Ecological filtering shapes the impacts of agricultural deforestation on biodiversity

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Abstract

The biodiversity impacts of agricultural deforestation vary widely across regions. Previous efforts to explain this variation have focused exclusively on the landscape features and management regimes of agricultural systems, neglecting the potentially critical role of ecological filtering in shaping deforestation tolerance of extant species assemblages at large geographical scales via selection for functional traits. Here we provide a large-scale test of this role using a global database of species abundance ratios between matched agricultural and native forest sites that comprises 71 avian assemblages reported in 44 primary studies,

and a companion database of ten functional traits for all 2,647 species involved. Using meta-analytic, phylogenetic, and multivariate methods, we show that beyond agricultural features, filtering by the extent of natural environmental variability and the severity of historical anthropogenic deforestation shapes the varying deforestation impacts across species assemblages. For assemblages under greater environmental variability – proxied by drier and more seasonal climates under greater disturbance regime – and longer deforestation histories, filtering has attenuated the negative impacts of current deforestation by selecting for functional traits linked to stronger deforestation tolerance. Our study provides a heretofore largely missing piece of knowledge in understanding and managing the biodiversity consequences of deforestation by agricultural deforestation.

137

MAIN TEXT

As the earliest and most dominant form of human land use [1], agriculture has transformed almost 40% of the Earth's ice-free land area [2]. Among its many environmental impacts [3], deforestation for agriculture poses one of the gravest direct threats to biodiversity via habitat loss, fragmentation and degradation [4], with existing evidence overwhelmingly showing negative biodiversity responses [5,6]. However, the severity of these impacts appears to vary widely [7], with reports of substantial biodiversity loss following even small-scale forest conversions [8] contrasted by cases of agricultural landscapes providing positive conservation outcomes [9]. Understanding which factors underlie this apparent variation is fundamental in predicting the future biodiversity impacts of agricultural land use and informing conservation planning, including associated forest protection and restoration [6]. The urgency of such understanding is evident, given the ongoing expansion of agriculture globally (which saw ~107 million hectares of deforestation and natural vegetation conversion to croplands in 2003–2019 alone [10]) and the competing demands on limited land resources from food security and forest conservation [11].

Studies have traditionally focused on the landscape features and management regimes of agricultural systems to explore reasons for the varying biodiversity impacts of agricultural deforestation [7,12,13]. These efforts have generated a broad consensus on the ameliorating roles of higher landscape heterogeneity [14,15] and lower management intensities [16], providing useful guidance to minimise the biodiversity impacts of agriculture at the local scale [17]. However, these findings are focused on present-day factors and have neglected the potentially critical roles of natural and anthropogenic filtering in shaping biodiversity responses. At large geographical scales, natural habitat features and historical human impacts are well known to determine current species distributions via the selection for certain combinations of functional traits that govern species' persistence in the local environment (Fig. 1a) [18–23]. If such filtering affects species' inherent tolerance to habitat change because of their pre-existing or acquired functional traits, it could conceivably render inherently different tolerance to agricultural deforestation in extant species and their assemblages across different ecosystems. Yet despite the wide recognition of filtering [18–23], how it may underlie the tolerance of extant species and assemblages to agricultural deforestation has not been explicitly assessed beyond a handful of local studies [21,24], severely limiting the scope of inference attainable. Overall, the lack of a filtering perspective in existing large-scale assessments potentially omits a key process responsible for the observed variation in biodiversity responses to agricultural deforestation.

At large geographical scales, two sets of factors with clear geographical patterns are particularly likely to shape biodiversity responses to agricultural deforestation via filtering: natural variability of environmental conditions and historical anthropogenic deforestation ("environmental variability" and "historical deforestation" hereafter). In forest ecosystems where the environment is variable in such a way that vegetation bears natural resemblance to non-forest habitat, such as sparse canopy (whose interspersion of forest and non-forest conditions begets spatial environmental variability) or recurrent structural changes (*e.g.* seasonal defoliation or other structural changes linked to disturbance regime), species assemblages are naturally exposed to non-forest conditions. As such, they may be pre-adapted to deforestation including that associated with conversion to agriculture. This possibility has been demonstrated for avian assemblages in Central America and the Himalayas, where those in drier or more seasonal forest ecosystems are more tolerant of forest conversion to agriculture [24,25]. On the other hand, historical deforestation may further select against species sensitive to deforestation via extinction and adaptation [26,27]. In both cases, there should be a trait signature of filtering, whereby species assemblages under greater environmental variability or historical deforestation assume trait

profiles corresponding to greater deforestation tolerance (Fig. 1b). Filtering linked to this trait signature would thus predict less severe biodiversity impacts of current agricultural deforestation at the assemblage level, independent of the features of agricultural systems. Despite strong theoretical underpinnings [18] and empirical evidence of their influence on biodiversity responses to other anthropogenic threats [28,29], these filtering mechanisms and particularly the trait signature of such filtering have not been tested in large-scale assessments of the biodiversity impacts of agricultural deforestation.

Here, we combine meta-analytic, phylogenetic, and multivariate methods to test the hypothesis that filtering by environmental variability and historical deforestation explains global variations in the biodiversity impacts of agricultural deforestation, and that these filtering effects are reflected by the trait signatures of species assemblages. We use birds as a single, most data-rich representative taxon to avoid taxonomic identity confounding biodiversity responses, considering that different taxa may have inherently different responses to habitat change [30]. Through extensive compilation of paired data between matched agricultural and reference native forest sites ("agriculture-forest pair" hereafter), we constructed a global database of species-specific abundance records (individuals ha^{-1}; corrected for sampling effort) for entire avian assemblages [31]; we broadly defined agricultural land as including croplands, pastures, and agroforestry (Methods; Extended Data Fig. 1; Extended Data Table 1). For each record, we calculated an abundance response ratio of agricultural over native forest sites (on the natural log scale; "RR" hereafter) to represent the impact of agricultural deforestation on each species (and by extension, species' tolerance to agricultural deforestation), with more negative RRs indicating stronger negative impacts and lower deforestation tolerance (Methods).

For each assemblage, we additionally calculated the means of RR across all species ("assemblage RR" hereafter) to represent assemblage-level impacts. For the agricultural sites in each study, we also quantified remnant forest cover, distance to the nearest continuous forest, and surrounding human population density (people km^{-2}) to represent their landscape features. Our compilation yielded 7,625 RRs covering 2,647 bird species [31]. These records contained 71 agriculture-forest pairs – each involving an entire avian assemblage – reported in 44 primary studies from 25 countries, and they accounted for ~72% of all suitable primary studies identified (Fig. 2; Extended Data Table 2). For each bird species, we also compiled data on ten functional traits [31] – spanning the morphological, life-history, behavioural, and other ecological dimensions – that are considered predictive of species tolerance to forest loss or degradation [29,32–36] (Extended Data Tables 3 and 4; Methods).

To represent environmental variability, we used mean annual precipitation ("MAP" hereafter; mm y^{-1}), the standard deviation of mean monthly temperature ("seasonality" hereafter; °C), and the frequency of forest disturbance regime involving any of four disturbance types: storm, wildfire, flood, and drought ("disturbance regime" hereafter; in two categories: "no disturbance" versus "with regular disturbance") [28]. Native forests under lower MAP tend to have sparser canopy cover [37], while those under more seasonal climates or more frequent disturbance regime typically exhibit more pronounced defoliation or other structural change cycles [24,28] – features that both resemble non-forest habitat conditions associated with environmental variability. To represent the severity of historical deforestation, we calculated the length of agricultural history ("agricultural history" hereafter; y), considering that agricultural land use constitutes the dominant agent of anthropogenic deforestation [1,18], and that its filtering effect would most likely begin with the onset of agricultural land conversion [38]. We obtained data on

MAP, seasonality, and agricultural history from existing databases [39,40], and we scored disturbance regime by consulting authors of primary studies and the literature (Methods). In all, the study systems included in our database spanned wide ranges of variable values representing environmental variability (100–4,964 mm y^{-1} in MAP, 0.2–14.1 °C in seasonality, and varying disturbance regime scores; the 100-mm-y^{-1} MAP and 14.1-°C seasonality were both from a desert ecosystem with riparian forests), agricultural history (142–9,018 y), and agricultural landscape features (Fig. 2; Extended Data Figs. 2 and 3; Extended Data Table 2; ref 31).

Results

Biodiversity impacts of agricultural deforestation are less severe in study systems under greater environmental variability and historical deforestation

Meta-analyses of assemblage RR indicated that while the impacts of agricultural deforestation on avian abundance were overall negative, they depended on the type of agriculture and species considered (Figs. 3a and 3b; Methods). Whereas average impacts on whole assemblages were hardly negative (Fig. 3a, upper row), this pattern was a result of the mostly positive impacts of agroforestry (Fig. 3a, middle row) counteracting the overall negative impacts of open agriculture (Fig. 3a, lower row). More importantly, this pattern was clearly driven by a set of "winner" species that were absent from native forests but were found at agricultural sites: a separate set of meta-analyses on sub-assemblages that comprised only species present at the native forest sites showed clear negative impacts of agriculture (Fig. 3b, upper row), regardless of whether it was agroforestry (Fig. 3b, middle row) or open agriculture (Fig. 3b, lower row).

The above meta-analyses also showed that the impacts of agricultural deforestation on avian assemblages varied widely across study systems, as indicated by the consistently high values of I^2, the measure of heterogeneity of meta-analytic data [41] (Figs. 3a and 3b; Methods). Applying meta-regressions on assemblage RR to further assess such variation, we found that impacts were less negative in assemblages under higher remnant forest cover (β: 0.205, 95% confidence interval ["CI" hereafter]: 0.064–0.347) and in fact tended to be positive at high covers (Fig. 3c; Methods). Crucially, impacts were also less negative at lower MAP (β: -0.320, 95% CI: -0.650–0.009; Fig. 3d) and longer agricultural history (β: 0.227, 95% CI: 0.033–0.420; Fig. 3e). These results were robust to potential confounding effects of the types of agriculture and native forests being compared and the season of study (Extended Data Fig. 4), as well as to publication bias (Extended Data Fig. 4; Supplementary Information Table S1) and a set of sensitivity analyses involving map-extracted data, data scaling, outlier handling, and weighting schemes (Supplementary Information Tables S2–4; Methods). In sum, the negative biodiversity impacts of current agricultural deforestation were less severe in study systems subjected to greater filtering by historical deforestation and – to a lesser extent – environmental variability.

The trait signature of filtering: functional traits predicting greater deforestation tolerance

We further assessed the trait signature of such filtering effects by testing whether avian assemblages under greater environmental variability and historical deforestation had trait profiles predictive of greater tolerance to agricultural deforestation (Fig. 1b). To do this, we first asked what traits would predict species' greater tolerance to agricultural deforestation (represented by larger species-level RRs), using phylogenetically controlled mixed-effect modeling and accounting for the potential influence of covariates as informed by preliminary analyses (Methods). Our analyses showed all ten traits tested to be relevant, in ways consistent with

expectations (Extended Data Table 3): species' greater tolerance to deforestation was clearly associated with larger clutch sizes, shorter generation lengths, lower diet specialisation, lower foraging heights, weaker forest associations, larger natural ranges, and lower dependence on forest structures for nest placement, and to a lesser extent associated with lower body masses, larger hand-wing indices (representing stronger dispersal abilities [29]), and being migratory (Fig. 4a; Supplementary Information Table S5). These "tolerance traits" thus depicted a clear trait profile of species that were more tolerant of agricultural deforestation.

The trait signature of filtering: assemblage trait profiles in relation to filtering

Based on the above trait profile, we next derived the "tolerance trait profile" for individual assemblages, and assessed its relationship with environmental variability and historical deforestation. We represented the tolerance trait profile of a given assemblage by its "centroid" of each trait, *i.e.* the mean trait value weighed by the relative abundance of each species (pooled across agricultural and native forest sites, after correcting for potentially unequal sampling effort between the two habitat types; Methods). Thus, an assemblage more tolerant of agricultural deforestation had a trait profile involving lower assemblage-level centroid values for six traits: body mass, generation length, diet specialisation, foraging height, forest association, and dependence on forest structures for nest placement, as well as higher centroid values for the four other traits: hand-wing index, clutch size, migratory status, and natural range size (as shown in Fig. 4a). Mixed-effect models for the assemblage-level centroid of each trait indicated that they had clear relationships with seasonality and, to a lesser extent, MAP, disturbance regime, and agricultural history (Fig. 4b; Methods). Importantly, the directions of these relationships predominantly linked more tolerant assemblage trait profiles to greater environmental variability and historical deforestation. Take forest association as an example: its lower centroid values – indicating greater assemblage tolerance of deforestation (the top dashed box in Fig. 4a) – were linked to lower MAP, higher seasonality, and more frequent disturbance, all corresponding to greater environmental variability; they were also to a lesser extent linked to longer agricultural history that signifies more severe historical deforestation (Fig. 4b, the row corresponding to the top dashed box in Fig. 4a).

These relationships were not an artefact of multiple testing, according to a further analysis of the top principal component ("PC1" hereafter) of all ten trait centroids, which accounted for 49.0% of the total variance in principal component analysis ("PCA" hereafter; Supplementary Information Table S6; Methods). Variable loadings of PCA indicated that lower PC1 overwhelmingly corresponded to assemblage trait profiles more tolerant of agricultural deforestation, as evidenced by the negative loadings of traits that predicted greater tolerance to agricultural deforestation (*e.g.* hand-wing index) and vice versa (*e.g.* forest association; Supplementary Information Table S6). Mixed-effect models indicated that MAP, seasonality, disturbance regime, and agricultural history were all predictive of PC1 (Fig. 4c; Methods), in ways that linked lower PC1 to greater environmental variability – as represented by lower MAP (Fig. 4c, top panel), higher seasonality (Fig. 4c middle panel), and more frequent disturbance (Fig. 4c, slate blue over purple data points and fitted line in all panels) – and more severe historical deforestation (*i.e.* longer agricultural history; Fig. 4c, bottom panel).

Taken together, the above analyses (also robust to a suite of sensitivity analyses; Supplementary Information Tables S7–10; Methods) showed that the observed filtering effects of greater environmental variability and historical deforestation had a clear trait signature of "shifting" avian assemblages toward trait profiles that correspond to greater tolerance to

deforestation. Such shifts could occur in a number of ways. First, they could be the result of the filtered assemblages occupying a larger, more divergent trait space, particularly in regions of the trait space that correspond to greater tolerance of deforestation ("trait space expansion"; Fig. 1b, sub-panel (i)). Alternatively – and in the absence of trait space expansion – such shifts could occur by constituent species in filtered assemblages shifting collectively toward or clustering in the regions of the same trait space that correspond to greater tolerance ("trait shift" and "trait clustering" respectively; Fig. 1b, sub-panels (ii) and (iii)).

To assess how the above shift in assemblage trait profiles could have occurred, we used a set of multivariate trait metrics to measure the trait space occupation of each avian assemblage, which we then related to the PC1 of assemblage trait centroids, the metric we used in the above analyses to measure the trait profile and its shift for each assemblage. We used functional richness (corrected for species richness) to measure the hypervolume of the trait space occupied [42], functional dispersion to measure the divergence of trait profiles among species [43], and functional redundancy to measure the clustering of species around certain trait profiles [44] (Methods). Linear regressions indicated that lower PC1 – corresponding to more tolerant assemblage trait profiles (Supplementary Information Table S6) and associated with filtering by greater environmental variability and historical deforestation (Fig. 4c) – was strongly correlated with an increase in both functional richness and functional dispersion, but it was unrelated to functional redundancy (Fig. 5). These results suggested that in assemblages subjected to filtering by greater environmental variability and historical deforestation, the trait signature of filtering most likely occurred by constituent species exhibiting more divergent trait profiles, particularly those corresponding to greater tolerance of deforestation (*i.e.* via trait space expansion).

Discussion

Drawing on an extensive database of species abundance responses to agricultural deforestation for entire avian assemblages compiled from 25 countries, we demonstrated high levels of variation in the severity of assemblage-level deforestation impacts across a large collection of primary studies. Crucially, beyond features of the agricultural systems, this variation was linked to the filtering effects of environmental variability and historical anthropogenic deforestation, which operated on species' functional traits to render inherently different tolerances to deforestation across extant assemblages. Previous efforts to explain the varying impacts of agricultural deforestation on biodiversity were overwhelmingly limited to the features of agricultural systems [7,12], or were regionally focused so as to severely limit the ranges of filter types or filtering intensities testable [21,24]. Building on theoretical underpinnings [18,20] and empirical evidence in other contexts [19,28,29], our study provides a large-scale test of the roles of natural and anthropogenic filtering in shaping biodiversity responses to agricultural deforestation. The evidence we uncovered for such roles highlighted a heretofore largely neglected explanation for the observed variation in biodiversity responses, including the apparently more negative responses found in tropical assemblages [7], whose possible reasons were yet to be formally tested.

Enhancing such understanding enables better anticipation and management of biodiversity consequences of future agricultural land-use change. Globally, agricultural land use is predicted to shift and expand, with deforestation hotspots predicted particularly for sub-Saharan Africa, South and Southeast Asia, and to a lesser extent Central and South America [45]. Most of these hotspots are of high precipitation, low temperature seasonality, little disturbance

regime, and/or short agricultural histories (Extended Data Fig. 3), which likely render their extant biodiversity less tolerant to the negative impacts of deforestation. Such a prospect, combined with the fact that much of existing agricultural deforestation has happened in more "filtered" ecosystems [1,10] (*i.e.* ecosystems less subject to the filtering effects of high environmental variability or long deforestation histories), means that global biodiversity loss linked to future agricultural deforestation may be even more severe than has happened to date [4]. This is a grave possibility, and it underscores the need for managing agricultural landscapes using the best knowledge and practices available [12,17], and crucially, for proactive land-use planning to reduce deforestation in inherently high-impact regions – in ways sensitive to the livelihood and rights of the rural populations involved. The latter strategy should employ a range of approaches including reducing the footprint of agricultural land use – via optimizing land allocation among alternative production regimes [46] and/or relocating production to more cost-efficient regions [47] – and prioritizing already deforested land for agricultural expansion in coordination with forest restoration [48].

The trait signature of filtering we found further provided insights into how natural and anthropogenic filtering occurs to shape present-day biodiversity responses to anthropogenic environmental change, and it highlighted several functional traits as key determinants of such responses. Previous studies on the role of filtering in explaining the geographical variation of biodiversity responses are restricted to demonstrating the effect of filtering, stopping short of testing its potential trait signatures [19,28], although two recent species-level studies on avian tolerance of urbanisation [49] and forest fragmentation [29] have gone a step further to assess the relevance of traits to such tolerance and crucially, the geographical variation in this relevance. These studies mark an important advance toward understanding varied biodiversity responses to environmental change from a filtering perspective. Nevertheless, they do not test the signature of filtering on the level of entire species assemblages, which is critical for elucidating the role of filtering by bridging with the logic and expectations of the underlying ecological theory [18,20,23]. In addition, despite growing recognition of the links between species' tolerance to anthropogenic impacts and their functional traits [32,50], there is yet to be a rigorous large-scale test of these links for agricultural deforestation [33,35], particularly based on globally synthesised empirical data rather than the coarse proxy of IUCN threat levels [32,34]. Our study filled the above important gaps, and expanded current understanding of the conservation relevance of ecological filtering [23].

While based on paired data and robust to a suite of sensitivity analyses, our conclusions could be affected by several factors we could not account for. These include the management intensity of agricultural systems [7], potential pre-existing differences in biophysical conditions or anthropogenic pressures (*e.g.* hunting) between agricultural and native forest sites, and biotic factors capable of further filtering species assemblages in addition to the factors we considered [20], notably competition, a process recognised to shape community assembly via functional traits [51]. The first issue should be lessened by the fact that our analyses accounted for remnant forest cover at agricultural sites as well as the types of agriculture and native forests being compared, given the tendency for intensive agriculture to be associated with reduced remnant forest cover and non-agroforestry systems. The influence of the second issue should also be limited to that of noise rather than bias, because we have no reason to expect that potential differences in within-pair site conditions co-varied with MAP, seasonality, disturbance regime, or agricultural history to contradict our findings. For the third issue, while we were not able to explicitly account for the influence of competition and other biotic filters, we note that at large geographical scales – which is the scale our study is concerned with – these factors and processes are likely to be

ultimately shaped by such abiotic factors as the ones we tested [23]. Nevertheless, conclusions from our study should be interpreted with the caveat that we have not explicitly considered some potentially relevant filters. Finally, the lack of region-specific data on avian functional traits limited our assessment of the trait signature of filtering to the species level, regardless of how widely distributed a species may be. This forced us to neglect potential intraspecific trait variations across regions that may predict different deforestation tolerances even within the same species [52]. As the spatial resolution of trait data improves, future studies should incorporate intraspecific trait variations in assessing the trait signature of filtering.

Human activities continue to profoundly shape the Earth's ecosystems and the life forms therein. As we seek to understand the extent and nature of such impacts and manage them, it is critical to recognise that the observed impacts are influenced not just by current and ongoing human activities, but also by the nature and strength of historical legacies pertaining to ecosystems' evolutionary histories and past human impacts [28], including undocumented historical extinctions [53]. This legacy perspective particularly underscores humans' obligations to conserve the rapidly disappearing ecosystems so far spared of human impacts – the Earth's last strongholds of complete species assemblages. The otherwise inevitable filtering and loss of their sensitive species not only erodes the integrity of these ecosystems *per se*, but also spells further erosion of the Earth's life forms to aggravate the historical legacies humans leave. By illustrating this case for how agricultural deforestation – a leading threat to global biodiversity – impacts extant biodiversity, our study suggests the potentially strong relevance of natural and anthropogenic filtering to understanding and managing the biodiversity impacts of other forms of anthropogenic environmental change.

Methods

Data Collection

Data inclusion criteria: We targeted empirically measured abundance data for matched agricultural and native forest sites (*i.e.* "agriculture-forest pair") on the level of individual bird species for entire avian assemblages. We focused on species-level abundance to allow more nuanced assessment of deforestation impacts on biodiversity than is possible from coarser metrics such as species richness or presence/absence [54], and to relate species responses to functional traits. We considered a species part of an assemblage only if it was recorded at either the agricultural or native forest sites, or both.

As a benchmark for agricultural land, we included three types of native forest: old-growth forests that had not been anthropogenically degraded in extended recent history (*i.e.* ≥400 years), "generic native forests" that may have been degraded but had not been deforested in extended recent history, and secondary forests that had been regenerating after deforestation for ≥40 years [55]. For agricultural land, we included cropland of a wide range of food crops (mostly cereal and vegetables but also coffee, tea, and cocoa; we did not include oil palm and other orchard tree crops because unlike the shrub-like structure of coffee, tea, or cocoa plantations, plantations of oil palm or other orchard trees tend to have a much more tree-cover-like vegetation structure), pasture land for domestic livestock grazing, and agroforestry of crops or pasture (*i.e.* silvopasture). We considered coffee, tea and cocoa plantations as agroforestry (as opposed to cropland) only if they were noted by primary studies to be shade-grown, considering the generally open vegetation structure of sun-grown coffee, tea or cocoa.

While the true benchmark for agricultural land should be old-growth forests, we also accepted generic native forests and secondary forests as benchmarks because old-growth forests no longer existed in many study systems. We ensured that the use of these "degraded" benchmarks did not bias our findings (see "Statistical analysis: meta-analyses and meta-regressions" below), and we note that this use almost certainly rendered more conservative estimates of the negative impacts of agricultural deforestation. We considered a native forest as old-growth only when the primary studies explicitly labelled a forest as "primary", "old-growth", "pristine", or otherwise undisturbed by humans, and when we had no reason to doubt such labelling. For secondary forests, we used 40 years as the minimum acceptable regeneration age to allow a reasonable degree of biodiversity recovery in these forests [55]. This threshold age was nonetheless young and potentially rendered the native forest benchmark a highly degraded one, but secondary forests concerned only three out of the 71 avian assemblages studied (Extended Data Table 2). They therefore should not have driven our findings, and we tested for their potential influence on our findings via a set of sensitivity analyses (see "Sensitivity analyses" below).

We required the paired agricultural and native forest sites to provide matching abundance data capable of representing their habitat values for entire avian assemblages. Accordingly, we followed five criteria to assess the suitability of each primary study. (1) The avian assemblages studied (typically termed "communities" in primary studies) must not be defined by criteria potentially relevant to species' abundance response to habitat change (*e.g.* large body size or needing cavities for nesting). (2) The avian assemblages studied must include ≥6 species, and ≥10% of constituent species must have been recorded. (3) Sampling efforts for agricultural and native forest sites must be equivalent or known, such that abundance raw counts could be adjusted for equal sampling effort, or the quality and comparability of density estimates could be confirmed. (4) The size of the native forest patches sampled must be ≥5 ha such that the species-specific abundance data could be considered as reflecting the habitat value of the native forests being studied, although such data are still potentially affected by the wider landscapes [56] (as explained below, we have accordingly devised a "habitat certainty score" as part of the weight scheme used in meta-analyses and meta-regressions, to account for potential influences of the wider landscapes: 1 for "low habitat certainty", if the native forest sampled were fragmented or otherwise <50 ha in size; 2 for "high habitat certainty", if it was ≥50 ha in size; see "Data search and compilation"). Similarly, if the agricultural sites studied were in the form of agricultural patches situated in a forest landscape, we required the agricultural patches to be ≥5 ha. (5) The matching between agricultural and native forest sites concerned all biophysical (*e.g.* elevation, slope, landscape context) and study (sampling methods) conditions that may affect the measured species abundance. Correspondingly, we discarded data pairs that were obviously incomparable (*i.e.* major differences in biophysical or study conditions, or different sampling methods). Provided the above criteria were met, we allowed a range of data formats for species-specific abundance: raw counts, estimated density (*e.g.* individuals ha^{-1}), or abundance indices; we did not admit indices based on occurrence frequencies because they are fundamentally about species' presence / absence rather than abundance. Because of varied sampling designs and methods, data compiled from primary studies did not allow accounting for imperfect detection.

Data search and compilation: We conducted an extensive search for suitable primary studies up to 7th December 2021, using a combination of keyword searches and indexing from published syntheses and databases (Extended Data Fig. 1; Extended Data Table 1). In all, we

screened 5,899 abstracts and subsequently 451 full-text articles, through which we identified 61 suitable primary studies.

We extracted species-specific abundance data directly from these studies where available, and we corresponded with the first and corresponding authors of the other studies to request abundance data. Of the 61 suitable primary studies identified, we were able to compile species-specific abundance data for entire assemblages for 44 studies. We streamlined the resolution of abundance data such that a given primary study provided one set of species-specific abundance data (*i.e.* corresponding to an avian assemblage) for each agriculture-forest pair, which could consist of multiple sampling units. For abundance data in formats other than density, we adjusted their values by sampling effort (measured in the unit used in the primary studies) to ensure that data for agricultural land and native forests corresponded to equal sampling effort [54]. We assumed that density estimates were already corrected for sampling effort, and for studies that simultaneously reported raw counts and density estimates, we used the latter, assuming that they had accounted for factors that may affect the comparability of raw counts. In calculating RR for species-specific abundance, for data pairs involving zero abundance values (which would make it impossible to calculate RR), we handled zero values separately for each assemblage, by first identifying the smallest non-zero abundance value for any species in the assemblage, and adding half of that value to each zero value following [57].

For each agriculture-forest pair, we recorded three metrics to calculate the weight of its RRs in subsequent analyses (see "Statistical analysis: meta-analyses and meta-regressions" below). First, we assigned a "match rigor score" to gauge the extent of matching between agricultural and native forest sites: 1 for "high match rigor", if matching concerned most or all biophysical and methodological conditions; 2 for "likely or uncertain match rigor", if matching was partial or if little information was provided despite data being presented as matched. We note that primary studies often cannot fully eliminate site differences – *e.g.* agricultural sites may often be on more productive land than native forests in the same area. Second, we scored the duration of fieldwork (in months; "study duration" hereafter) to approximate the sampling effort for abundance data and in turn, data quality. The fact that primary studies used a range of sampling designs (*e.g.* point counts versus transect surveys) precluded the use of sampling units to assess sampling effort. Third, we assigned a "habitat certainty score" to represent the extent to which abundance data for native forests reflected the habitat value of the forests *per se* rather than the influence of the wider landscapes: 1 for "low habitat certainty", if the native forest sampled were fragmented or otherwise <50 ha in size; 2 for "high habitat certainty", if it was ≥50 ha in size. We gave greater weights to records with higher match rigor, longer study durations, and higher habitat certainty, by calculating the weight of the species-level RRs (and correspondingly, the assemblage-level RRs) for each agriculture-forest pair using Equation 1 (we ensured the robustness of our results to this weight formulation using a set of sensitivity analyses; see "Sensitivity analysis" below):

$$\text{Weight score} = \frac{\sqrt{\text{Study duration}} \times \text{Habitat certainty score}}{\text{Match rigor score}} \quad \text{(Equation 1)}$$

For each agriculture-forest pair, we additionally extracted data on the season of study ("study season" hereafter), and for the agricultural site, the amount of remnant forest cover in the

landscape and the distance to the nearest large, continuous forest ("distance to the nearest continuous forest" hereafter). For study season, we differentiated between studies conducted during the non-breeding season of the avian assemblages studied *versus* those conducted during the breeding season or all-year, considering the possible shift of habitat needs during the breeding cycle for some species [9]. We defined the study season as "non-breeding" if the primary study explicitly indicated as such, and otherwise as "breeding or all-year" (tropical studies in our database that did not specify their study season relative to the avian breeding cycle were therefore classified as the latter). For the amount of remnant forest cover at agricultural sites, because of varying and limited amounts of information provided across primary studies, we used an ordinal system of six categories represented by scores 0–5 in sequential order: 0, (0–5]%, (5, 10]%, (10, 20]%, (20, 40]%, (40, 60]%; no study included in our database had >60% remnant forest cover in the agricultural landscapes.

For distance of agricultural sites to the nearest continuous forest, we defined continuous forest as forest expanses ≥50 ha in size, and we measured this distance from the FROM-GLC Plus land-cover map (covering years 1982–2021, at a 30-m resolution; "FGP map" hereafter) [58], from layers matched to the year of the avian surveys. Our use of land-cover maps for extracting this information was again because of the lack of consistent, quantitative information from primary studies on distances between agricultural and forested sites. We selected the FGP map because it is the highest-resolution land-cover product that adequately covers the temporal extent of primary studies in our database. The only other land-cover product that covers a sufficiently wide temporal extent is the ESA CCI Land Cover time-series map (covering years 1992–2020) [59], but its spatial resolution is 10 times coarser than that of the FGP map (30 m), which we deemed too coarse to provide reliable distance measures. The FGP map also shows higher overall accuracies than the ESA CCI maps [58]. For the three primary studies whose avian surveys occurred outside the year range of these maps, we used the map layers for the years nearest to them. Considering potential limitations on data accuracy imposed by map resolution, we set all distance values below 30 m (the map pixel size) to 30 m. We additionally used an alternative size criterion of ≥100 ha for continuous forest [60] in a set of sensitivity analyses (see "Sensitivity analysis" below). Finally, considering potential map inaccuracies and its inclusion of plantations – by nature not "forests" that could serve as population sources – we also compiled the distance between agricultural sites and its matching native forest sites from primary study authors, as a complementary distance measure. For this measure, we again adopted a simplified classification system because of limited information reliability, based on the smallest distance between any sampling unit of the agricultural and native forest sites: "close" for distance ≤1 km, and "far" for distance >1 km. Because data on this measure were of coarse resolution and were sometimes noted by primary study authors to be uncertain, we used this measure only in a corroborative assessment (see "Sensitivity analysis" below).

For each agriculture-forest pair, we obtained its corresponding MAP and the standard deviation of mean monthly temperature from WorldClim 2.1 [39] based on study coordinates. For disturbance regime, authors of primary studies scored the frequency of each of four major disturbance types for the forest ecosystems in their studies: storms (including hurricanes), wildfires, floods, and droughts. Scoring was conducted for each agriculture-forest pair, and concerned three categories based on the following criteria:

0: (Almost) never – *i.e.* the disturbance (almost) never happens, or its incidence is considered exceptional;

1: Occasional – *i.e.* the disturbance sometimes happens, but is not considered a regular phenomenon (below a 50% chance);

2: Frequent – *i.e.* the disturbance regularly happens (above a 50% chance).

We opted to obtain first-hand information from primary study authors rather than existing maps because the latter are typically of coarse resolutions [28]. Of all 44 primary studies, we were able to get author-provided scores of the four disturbance types for 35 studies; for the remaining nine studies, two co-authors (FH and WW) independently scored the four disturbance types by consulting literature and web sources, then discussed to harmonise any discrepancies. For each agriculture-forest pair, we then took the highest score across the four disturbance types to produce an overall disturbance regime score, which represented the extent to which a given ecosystem was subject to regular disturbances of any kind. Finally, because only four primary studies had an overall disturbance regime score of 2, we converted their scores to 1 to avoid computational problems, thus effectively streamlining the disturbance regime variable into a two-category variable: 0 (*i.e.* almost no disturbance; "no disturbance" hereafter) versus 1 (*i.e.* occasional or more frequent disturbances; "with regular disturbance" hereafter).

We additionally used study coordinates to derive the length of agricultural history for each agriculture-forest pair from the HYDE 3.2 database [40] (which covers the temporal span of year 10,000 BCE – 2017 CE), by calculating the number of years that had passed between the year when any form of agriculture (cropland or pasture, irrigated or non-irrigated) first appeared anywhere within a 10-km radius of the study location and the year when the primary study was conducted. We also used the HYDE 3.2 database to extract the average human population density within a 10-km radius of the study location in the year of the primary study.

For each bird species in our database, we compiled data on ten functional traits, following the taxonomic nomenclature used in [61]. These traits are all considered predictive of species sensitivity to forest loss and degradation [29,32–36], and they include the following: two morphological traits – body mass, hand-wing index (a measure of the relative elongation of a bird's wing and a widely used proxy for dispersal capability [62]; Extended Data Table 3), two life-history traits – clutch size, generation length, and six ecological traits – diet specialisation, foraging height, forest association (the extent to which a species is associated with forest habitats), migratory status (whether or not a species is considered migratory), natural range size, nest placement (the extent to which a species depends on forest structures for nest placement); we provide detailed definition, reasons of inclusion into our study, and data sources for these traits in Extended Data Table 3. Our classification system for forest association went beyond the coarse "forest versus non-forest" classification of most studies (*e.g.* [33]) by distinguishing among four categories: late-successional-forest, early-successional-forest, generalist, and open-country (Extended Data Tables 3 and 4), allowing for finer distinction of species' forest association that was also specific to the study season. To ensure data quality, two co-authors (WW and SL) independently scored forest association for each species and discussed to harmonise any discrepancies, and we double-checked all extracted data to minimise data entry error.

For each trait and each species assemblage (*i.e.* that corresponded to a given agriculture-forest pair), we calculated its assemblage-level "centroid", *i.e.* the assemblage mean value weighted by the relative abundance of each species (pooled across agricultural and native forest sites after correcting for sampling effort) following Equation 2:

$$\text{Trait centroid} = \sum_{i=1}^{n} Trait\ value_i \times \frac{Abun_{i,agriculture} + Abun_{i,native\ forest}}{Abun_{assemblage}} \quad \text{(Equation 2)}$$

Where i represents each species in the assemblage that consists of n species, $Abun_{i,agriculture}$ and $Abun_{i,native\ forest}$ refer to the abundance of species i at the agricultural and native forest sites (after being corrected for potentially unequal sampling effort between the two habitat types), respectively, and $Abun_{assemblage}$ refers to the total abundance (corrected for sampling effort) of all n species pooled across agricultural and native forests.

Statistical Analysis

Meta-analyses and meta-regressions: We conducted weighted multi-level meta-analyses and meta-regressions [63] of assemblage RR using the "lme()" function of package "nlme" (version 3.1-157 [64]) in programme R (version 4.2.0 [65]). For meta-analyses, we used an intercept-only fixed effect, and we fitted a group of random intercept variables to account for potential shared variation and data non-independence, in descending order of nestedness as below (*i.e.* later variables were nested within earlier ones):

Level 1: study season, involving two categories: breeding/all-year *versus* non-breeding; random effects with a small number of categories have been shown to not bias model estimates [66], and we confirmed that our models did produce reasonable estimates for this variable;

Level 2: the types of agriculture and native forest being compared ("comparison type" hereafter); for native forest, we combined generic native forests and secondary forests – both were degraded benchmarks – to form "non-old-growth forests"; this variable therefore involved six categories (three types of agriculture by two types of native forests);

Level 3: the identity of the primary study.

Finally, we added one more, lowest-tier variable to estimate I^2, the measure of the heterogeneity of meta-analytic data that represents variation not due to sampling variance arising from differences in sampling efforts among effect sizes [41], following the method developed in [54].

For meta-regressions on the relationship between assemblage RR and predictor variables, we conducted model selection based on small-sample-corrected Akaike Information Criterion (AICc) [67], then used the model(s) with the most complete set of predictor variables from within the top model set (ΔAICc $\leq$2) to make inference. We used the same random effect structure as in the above meta-analyses, and we calculated marginal R^2 based on the lowest-tier random intercept variable [68]. Fixed effects of the global models followed Equation 3:

RR ~ remnant forest cover + distance to nearest continuous forest + surrounding human population density + MAP + seasonality + disturbance regime + agricultural history (Equation 3)

Where remnant forest cover (in ordinal values of 0–5), distance to the nearest continuous forest (in m), and surrounding human population density (in 100 persons km^{-2}) represented features of the agricultural landscapes; MAP (in mm y^{-1}), seasonality (in °C), and disturbance regime ("no disturbance" versus "with regular disturbance") represented natural filtering; and agricultural history (in y) represented anthropogenic filtering. We modelled the effects of all continuous variables (*i.e.* all except for remnant forest cover) on the natural log scale,

considering that the same absolute difference in the lower range of their values (*e.g.* 100 versus 300 m distance, or 300 versus 600 mm MAP) was most likely of much greater ecological magnitude than in the upper range (*e.g.* 2,100 versus 2,300 m distance, or 2,300 versus 2,600 mm MAP). Pre-analysis assessment of collinearity indicated the absence of strong collinearity among all variables (all $|r_{Pearson}| < 0.52$). We therefore did not exclude any variable from analyses.

For our meta-regression global models (one global model for each set of sensitivity analyses), we checked and confirmed that the random-effect variables of study season and comparison type did not have strong collinearity with the four filtering variables (MAP, seasonality, disturbance regime, and agricultural history), and therefore would not have confounded their relationship with assemblage RR (Extended Data Fig. 4a–d as an example for the main analysis). We then identified the top model set for each global model, *i.e.* models whose ΔAICc was ≤2 from the lowest AICc score of the full model set, using package "MuMIn" (version 1.47.5 [69]) in programme R. From the top model set, we adopted the model(s) with the most complete set of predictor variables to obtain predictor coefficients and their 95% CIs ("most complete top model" hereafter), admitting as many most complete top models as necessary to include all predictor variables present in the top model set. In reality, none of our meta-regressions entailed more than one most complete top model.

In all meta-analyses and meta-regressions above, we applied the weight score calculated above in a weighting scheme (Equation 1). Because of the way the function "lme()" in package "nlme" works, we supplied the above weight scores in the form of 'weights = ~I(1/weight score)' in running the function "lme()". The species-level RR format of our data did not allow us to follow the sampling-variance-based weighting scheme used in conventional meta-analyses/regressions, because species-level abundance data reported rarely had sampling variance information. For all meta-analyses and meta-regressions, we visually assessed residual and QQ plots, which indicated general satisfaction of the assumption of residual normality (Extended Data Fig. 5). Concerns about any potential violation of this assumption should be alleviated by the fact that mixed-effect models are known to be generally robust to violations of model assumptions [70]. Funnel plots produced using package "metafor" (version 3.4-0 [71]) in programme R and Egger's test following [72] additionally indicated our meta-analytic findings to be generally free of publication bias: any apparent data asymmetry did not appear to be linked to studies with lower sampling efforts (Extended Data Fig. 4g), and the coefficient for the square-root of data weight (inverse form, in accordance with the way we supplied weight scores in the above meta-analyses) in relation to RR was non-significant for all but one meta-analyses (Supplementary Information Table S1), further indicating a lack of data asymmetry.

Other linear mixed models: To assess the relationship of assemblage-level trait centroids and their PC1 (from principal component analysis; see "Statistical analysis: multivariate analysis of trait data" below) with the filtering factors, we used the same regression approach followed by model selection and inference from the most complete top model as we used in the meta-regressions above, with two modifications. First, we did not include landscape features of agricultural sites as fixed effects (*i.e.* remnant forest cover, distance to the nearest continuous forest, and human population density) or the weighting scheme, because the response variables concerned the profile of the regional species pool rather than the comparison between agricultural and native forest sites. Second, we did not include the lowest-tier random intercept variable because conceptually, this set of analyses was not for meta-analytic synthesis.

Diagnostic residual and QQ plots showed the general satisfaction of the residual-normality assumption for these analyses. Fixed effects of the global models thus followed Equation 4:

Trait centroids or PC1 ~ MAP + seasonality + disturbance regime + agricultural history (Equation 4)

Phylogenetically controlled mixed-effect models: We used the function "MCMCglmm()" of package "MCMCglmm" (version 2.34 [73]) in programme R to conduct phylogenetically controlled mixed-effect models on the relationship between species-level RR and all ten functional traits, while considering the potential influence of covariates, *i.e.* the three variables representing landscape features of agricultural sites (remnant forest cover, distance to the nearest continuous forest, and surrounding human population density). Pre-analysis assessment of collinearity using Pearson correlations indicated the absence of strong collinearity (all $|r_{Pearson}|$ <0.37) among all variables except between body mass and generation length ($r_{Pearson}$ = 0.84 for centred-and-scaled values). We therefore conducted two sets of analyses, one dropping body mass and the other dropping generation length.

As preliminary analyses, we first used regular mixed-effect models without considering phylogeny, to identify relevant covariates to include in the formal phylogenetically controlled mixed-effect models. We followed the same model building, selection and inference approaches as used in previous meta-regressions (see "Statistical analysis: meta-analyses and meta-regressions" above). Similarly, we followed the same random-effect structures as previous meta-regressions, but we replaced the lowest-tier random effect with the identity of the agriculture-forest pair (*i.e.* the identity of the assemblage to which each species belonged) to account for potential data non-independence among records from the same assemblage, and we removed study season because its estimates as could not be properly produced in subsequent phylogenetically controlled mixed-effect models. We instead modelled study season as a fixed effect variable. Fixed effects of our global model thus followed Equation 5:

RR ~ remnant forest cover + distance to the nearest continuous forest + surrounding human population density + body mass (or generation length) + hand-wing index + clutch size + diet specialisbation + foraging height + forest association + migratory status + natural range size + nest placement (Equation 5)

We centred and scaled all continuous variables and remnant forest cover (distance to the nearest continuous forest and surrounding human population density were on natural-log scale before being centred and scaled); for the three categorical traits (forest association, migration status, and nest placement) and study season, we used open-country, non-migratory, and ground nest placement during the non-breeding season as baseline. For the two sets of analyses dropping either body mass or generation length, model selection indicated all fixed predictors to have entered the top model set except for the distance to the nearest continuous forest; we therefore included all variables except the distance variable in subsequent formal analyses that controlled for phylogenetic correlation. In subsequent sensitivity analyses (*i.e.* those involving alternative data on the distance to the nearest continuous forest, and on surrounding human population density; see "Sensitivity analysis" below), we again conducted model selection to decide the predictor variables to be included in phylogenetically controlled mixed-effect models.

For phylogenetically controlled mixed-effect models, we similarly conducted two sets of analyses, one dropping body mass and the other dropping generation length. Our models differed from the above preliminary analyses by (1) not including distance to the nearest continuous forest as a fixed variable, (2) modelling remnant forest cover on the original ordinal scale of 0–5, and (3) including the phylogenetic relationship among species as an additional random variable. Our fixed effects thus followed Equation 6:

RR ~ remnant forest cover + surrounding human population density + (Equation 6)
body mass (or generation length) + hand-wing index + clutch size +
diet specialisation + foraging height + forest association +
migratory status + natural range size + nest placement

We used the default uninformative prior for fixed effects, the inverse gamma prior (V = 1 and nu = 0.002) for the residual variance, and the parameter-expanded prior (V = 1, nu = 1, alpha.V = 1,000, alpha.mu = 0) for all random effects. We ran 120,000 iterations with a burn-in of 20,000 and a thinning value of 50. For each set of analyses, we conducted 100 model runs, each on a randomly drawn phylogenetic tree [61], and we obtained the coefficient and its 95% CIs for each predictor variable by averaging the outputs of all 100 model runs (note a previous simulation showed that using 50 trees is usually sufficient to account for the uncertainty of phylogenetic trees [74]). Diagnostic plots indicated convergence for all model runs (Extended Data Fig. 6, as example for one model).

Multivariate analysis of trait data: We calculated the assemblage-level centroid for each functional trait using weighted averaging, with weights being the abundance of each species summed across the agricultural and native forest sites in each agriculture-forest pair. For this purpose, we expressed the three categorical traits (forest association, migration status, and nest placement) in integer values: 1–4 respectively for open-country, generalist, early-successional-forest, and late-successional-forest regarding forest association, 1 and 2 respectively for non-migratory and migratory regarding migratory status, and 1–3 respectively for ground-nesting, elevated open-nesting, and cavity-nesting regarding nest placement. We conducted principal component analysis on the assemblage-level trait centroids (centred-and-scaled) using function "princomp()" in programme R.

To calculate functional richness and functional dispersion for each species assemblage, we used the function "alpha.fd.multidim" of package "mFD" (version 1.0.1 [75]) in programme R and the first four axes of the Gower-based functional distance. Because functional richness is by definition closely linked to species richness [43], we corrected it using Equation 7 to remove the influence of species richness:

$$\text{Corrected functional richness} = \frac{Raw\ functional\ richness \times 100}{Species\ richness} \quad \text{(Equation 7)}$$

Finally, we calculated functional redundancy for each species assemblage following [76], by first classifying each species into a "unique trait combination" ("UTC" hereafter) based on its trait profile. To do this, we followed [76] to bin the seven continuous traits using the Sturges algorithm. We then calculated functional redundancy by dividing species richness for each

assemblage by the number of UTCs [44,76]. We conducted simple linear regressions between PC1 and the three multivariate trait metrics. Diagnostic residual and QQ plots showed the general satisfaction of the residual-normality assumption for these analyses.

Sensitivity analysis: We conducted six sets of sensitivity analyses where applicable. They concerned: (1) the radius for data extraction on agricultural history and surrounding human population density from the HYDE 3.2 database [40] (2 km and 50 km, versus the 10 km in main analyses); (2) the size criterion for defining continuous forest in measuring the distance between agricultural sites and the nearest continuous forest (100 ha, versus the 50 ha used in main analyses); (3) the mathematical scale on which seasonality, MAP, agricultural history, distance to the nearest continuous forest, and surrounding human population density were analysed (original scale, versus the natural log scale in main analyses; we divided MAP, agricultural history, distance to the nearest continuous forest, and surrounding human population density by 100 such that results represented the effect of every 100-mm, 100-year, 100-m, and 100-person increase); (4) the removal of two primary studies – containing four avian assemblages – with extreme MAP [77,78] or seasonality [78] (versus their inclusion in main analyses); (5) the removal of two primary studies – containing three avian assemblages – that had secondary forest as the baseline against which agricultural sites were compared [79,80] (versus their inclusion in main analyses); and (6) weighting schemes in mixed-effect models (using simply the inverse of the match rigor score as weights and not using weights altogether, versus using Equation-1 derived weight scores in main analyses). The last set of sensitivity analyses was in light of the potential subjectivity and varying standards of reporting from primary studies involved in the calculation of the weight scores, and it applied only to the meta-analyses and meta-regressions.

Finally, considering the potential data quality issue for the distance between agricultural sites and the nearest continuous forest extracted from the FGP maps, we checked whether greater assemblage RR was associated with lower distance between agricultural sites and their matching native forests, our complementary distance measure compiled from primary study authors. This assessment was to corroborate our formal analyses using distance data from the FGP maps (which may have potentially low data quality), and to rule out the possibility that variation in the impacts of agricultural deforestation found in our database was linked to the proximity of agricultural sites to native forests [7]. We conducted this assessment with simple visualisation in light of the limited data quality of this complementary distance measure (Extended Data Fig. 4h).

Data availability

All data used in this study have been uploaded to a public repository, and can be accessed at ref 31.

Code availability

All code used in this study have been uploaded to a public repository, and can be accessed at ref 31.

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Author contributions

FH conceived the study and led the study design. WW compiled species-level abundance data and associated meta-data with assistance from all co-authors. WW compiled species trait data with assistance from SL and XM. FH designed and coded data analysis with assistance from SN and PE, and along with WW implemented all analyses. FH designed results visualisation, and along with WW implemented results visualisation. FH wrote the first draft of the manuscript with assistance from WW and SN, and all authors contributed to manuscript revisions.

Competing interests: The authors declare no competing interests.

Figure legends

Fig. 1 | Conceptual diagrams of natural and anthropogenic filtering shaping the observed biodiversity responses to agricultural deforestation. (**a**) Filtering by natural habitat features (natural filtering; also termed "habitat filtering" [18,20]) and historical human impacts (anthropogenic filtering) – both of which can operate via biotic and abiotic mechanisms [23] – selects for species with certain functional trait profiles (pre-existing or acquired in the process of adaptation) that allow them to persist in the local environment, such that present-day species assemblages studied for deforestation impacts contain only a subset of species that (could) have existed. Circles with different colours represent species with different trait profiles. (**b**) The trait signature of natural and anthropogenic filtering. Species of hypothetical assemblages (small gray dots) are displayed in three-dimensional trait space along with the trait centroid of each assemblage (large pink dots), calculated as the abundance-weighted mean for each trait. Compared to species assemblages under low filtering (upper left panel), assemblages under high natural or anthropogenic filtering (the three panels in dashed box) should in theory occupy trait spaces that correspond to greater deforestation tolerance. This contrast can be achieved through different mechanisms, such that strongly filtered assemblages (i) occupy a larger trait space, particularly in regions of the trait space that correspond to greater tolerance ("trait space expansion"), (ii) shift collectively toward regions of the trait space that correspond to greater tolerance while assuming the same trait space size ("trait shift"), and/or (iii) occupy the same trait space in size and location, but have a considerable portion of constituent species clustering in the regions of trait space that correspond to greater tolerance ("trait clustering").

Fig. 2 | The geographical distribution of paired abundance data in our database. Circles represent datasets of entire avian assemblages for agriculture-forest pairs contributed by each primary study, sized proportional to the number of assemblages (each representing an agriculture-forest pair) and coloured by agricultural history of the study system. Symbols

accompanying each circle indicate the type of agriculture (cropland, pasture, or agroforestry) involved in each primary study. Distributions of MAP and seasonality for primary studies are displayed as boxplot insets (n=44 primary studies). For each boxplot, the box demarcates the first quartile (*i.e.* Q1; left rim), median value (middle line), and third quartile (*i.e.* Q3; right rim), while the lower and upper whiskers reach the most extreme data points within the 1.5 interquartile range (*i.e.* 1.5 times the difference between Q3 and Q1) as measured below Q1 and above Q3, respectively.

Fig. 3 | Variation in assemblage-level impacts of agricultural deforestation across studies and their underlying factors. (**a**) Assemblage-level impacts of agricultural deforestation (upper row; n=71 assemblages), distinguished between agroforestry (middle row; n=16 assemblages) versus open agricultural systems (cropland or pasture; lower row; n=55 assemblages). Scattered points represent assemblage-level RRs (*i.e.* the abundance response ratios [RRs] of agricultural over native forest sites on the natural log scale, averaged across all species within an assemblage), with those involving pasture in the lower row indicated by darker dots. See dashed box in (b) for symbol legend. (**b**) Impacts of agricultural deforestation on sub-assemblages that comprised species present at the native forest sites (upper row), shown separately for agroforestry (middle row) and open agricultural systems (lower row). The clear contrasts between agricultural and native forest sites suggested that the less marked contrasts in panel (a) were driven by a set of "winner" species, which were absent from native forests but were found at agricultural sites. Sample sizes and symbols are the same as in panel (a). (**c**)–(**e**) The relationship between assemblage-level RR and remnant forest cover (c), MAP (d), and agricultural history (e), the three variables identified by model selection to be predictive of assemblage-level RR; MAP and agricultural history were analysed on a natural log scale (Methods). Sample size n=60 assemblages, after removing records with missing information on remnant forest cover. Each point represents an avian assemblage, sized proportional to its weight in analysis. Black lines and coloured bands represent fitted curves along with their 95% confidence bands, based on the mean (*i.e.* β in the upper right of each panel) and 95% CI (*i.e.* range in the parentheses after β) estimated for the slope of each focal variable, according to the model with the most complete set of predictor variables from within the top model set identified by model selection.

Fig. 4 | The trait signature of filtering by environmental variability and historical deforestation. (**a**) Relationship of species-level RR with functional traits and other covariates, based on phylogenetically controlled mixed-effect models (n=5,866 RRs, after removing records with missing information). For the three categorical traits (indicated with dashed boxes) and study season, this relationship was based on the baseline of open-country, non-migratory, ground-nesting species during non-breeding season; for all continuous variables, this relationship was based on ordinal values for remnant forest cover (0–5) and centred-and-scaled values for others. Because of collinearity between body mass and generation length, effects displayed for all traits other than generation length were from the set of analyses dropping generation length, and they were similar to estimates by the alternative set of analyses dropping body mass (Supplementary Information Table S5). (**b**) Relationships between the assemblage-level centroid of individual traits and filtering factors, based on model selection (n=71 assemblages). Relationships are expressed as the coefficients of filtering factors, displayed in bubbles that are sized proportional to the absolute coefficient value and coloured by its sign and overlap of 95%

CI with zero; "–" indicates that the filtering factor concerned did not enter the top model set. Categorical traits were analysed as ordinal variables, with higher values corresponding to stronger forest association, being migratory, and stronger forest dependence for nest placement, respectively. (**c**) Relationships between PC1 of the assemblage-level trait centroids and filtering factors based on model selection (n=71 assemblages). Each point represents an avian assemblage. Black lines and coloured bands represent fitted curves and their 95% confidence bands, based on the mean (*i.e.* β in the upper right of each panel) and 95% CI (*i.e.* range in the parentheses after β) estimated for the slope of each filtering factor; assemblages and fitted lines are displayed separately for study systems deemed to not have (slate blue) or regularly have (purplish red) disturbance regime. *: According to variable loadings of PCA (Supplementary Information Table S6), PC1 had an overwhelmingly negative relationship with traits that predicted greater tolerance to deforestation, thus higher PC1 values corresponded to lower deforestation tolerance.

Fig. 5 | How the "greater-tolerance shift" of assemblage trait centroids may have occurred under natural and anthropogenic filtering. We assessed possible mechanisms by testing, on the assemblage level, the relationship between PC1 of the PCA on assemblage-level trait centroids and three multivariate trait metrics, including (**a**) functional richness (after correcting for species richness), (**b**) functional dispersion, and (**c**) functional redundancy (n=71 assemblages). Each point represents an avian assemblage, and black lines and coloured bands represent fitted lines along with their 95% confidence intervals from simple linear regressions, based on the mean (*i.e.* β in the upper right of each panel) and 95% CI (*i.e.* range in the parentheses after β) estimated for the slope of each multivariate trait metric.

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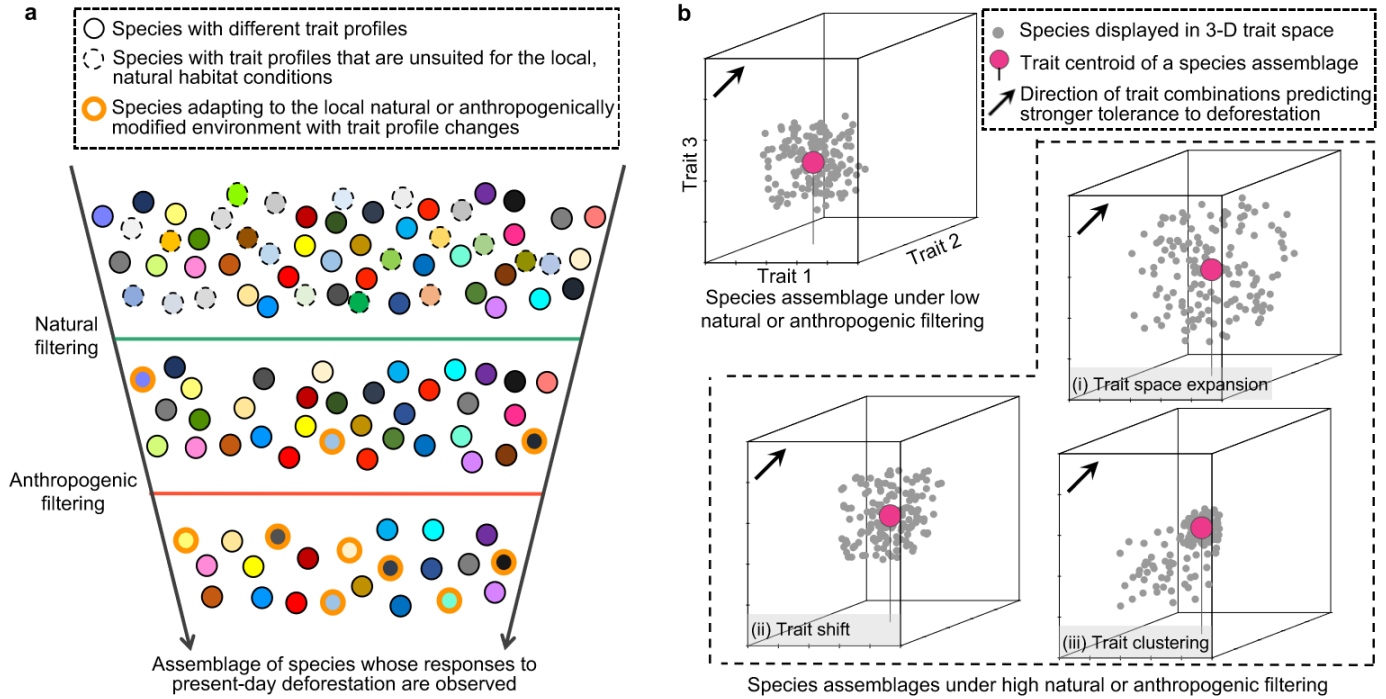
a
Species with different trait profiles
Species with trait profiles that are unsuited for the local, natural habitat conditions
Species adapting to the local natural or anthropogenically modified environment with trait profile changes
Natural filtering
Anthropogenic filtering
Assemblage of species whose responses to present-day deforestation are observed
b
Species displayed in 3-D trait space
Trait centroid of a species assemblage
Direction of trait combinations predicting stronger tolerance to deforestation
Trait 3
Trait 1
Trait 2
Species assemblage under low natural or anthropogenic filtering
(i) Trait space expansion
(ii) Trait shift
(iii) Trait clustering
Species assemblages under high natural or anthropogenic filtering

Figure 1:

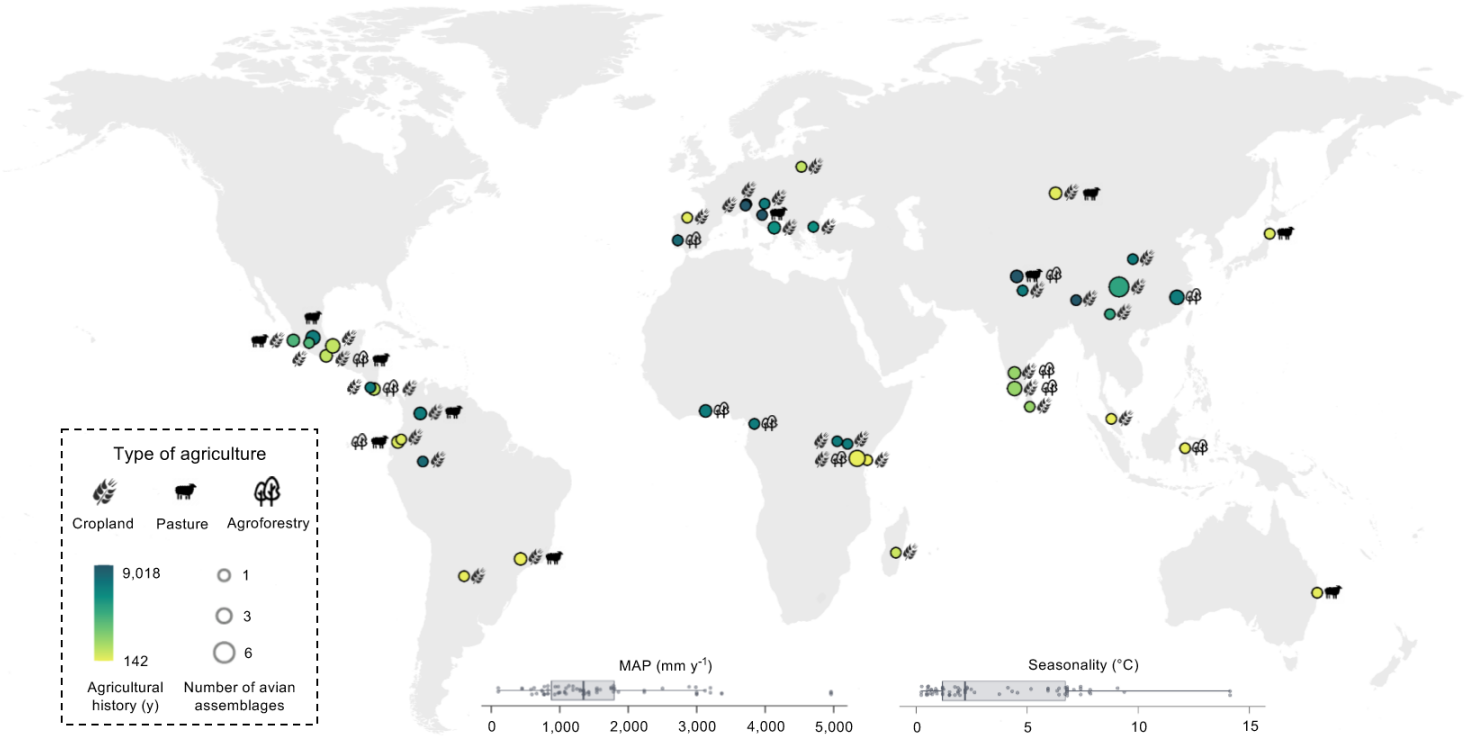
Type of agriculture
Cropland
Pasture
Agroforestry
9,018
142
Agricultural history (y)
1
3
6
Number of avian assemblages
MAP (mm y-1)
0
1,000
2,000
3,000
4,000
5,000
Seasonality (°C)
0
5
10
15

Figure 2:

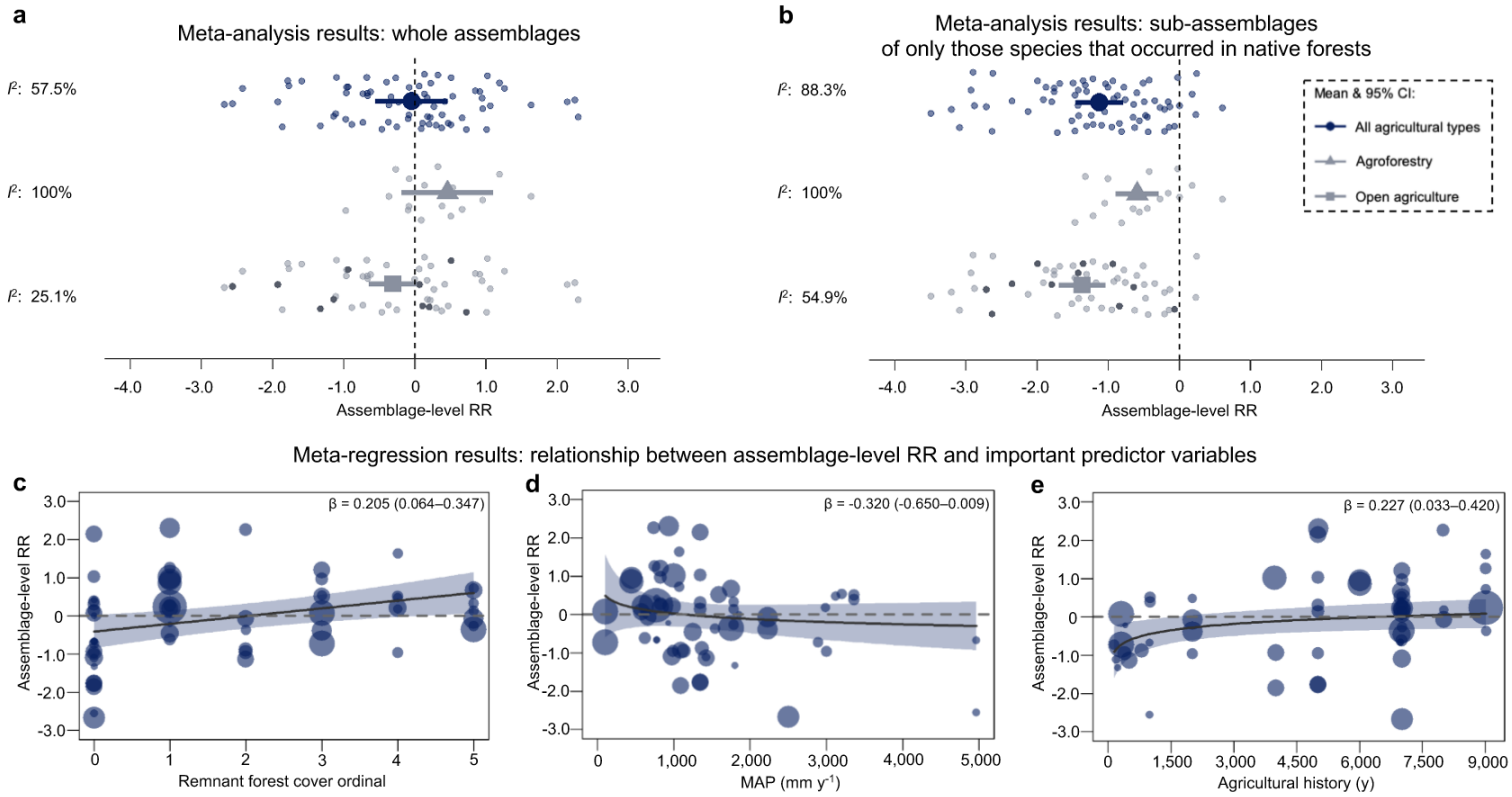
a
Meta-analysis results: whole assemblages
I²: 57.5%
I²: 100%
I²: 25.1%
-4.0
-3.0
-2.0
-1.0
0
1.0
2.0
3.0
Assemblage-level RR
b
Meta-analysis results: sub-assemblages
of only those species that occurred in native forests
I²: 88.3%
I²: 100%
I²: 54.9%
Mean & 95% CI:
All agricultural types
Agroforestry
Open agriculture
Assemblage-level RR
Meta-regression results: relationship between assemblage-level RR and important predictor variables
c
β = 0.205 (0.064–0.347)
Assemblage-level RR
Remnant forest cover ordinal
d
β = -0.320 (-0.650–0.009)
MAP (mm y⁻¹)
e
β = 0.227 (0.033–0.420)
Agricultural history (y)

Figure 3:

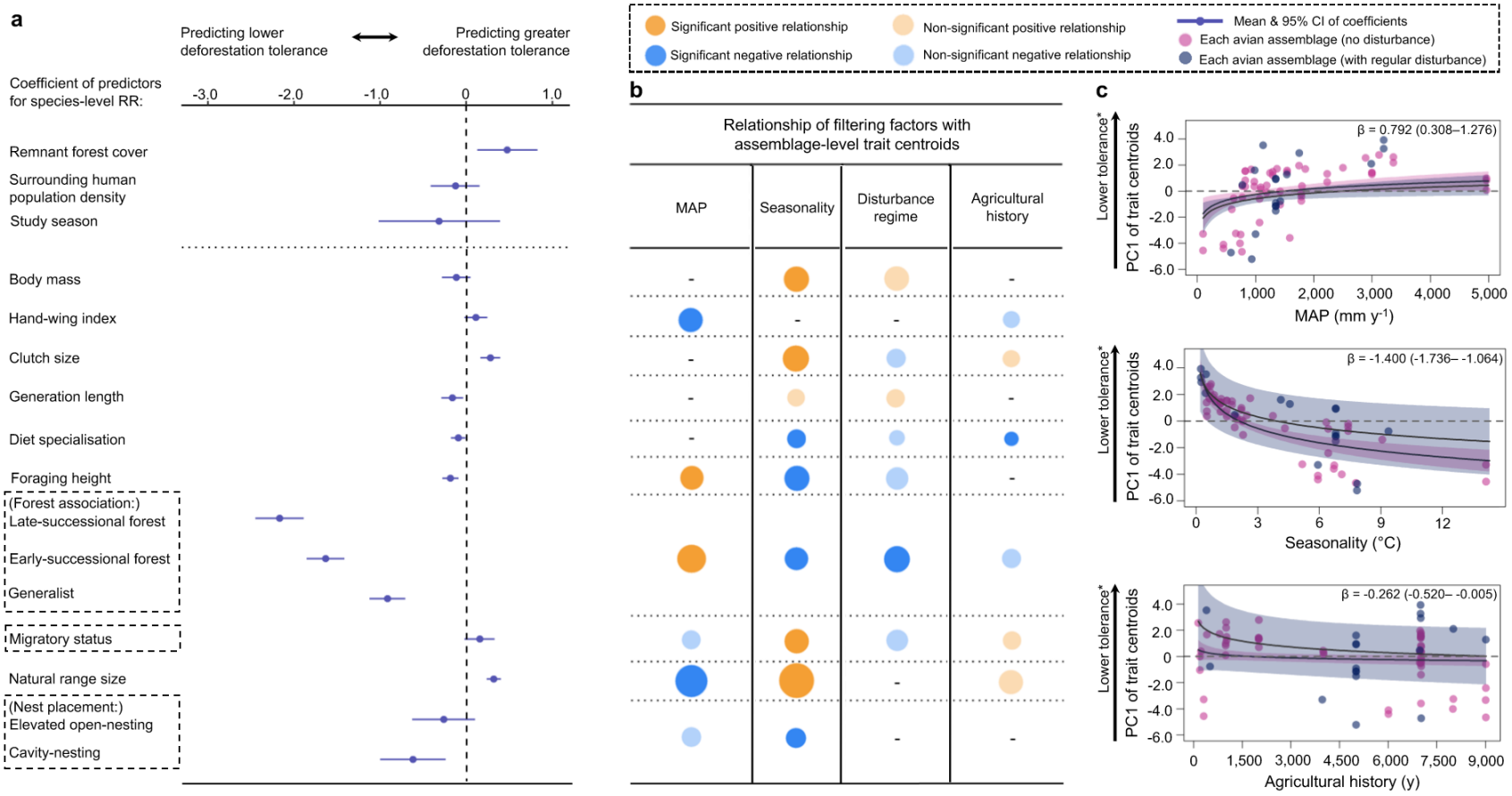
a
Predicting lower deforestation tolerance
Predicting greater deforestation tolerance
Coefficient of predictors for species-level RR:
-3.0
-2.0
-1.0
0
1.0
Remnant forest cover
Surrounding human population density
Study season
Body mass
Hand-wing index
Clutch size
Generation length
Diet specialisation
Foraging height
(Forest association:)
Late-successional forest
Early-successional forest
Generalist
Migratory status
Natural range size
(Nest placement:)
Elevated open-nesting
Cavity-nesting
Significant positive relationship
Significant negative relationship
Non-significant positive relationship
Non-significant negative relationship
Mean & 95% CI of coefficients
Each avian assemblage (no disturbance)
Each avian assemblage (with regular disturbance)
b
Relationship of filtering factors with assemblage-level trait centroids
MAP
Seasonality
Disturbance regime
Agricultural history
c
Lower tolerance*
PC1 of trait centroids
β = 0.792 (0.308–1.276)
MAP (mm y-1)
β = -1.400 (-1.736– -1.064)
Seasonality (°C)
β = -0.262 (-0.520– -0.005)
Agricultural history (y)

Figure 4:

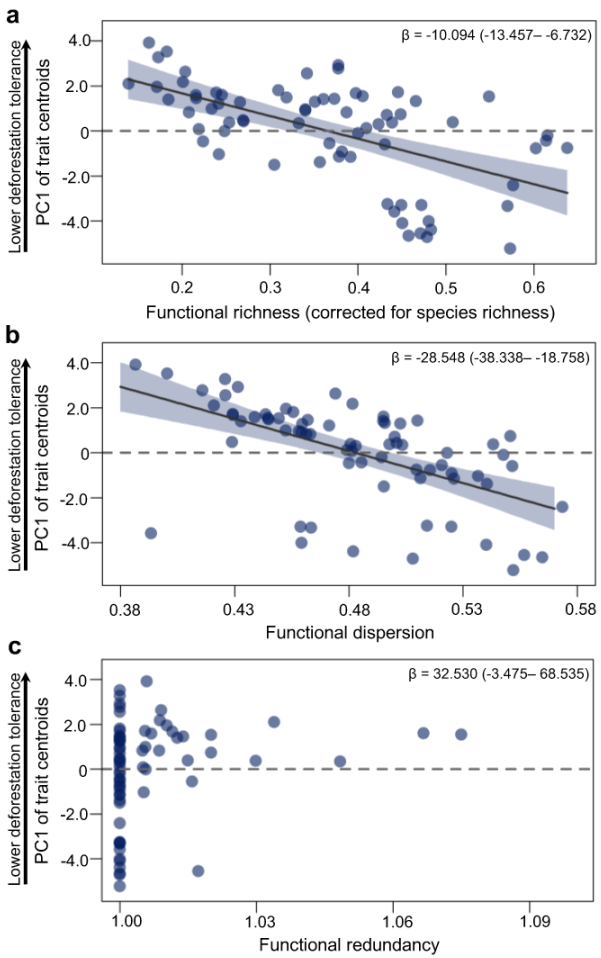
a
β = -10.094 (-13.457– -6.732)
Lower deforestation tolerance
PC1 of trait centroids
4.0
2.0
0
-2.0
-4.0
0.2
0.3
0.4
0.5
0.6
Functional richness (corrected for species richness)
b
β = -28.548 (-38.338– -18.758)
Lower deforestation tolerance
PC1 of trait centroids
4.0
2.0
0
-2.0
-4.0
0.38
0.43
0.48
0.53
0.58
Functional dispersion
c
β = 32.530 (-3.475– 68.535)
Lower deforestation tolerance
PC1 of trait centroids
4.0
2.0
0
-2.0
-4.0
1.00
1.03
1.06
1.09
Functional redundancy

Figure 5: