

# Ecological filtering shapes the impacts of agricultural deforestation on biodiversity

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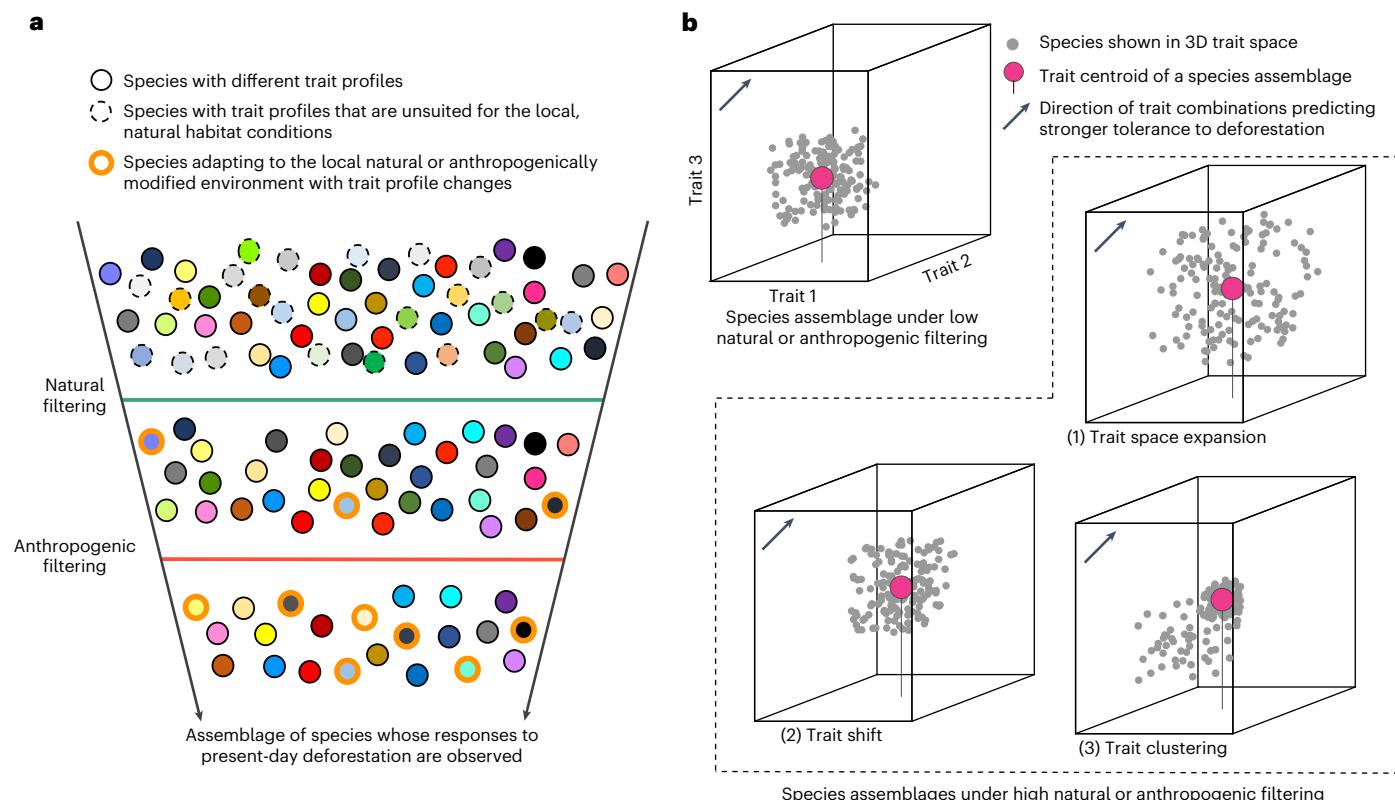
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The biodiversity impacts of agricultural deforestation vary widely across regions. Previous efforts to explain this variation have focused exclusively on the landscape features and management regimes of agricultural systems, neglecting the potentially 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 10 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 a 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 previously largely missing piece of knowledge in understanding and managing the biodiversity consequences of deforestation by agricultural deforestation.

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

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<sup>7,12,13</sup>. These efforts have generated a broad consensus on the ameliorating roles of higher landscape heterogeneity<sup>14,15</sup> and lower management intensities<sup>16</sup>, providing useful guidance to minimize the biodiversity impacts of agriculture at the local scale<sup>17</sup>. 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)<sup>18–23</sup>. 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



**Fig. 1 | How natural and anthropogenic filtering can shape the observed biodiversity responses to agricultural deforestation.** **a**, Filtering by natural habitat features (natural filtering; also termed habitat filtering<sup>18,20</sup>) and historical human impacts (anthropogenic filtering)—both of which can operate via biotic and abiotic mechanisms<sup>23</sup>—can select 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. Different-coloured circles represent species with different trait profiles. **b**, The trait signature of natural and anthropogenic filtering. Species of hypothetical assemblages (grey circles) are shown in three-dimensional (3D) trait space along with the trait centroid of each assemblage (pink circles),

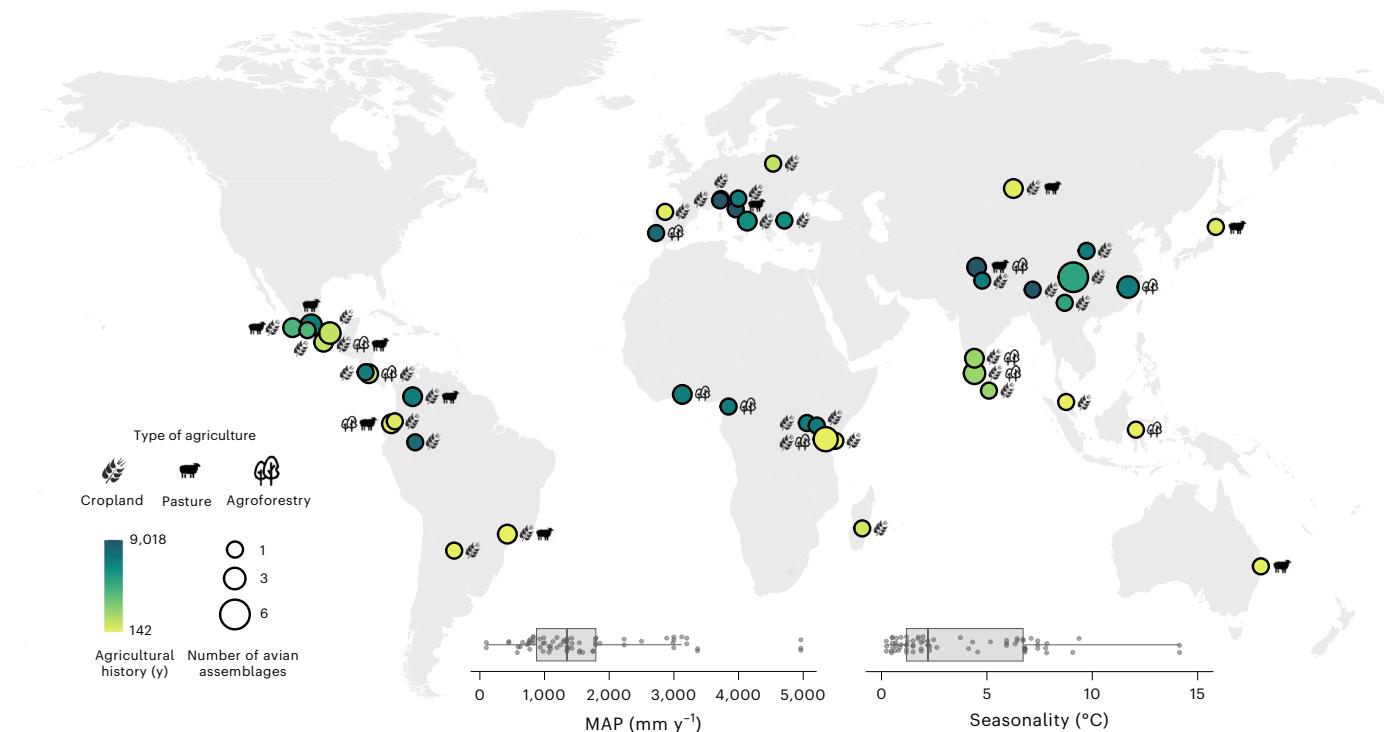
calculated as the abundance-weighted mean for each trait. Compared with species assemblages under low filtering (top left), assemblages under high natural or anthropogenic filtering (assemblages within the dashed box) should in theory occupy trait spaces that correspond to greater deforestation tolerance. This contrast can be achieved through different mechanisms, such that strongly filtered assemblages (1) occupy a larger trait space, particularly in regions of the trait space that correspond to greater tolerance (trait space expansion); (2) shift collectively towards regions of the trait space that correspond to greater tolerance while assuming the same trait space size (trait shift); and/or (3) 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).

ecosystems. Yet despite the wide recognition of filtering<sup>18–23</sup>, 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<sup>21,24</sup>, 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', respectively, 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 results in spatial environmental variability) or recurrent structural changes (for example, 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 deforestation associated with conversion to agriculture. This possibility has been shown 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<sup>24,25</sup>. In contrast, historical deforestation may further select against species sensitive to deforestation via extinction and adaptation<sup>26,27</sup>. 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<sup>18</sup> and empirical evidence of their influence on biodiversity responses to other anthropogenic threats<sup>28,29</sup>, 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.

In this study, 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<sup>30</sup>. Through extensive compilation of paired data between



**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, with sizing proportional to the number of assemblages (each representing an agriculture–forest pair) and colours representing the 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 shown as box plots ( $n = 44$  primary studies). For each box plot, the box demarcates the first quartile (that is, Q1; left edge), median value (middle line) and third quartile (that is, Q3; right edge), and the lower and upper whiskers reach the most extreme data points within the  $1.5 \times$  interquartile range (that is,  $1.5 \times$  the difference between Q3 and Q1) as measured below Q1 and above Q3, respectively.

matched agricultural and reference native forest sites ('agriculture–forest pair' hereafter), we constructed a global database of species-specific abundance records (in individuals per hectare; corrected for sampling effort) for entire avian assemblages<sup>31</sup>; we broadly defined agricultural land to include croplands, pastures and agroforestry (Methods, Extended Data Fig. 1 and Extended Data Table 1). For each record, we calculated an abundance response ratio (RR) of agricultural to native forest sites (on the natural log scale) 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 also 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 per km<sup>2</sup>) to represent their landscape features. Our compilation yielded 7,625 RRs covering 2,647 bird species<sup>31</sup>. 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 and Extended Data Table 2). For each bird species, we also compiled data on ten functional traits<sup>31</sup> (spanning the morphological, life-history, behavioural and other ecological dimensions) that are considered predictive of species tolerance to forest loss or degradation<sup>29,32–36</sup> (Extended Data Tables 3 and 4 and Methods).

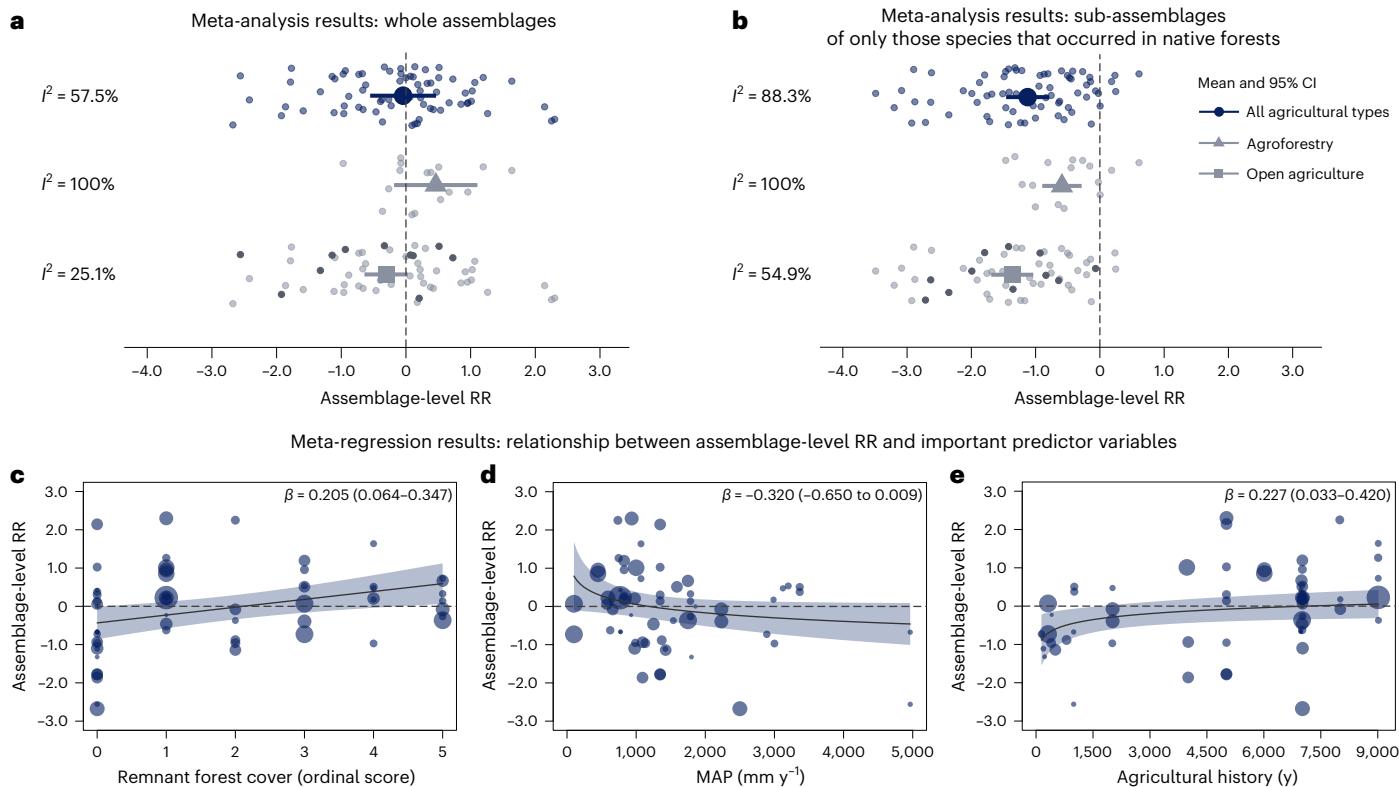
To represent environmental variability, we used mean annual precipitation (MAP; in mm y<sup>-1</sup>), the s.d. of mean monthly temperature ('seasonality' hereafter; in °C) and the frequency of forest disturbance regime involving any of four disturbance types: storm, wildfire, flood

and drought ('disturbance regime' hereafter; in the two categories no disturbance versus with regular disturbance)<sup>28</sup>. Native forests under lower MAP tend to have sparser canopy cover<sup>37</sup>, whereas those under more seasonal climates or a more frequent disturbance regime typically show more pronounced defoliation or other structural change cycles<sup>24,28</sup>—both are features that 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; in years), considering that agricultural land use constitutes the dominant agent of anthropogenic deforestation<sup>1,18</sup>, and that its filtering effect would most likely begin with the onset of agricultural land conversion<sup>38</sup>. We obtained data on MAP, seasonality and agricultural history from existing databases<sup>39,40</sup>, and we scored disturbance regime by consulting authors of the primary studies and the literature (Methods). The study systems included in our database spanned wide ranges of variable values representing environmental variability (100–4,964 mm y<sup>-1</sup> in MAP, 0.2–14.1 °C in seasonality and varying disturbance regime scores; the 100 mm y<sup>-1</sup> 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, and 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 although the impacts of agricultural deforestation on avian abundance were negative overall, they depended on the type of agriculture and species considered (Fig. 3a,b and Methods). Whereas average impacts on whole assemblages were hardly negative (Fig. 3a, top), this pattern was a result of the



**Fig. 3 | Variation in assemblage-level impacts of agricultural deforestation across studies and their underlying factors.** **a**, Assemblage-level impacts of agricultural deforestation (top;  $n = 71$  assemblages), distinguished between agroforestry (middle;  $n = 16$  assemblages) versus open agricultural (cropland or pasture; bottom;  $n = 55$  assemblages) systems. Scattered points represent assemblage-level RRs (that is, the 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 bottom row indicated by darker dots. See **b** for symbol legend. **b**, Impacts of agricultural deforestation on subassemblages that comprised species present at the native forest sites (top), shown separately for agroforestry (middle) and open agricultural systems (bottom). The clear contrasts between agricultural and native forest sites suggested that the less marked contrasts in **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 **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 of  $n = 60$  assemblages, after removing records with missing information on remnant forest cover. Each point represents an avian assemblage, with sizing proportional to its weight in analysis. Lines and coloured bands represent fitted curves along with their 95% confidence bands, based on the mean (that is,  $\beta$  in the top right) and 95% CI (that is, range in parentheses after  $\beta$ ) 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.

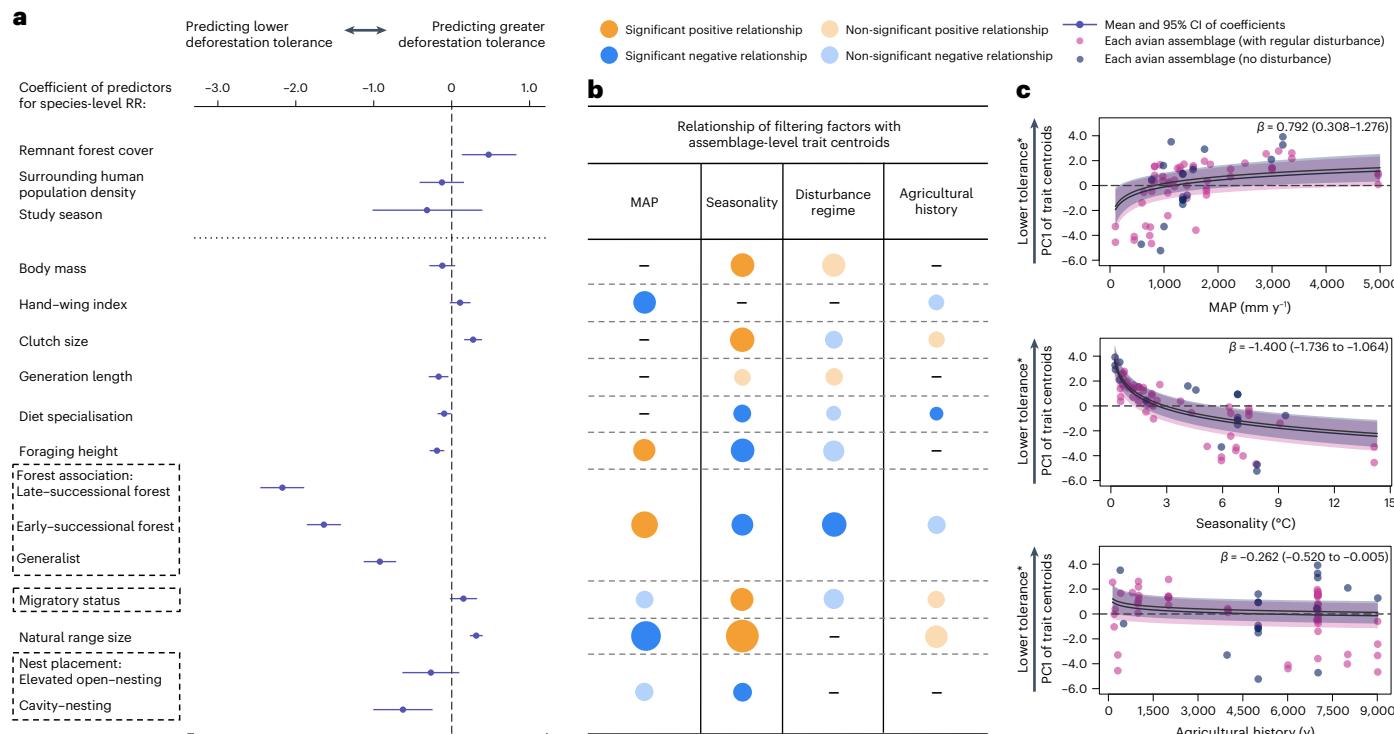
mostly positive impacts of agroforestry (Fig. 3a, middle) counteracting the overall negative impacts of open agriculture (Fig. 3a, bottom). More importantly, this pattern was clearly driven by a set of 'winner' species that were absent from native forests but were found at agricultural sites: a separate set of meta-analyses on subassemblages that comprised only species present at the native forest sites showed clear negative impacts of agriculture (Fig. 3b, top), regardless of whether it was agroforestry (Fig. 3b, middle) or open agriculture (Fig. 3b, bottom).

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<sup>41</sup> (Fig. 3a,b and 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 (meta-regression slope  $\beta = 0.205$ ; 95% confidence interval (CI), 0.064–0.347) and in fact tended to be positive at high cover (Fig. 3c and Methods). Crucially, impacts were also less negative at lower MAP ( $\beta = -0.320$ ; 95% CI, -0.650 to 0.009; Fig. 3d) and longer agricultural history ( $\beta = 0.227$ ; 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), to publication bias (Extended Data Fig. 4 and Supplementary Table 1), and to a set of sensitivity analyses involving

map-extracted data, data scaling, outlier handling and weighting schemes (Supplementary Tables 2–4 and 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.

#### Functional traits predict species tolerance to agricultural deforestation

We further assessed the trait signature of 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 modelling 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 specialization, lower foraging heights, weaker forest associations, larger natural ranges, and lower dependence on forest structures for nest placement, and to a lesser extent were associated with lower body masses, larger



**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). The vertical dashed line indicates a slope of zero for predictor variables (that is, no relationship); the horizontal dashed line separates functional trait variables (below the line) from other covariates (above the line). For the three categorical traits (shown in 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 shown 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 Table 5). **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, shown in circles that are

sized proportionally to the absolute coefficient value, with colours representing coefficient sign and the overlap of its 95% CI with zero (noted as ‘significant’ if not overlapping with zero, and ‘non-significant’ otherwise); dashes (–) indicate 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. **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. Lines and coloured bands represent fitted curves and their 95% confidence bands, based on the mean (that is,  $\beta$  in the top right) and 95% CI (that is, range in parentheses after  $\beta$ ) estimated for the slope of each filtering factor; assemblages and fitted lines are shown separately for study systems deemed to not have (slate blue) or regularly have (purplish red) a disturbance regime. \*According to variable loadings of PCA (Supplementary Information Table 6), PC1 had an overwhelmingly negative relationship with traits that predicted greater tolerance to deforestation, thus higher PC1 values corresponded to lower deforestation tolerance.

hand-wing indices (representing stronger dispersal abilities<sup>29</sup>) and being migratory (Fig. 4a and Supplementary Table 5). These ‘tolerance traits’ thus depicted a clear trait profile of species that were more tolerant of agricultural deforestation.

### Assemblage trait profiles are related to environmental variability and historical deforestation

On the basis of 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, that is, 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 specialization, foraging height, forest association and dependence on forest structures for nest placement) and higher

centroid values for the four other traits (hand-wing index, clutch size, migratory status and natural range size) (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 and 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 (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) of all 10 trait centroids, which accounted for 49.0% of the total variance in principal component analysis (PCA; Supplementary Table 6 and

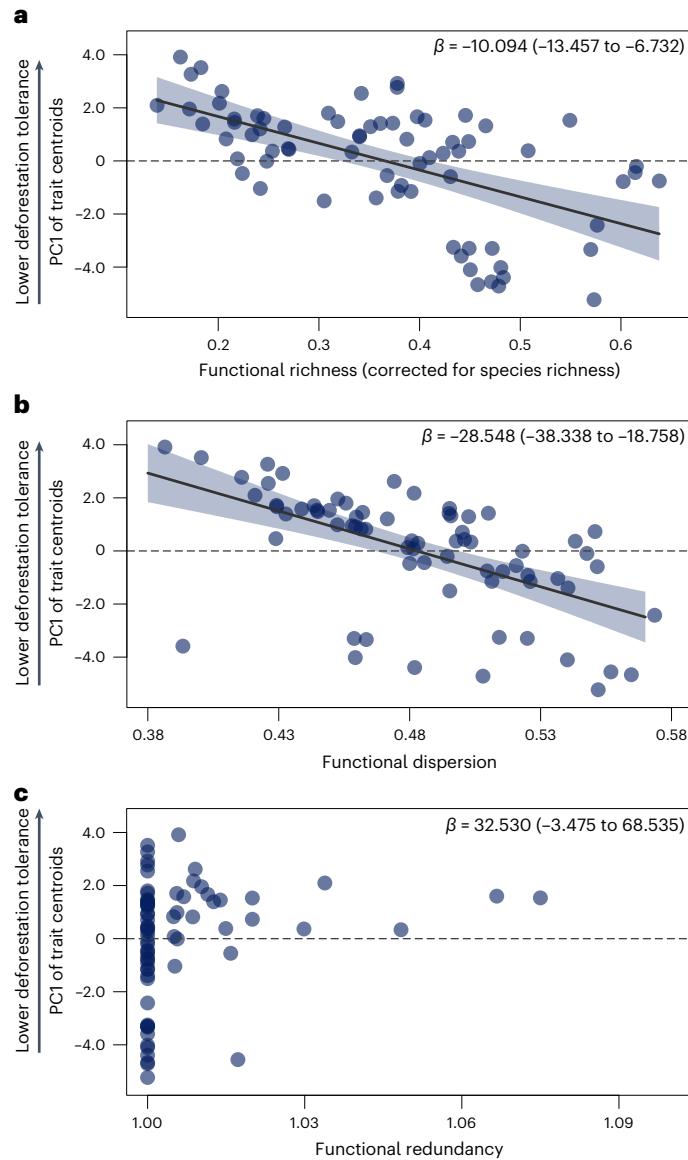
Methods). Variable loadings of PCA indicated that a lower PC1 overwhelmingly corresponded to assemblage trait profiles more tolerant of agricultural deforestation, as evidenced by the negative loadings of traits that predicted greater tolerance to agricultural deforestation (for example, hand-wing index) and vice versa (for example, forest association; Supplementary Table 6). Mixed-effect models indicated that MAP, seasonality, disturbance regime and agricultural history were all predictive of PC1 (Fig. 4c and Methods) in ways that linked a lower PC1 to greater environmental variability—as represented by lower MAP (Fig. 4c, top), higher seasonality (Fig. 4c, middle) and more frequent disturbance (Fig. 4c, slate blue over pink data points and fitted line)—and more severe historical deforestation (that is, longer agricultural history; Fig. 4c, bottom).

Taken together, the above analyses (also robust to a suite of sensitivity analyses; Supplementary Tables 7–10 and Methods) showed that the observed filtering effects of greater environmental variability and historical deforestation had a clear trait signature of ‘shifting’ avian assemblages towards 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 in Fig. 1b). Alternatively, and in the absence of trait space expansion, such shifts could occur by constituent species in filtered assemblages collectively shifting towards or clustering in the regions of the same trait space that correspond to greater tolerance (trait shift and trait clustering, respectively, in Fig. 1b).

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<sup>42</sup>, functional dispersion to measure the divergence of trait profiles among species<sup>43</sup> and functional redundancy to measure the clustering of species around certain trait profiles<sup>44</sup> (Methods). Linear regressions indicated that a lower PC1—corresponding to more tolerant assemblage trait profiles (Supplementary Table 6) 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 showing more divergent trait profiles, particularly those corresponding to greater tolerance of deforestation (that is, 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 showed 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<sup>7,12</sup>, or were regionally focused so as to severely limit the ranges of testable filter types or filtering intensities<sup>21,24</sup>. Building on theoretical underpinnings<sup>18,20</sup> and empirical evidence in other contexts<sup>19,28,29</sup>, our study provides a large-scale test of the roles of natural and anthropogenic filtering in shaping biodiversity responses to agricultural



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

deforestation. The evidence we uncovered for such roles highlighted a previously largely neglected explanation for the observed variation in biodiversity responses, including the apparently more negative responses found in tropical assemblages<sup>7</sup>, the reasons for which were yet to be formally tested.

Enhancing our 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<sup>45</sup>. 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 the existing agricultural deforestation occurred in more ‘filtered’ ecosystems<sup>1,10</sup> (that is, ecosystems less subjected 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 that which has occurred so far<sup>4</sup>. This grave possibility underscores the need for managing agricultural landscapes using the best knowledge and practices available<sup>12,17</sup>, 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. Proactive land-use strategies should use a range of approaches, including reducing the footprint of agricultural land use (via optimizing land allocation among alternative production regimes<sup>46</sup> and/or relocating production to more cost-efficient regions<sup>47</sup>) and prioritizing already deforested land for agricultural expansion in coordination with forest restoration<sup>48</sup>.

The trait signature of filtering we found provided further insights into how natural and anthropogenic filtering occurs to shape current 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 showing the effects of filtering, stopping short of testing its potential trait signatures<sup>19,28</sup>, although two recent species-level studies on avian tolerance of urbanization<sup>49</sup> and forest fragmentation<sup>29</sup> have gone a step further to assess the relevance of traits to such tolerance and, crucially, the geographical variation involved in this relevance. These studies mark an important step towards 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 the logic and expectations of the underlying ecological theory<sup>18,20,23</sup>. In addition, despite growing recognition of the links between species’ tolerance to anthropogenic impacts and their functional traits<sup>32,50</sup>, there is yet to be a rigorous large-scale test of these links for agricultural deforestation<sup>33,35</sup>, particularly based on globally synthesized empirical data rather than the coarse proxy of species threat levels delineated by the International Union for Conservation of Nature<sup>32,34</sup>. Our study filled the above important gaps, and expanded current understanding of the conservation relevance of ecological filtering<sup>23</sup>.

Although our study was based on paired data and robust to a suite of sensitivity analyses, our conclusions could be affected by several factors for which we could not account. These include (1) the management intensity of agricultural systems<sup>7</sup>, (2) potential pre-existing differences in biophysical conditions or anthropogenic pressures (for example, hunting) between agricultural and native forest sites, and (3) biotic factors capable of further filtering species assemblages in addition to the factors we considered<sup>20</sup>, notably competition, a process known to shape community assembly via functional traits<sup>51</sup>. The first issue should be lessened by the fact that our analyses accounted for remnant forest cover at agricultural sites and 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, although 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 similar abiotic factors to those we tested<sup>23</sup>. 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<sup>52</sup>. 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 recognize that the observed impacts are influenced not only 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<sup>28</sup>, including undocumented historical extinctions<sup>53</sup>. This legacy perspective particularly underscores humans’ obligations to conserve the rapidly disappearing ecosystems that have so far been spared of human impacts—the Earth’s last strongholds of complete species assemblages. The otherwise inevitable filtering and loss of 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 (that is, agriculture–forest pairs) on the level of individual bird species for entire avian assemblages. We focused on species-level abundance to allow for more nuanced assessment of deforestation impacts on biodiversity than is possible from coarser metrics, such as species richness or presence/absence<sup>54</sup>, 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 (that is,  $\geq 400$  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  $\geq 40$  years<sup>55</sup>. 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 (that is, 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 crops, considering the generally open vegetation structure of sun-grown coffee, tea or cocoa.

Although 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 ‘Meta-analyses and meta-regressions’), 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<sup>55</sup>. Still, this threshold age was young and potentially rendered the native forest benchmark a highly degraded one, but secondary forests were involved in only 3 out of the 71 avian assemblages studied (Extended Data Table 2). Therefore, these forests 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').

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 (for example, large body size or needing cavities for nesting). (2) The avian assemblages studied must include  $\geq 6$  species, and  $\geq 10\%$  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  $\geq 5$  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<sup>56</sup> (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  $\geq 50$  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  $\geq 5$  ha. (5) The matching between agricultural and native forest sites concerned all biophysical (for example, elevation, slope and landscape context) and study (sampling methods) conditions that may affect the measured species abundance. Correspondingly, we discarded data pairs that were obviously incomparable (that is, 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 (for example, individuals per hectare) or abundance indices; we did not admit indices based on occurrence frequencies because they are fundamentally about species' presence or 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 7 December 2021 using a combination of keyword searches and indexing from published syntheses and databases (Extended Data Fig. 1 and Extended Data Table 1). Overall we screened 5,899 abstracts and subsequently 451 full-text articles, from which we identified 61 suitable primary studies.

We extracted species-specific abundance data directly from these studies where available, and we contacted 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 (that is, 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<sup>54</sup>. 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 the 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<sup>57</sup>.

For each agriculture–forest pair, we recorded three metrics to calculate the weight of its RRs in subsequent analyses (see 'Meta-analyses and meta-regressions'). First, we assigned a 'match rigour score' to gauge the extent of matching between agricultural and native forest sites: 1 for 'high match rigour', if matching concerned most or all biophysical and methodological conditions; and 2 for 'likely or uncertain match rigour', 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; for example, agricultural sites may often be on more productive land than native forests in the same area. Second, we scored the duration of fieldwork ('study duration' hereafter; in months) to approximate the sampling effort for abundance data and, in turn, data quality. The fact that primary studies used a range of sampling designs (for example, 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 was fragmented or otherwise  $<50$  ha in size; and 2 for 'high habitat certainty', if it was  $\geq 50$  ha in size. We gave greater weights to records with higher match rigour, 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'):

$$\text{weight score} = \frac{\sqrt{\text{study duration} \times \text{habitat certainty score}}}{\text{match rigour score}} \quad (1)$$

For each agriculture–forest pair, we also 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<sup>9</sup>. 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 6 categories represented by scores 0–5 in sequential order: 0 for 0%; 1, (0%–5%]; 2, (5%, 10%]; 3, (10%, 20%]; 4, (20%, 40%]; and 5, (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  $\geq 50$  ha in size, and

we measured this distance from the FROM-GLC Plus land-cover map (FGP map; covering years 1982–2021, at a 30 m resolution)<sup>58</sup> using layers matched to the year of the avian surveys. We used land-cover maps for extracting this information 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 (that is, the global land cover map produced by the European Space Agency Climate Change Initiative; it covers years 1992–2020)<sup>59</sup>, but its spatial resolution is 10× 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<sup>58</sup>. 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 also used an alternative size criterion of  $\geq 100$  ha for continuous forest<sup>60</sup> in a set of sensitivity analyses (see ‘Sensitivity analysis’). 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 their 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 a distance  $\leq 1$  km, and ‘far’ for a distance  $> 1$  km. As data on this measure were of coarse resolution and were sometimes noted by primary study authors to be uncertain, we only used this measure in a corroborative assessment (see ‘Sensitivity analysis’).

For each agriculture–forest pair, we obtained its corresponding MAP and the s.d. of mean monthly temperature from WorldClim 2.1 (ref. 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:

- (1) (Almost) never, that is, the disturbance (almost) never happens, or its incidence is considered exceptional
- (2) Occasional, that is, the disturbance sometimes happens, but is not considered a regular phenomenon (<50% chance)
- (3) Frequent, that is, the disturbance regularly happens (>50% chance)

We opted to obtain first-hand information from primary study authors rather than from existing maps because the latter are typically of coarse resolutions<sup>28</sup>. Of all 44 primary studies, we were able to get author-provided scores of the 4 disturbance types for 35 studies; for the remaining 9 studies, 2 co-authors (F.H. and W.W.) independently scored the 4 disturbance types by consulting literature and web sources, and then discussed to harmonize 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 subjected to regular disturbances of any kind. Finally, because only four primary studies had an overall disturbance regime score of two, we converted their scores to one to avoid computational problems, thus effectively streamlining the disturbance regime variable into a two-category variable: zero (that is, almost no disturbance; ‘no disturbance’ hereafter) versus one (that is, occasional or more frequent disturbances; ‘with regular disturbance’ hereafter).

We also used study coordinates to derive the length of agricultural history for each agriculture–forest pair from the HYDE 3.2 database<sup>40</sup>

(which covers the temporal span of year 10,000 BC to 2015 AD) 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 ref. 61. These traits are all considered predictive of species sensitivity to forest loss and degradation<sup>29,32–36</sup>, and they include the following: two morphological traits (body mass and hand-wing index (a measure of the relative elongation of a bird’s wing and a widely used proxy for dispersal capability<sup>62</sup>; Extended Data Table 3)), two life-history traits (clutch size and generation length) and six ecological traits (diet specialization, 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 and nest placement (the extent to which a species depends on forest structures for nest placement)). We provide detailed definition, reasons for 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 (for example, ref. 33) by distinguishing between four categories: late successional forest, early successional forest, generalist and open country (Extended Data Tables 3 and 4). These categories allowed for finer distinction of species’ forest association that was also specific to the study season. To ensure data quality, two co-authors (W.W. and S.L.) independently scored forest association for each species and then discussed to harmonize any discrepancies, and we double-checked all extracted data to minimize data entry error.

For each trait and each species assemblage (that is, corresponding to a given agriculture–forest pair), we calculated its assemblage-level centroid, that is, 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):

$$\text{trait centroid} = \sum_{i=1}^n \text{trait value}_i \times \frac{\text{Abun}_{i,\text{agriculture}} + \text{Abun}_{i,\text{native forest}}}{\text{Abun}_{\text{assemblage}}} \quad (2)$$

Where  $i$  represents each species in the assemblage that consists of  $n$  species,  $\text{Abun}_{i,\text{agriculture}}$  and  $\text{Abun}_{i,\text{native forest}}$  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  $\text{Abun}_{\text{assemblage}}$  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<sup>63</sup> of assemblage RR using the ‘lme()’ function of package nlme (v.3.1-157 (ref. 64)) in program R (v.4.2.0 (ref. 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 (that is, later variables were nested within earlier ones):

- Level 1: study season, involving the two categories breeding or all year versus non-breeding; random effects with a small number of categories have been shown to not bias model estimates<sup>66</sup>, 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<sup>41</sup>, following the method developed in ref. 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)<sup>67</sup>, and then used the model(s) with the most complete set of predictor variables from within the top model set ( $\Delta\text{AICc} \leq 2$ ) to make an inference. We used the same random-effect structure as in the above meta-analyses, and we calculated marginal  $R^2$  (that is, the variance explained by the models) based on the lowest-tier random intercept variable<sup>68</sup>. Fixed effects of the global models followed equation (3):

$$\begin{aligned} \text{RR} \sim & \text{remnant forest cover} + \text{distance to nearest continuous forest} + \\ & \text{surrounding human population density} + \\ & \text{MAP} + \text{seasonality} + \text{disturbance regime} + \text{agricultural history} \end{aligned} \quad (3)$$

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  $\text{km}^{-2}$ ) represented features of the agricultural landscapes; MAP (in  $\text{mm y}^{-1}$ ), seasonality (in  $^{\circ}\text{C}$ ) and disturbance regime (no disturbance versus with regular disturbance) represented natural filtering; and agricultural history (in years) represented anthropogenic filtering. We modelled the effects of all continuous variables (that is, all except for remnant forest cover) on the natural log scale, considering that the same absolute difference in the lower range of their values (for example, 100 m versus 300 m distance, or 300 mm versus 600 mm MAP) was most likely of much greater ecological magnitude than that in the upper range (for example, 2,100 m versus 2,300 m distance, or 2,300 mm versus 2,600 mm MAP). Pre-analysis assessment of collinearity indicated the absence of strong collinearity among all variables (all  $|r_{\text{Pearson}}| < 0.52$ ). Therefore, we 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, that is, models whose  $\Delta\text{AICc}$  was  $\leq 2$  from the lowest AICc score of the full model set, using the package MuMIn (v.1.47.5 (ref. 69)) in program 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 = ~(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 and meta-regressions because the species-level abundance data reported

rarely had sampling variance information. For all meta-analyses and meta-regressions, we visually assessed residual and quantile–quantile (Q–Q) 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<sup>70</sup>. Funnel plots produced using package metafor (v.3.4-0 (ref. 71)) in program R and Egger’s test following ref. 72 also 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 Table 1), further indicating a lack of data asymmetry.

**Other linear mixed models.** To assess the relationship of assemblage-level trait centroids and their PC1 (from PCA; see ‘Multivariate analysis of trait data’) 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 (that is, 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 Q–Q plots showed the general satisfaction of the residual-normality assumption for these analyses. Fixed effects of the global models thus followed equation (4):

$$\begin{aligned} \text{trait centroids or PC1} \sim & \text{MAP} + \text{seasonality} + \text{disturbance regime} + \\ & \text{agricultural history} \end{aligned} \quad (4)$$

**Phylogenetically controlled mixed-effect models.** We used the function ‘MCMCglmm()’ of package MCMCglmm (v.2.34 (ref. 73)) in program 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, that is, 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  $|r_{\text{Pearson}}| < 0.37$ ) among all variables, except between body mass and generation length ( $r_{\text{Pearson}} = 0.84$  for centred-and-scaled values). Therefore, we 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 ‘Meta-analyses and meta-regressions’). 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 (that is, 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 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):

$$\begin{aligned} \text{RR} \sim & \text{ remnant forest cover} + \text{distance to the nearest continuous forest} \\ & + \text{surrounding human population density} \\ & + \text{body mass (or generation length)} + \text{hand-wing index} + \text{clutch size} \\ & + \text{diet specialization} + \text{foraging height} + \text{forest association} \\ & + \text{migratory status} + \text{natural range size} + \text{nest placement} \end{aligned} \quad (5)$$

We centred and scaled all continuous variables and remnant forest cover (distance to the nearest continuous forest and surrounding human population density) were on the 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 that all fixed predictors entered the top model set except for the distance to the nearest continuous forest; therefore, we included all variables except the distance variable in subsequent formal analyses that controlled for phylogenetic correlation. In subsequent sensitivity analyses (that is, those involving alternative data on the distance to the nearest continuous forest, and on surrounding human population density; see ‘Sensitivity analysis’), 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 between species as an additional random variable. Our fixed effects thus followed equation (6):

$$\begin{aligned} \text{RR} \sim & \text{ remnant forest cover} + \text{surrounding human population density} \\ & + \text{body mass (or generation length)} + \text{hand-wing index} + \text{clutch size} \\ & + \text{diet specialization} + \text{foraging height} + \text{forest association} \\ & + \text{migratory status} + \text{natural range size} + \text{nest placement} \end{aligned} \quad (6)$$

We used the default uninformative prior for fixed effects, the inverse gamma prior (with the following parameter setting: scale matrix  $V=1$ , and degree of freedom  $\text{nu}=0.002$ ) for the residual variance, and the parameter-expanded prior (with the following parameter setting: scale matrix  $V=1$ , degree of freedom  $\text{nu}=1$ , covariance matrix  $\text{alpha.V}=1,000$  and mean  $\text{alpha.mu}=0$ ) 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<sup>61</sup>, 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<sup>74</sup>). Diagnostic plots indicated convergence for all model runs (Extended Data Fig. 6 for an example of 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 to 4, for open-country, generalist, early successional forest and late successional forest, respectively, regarding forest association; 1 and 2 for non-migratory and migratory, respectively, regarding migratory status; and 1 to 3 for ground nesting, elevated open nesting and cavity

nesting, respectively, regarding nest placement. We conducted PCA on the assemblage-level trait centroids (centred and scaled) using the function ‘princomp()’ in program R.

To calculate functional richness and functional dispersion for each species assemblage, we used the function ‘alpha.fd.multidim’ of package mFD (v.1.0.1 (ref. 75)) in program R and the first four axes of the Gower-based functional distance. As functional richness is by definition closely linked to species richness<sup>43</sup>, we corrected it using equation (7) to remove the influence of species richness:

$$\text{corrected functional richness} = \frac{\text{raw functional richness} \times 100}{\text{species richness}} \quad (7)$$

Finally, we calculated functional redundancy for each species assemblage, following ref. 76, by first classifying each species into a ‘unique trait combination’ based on its trait profile. To do this, we followed ref. 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 unique trait combinations<sup>44,76</sup>. We conducted simple linear regressions between PCI and the three multivariate trait metrics. Diagnostic residual and Q–Q plots showed the general satisfaction of the residual-normality assumption for these analyses.

**Sensitivity analysis.** We conducted six sets of sensitivity analyses where applicable. These concerned (1) the radius for data extraction on agricultural history and surrounding human population density from the HYDE 3.2 database<sup>40</sup> (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 so 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<sup>77,78</sup> or seasonality<sup>78</sup> (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<sup>79,80</sup> (versus their inclusion in main analyses); and (6) weighting schemes in mixed-effect models (using simply the inverse of the match rigour 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<sup>7</sup>. We conducted this assessment with simple visualization in light of the limited data quality of this complementary distance measure (Extended Data Fig. 4h).

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

All data used in this study have been uploaded to a public repository, and can be accessed at <https://doi.org/10.5281/zenodo.10031327> (ref. 31).

## Code availability

All code used in this study have been uploaded to a public repository, and can be accessed at <https://doi.org/10.5281/zenodo.10031327> (ref. 31).

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## Author contributions

F.H. conceived the study and led the study design. W.W. compiled species-level abundance data and associated meta-data with assistance from all co-authors. W.W. compiled species trait data with assistance from S.L. and X.M. F.H. designed and coded data analysis

with assistance from S.N. and P.R.E., and along with W.W. implemented all analyses. F.H. designed visualization of the results, and along with W.W. implemented visualization of the results. F.H. wrote the first draft of the article with assistance from W.W. and S.N., and all authors contributed to revisions of the article.

## Competing interests

The authors declare no competing interests.

## Additional information

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Comprehensive primary search  
on Web of Science on December  
7<sup>th</sup>, 2021  
(number of hits: n = 5,879)

#### Search terms

(bird\* OR avian OR avifauna)  
AND forest\*  
AND (agricultur\* OR cropland\*  
OR farm\* OR agroforest\* OR  
pastur\* OR silvopastur\*)  
AND (abundan\* OR communit\*  
OR diversit\* OR densit\*)

Screening relevant databases:  
BIOFRAG  
(number of hits: n = 3)

PREDICTS  
(number of hits: n = 5)

+

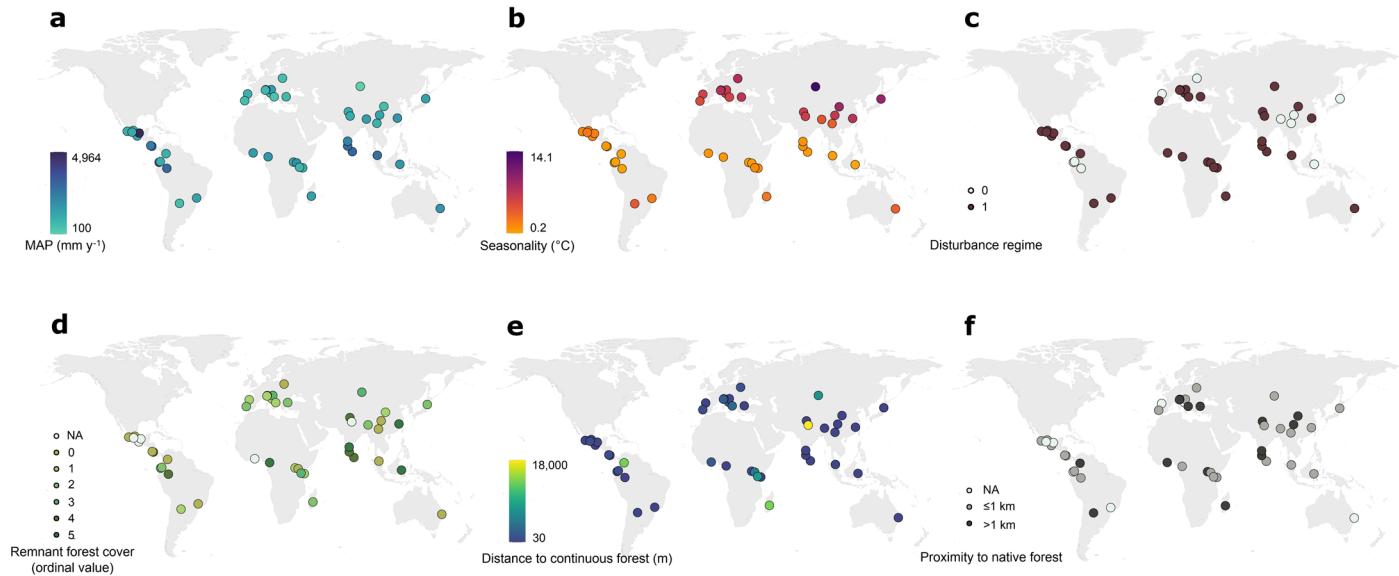
Screening primary studies  
cited in two reviews on land  
sharing and sparing  
(number of hits: n = 12)

Screening abstract to identify primary studies for full-text screening  
(number of hits remaining: n = 451)

Screening full text to identify primary studies meeting inclusion criteria  
(number of hits remaining: n= 61)

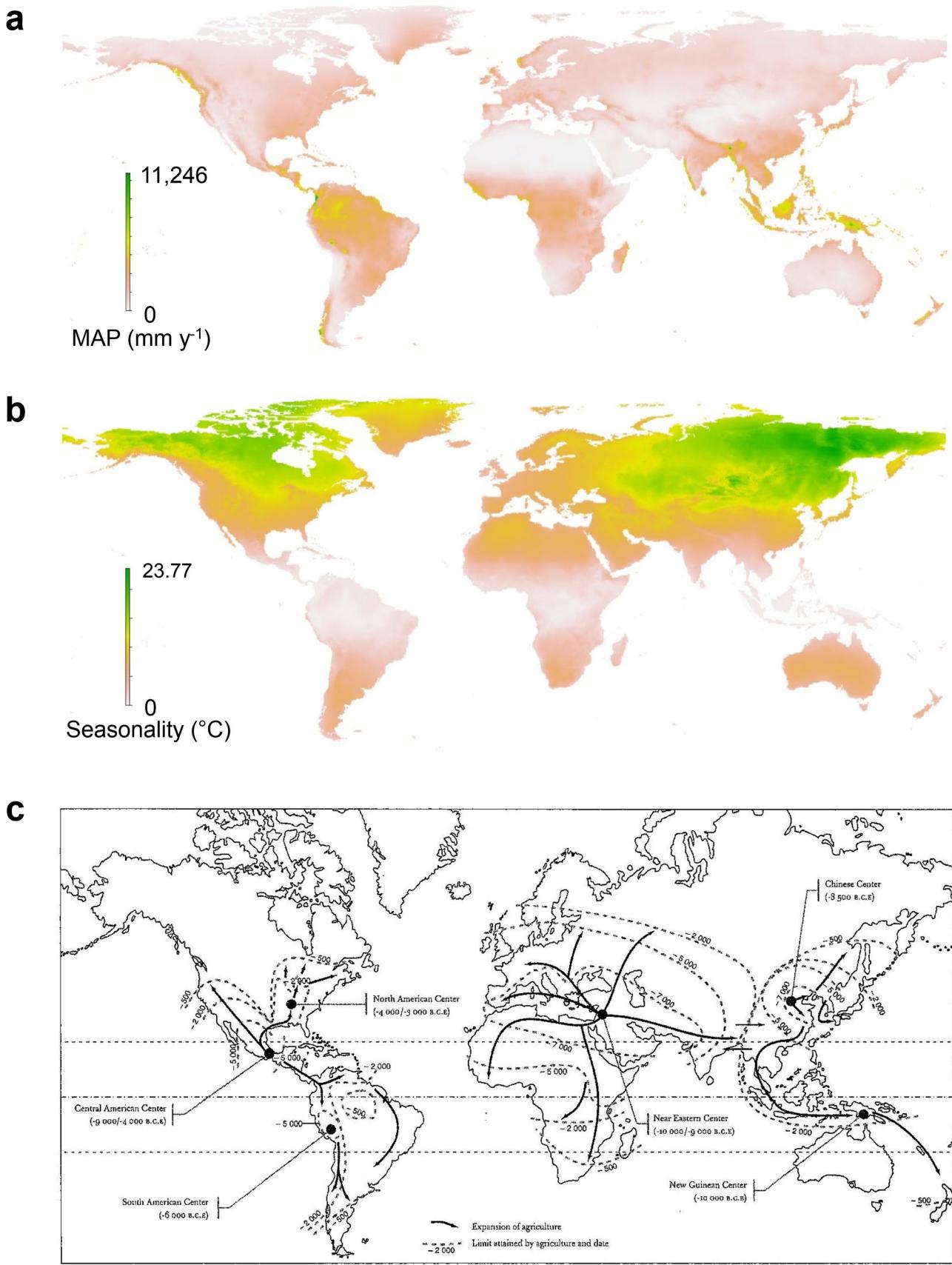
Requesting data from primary study authors where necessary and  
compiling data (number of primary studies included: n = 44)

**Extended Data Fig. 1 | PRISMA plot for data compilation.** Reference information for the two databases and reviews consulted is provided in Extended Data Table 1.



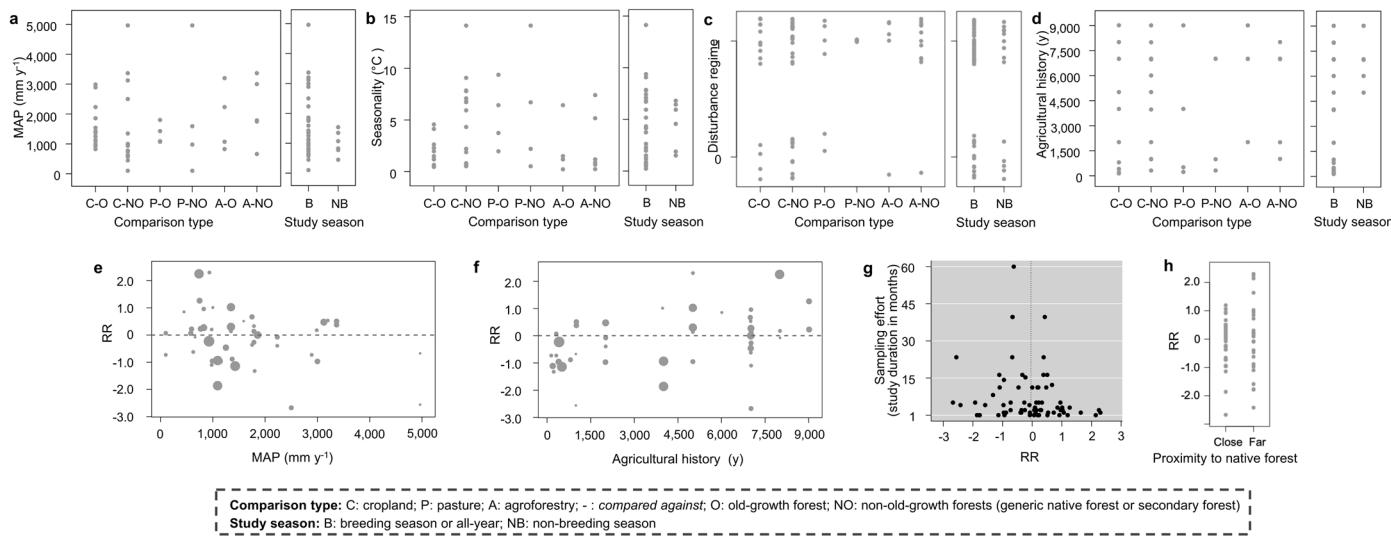
**Extended Data Fig. 2 | Additional information on the range of data covered by our database.** As with Fig. 2, circles represent datasets of entire avian assemblages for agriculture-forest pairs contributed by each primary study, sized proportional to the number of avian assemblages and colored by (a) MAP,

(b) seasonality, and (c) disturbance regime of the study system, as well as (d) remnant forest cover, distance to (e) the nearest continuous forest and (f) native forest surveyed for the agricultural sites in each primary study.



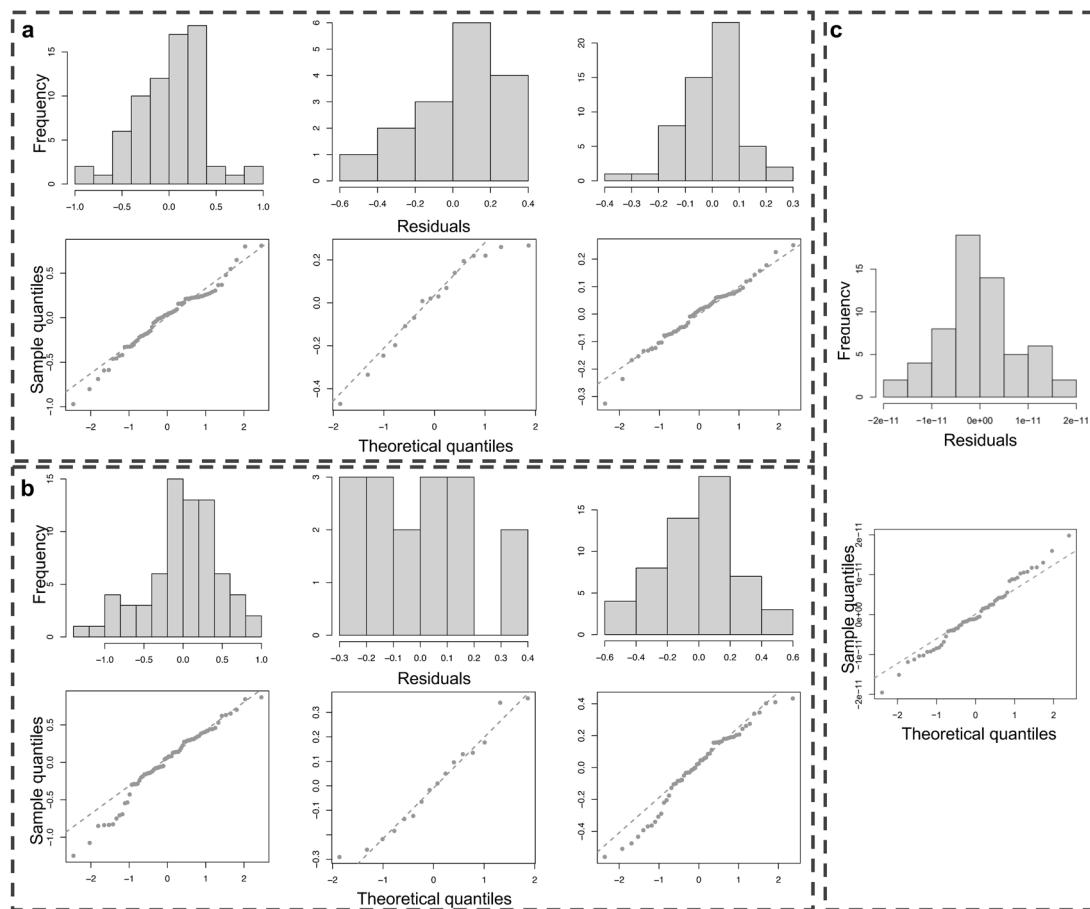
**Extended Data Fig. 3 | Geographical patterns of three filtering factors across the world.** (a) MAP, (b) temperature seasonality, and (c) agricultural history. Data for temperature seasonality and MAP are from WorldClim 2.1<sup>39</sup>.

Map boundaries in c show the centres of origin and areas of expansion of the Neolithic Agricultural Revolution, as reproduced with permission from ref. 81, Monthly Review Press.



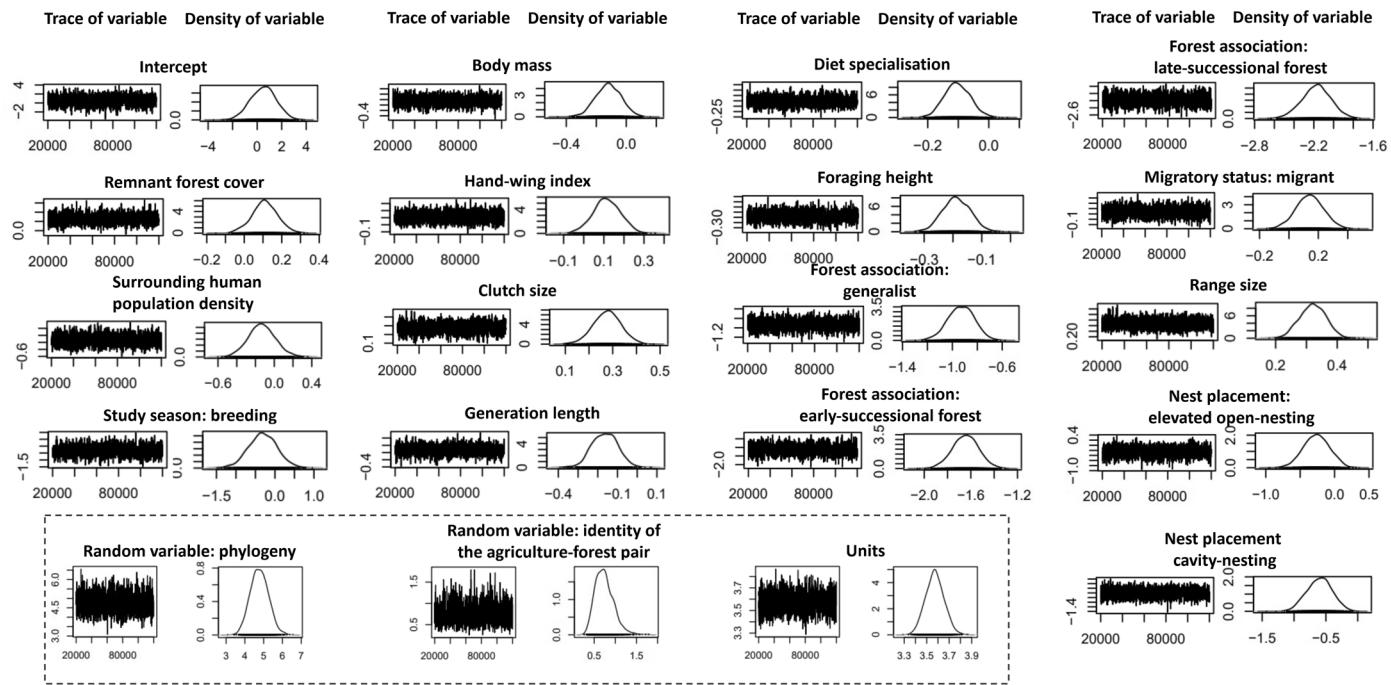
**Extended Data Fig. 4 | Evidence that the influence of filtering on the observed impacts of agricultural deforestation was not an artefact of confounding variables or publication bias.** (a–d) The relationship between the four filtering variables and comparison type (left part) or study season (right part). While none of the filtering factors had no strong collinearity with comparison type, for at least MAP and agricultural history, there appeared to be some difference between breeding/all-year versus non-breeding seasons. (e, f) We therefore focused on a subset of data concerning the breeding season only (80% of all data) to visually assess the relationship between assemblage RR with MAP and agricultural history, using the same graph format as in Fig. 3. This subset of data also showed the negative effect of MAP (Fig. 3d) and the positive effect of agricultural history (Fig. 3e) on assemblage RR that were found by formal meta-regressions, suggesting that these effects were not spuriously driven by

possible collinearity between filtering variables and study season. (g) Funnel plot for meta-analysis, based on effect size (RR) and study size (sampling effort; measured as the study duration in months). The dotted vertical line represents the mean effect size indicated by meta-analysis (*that is* corresponding to the mean of Fig. 3A, upper row). (h) The relationship between assemblage RR and the distance of agricultural sites to their matching native forests. We represented distance by the smallest distance from any sampling unit of the agricultural sites to matching native forest sites, with ‘close’ representing distances  $\leq 1$  km and ‘far’ those  $> 1$  km. This visual assessment showed that greater assemblage RR was not associated with shorter distances between agricultural sites and native forests, corroborating our main findings based on the FGP map data that distance to nearest continuous forest did not drive variation in biodiversity responses to agricultural deforestation.



**Extended Data Fig. 5 | Diagnostic plots for meta-analyses and meta-regressions corresponding to (a) Fig. 3a, (b) Fig. 3b, and (c) Fig. 3c–e.** For (a) and (b), residual plots (upper) and Q-Q plots (lower) are displayed for each of the meta-analyses concerning all agricultural types (left column), agroforestry

(middle column), and open agricultural systems (right column) displayed in Fig. 3a, b. For (c), the residual plot (upper) and Q-Q plot (lower) correspond to the meta-regression global model.



**Extended Data Fig. 6 | Diagnostic plots for the phylogenetically controlled mixed-effect model on the relationship between species-level RR and predictor variables, run on one randomly drawn phylogenetic tree.** Plots for all variables other than generation length were from a model that dropped

generation length, while the plot for generation length was from a model that dropped body mass. Pairs of plots on the trace (left) and density (right) of posterior estimates are displayed for each fixed factor and random factor including residual variance, or ‘Units’ (in dashed box).

**Extended Data Table 1 | List of syntheses, databases, and other studies consulted for identifying suitable primary studies.**  
These studies are listed by type<sup>82–93</sup>

Type	No.	Study
Synthesis on agriculture- or forest-related land-use change	1	De Beenhower et al. 2013 <sup>82</sup>
	2	Dunn 2004 <sup>83</sup>
	3	Norris et al. 2010 <sup>84</sup>
	4	Philpott et al. 2008 <sup>85</sup>
	5	Plexida et al. 2018 <sup>86</sup>
	6	Núñez-Regueiro et al. 2019 <sup>87</sup>
	7	Sekercioglu 2012 <sup>88</sup>
	8	Sodhi et al. 2009 <sup>89</sup>
Database on biodiversity response to agriculture- or forest-related land-use change	9	Pfeifer et al. 2014 <sup>90</sup>
Reviews on agriculture- or forest-related land-sharing/sparing	10	Hudson et al. 2016 <sup>91</sup>
	11	Fischer et al. 2014 <sup>92</sup>
	12	Luskin et al. 2017 <sup>93</sup>

**Extended Data Table 2 | Full list of primary studies included in our database. These studies are listed in alphabetical order<sup>94–130</sup>**

Primary study	Country	Native forest type†	Agriculture type	MAP (mm y <sup>-1</sup> )	Seasonality (°C)	Disturbance regime	Agricultural history (y)	Primary study	Country	Native forest type†	Agriculture type	MAP (mm y <sup>-1</sup> )	Seasonality (°C)	Disturbance regime	Agricultural history (y)
Abrahamczyk et al. 2008 <sup>94</sup>	Indonesia	GNF	Agroforestry	1,750	0.25	0	7,007	Macchi et al. 2019 <sup>112</sup>	Argentina	GNF	Cropland	625	4.32	1	7,009
Arias-Sosa et al. 2021 <sup>80</sup>	Colombia	SF (≥40 y)	Pasture	978	0.52	1	7,019	MacGregor-Fors & Schondube 2011 <sup>113</sup>	Mexico	OGF	Cropland	1,092	1.97	1	4,007
Bongiorno 1982 <sup>95</sup>	Spain	GNF	Cropland	1,000	5.93	0	3,972			Pasture				1	
Chandler et al. 2013 <sup>96</sup>	Costa Rica	GNF	Agroforestry	3,366	0.68	1	1,006	Martin et al. 2012 <sup>114</sup>	Madagascar	OGF	Cropland	1,370	2.63	1	804
Chiariate & Meriggi 2016 <sup>97</sup>	Italy	GNF	Cropland	448	5.93	1	6,011	Morelli et al. 2013 <sup>115</sup>	Italy	GNF	Cropland	747	6.73	1	9,011
Chiariate et al. 2019 <sup>98</sup>	Italy	GNF	Cropland	768	7.79	1	9,015	Mulwa et al. 2013 <sup>116</sup>	Kenya	OGF	Cropland	1,857	0.65	1	7,009
Chiariate et al. 2021 <sup>99</sup>	Italy	GNF	Cropland	935	7.83	0	5,016	Norfolk et al. 2017 <sup>117</sup>	Kenya	OGF	Cropland	826	1.5	1	7,014
Chiawo et al. 2018 <sup>100</sup>	Kenya	OGF	Cropland	927	1.22	1	412	O'Dea & Whittaker 2007 <sup>118</sup>	Ecuador	OGF	Cropland	3,200	0.23	0	7,003
Cresswell et al. 1999 <sup>101</sup>	Ecuador	OGF	Cropland	1,132	0.48	0	397	Ortega-Álvarez et al. 2018 <sup>119</sup>	Mexico	GNF	Agroforestry			0	
Echeverri et al. 2019 <sup>102</sup>	Costa Rica	GNF	Cropland	2,500	0.81	1	7,016	Penteado et al. 2016 <sup>120</sup>	Brazil	OGF	Cropland	1,297	1.74	1	1,016
Elsen et al. 2017 <sup>9</sup>	India	OGF	Pasture	1,070	6.43	1	9,013	Phalan et al. 2011 <sup>121</sup>	Ghana	GNF	Pasture	1,422	2.29	1	193
			Agroforestry			1		Raman et al. 2021 <sup>122</sup>	India	OGF	Agroforestry	1,542	0.93	1	7,007
Estrada et al. 1997 <sup>77</sup>	Mexico	GNF	Cropland	4,964	2.2	1	990	Salgueiro et al. 2018 <sup>123</sup>	Portugal	GNF	Cropland	2,232	1.19	1	2,016
			Pasture			1		Shahabuddin et al. 2021 <sup>124</sup>	India	OGF	Agroforestry	661	5.17	1	8,013
			Agroforestry			1		Sidhu et al. 2010 <sup>125</sup>	India	GNF	Cropland	1,193	6.35	1	7,016
Garcia et al. 1998 <sup>103</sup>	Mexico	GNF	Pasture	1,192	2.48	1	3,994	Socobar et al. 2019 <sup>8</sup>	Peru	OGF	Cropland	3,000	1.19	1	2,008
Hua et al. 2016 <sup>104</sup>	China	GNF	Cropland	1,347	6.81	0	5,014	Soh et al. 2005 <sup>126</sup>	Malaysia	OGF	Cropland	2,987	0.46	0	8,013
Huang & Catterall 2021 <sup>105</sup>	Australia	OGF	Pasture	1,800	3.74	1	227	Sreekar et al. 2017 <sup>127</sup>	Sri Lanka	GNF	Agroforestry	2,890	0.54	1	142
Hulme et al. 2013 <sup>106</sup>	Uganda	OGF	Cropland	1,250	0.51	1	7,006	Srinivasan et al. 2019 <sup>24</sup>	India	OGF	Cropland	3,122	0.72	1	2,014
Hutto 2020 <sup>107</sup>	Mexico	GNF	Cropland	773	1.89	1/0*	6,975	Yamaura et al. 2012 <sup>128</sup>	Japan	OGF	Pasture	1,538	4.56	0	9,018
Imboma et al. 2020 <sup>108</sup>	China	GNF	Agroforestry	1,786	7.41	1	7,018	Zhang et al. 2021 <sup>129</sup>	China	GNF	Cropland	1,427	9.38	0	509
Jarrett et al. 2021 <sup>109</sup>	Cameroon	GNF	Agroforestry	1,749	0.88	1	6,990	Zhou et al. 2019 <sup>130</sup>	China	OGF	Cropland	593	9.08	1	7,016
Kati & Sekercioğlu 2006 <sup>110</sup>	Greece	GNF	Cropland	736	7.1	1	7,999			Cropland	988	4.13	0	5,015	
Kmed & Denac 2018 <sup>79</sup>	Slovenia	SF (≥40 y)	Pasture	1,590	6.71	1	7,012								
Kulaga & Budka 2019 <sup>111</sup>	Poland	GNF	Cropland	579	7.85	0	7,018								
Li et al. 2019 <sup>78</sup>	China	GNF	Cropland	100	14.14	1	315								
			Pasture			1									

Note: † – GNF for generic native forest; SF for secondary forest; OGF for old-growth forest.

\* – 1 for low and high elevations; 0 for mid elevation.

**Extended Data Table 3 | List of species functional traits considered in this study. Traits are listed by type (morphological, life history, and ecological), along with information on their definition, rationale for consideration in our study, and data sources<sup>131-135</sup>**

Trait type	Trait	Definition	Reason for inclusion	Data source
Morphological trait	Body mass	Weight of body measured in g; continuous variable on the natural log scale	Numerous previous studies have indicated that larger-bodied birds and other species tend to be more sensitive to forest loss and degradation, and habitat change in general <sup>32-35</sup> . This could be linked to the slow(er) reproductive rates typically associated with larger-bodied species, which render their population less able to recover from disturbance impacts.	<sup>131</sup>
	Hand-wing index	A measure of the relative elongation of a bird's wing and proxy for dispersal capability <sup>29</sup> , measured by the function $100*D_w/L_w$ , where $L_w$ is wing length, as measured by the distance from the tip of the longest primary feather to the carpal joint, and $D_w$ is Kipp's distance, as measured by the difference between $L_w$ and the length of the secondaries, which is in turn measured as the distance from the first secondary feather to the carpal joint); unitless continuous variable on the natural log scale	Dispersal capability is increasingly recognised as an important predictor for avian tolerance to forest habitat degradation, notably fragmentation <sup>29</sup> , with species more capable of dispersing generally more tolerant.	<sup>62</sup>
Life-history trait	Clutch size	Average number of eggs per clutch; continuous variable on the natural log scale	Clutch size is a frequently used measure of avian fecundity. In theory, species with higher fecundity (capable of reproducing faster) should be better able to recover from disturbance impacts <sup>33</sup> , and this has been supported by numerous previous studies linking larger clutch sizes to bird species' greater tolerance to environmental change <sup>32,33,35</sup> .	<sup>32,132</sup>
	Generation length	The average age of parents of the current cohort; continuous variable on the natural log scale	Similar to clutch size, generational length is frequently used to represent avian fecundity: species with longer generation lengths tend to reproduce more slowly, and are expected to be less capable of recovering from disturbance impacts <sup>33</sup> . The relevance of generation length to birds' tolerance of forest loss and degradation, and habitat change in general has been supported by previous studies <sup>33</sup> .	<sup>133</sup>
Ecological trait	Diet specialisation	A modified Gini coefficient calculated based on all diet categories a species consumes, following <sup>134</sup> ; R code in associated data upload; continuous variable, with higher scores indicating more specialised diet	Diet is widely recognised as a relevant trait predicting bird species' tolerance to habitat change <sup>32-35</sup> , which directly affects species food resources. Diet specialisation in particular, determines the breadth of food resources a species can utilise. It is thus an important aspect of species specialisation <sup>134</sup> , and has been suggested to be a trait relevant to species tolerance to habitat change and endangerment <sup>33</sup> .	<sup>131</sup> (for information on diet category)
	Foraging height	A weighted average of height at which a species forages, calculated based on the proportion of time it spends foraging at each stratum (expressed in ordinal scores of 1–5 for below-water-surface/water surface/ground, understory, mid-height, canopy, and aerial strata, respectively); continuous variable, with higher scores indicating higher average foraging height	Foraging height describes an important aspect of species' foraging behavior and its ecological relationship with habitat. Species foraging at higher vegetation strata should generally rely on (tall) forest vegetation structure for its food resources. In our study's context of forest conversion to agriculture, we therefore expected such species to be more heavily impacted.	<sup>131</sup> (for information on foraging stratum)
	Forest association	The extent to which a species is associated with forest habitats; four categories in increasing degree of association: open country, generalist, early-successional forest, late-successional forest (expressed as 1, 2, 3, and 4, respectively, when used as an ordinal variable)	Species' habitat association is a direct – albeit composite – description of its habitat needs. By describing the level of reliance on forest habitat, a species' forest association should constitute a trait of direct relevance to its response to deforestation. This relevance has been supported by numerous studies <sup>32-36</sup> .	<sup>132,135</sup>
	Migratory status	Whether or not a species is considered migratory; resident species are considered non-migratory, while all other species are considered migratory; when used in ordinal values, expressed as 1 and 2 for non-migratory and migratory, respectively	Some studies have indicated different levels of sensitivity to habitat change between migratory and resident species <sup>33</sup> , with migratory species generally more tolerant. This could be linked to the exposure of migratory species to a greater variety of environmental conditions, compared to the more localised exposure of resident species.	<sup>135</sup>
	Natural range size	The size of a species' natural distribution range measured in km <sup>2</sup> ; continuous variable on the natural log scale	It is generally recognised that more widely distributed species are more abundant, less of conservation concern, and more tolerant to habitat change. Numerous studies have indicated positive relationships between species' natural range size and their tolerance to forest loss, degradation, and habitat change in general <sup>35,36</sup> .	<sup>32,135</sup>
	Nest placement	The extent to which a species depends on forest structures for nest placement; three categories in increasing degree of dependence: ground-nesting, elevated open-nesting, cavity-nesting (expressed as 1, 2, and 3, respectively, when used as an ordinal variable)	Similar to foraging height and forest association, the extent to which a bird species depends on forest structures for nest placement describes an important aspect of its habitat needs: in terms of reproduction. Species with greater levels of dependence – as measured by our ordinal scoring system – should generally rely more on (mature) forest vegetation structure for its nesting needs. In our study's context of forest conversion to agriculture, we therefore expected such species to be more heavily impacted.	<sup>32</sup>

**Extended Data Table 4 | Two criteria that must be met simultaneously for classifying species into forest association categories**

Category	Criterion 1, based on information from <sup>135</sup>	Criterion 2, based on information from <sup>132</sup>
Late-successional-forest	The section "habitat type" only involves "forest"	The section "habitat" notes the species to only/mostly use habitats typical of mature or late-successional forests, represented by descriptive terms (for the forest habitat) including: "primary", "pristine", "old-growth", "large trees", "dense forest", and "old secondary growth".
Early-successional-forest	The section "habitat type" only involves "forest"	The section "habitat" notes the species to only/mostly use habitats typical of early-successional forests, represented by descriptive terms (for the forest habitat) including: "open forest", "forest edge", "secondary growth", "gallery forest", and "scattered trees".
Generalist	The section "habitat type" involves "forest" and other non-forest habitats	The section "habitat" notes the species to use forest as well as non-forest habitats.
Open-country	The section "habitat type" only involves non-forest habitats	The section "habitat" notes the species to only use non-forest habitats ( <i>i.e.</i> the species does not use any forest habitats), represented by terms including "urban", "farmland", "water area", and "wetland".

## Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

### Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
  - Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted
  - Give  $P$  values as exact values whenever suitable.*
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

Data collection No software was used in data collection for this study.

Data analysis We used the programme R (versio 4.2.0) for data analysis in this study.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

### Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
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All data came from published sources or were contributed by co-authors.

## Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	<input type="checkbox"/> This study did not involve human participants.
Reporting on race, ethnicity, or other socially relevant groupings	<input type="checkbox"/> This study did not involve human participants.
Population characteristics	<input type="checkbox"/> This study did not involve human participants.
Recruitment	<input type="checkbox"/> This study did not involve human participants.
Ethics oversight	<input type="checkbox"/> This study did not involve human participants.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences       Behavioural & social sciences       Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study tested the hypotheses that filtering by habitat resemblance to non-forest conditions and historical deforestation explains global variations in the biodiversity impacts of agricultural deforestation, and that these filtering effects are reflected by trait signatures of species assemblages.
Research sample	Seventy one avian assemblages reported in 44 primary studies from 25 countries for which paired species abundance records are available on the species level for the entire assemblage.
Sampling strategy	We systematically searched for published studies that met our predetermined data inclusion criteria (explained in the manuscript), and we reached out to study authors to request data if the assemblage-level data were not available from the publications.
Data collection	We compiled data from published studies, including data on functional traits.
Timing and spatial scale	The temporal and spatial scales of this study were determined by the primary studies included into our database. The temporal range of our avian abundance data is 1972–2019 (i.e. for the year of field data collection); the spatial range of our data is 25 countries across the globe. In addition, the variable agricultural history was compiled from an existing global map that covered the temporal range of 10,000 BCE – 2017 CE.
Data exclusions	Of the 61 studies we identified that met our data inclusion criteria, we were able to include only 44 because species-level abundance data for the entire avian assemblage were not available for the other 17 studies.
Reproducibility	Not applicable because data were from published sources.
Randomization	Not applicable because data were from published sources.
Blinding	Not applicable because data were from published sources.

Did the study involve field work?  Yes     No

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

**Materials & experimental systems**

- |                                     |                               |
|-------------------------------------|-------------------------------|
| n/a                                 | Involved in the study         |
| <input checked="" type="checkbox"/> | Antibodies                    |
| <input checked="" type="checkbox"/> | Eukaryotic cell lines         |
| <input checked="" type="checkbox"/> | Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | Animals and other organisms   |
| <input checked="" type="checkbox"/> | Clinical data                 |
| <input checked="" type="checkbox"/> | Dual use research of concern  |
| <input checked="" type="checkbox"/> | Plants                        |

**Methods**

- |                                     |                        |
|-------------------------------------|------------------------|
| n/a                                 | Involved in the study  |
| <input checked="" type="checkbox"/> | ChIP-seq               |
| <input checked="" type="checkbox"/> | Flow cytometry         |
| <input checked="" type="checkbox"/> | MRI-based neuroimaging |