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LETTER

Global impacts of climate change on avian functional diversity

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Abstract

Climate change is predicted to drive geographical range shifts, leading to fluctuations in species richness (SR) worldwide. However, the effect of these changes on functional diversity (FD) remains unclear, in part because comprehensive species-level trait data are generally lacking at global scales. Here, we use morphometric and ecological traits for 8268 bird species to estimate the impact of climate change on avian FD. We show that future bird assemblages are likely to undergo substantial shifts in trait structure, with a magnitude of change greater than predicted from SR alone, and a direction of change varying according to geographical location and trophic guild. For example, our models predict that FD of insect predators will increase at higher latitudes with concurrent losses at mid-latitudes, whereas FD of seed dispersing birds will fluctuate across the tropics. Our findings highlight the potential for climate change to drive continental-scale shifts in avian FD with implications for ecosystem function and resilience.

KEYWORDS
climate change, ecological forecasting, ecosystem function, functional diversity, functional traits, range-shift modelling

INTRODUCTION

Climate change is driving substantial shifts in species distributions worldwide (Chen et al., 2011; Parmesan & Yohe, 2003; Walther et al., 2002). The magnitude and direction of these shifts vary across species, generating novel species assemblages, which differ in structure and composition to those observed today (Williams & Jackson, 2007), potentially resulting in changes to ecosystem functions and services (Barbet-Massin & Jetz, 2015). Understanding and forecasting these changes to assemblage structure is an important step towards developing effective conservation strategies targeted at regions where ecosystem functions are likely to be affected by climate change (Oliver & Roy, 2015). However, few previous studies have gone beyond relatively simplistic estimates of changes in species distributions (Barbet-Massin & Jetz, 2015; Gaüzère et al., 2015), and thus the likely trophic structure and functioning of future assemblages under climate change remains unclear.

One method for estimating climate change's impacts on the functioning of future ecosystems is to assess

changes in the functional traits present in species assemblages (Barbet-Massin & Jetz, 2015). In particular, functional traits can provide relatively precise information about key dimensions of the ecological niche (Pigot et al., 2016, 2020; Winemiller et al., 2015), while the structure and distribution of these traits within an assemblage can be quantified using metrics such as functional diversity (FD; Petchey & Gaston, 2002). Projected shifts in FD can, therefore, reveal how the diversity and characteristics of occupied niches within an assemblage are likely to change in future (Mouillot et al., 2013; Pigot et al., 2020), which in turn provides information about the ability of assemblages to sustain important ecological processes (Leitão et al., 2016; Petchey & Gaston, 2002; Tilman, 2001; Villéger et al., 2008). Specifically, a reduction or shift in the trait structure of an assemblage suggests that ecosystem functions will be lost or altered (Tilman et al. 2010; Cardinale et al. 2002; Díaz et al. 2013), potentially impacting ecosystem multifunctionality (Mouillot et al., 2011) and resilience (Bregman et al., 2016).

Assessing these functional impacts at macroecological scales has proved challenging because detailed trait data are generally available only patchily across large numbers of species. Most previous research has therefore focused at smaller spatial or taxonomic scales (e.g. Biswas et al., 2017; Gaüzère et al., 2015; Mokany et al., 2015; Van Zuiden et al., 2016), making it difficult to know how far their findings can be generalised. The only data sets currently available at a global scale and that have previously been used to assess climate change impacts on assemblage trait structure are largely based on relatively crude species traits, such as diet categories or binary characters (e.g. diurnal vs. nocturnal) (Barbet-Massin & Jetz, 2015). The main drawback of these categorical traits is that vital information is lost during the process of categorisation, with many distinctly different species lumped within each particular category (Kohli & Jarzyna, 2021; Weiher et al., 1999).

To address this issue, we compared the functional structure of current and future avian assemblages using a comprehensive data set of morphological and ecological traits for 8268 landbird species worldwide (Pigot et al., 2020; Tobias et al., 2022). For all species, we compiled eight continuous variables to capture morphological variation in body mass, beak shape, wing shape and the length of tarsus and tail. Together, these morphological traits provide an index of avian dispersal ability and trophic niche (Claramunt et al., 2012; Pigot et al., 2020; Tobias et al., 2014). By comparison, previous global studies have generally been limited to a single continuous ecological trait – body mass – which is generally a poor predictor of avian dispersal (Sheard et al., 2020), and only weakly informative about ecological niche differences (Pigot et al., 2020). We used this comprehensive trait data set to calculate the FD of future species assemblages estimated using range projections under two climate change scenarios (Hof et al., 2018) with a time horizon centred on 2050.

To explore the potential impact of these changes on ecosystem function, we partitioned avian assemblages into two major dietary groups – frugivores and invertivores – which underpin important ecological processes. Specialist avian frugivores are vital seed dispersal agents, especially for large-fruited or large-seeded plants in tropical regions (Corlett, 2017; Snow, 1981). Avian invertivores in terrestrial ecosystems exert top-down control on invertebrate populations, including numerous phytophagous (herbivorous) insects and their larvae, thereby indirectly benefitting plant populations (Mäntylä et al., 2011) and boosting ecosystem productivity (Marquis & Whelan, 1994). Invertivores also provide an important ecosystem service by limiting the impact of insect pests on agricultural crops (Jones et al., 2005; Karp et al., 2013; Mols & Visser, 2002).

The main aims of our study are to (1) re-evaluate the possible future impacts of climate change on the FD of avian assemblages, with particular focus on the structure of frugivore and invertivore communities and (2) quantify how changes in FD relate to changes in species richness (SR) to determine whether these changes in FD are primarily driven by the loss or gain of morphologically distinct species. This second aim is related to the findings of Barbet-Massin and Jetz (2015), who reported that projected FD shifts were generally smaller than expected from observed changes in avian SR, suggesting a tendency for gains or losses of morphologically similar species, which contribute relatively little to the overall FD of the assemblage. We revisit this question in the context of continuous traits to examine the role of species' distinctiveness in explaining projected shifts in avian FD.

MATERIALS AND METHODS

Current and projected bird distributions

We used baseline and projected distributions for 8268 landbird species worldwide from Hof et al. (2018) to produce binary presence-absence matrices for 65521 0.5° × 0.5° latitude-longitude terrestrial grid cells (henceforth, "grid-cell assemblages"; see Supporting Information). Baseline distributions were derived from expert range maps produced by BirdLife International and NatureServe (2015). Species distribution models were used to generate projected current and future distributions for each species under the RCP6.0 and RCP2.6 emissions scenarios (see Supporting Information). As a realistic medium-high climate-policy intervention scenario, we focused primarily on RCP6.0, which assumes a shift away from coal and towards oil, gas and renewables for energy (Masui et al., 2011); RCP2.6 represents a stronger mitigation scenario (van Vuuren et al., 2011).

To estimate the ability of species to track their future potential distribution, we produced a species-specific dispersal buffer around all baseline distributions using established predictors of dispersal ability, including species' hand-wing index, wing length, body mass and geographic range size (see Supporting Information). We allowed all species to disperse to grid cells within their dispersal buffer, with overall dispersal constrained to neighbouring zoogeographic realms, following Hof et al. (2018). Further aspects, such as anthropogenic land use change, may limit the ability of some species to track climatic niches, although in theory this constraint should only apply to species with low dispersal ability, which is accounted for by our dispersal buffer.

Functional traits

We assembled morphological and ecological trait data from comprehensive global datasets (Pigot et al., 2020; Tobias et al., 2022; Tobias & Pigot, 2019). For all species in our sample, we compiled information on eight continuous traits (Table S1), which provide information about key dimensions of the avian niche. Specifically, beak length, width and depth are linked to the size and type of food consumed, and thus the trophic niche (Hsu et al., 2014; Lederer, 1975; Pigot et al., 2020; Wheelwright, 1985). Tarsus length, wing chord, first-secondary length and tail length are locomotory traits related to microhabitat utilisation, foraging strategy, and dispersal (Claramunt et al., 2012; Miles & Ricklefs, 1984; Miles et al., 1987; Sheard et al., 2020). Finally, body mass is related to various aspects of the avian niche including metabolic requirements (McGill et al., 2006), movement (Wotton & Kelly, 2012), and foraging behaviour (Dial et al., 2008). In combination, these traits provide an eight-dimensional quantitative morphological space (hereafter, "morphospace") in which the position of each species reflects key aspects of the trophic niche, including trophic level, diet and foraging behaviour (Pigot et al., 2020).

All trait values were log-transformed, then z-transformed and converted into a distance matrix with the package Cluster (Maechler et al., 2018). We further adapted the matrix into a nested functional dendrogram using the "average" clustering algorithm in the ape package (Paradis & Schliep, 2018). Additionally, we combined the z-transformed traits in a principal component analysis (PCA). We retained the first four principal component (PC) axes for further analysis because the computational requirements of FD indices increase rapidly with increasing dimensionality and a four-dimensional morphospace is sufficient to describe variation in avian trophic niches (Pigot et al., 2020). Together, these axes accounted for >95% of the variance in the functional trait data (see Table S2 for PC scores). All analyses were performed in R v4.0.3 (R Core Team, 2020).

Analysing functional trait structure of entire assemblages combines information across multiple different trophic levels and niches. Although this provides a useful overview of general patterns, it can mask effects specific to particular ecological processes, unless these processes are partitioned into separate analyses (Bregman et al. 2014; Bregman et al., 2016; Cannon et al. 2019). To address this issue, we used published datasets (Pigot et al., 2020; Tobias & Pigot, 2019) to subdivide our species sample into frugivores and invertivores, that is, landbird species for which >50% of the diet consists of fruit or invertebrates, respectively. We selected these two groups because together they make up the majority of landbirds worldwide and have clearly defined links to important ecological processes, namely seed dispersal and the top-down control of invertebrates, respectively (Bregman et al., 2016; Karp et al., 2013; Şekercioğlu, 2006).

Analysis of trait structure

To quantify the trait structure of each grid-cell assemblage, we calculated four FD metrics: FD (Petchey & Gaston, 2002), functional richness (FRic; Villéger et al., 2008) and Gaussian hypervolume (Blonder, 2017) measured as both volume (H_{vol}) and centroid coordinates (H_{cent}). We also calculated the SR of each assemblage. We conducted analyses for all species (n = 8268) and then repeated analyses separately for frugivores (n = 885 species) and invertivores (n = 4115 species).

FD, the sum of branch lengths on a functional dendrogram, measures how species are dispersed in trait space, with greater values of FD indicating a greater degree of trait complementarity. We calculated FD from the functional trait dendrogram for each assemblage, using the 'ape' package (Paradis & Schliep, 2018).

FRic, the volume of the smallest convex hull enclosing all trait values in an assemblage (Villéger et al., 2008), does not measure 'functional richness' per se because it is entirely dependent on the species with the most extreme trait values. However, it provides a useful indicator of the gain or loss of functionally extreme species. We calculated FRic based on the trait PC scores for each presence-absence-matrix row in all assemblages with five or more species using the 'geometry' package (Habel et al., 2015).

The volume of a Gaussian hypervolume (H_{vol}) provides a different perspective to dendrogram-based approaches in that it focuses on the volume of morphospace occupied by species in an assemblage (Blonder, 2017; Maire et al., 2015). Finally, the position of the hypervolume centroid (H_{cent}) can indicate important shifts in trait structure even when the current and future assemblages occupy a similar volume of morphospace. H_{vol} and H_{cent} were calculated for each assemblage from the trait PC scores using the Silverman bandwidth estimate in the 'hypervolume' package (Blonder & Harris, 2018).

To measure how FD differed between current and future assemblages, the difference in SR, FD, FRic and H_{vol} values between the baseline and projected distributions (ΔSR, ΔFD, ΔFRic, and ΔH_{vol}) was calculated for each assemblage, as well as the Euclidean distance between the baseline and projected H_{cent} coordinates. To examine whether changes in FD were primarily driven by the gain or loss of morphologically distinct species, observed ΔFD was compared to ΔFD values predicted from ΔSR (see Supporting Information). Furthermore, as assemblage-level level ΔFD represents a combination of gains and losses, meaning that losses may be masked by the influx of new species (or vice versa), we separated ΔFD into its gain and loss components (see Supporting Information). Finally, to examine the how the RCP6.0 and RCP2.6 climate scenarios differ in their projections, we calculated the absolute value of difference between the ΔFD values (RCP6.0 ΔFD – RCP2.6 ΔFD), expressed as a proportion of baseline FD.

RESULTS

Changes in functional diversity for whole assemblages

In our geographical range forecasts under the RCP6.0 climate scenario, 1.2% of bird species (n = 101) had no suitable climate within their projected range and were thus considered to become extinct by 2050. Shifts in the geographical distribution of the remaining species altered the diversity and structure of most grid-cell assemblages. Our projections for RCP6.0 showed substantial changes in SR (Figure 1a) and all FD metrics (Figures 1b, 2a, b, Figure S1), with the direction and magnitude of effects varying according to geographical location. A prominent pattern in these results was the widespread, consistent increases in FD and H_{vol} at higher latitudes, concurrent with losses in these metrics in mid-latitude regions (Figures 1b, 2b, Figure S1). Proportional changes in FRic also revealed this trend (Figure S1), suggesting that some species will disperse into these regions from areas of morphospace not occupied by the baseline assemblage. Some northern regions, particularly in Canada, also showed relatively large distances between baseline and projected H_{cent} coordinates, indicating a shift of the assemblages towards a different region of morphospace (Figure S1).

At a global scale, changes in FD were often greater than predicted from ΔSR, indicating that they were driven by the loss or gain of morphologically distinct species. This was especially true for FD losses, which were typically >50% greater than expected and included around 3000 assemblages in which FD was lost despite being expected to increase (Figure 1c, d), with these larger-than-expected losses occurring across a multitude of geographic locations (Figure 1e, red regions). Gains in FD were also more often larger than expected, although less prominently (Figure 1d) and with less clear spatial patterning; northern latitudes, for instance, were a mosaic of assemblages in which FD gains were higher or lower than expected (Figure 1e, dark blue and cyan regions respectively).

Partitioning FD change into gain and loss components revealed that nearly all assemblages were projected to lose some proportion of their baseline FD (Figure S3). In some regions, particularly North Africa and Arabia, large FD gains co-occurred with losses, indicating substantial functional turnover (Figure S3). In contrast, widespread shifts in FD in northern latitudes were mainly driven by simple increases or decreases in diversity, with relatively little turnover.

Frugivores

Under the RCP6.0 climate scenario, 1014 (3.4%) of 29490 assemblages are predicted to lose all frugivore species (Figure S9), of which 20 species have no suitable climate within their projected range and are thus assumed to be extinct by 2050. Conversely, 1355 previously unoccupied assemblages are predicted to be colonised by at least one frugivore species (Figure S4), resulting in a net gain of 341 assemblages (+1.1% relative to baseline).

Shifts in the structure of frugivore assemblages were not associated with latitude, as both gains and losses of SR (Figure 3a) and FD occurred patchily across the tropics (Figures 2c,d, 3b, S1). We projected that many regions will undergo substantial proportional losses (often >20%) in FD and H_{vol}, with complete losses projected for some areas where assemblages lose their component of frugivores (Figure S9). We also projected large decreases in FRic for some regions, particularly in South America (Figure S1c), accompanied by the greatest shifts in H_{cent} position (Figure S1d). In contrast, several areas were projected to undergo large proportional gains in FD and H_{vol}, often over 20% and occasionally over 100% of their baseline value (Figure 2c, d). In most frugivore assemblages, changes in FD were more extreme than predicted from ΔSR (Figure 3c,d), especially for losses in FD (Figure 3d). Most losses were more than 50% greater than predicted from ΔSR (Figure 3c,d), indicating the loss of morphologically distinct seed dispersers in many parts of South America, Australia, and India (Figure 3e, red regions).

Separating FD changes into gain and loss components revealed that FD losses were projected to be common throughout much of the tropics, but generally smaller or absent in other regions (Figure S3). Conversely, gains in FD were projected to be relatively rare and typically not co-occurring with losses, except in southern Africa where functional turnover was predicted to be relatively high (Figure S3).

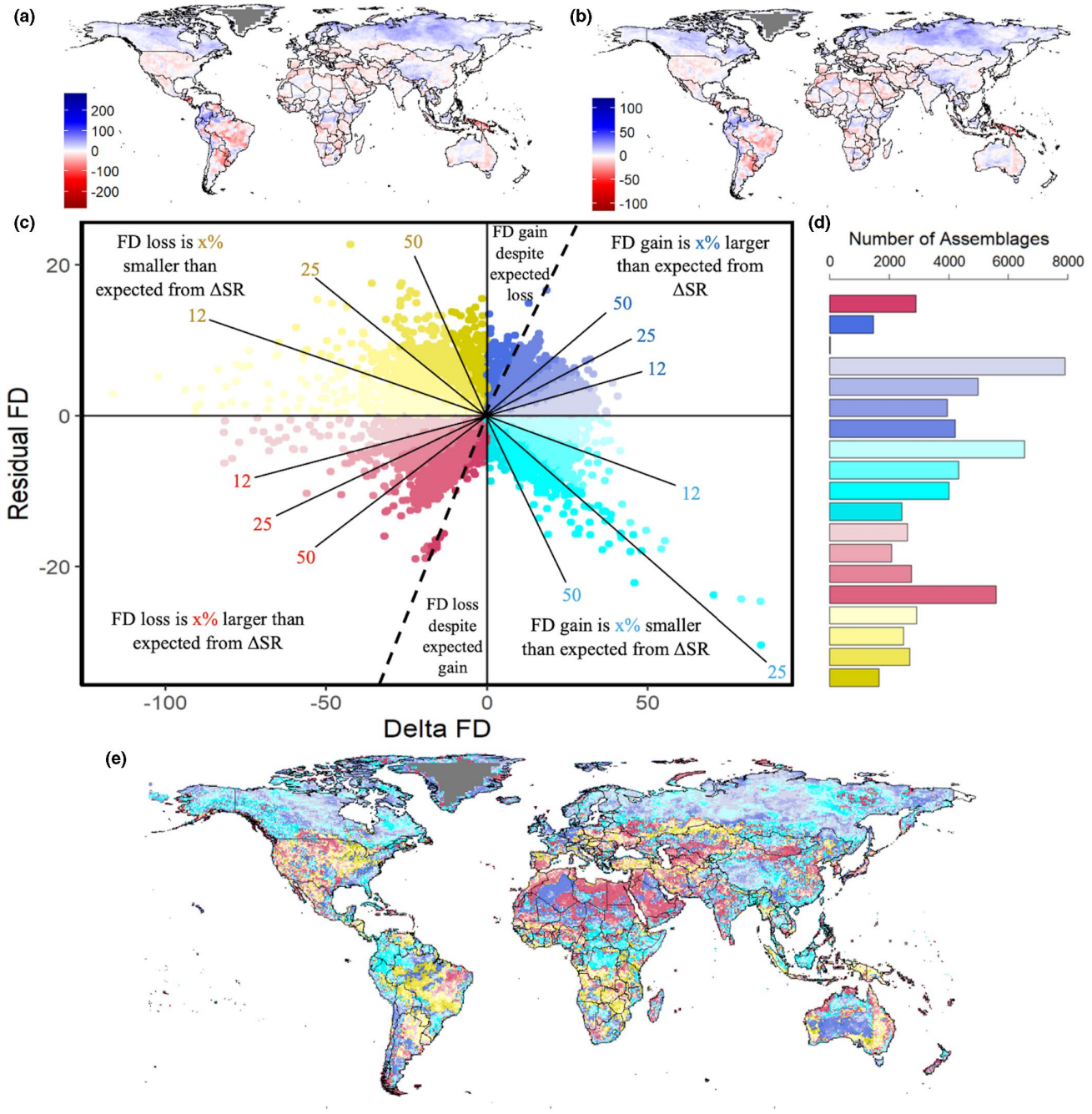

FIGURE 1 Projected changes in avian species richness (SR) and functional diversity (FD) from 1995 to 2050 under the RCP6.0 emissions scenario. (a) Absolute change in SR; (b) Absolute change in FD; (c) The relationship between observed ΔFD and Residual FD (the difference between observed ΔFD and ΔFD predicted from ΔSR). Annotations denote regions where ΔFD is larger or smaller than predicted from ΔSR. Dashed line separates assemblages where ΔSR predicts FD loss (left) and FD gain (right); (d) The number of assemblages belonging to each scenario presented in (c) or which underwent no change in assemblage composition (light grey bar); (e) Geographical distribution of the scenarios presented in (c). Light grey areas indicate no observed change in assemblage composition; dark grey areas indicate regions for which no data were available

Invertivores

In contrast to specialist frugivores, invertivores are global in their distribution (Figure 4a). In our RCP6.0 projections, 48 (1.1%) of the 4115 invertivore species in baseline assemblages had no suitable climate within their projected range and were thus assumed to become extinct by 2050. The surviving invertivores shifted in distribution, driving changes in SR (Figure 4a) and FD worldwide. Overall, these changes were far less patchy than those observed for frugivores, with the clearest pattern being substantial (often >20%) increases across higher latitudes in the northern hemisphere, with concurrent losses at mid-latitudes (Figures 2e,f, 4b). The

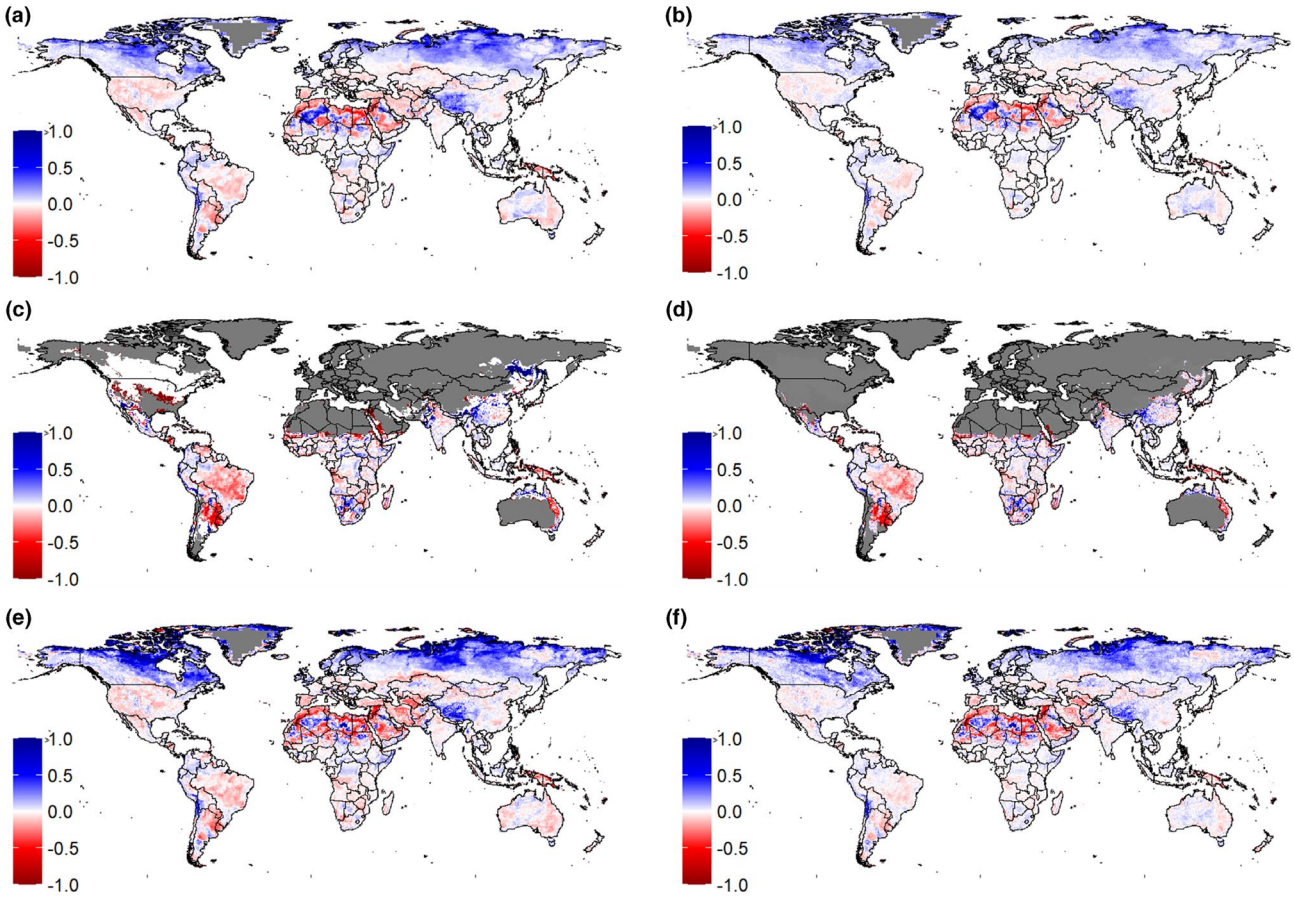

FIGURE 2 Projected changes in functional diversity (FD) and Gaussian hypervolume metrics from 1995 to 2050 under the RCP6.0 climate scenario, expressed as a proportion of their value in 1995. (a) all species FD; (b) all species H_{vol}; (c) frugivores FD; (d) frugivores H_{vol}; (e) invertivores FD; (f) invertivores H_{vol}. Dark grey areas indicate assemblages for which no data were available

same effect explained regional-scale patterns in FRic and H_{cent} (Figure S3e,f). Outcomes in the tropics were slightly less consistent, with large (typically 10–20%) decreases in New Guinea and parts of South America, and a mosaic of changes in other regions (Figures 2e,f, 4b).

Changes in invertivore FD were again dominated by values greater than predicted from ΔSR, especially for FD losses (Figure 4c,d), suggesting that shifts in FD were primarily driven by the loss or gain of morphologically distinct species (dark red and blue in Figure 4e, respectively). Separating FD changes into gain and loss components showed that projected patterns of FD losses were quite similar to those found across all birds, with the increase in FD at northern latitudes again being driven largely by simple increases in diversity, not turnover (Figure S3).

Comparing alternative climate scenarios

The difference between the projections obtained under the RCP6.0 and RCP2.6 scenarios were one of degree, not of kind; the patterns of change in FD were qualitatively similar (Figures S2–S8). These differences were also quantitatively similar across scenarios. For example, in all birds, the difference in ΔFD between the two scenarios was usually less than 2.6% of baseline FD (1st quartile = 0.6%, median = 1.3%, 3rd quartile = 2.6%), although in a few regions the difference was larger, around 10% (Figure S10). Similar results were observed for frugivore and invertivore subsets, although in general the difference between the scenarios was slightly larger for invertivores than it was for frugivores or the cladewide analysis (first quartile = 0.5%, median = 1.7%, third quartile = 3.8%) and larger (~10%) differences were geographically more widespread for invertivores (Figure S10).

DISCUSSION

Our analyses show that climate change is likely to drive substantial shifts in FD for landbird assemblages worldwide, with the direction and magnitude of these shifts varying according to geographic location. A previous analysis by Barbet-Massin and Jetz (2015) predicted that most bird species lost from future assemblages would be functionally redundant, leading to lower-than-expected

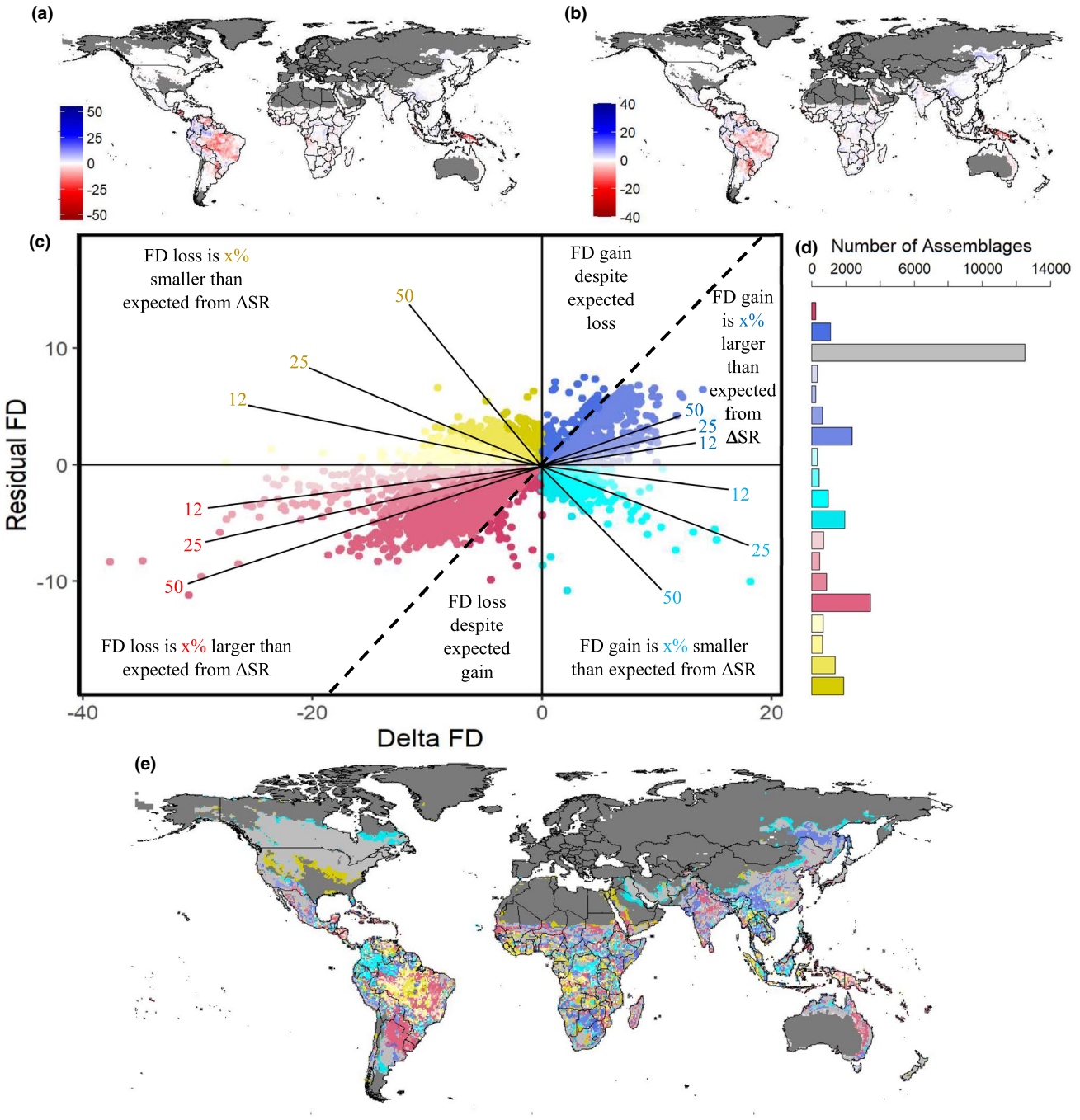

FIGURE 3 Projected changes in avian frugivore species richness (SR) and functional diversity (FD) from 1995 to 2050 under the RCP6.0 emissions scenario. (a) Absolute change in SR; (b) Absolute change in FD; (c) The relationship between observed ΔFD and residual FD (the difference between observed ΔFD and ΔFD predicted from ΔSR). Annotations denote regions where ΔFD is larger or smaller than predicted from ΔSR. Dashed line separates assemblages where ΔSR predicts FD loss (left) and FD gain (right); (d) The number of assemblages belonging to each scenario presented in C, or which underwent no change in assemblage composition (light grey bar); (e) Geographical distribution of the scenarios presented in C. Light grey areas indicate no observed change in assemblage composition; dark grey areas indicate regions for which no data were available

shifts in FD. In contrast, our projections show widespread changes in FD greater than predicted from changes in SR alone, indicating that shifts in trait structure are primarily driven by the loss or gain of morphologically distinct species, with potentially unique functional roles. This discrepancy is likely to be caused by major differences in the trait data used. Whereas Barbet-Massin and Jetz (2015) were mainly restricted to using categorical data, our use of multiple continuous morphological traits may allow us to more readily detect functional differences – and therefore complementarity – among species (Kohli & Jarzyna, 2021; Tobias et al., 2022).

The opposite pattern – that is, changes in FD lower than expected from the projected change in SR – were

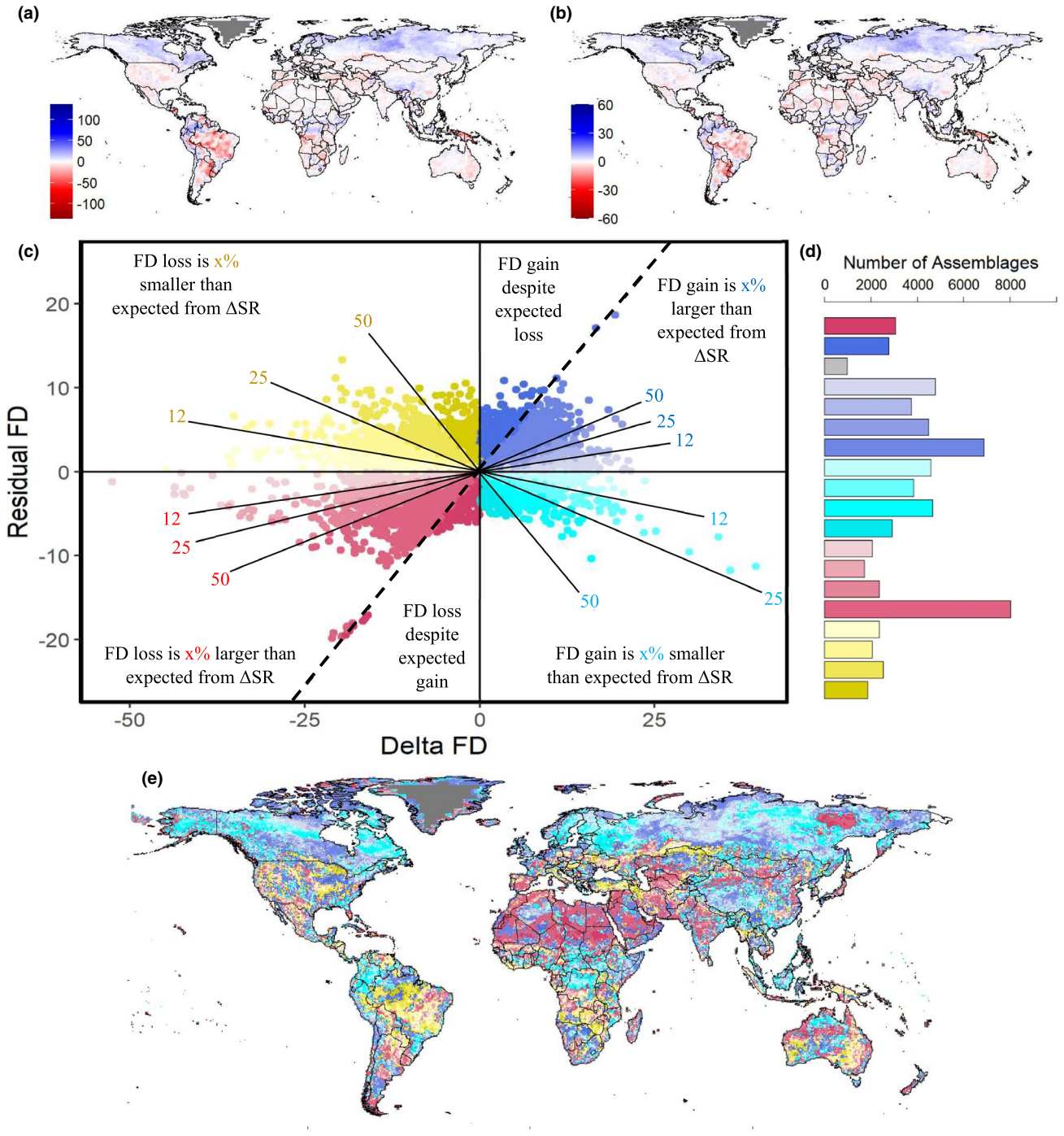

FIGURE 4 Projected changes in avian invertivore species richness (SR) and functional diversity (FD) from 1995 to 2050 under the RCP6.0 emissions scenario. (a) Absolute change in SR; (b) Absolute change in FD; (c) The relationship between observed ΔFD and Residual FD (the difference between observed ΔFD and ΔFD predicted from ΔSR). Annotations denote regions where ΔFD is larger or smaller than predicted from ΔSR. Dashed line separates assemblages where ΔSR predicts FD loss (left) and FD gain (right); (d) The number of assemblages belonging to each scenario presented in (c), or which underwent no change in assemblage composition (light grey bar); (e) Geographical distribution of the scenarios presented in (c). Light grey areas indicate no observed change in assemblage composition; dark grey areas indicate regions for which no data were available

less common across all metrics but occurred in some regions. In these cases, we can infer that the species gained in these regions are not morphologically distinctive in relation to the set of species projected to persist. This raises the question of whether functionally similar species will be able to invade these novel assemblages as predicted. Coexistence between bird species is facilitated by divergence in functional traits and associated ecological niches (Barnagaud et al., 2014; Pigot et al., 2018), whereas coexistence of functionally similar, closely

related species may be constrained by competitive exclusion (Diamond, 1975; Pigot & Tobias, 2013). In the context of range shifts, one species may therefore be unable to colonise the range of another. Even where geographical range overlap occurs, interspecific competition may reduce the abundance of some species (Fitt & Lancaster, 2017), rendering them vulnerable to extinction via stochastic causes (Lande, 1993).

Implications of species losses

The loss of distinctive species from assemblages may create a shortfall in ecosystem functions. The presence of functionally distinct species in an assemblage is vital for maintaining a breadth of ecosystem functions and services (Leitão et al., 2016), increasing the speed of ecological processes (Hedde et al., 2010) and promoting ecosystem stability (O'Gorman et al., 2011). As such, the loss of these species can have serious effects on ecosystem processes, including the unpredictable loss of function (O'Gorman et al., 2011). We, therefore, expect that regions in which more FD was lost than predicted from SR are likely to undergo the greatest immediate negative impacts.

In principle, the loss of morphologically similar species is less likely to have such immediate impacts because functionally similar species still remain to maintain ecosystem functions. There is, of course, no guarantee that one morphologically similar species will be able to compensate for the loss of another, particularly if the replacement species differs in an undetected niche dimension – for example, behaviour – or is simply much rarer (Rosenfeld, 2002). This type of hidden complementarity often means that the loss of seemingly functionally redundant species has negative effects, while the provision of adequate functional redundancy may also increase ecosystem stability and resilience (Ehrlich & Walker, 1998; Naeem & Li, 1997). Nonetheless, a range of ecological functions and interactions is more likely to be maintained by morphologically distinct species than an equivalent number of morphologically similar species.

Disentangling the impacts of climate change on different ecological functions

Two key limitations of our models focusing on all birds are, first, that general patterns can mask important changes occurring within different functional groups and, second, it is not possible to interpret general patterns in the context of specific ecological functions (Bregman et al., 2016). When we repeated our analyses on frugivores and invertivores separately, we found contrasting patterns of impacts on these two trophic groups. In particular, our results point to a future increase in FD of invertivores at higher latitudes with concurrent losses at mid-latitudes, whereas projected shifts in frugivore FD show a mosaic of different directional effects throughout the tropics.

Focusing on frugivores, many mid- and high-latitude frugivore assemblages were projected to retain similar structure under climate change. However, these regions typically contain only one or two specialist frugivore species, reflecting the much-reduced incidence of specialist frugivory outside the tropics (Clark et al., 1999; Kissling et al., 2009). Consequently, the provision of mid- to high-latitude seed dispersal is unlikely to be strongly affected by climate change. Conversely, our projections forecast a dramatic decline in frugivore FD across much of tropical South America, New Guinea, Central America, and eastern Australia. As specialist frugivores are vital dispersal agents, especially for large-fruited or large-seeded plants (Corlett, 2017; Snow, 1981), these declines in FD could impair the seed dispersal system in these regions. The main negative impacts would theoretically involve reduced dispersal distance and survival of juvenile plants, potentially altering vegetation structure, reducing reforestation in cleared areas, and limiting the ability of plants to track climate change (Bregman et al., 2016; Cordeiro & Howe, 2003; McConkey et al., 2011; Mokany et al., 2014). In tropical forests, these effects could drive declines in carbon storage (Bello et al., 2015). However, the scarcity of data on how fruiting plants will respond to climate change hinders our ability to predict exactly how ecosystem functions will be affected (Corlett, 2011).

Our projections for invertivores show a far more distinct pattern of poleward shifts in diversity, particularly in the northern hemisphere, consistent with species ranges tracking climatic niches towards the poles (Sorte & Thompson, 2007; McQuillan & Rice, 2015). At mid-latitudes, the sharp decline in invertivore FD may have important implications for the top-down control of invertebrate populations, which in turn will affect other important ecosystem processes. For instance, forest productivity is likely to decline due to increased leaf damage from insects which are currently controlled by avian invertivores (Marquis & Whelan, 1994). Additionally, the productivity of arable farms and orchards may decline owing to increased populations of invertebrate pests released from top-down control by birds (Jones et al., 2005; Karp et al., 2013; Mols & Visser, 2002).

Meanwhile, the ecological effects of gains in invertivore FD at higher latitudes depend largely on how invertebrate populations respond to climate change. Long-term studies report northward shifts in European odonata (Hickling et al., 2005) and lepidoptera (Parmesan et al., 1999) in response to warming over recent decades. If similar northward shifts are a general trend across invertebrates, an overall increase in invertebrate diversity may match the increased diversity of invertivorous birds. However, other studies suggest that climate-driven changes in arthropod abundance and diversity are highly taxon- and habitat-specific (Koltz et al., 2018; Buddle &

Schmidt, 2018). Furthermore, invertebrate declines may be exacerbated by a reduction in flowering season arising from phenological differences between plant species in different areas (Høye et al., 2013). Together, these studies suggest that complex changes in invertebrate community structure are likely to occur (Callaghan et al., 2004), disrupting the balance between predator and prey populations, and potentially impairing ecosystem functions (Durant et al., 2007; Schweiger et al., 2008).

Potential limitations and future directions

Our approach relies on assumptions common to all multi-species studies based on species distribution models. As such, certain caveats must be borne in mind. First, these models assume that species are in equilibrium with the environment and that all relevant climatic factors that may influence species presence are considered, so that climatic tolerance can be inferred from the observed distribution of the species. The main weaknesses of this approach are that key climatic variables may be omitted from models, while a range of factors other than climatic tolerance may shape the current distribution of bird species, including habitat loss, hunting and exploitation. The assumptions of species distribution models are, therefore, often violated, suggesting that model validation is overly generous (Santini et al., 2021).

As with all global analyses of this type, our projections are relatively coarse (grid cells represent areas over 3000 km^2 at the equator). As species may be confined to microhabitats within each grid cell, and the climatic data represent an average of conditions over each grid cell, mismatches may occur both between our projections and reality, and between different models in our ensemble projections. Overall, while we believe our approach provides the best possible current estimate of broad macroecological trends under climate change, our findings should not be used to infer changes for specific grid-cell assemblages or individual species. For example, where our projections show no suitable climate within the dispersal buffer for species in the future, this should not be taken to mean that these species will certainly become extinct.

We only considered resident and breeding ranges in our analysis due to constraints imposed by our dietary data, and problems associated with pooling breeding and non-breeding ranges in the same models (Freeman et al., 2022). Therefore, we overlook the non-breeding range of the relatively small proportion (<10%) of landbird species that are migratory. The influx of these non-breeding migrants to some tropical and subtropical regions may have a substantial impact on FD of bird assemblages, although non-breeding ranges in these cases are much less likely to undergo major climate-driven shifts than breeding ranges, most of which are in the temperate or boreal zones. Nonetheless, the impacts of climate-change on avian functional traits in non-breeding species assemblages is an important question for future research.

A further caveat is that species distribution models assume that species respond individually to climate change, and therefore ignore interactions among species. This is arguably a serious weakness because species interactions within and between trophic levels may have a pivotal influence on whether a particular taxon can persist in its current range, or colonise new areas (Early & Keith, 2019; Pigot & Tobias, 2013). In a general sense, understanding how species interactions structure novel assemblages under climate change is an important priority (Araújo & Luoto 2007; Lavergne et al. 2010; Pigot & Tobias, 2013; Schleuning et al., 2016, 2020). Morphological traits may provide insights into this issue, such as by using trait matching to explore connections between avian frugivores and their food plants (Dehling et al., 2016; McFadden et al., 2022; Moran & Catterall, 2010). In combination with species distribution models for both birds and plants, this approach could help to fill gaps in knowledge about how novel species combinations are likely to function (Corlett, 2011; Høye & Culler, 2018).

CONCLUSIONS

By modelling the future ranges of all extant landbirds, we show that avian FD is projected to undergo substantial, continental-scale shifts under climate change, which are largely consistent across different climate scenarios. In contrast to previous research, our analyses suggest that these shifts will be primarily driven by the loss or gain of morphologically distinct species from assemblages. In addition, we show how the impacts of climate change are predicted to vary geographically, and across different dietary categories associated with the delivery of seed dispersal and insect predation services by birds. This suggests that broad-scale predictions and interventions need to be formulated independently for different components of ecosystem function. Our findings highlight the importance of continuous morphological trait data as a basis for exploring the structure of future assemblages, and the impacts of climate change on trophic interactions.

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AUTHOR CONTRIBUTIONS

PS and JAT developed the conceptual framework; JAT, SW, CH, AV, MB and AD compiled and organised data sets; PS, AV and LS conducted analyses; PS wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Geographical range maps and future range projections have been published previously; morphometric and ecological data are released in a companion paper (Tobias et al. 2022); all other data and R scripts are freely available on Dryad (https://doi.org/10.5061/dryad.dfn2z351n).

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SUPPORTING INFORMATION

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