

# Dietary guild composition and disaggregation of avian assemblages under climate change

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## Abstract

Climate change is expected to cause geographic redistributions of species. To the extent that species within assemblages have different niche requirements, assemblages may no longer remain intact and dis- and reassemble at current or new geographic locations. We explored how climate change projected by 2100 may transform the world's avian assemblages (characterized at a 110 km spatial grain) by modeling environmental niche-based changes to their dietary guild structure under 0, 500, and 2000 km-dispersal distances. We examined guild structure changes at coarse (primary, high-level, and mixed consumers) and fine (frugivores, nectarivores, insectivores, herbivores, granivores, scavengers, omnivores, and carnivores) ecological resolutions to determine whether or not geographic co-occurrence patterns among guilds were associated with the magnitude to which guilds are functionally resolved. Dietary guilds vary considerably in their global geographic prevalence, and under broad-scale niche-based redistribution of species, these are projected to change very heterogeneously. A nondispersal assumption results in the smallest projected changes to guild assemblages, but with significant losses for some regions and guilds, such as South American insectivores. Longer dispersal distances are projected to cause greater degrees of disassembly, and lead to greater homogenization of guild composition, especially in northern Asia and Africa. This arises because projected range gains and losses result in geographically heterogeneous patterns of guild compensation. Projected decreases especially of primary and mixed consumers most often are compensated by increases in high-level consumers, with increasing uncertainty about these outcomes as dispersal distance and degree of guild functional resolution increase. Further exploration into the consequences of these significant broad-scale ecological functional changes at the community or ecosystem level should be increasingly on the agenda for conservation science.

**Keywords:** avian, climate change, community composition, dispersal, guild assembly, species distributions

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## Introduction

The Earth is undergoing environmental changes that stand to cause shifts in the geographic distributions of species and thereby reorganize species compositions of communities through temporal disassembly and reassembly (Rogers & McCarty, 2000; Walther *et al.*, 2002; Perry *et al.*, 2005; Buckley & Jetz, 2008; Schaefer *et al.*, 2008; Zavaleta *et al.*, 2009; Zuckerberg *et al.*, 2009; Chen *et al.*, 2011). Most analyses of climate change effects on species distributions treat species individually. But interdependencies (e.g., groups of species share food resources or predator–prey interactions) among species within communities (Pounds *et al.*, 1999; Schmitz *et al.*, 2003; Tylianakis *et al.*, 2008) mean that future changes

in species distributions and co-occurrence patterns will likely have consequences for the functional structure of communities.

One way to ecologically characterize species co-occurrence patterns and aspects of the functional structure of assemblages is through the analysis of dietary guilds (Adams, 1985; Simberloff & Dayan, 1991; Duffy, 2002; Carnicer & Díaz-Delgado, 2008; Kissling *et al.*, 2012). Variation in the spatiotemporal availability of energy inputs and food resources is known to be a critical determinant in shaping broad-scale gradients of dietary guild structure of communities. For example, the high species richness of avian insectivores, frugivores, and carnivores of (sub)tropical regions corresponds to high resource availability (e.g., great abundance of insects, fleshy fruits, and vertebrate prey) and low seasonality (Hawkins *et al.*, 2003; Kissling *et al.*, 2012). High grassland productivity in some

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subtropical and temperate regions has been suggested to beget the high diversity and abundance of large ungulates which in turn support the occurrence of herbivores and scavengers (Duffy, 2002; Holdo *et al.*, 2007). In contrast to the increasing detail about other aspects of the full global biogeography of vertebrates, to date the global knowledge of geographic variation in dietary guilds is limited to species counts (Kissling *et al.*, 2012) and assessment of relative dietary guild richness or dietary structure of assemblages to only very specialist (Kissling *et al.*, 2009) or generalist groups (Jetz *et al.*, 2009). The vast variation in the absolute richness of dietary guilds in birds (Kissling *et al.*, 2012) suggests significant differences in the prevalence of dietary strategies and in the ecological structure of communities worldwide that only a broad-scale perspective may appropriately capture.

Diet also represents a good starting point to understand how changes in the composition of communities may influence their function because trophic interactions and species interdependencies vary with dietary guilds (Chapin *et al.*, 1997; Duffy, 2002; Kinzig *et al.*, 2002). For example, the disappearance and recovery of many tropical tree species are the result of losses and recovery of guilds of seed dispersing and pollinating frugivore bird species (Silva & Tabarelli, 2000). Losses or geographic rearrangement of terrestrial carnivore species (e.g., birds, lizards, or insects) stand to have significant effects on herbivore and plant species comprising communities (Schmitz *et al.*, 2000, 2003; Tylianakis *et al.*, 2008; Estes *et al.*, 2011). However, despite the important potential for changes in guild structure to alter community functioning, we still have only a limited understanding of the kinds of changes in guild structure that are expected under future climate warming.

We address this uncertainty here using a global dataset of well-characterized bird species distributions (Jetz *et al.*, 2007; Kissling *et al.*, 2012) and well-quantified dietary preferences (Belmaker & Jetz, 2013) to explore how climate change projected for this century may influence avian dietary guild structure across different geographic regions of the globe. We use both a coarse (i.e. primary, high-level, and mixed consumers) and fine dietary guild classification for birds (frugivores, nectarivores, insectivores, herbivores, granivores, scavengers, omnivores, and carnivores). Examining guild structure at these two ecological resolutions enable us to determine whether or not geographic co-occurrence patterns among guilds were associated with the magnitude to which guilds are functionally resolved.

To compare guild projections, we use species distribution modeling (SDM), a widely used tool to estimate species environmental niches (specifically, their realized

niches) using the characteristics of occupied (and unoccupied) locations (Elith *et al.*, 2006; Soberón, 2007; Elith & Leathwick, 2009). Comparing these characteristics and the resulting distribution predictions in time and space among species assumes that in different species the approach is similarly successful in capturing vital niche characteristics and their individual distributions are similarly at equilibrium with climate; violations to this assumption might affect the comparison of projected potential distributions (Pearson & Dawson, 2003; Araújo & Guisan, 2006; Zimmermann *et al.*, 2010). As long as these sorts of SDM limitations and assumptions are recognized, they represent a useful tool for baseline assessments and ecological comparisons (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith *et al.*, 2006; Elith & Leathwick, 2009). Global applications of SDMs may also be hampered by presence data that are biased by sampling effort (Boakes *et al.*, 2010; Jetz *et al.*, 2012) or geographically/environmentally truncated (Barbet-Massin *et al.*, 2010).

We here apply SDMs to global (full-extent) species range maps and use an appropriate spatial analysis grain that allows us to do a first-order, globally comparable characterization of species' realized climatic niches and, assuming temporally similar climatic equilibrium conditions of individual species, use them to compare projections of their future distributions. At the chosen grain of analysis (ca. 100 km) climatic variables have previously been demonstrated to strongly affect the distributions of single species (Pigot *et al.*, 2010; Barbet-Massin *et al.*, 2011; Jiménez-Valverde *et al.*, 2011) and richness of guilds and trophic levels (Jetz *et al.*, 2009; Kissling *et al.*, 2012). While a strong grain size dependence of these relationships has been recognized (Belmaker & Jetz, 2011), climatic conditions pose numerous vital constraints on species distributions. These include direct ecophysiological limits to existence (Root, 1988; McKechnie & Wolf, 2010; Sinervo *et al.*, 2010) due to high or low temperature or precipitation and limits imposed by resource availability (Hurlbert & Jetz, 2010; Buckley *et al.*, 2012). For example, frugivores and insectivores show strong association with the productivity of tropical ecosystems (i.e. there are always high abundance and diversity of fruits and insects with high temperature). The richness of nectarivores depends highly on the seasonal availability of flower resources that elevated temperatures and decreased precipitation are known to affect the physiology of flowering plants resulting in altered production of flowers and nectar. Jetz *et al.* (2009) and Kissling *et al.* (2009, 2012) demonstrated the generally strong, but heterogeneous environmental associations worldwide of different avian trophic levels and guilds with climatic conditions.

Here, we extend these insights by carefully developing species-level models of the environmental associations in different guilds and projected future climate to infer (i) potential future changes in guild structure of avian assemblages worldwide; (ii) potential compensatory patterns in the guild structure; and (iii) the influence of dispersal distances on outcomes.

## Materials and methods

We examined present avian dietary guild structure on a global  $110 \times 110$  km equal-area grid in Behrman equal-area cylindrical projection (see Hurlbert & Jetz, 2007 for grain size justification). Within each grid cell, we quantified the present relative richness (proportions of total) of each guild and projected the relative richness of each guild under climate change and under different assumptions about species dispersal capabilities.

### Species data

We used breeding distributions of 8472 bird species (of 9993 total; 847 pelagic and marine species and 674 species with 1–3 presence grid cell(s) were excluded; see Jetz *et al.*, 2012, for details and taxonomic treatment).

We compiled a database of avian diets from the literature (predominantly Handbook of the Birds of the World, see Belmaker & Jetz, 2013, for details) that includes an estimate of the relative importance of each of seven food categories in the diet of every bird species (fruits, nectar, plants, seeds, invertebrates, vertebrates, and scavengers). The relative importance score of the seven categories summed to a total of 10 (i.e., 100%). We then used these scores to assign birds to three and eight dietary guilds at coarse and fine levels of 'ecological resolution', respectively. In the coarse dietary guild classification, species with a summed score for fruits, nectar, plants, and seeds  $>5$  (i.e., predominantly feeding on plant materials) were assigned to be 'primary consumers'; species with a summed score for invertebrates, vertebrates, and scavengers  $>5$  (i.e., predominantly feeding on animal materials) were declared as 'high-level consumers', and the remaining species (i.e., equally feeding on plant and animal materials) were treated as 'mixed consumers'. In the finer dietary guild classification, species were classified based on their primary diet (i.e., score  $>5$  in a category): (i) frugivores (predominantly feeding on fruits); (ii) nectarivores (predominantly feeding on nectar); (iii) herbivores (predominantly feeding on plants), (iv) granivores (predominantly feeding on seeds); (v) insectivores (predominantly feeding on invertebrates); (vi) carnivores (predominantly feeding on vertebrates); and (vii) scavengers (predominantly feeding on scavengers). Species in which the score of no single category exceeded 5 were further distinguished as feeding on either plants only (i.e., greatest scores for fruits, nectar, plants, and seeds), or animals only (i.e., greatest scores for invertebrates, vertebrates, and scavengers). These were then assigned into guilds (i)–(iv) or guilds (v)–(vii), respectively, according to the highest score among the food categories (e.g., a species with score 3, 3, and 4 in fruits, nectar, and plants). If neither

applied, a species was classified as an omnivore (e.g., a species with score 3, 3, and 4 in fruits, plants, and invertebrates, a species with score 3, 3, and 4 in invertebrates, vertebrates, and plants, or a species with score 5 and 5 in plants and invertebrates) because it feeds almost equally on plant and animal materials. Although here applied to bird species, this classification approach is generalizable for other taxa. The full dataset is available here <http://www.mappinglife.org/>.

### Environmental data

We included eight climatic variables for both present and projected climate scenarios: mean annual temperature and its seasonality, mean temperature of the coldest and warmest month, total annual precipitation and its seasonality, and total precipitation of the driest and wettest month. Projected temperature and precipitation were taken from the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report on Emission Scenario A2 (IPCC, 2007). This scenario approximates the current greenhouse gas emission rates (Raupach *et al.*, 2007; Beaumont *et al.*, 2008), and it assumes a continuously increasing population and a regionally oriented economic development. Gridded climate data of 20-year time period in 2080–2099 were developed using the 1980–1999 base period from the climate of the 20th Century experiment (20C3M) prescribed by IPCC. Seasonality was estimated for each period (i.e., 1980–1999 and 2080–2099) using the standard deviation of monthly values for each year averaged over 20 years. Hereafter, we refer to the time periods 1980–1999 and 2080–2099 as '2000' and '2100', respectively. We generated and compiled projected temperature and precipitation values using the following four atmosphere–ocean general circulation models (AOGCMs): CCCMA-CGCM, CSIRO-MK2, HADCM3, and CCSR-NIES. All climate variables were bilinearly interpolated to the  $110 \text{ km} \times 110 \text{ km}$  equal-area grid.

We also characterized topographic conditions in each grid cell using the range between minimum and maximum altitudes in a grid cell, derived from the GTOPO30 dataset (<http://eors.usgs.gov/>, spatial resolution 30 arc seconds, ca. 1 km) to constrain ranges of elevational specialist species. All nine variables (eight climatic and one topographic) were  $\log_{10}$  transformed for analysis.

### Species distribution modeling

We used a species-level 'stacked' distribution modeling approach, which predicts the distribution of individual species first and then estimates the species compositions of communities based on the aggregate of the predicted individual species' distribution. This approach has greatly matured over the last two decades and is now most commonly used to address impacts of future climate change on community structure (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Schröder, 2008; Elith & Leathwick, 2009).

We used seven common SDM algorithms based on species presence–absence data (Elith *et al.*, 2006; Thuiller *et al.*, 2009). The first three methods were based on regression modeling:

generalized linear models, generalized additive models, and multivariate adaptive regression splines. The remaining methods were based on nonparametric classification and machine-learning algorithms: mixture discriminant analysis, general boosting method, random forests, and maximum entropy (Phillips *et al.*, 2004, 2006). These models had good predictive performances in previous analyses of species distributions in different global regions and for different species groups (Elith *et al.*, 2006; Phillips *et al.*, 2006; Thuiller *et al.*, 2009). All models were run in 'dismo' and 'BIOMOD' packages in R, version 2.12 (R Development Core Team, 2011).

As in all models of this type, very distant absences (i.e. unoccupied grid cells) are less informative than those closer to presences (VanDerWal *et al.*, 2009). We weighted absence data in the models by the inverse of the distance to the nearest presence grid cell and excluded any absence grid cells that were more than 4000 km away. We considered any location beyond 4000 km threshold as unreachable during the study time frame. The ratio of presences-to-absences affects the accuracy of SDMs (McPherson *et al.*, 2004; Barbet-Massin *et al.*, 2012). We therefore selected the same number of species presence and absence data used in each algorithm, except for the species with less than 100 occurrence grid cells for which we used 100 absences. For species with at least or less than 100 presence grid cells, we randomly drew absences from the possible pool (i.e., grid cells within 4000 km of individual species' presences) five and ten times, respectively.

We ran each SDM in two steps. We first used all species presence-absence data to find six (of nine) most important environmental predictors, given high values of contribution, and then performed the SDMs using only the aforementioned six most important predictors. We fitted each of the SDMs to the data on current species distributions. Here, an 80% random sample from the species presence-absence data was used for model training and the remaining 20% of the data were used to test model performance. The 80/20 splitting was repeated five times. Overall, to decrease biases caused by geographic distances of training/testing presences/absences, multiple repetitions were implemented in our study. We repeated SDMs for each species at least 175 times (for species with at least 10 occurrences, absence selection 5 times  $\times$  data split 5 times  $\times$  7 SDM algorithms; for species with less than 10 occurrences, absence selection 10 times  $\times$  data split 5 times  $\times$  7 SDM algorithms). Generally, our models achieved overall good predictive accuracies (model performance values on different SDM algorithms see Figure S1 a-c). We then projected future distributions using future climate projections in conjunction with the fitted SDMs to predict the probabilities of future species presences. Altogether, we ran models for 8472 species  $\times$  7 SDM algorithms  $\times$  4 GCMs  $\times$  1 climate change scenario (i.e., A2 scenario by 2100) resulting in 237 216 model realizations (not accounting for repetitions here).

To minimize the uncertainty of predictions, for species with at least 10 occurrence grid cells, we calculated the species final ensemble maps based on the weighted average consensus method (Marmion *et al.*, 2009). This method uses weighted averages of the preevaluated values of the area under the receiver-operating characteristic curve (AUC) of the

single-species models. The four (of seven) SDM techniques with the highest AUC values were selected and assigned weights using the calculated ratio of the AUC value of one model technique to sum of the AUC values by the four model algorithms. The final relative probabilities of presence of a species in a given grid cell were calculated by summing the weighted relative probabilities predicted by the best four model algorithms. The binary species distributional maps (i.e., presence and absence maps) were then produced by using species-specific maximum sum of sensitivity and specificity as threshold. For the 717 species with less than 10 occurrence grid cells, we evaluated each algorithm according to a jackknife procedure (Pearson *et al.*, 2007). The better accurate model algorithms for predicting these species with less than 10 occurrence grid cells showed a corresponding *P* value less than 0.01 in the procedure. The final probabilities of presence of these species were obtained by calculating the mean distribution of those better accurate model algorithms (for final SDM algorithms used for the species with less than 10 occurrence grid cells see Figure S1 d-e).

Notably, the random splits of training and testing data or cross-validation generally used in SDMs does not ensure spatial independence/nonindependence and measures of model accuracy may be inflated (Segurado *et al.*, 2006; Hijmans, 2012). Even with spatial filters or striped or checkerboard designs complete nonindependence is hard to achieve and would very likely lead to a truncated estimation of the climatic niche and therefore an underestimation of the projected distribution (Barbet-Massin *et al.*, 2010). This leaves spatial null models as potentially only fully appropriate solution (Beale *et al.*, 2009; Hijmans, 2012). The methodology in this area is still the focus of ongoing research and therefore outside the scope of our study. Absolute measures of model performance were not central to our work and we expect the spatial independence/nonindependence to not majorly affect guild differences. We herewith acknowledge this issue and flag it as an important area for future work.

#### *Species dispersal distance assumptions*

Empirical evidence shows that species dispersal ability can determine the fate of species across geographic space and can be quite rapid in response to global climate change (Parmesan & Yohe, 2003; Hitch & Leberg, 2007; Chen *et al.*, 2011). Failure to consider the importance and degree of species dispersal ability may result in naïve or incorrect predicted future distributions (Schloss *et al.*, 2012). Evidence indicates rapid range shifts in bird species from ca. 6.1 km to ca. 17.6 km per decade in recent years (Parmesan & Yohe, 2003; Moore *et al.*, 2008; Chen *et al.*, 2011), which extrapolates linearly to 200 km or more per century. We therefore modeled dispersal distances of greater than 200 km for our projections. In the absence of complete information on each species' dispersal ability and the lack of simple allometric relationships for dispersal ability in birds (see, e.g., Moore *et al.*, 2008), we here assumed a uniform potential dispersal rate in the stacked SDMs and used scenarios of 0, 500, and 2000 km-dispersal distances to bracket the potential variation. These dispersal assumptions should be

able to represent the range of species changes between without and with dispersal and the real changes in the future should be covered.

### Statistics

Using present species distributions in conjunction with climatic and topographic variables, we were able to predict present bird species distributions. These predictions were then used to compare present patterns with projected patterns under future climate change.

To avoid data noise from certain extreme values (e.g., a grid cell with no present occupation by a specific guild, but projected to have high relative richness by that guild), we used data within 5–95% quantiles to understand relationships between predicted present and projected future relative guild richness. Equations and  $R^2$  values in accordance with linear regression were calculated and used to compare difference among three dispersal distance scenarios. For each guild, we then used paired t-tests to examine differences between predicted present and projected future relative guild richness under individual dispersal distance scenarios.

## Results

### Global dietary structure of avian assemblages

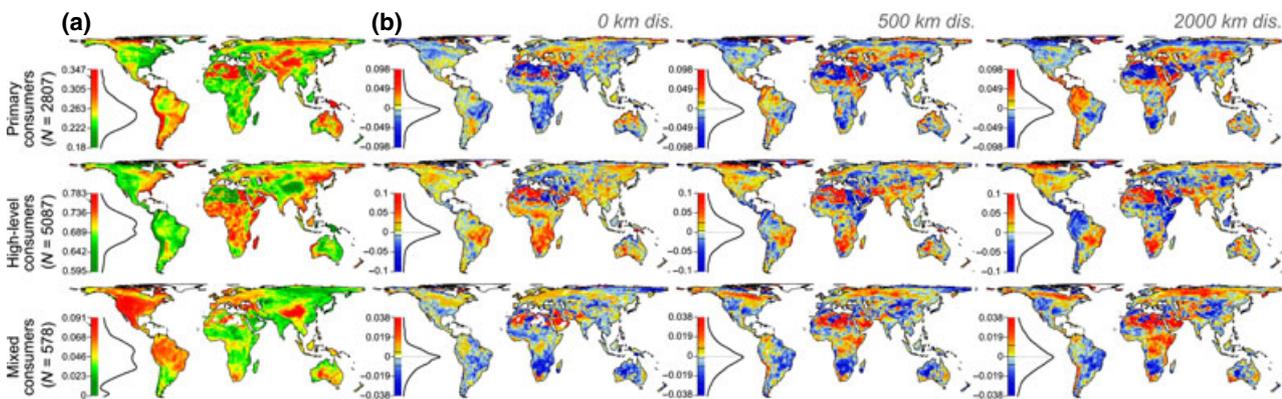
Birds show substantial geographic variation in the relative richness (proportions of total) of three coarse dietary guilds (Fig. 1a; Figure S2a). A total of 2807 species, i.e., 33% of all birds, are primary consumers, but in grid cell assemblages worldwide their proportional richness varies from only 18% to 35%. They are relatively dominant in the higher elevation regions of South America and Asia, as well as much of India, New Guinea, and Australia. Higher level consumers are more dominant

among birds (5087 species, 60% of all), but show similarly strong variation ranging from just 60% in many of the aforementioned regions to up to 78% in much of Africa, eastern North America, eastern Asia, and Madagascar. Birds that frequently consume both primary and higher trophic level prey (i.e., mixed consumers) are relatively rare (578 species, 7% of total) and contribute relatively little assemblage richness (2–9%).

As may be expected with increasing level of specialization, this heterogeneity is even greater for many of the finer guilds (Fig 2a, Figure S2b). Avian clades with predominantly frugivorous and nectarivorous species are largely absent from Europe and northern Asia, but are common in tropical and, in the case of nectar feeders (such as the honeyeaters, Meliphagidae), Australian assemblages. The other two guilds of mostly primary consumers show similar median and maximum relative richness, but are more ubiquitous and have a largely temperate/boreal distribution (especially herbivores) and interesting continental contrasts of North American (relatively high herbivore assemblage richness) vs. African and Australian (relatively high granivores assemblage richness). Tropical bird assemblages worldwide are dominated by insectivores contributing 37–58%, whereas carnivores and omnivores most strongly contribute to higher latitude assemblages.

### Projected changes to guild structure under climate change

Under climate change forecasted for 2100 many assemblages are projected to see significant and geographically highly nonuniform changes to the described dietary guild structure. We first assessed a nondispersal



**Fig. 1** Relative richness (proportions of total) and its changes for three coarse dietary guilds predicted for the present (2000) and projected for the future (by 2100). The changes are measured as differences between predicted present and projected future relative guild richness for each grid cell assemblage, and provided for three dispersal scenarios (0 km, 500 km, and 2000 km). White colors represent absences or no relative richness changes in guilds. Black lines in the color legend indicate 25%, 50% (i.e., median), and 75% quantiles, respectively; black curves represent the frequency histogram; and dotted black lines connect zero with the histogram line. Maps are displayed by a Behrman equal-area cylindrical projection at a spatial grain of 110 km.

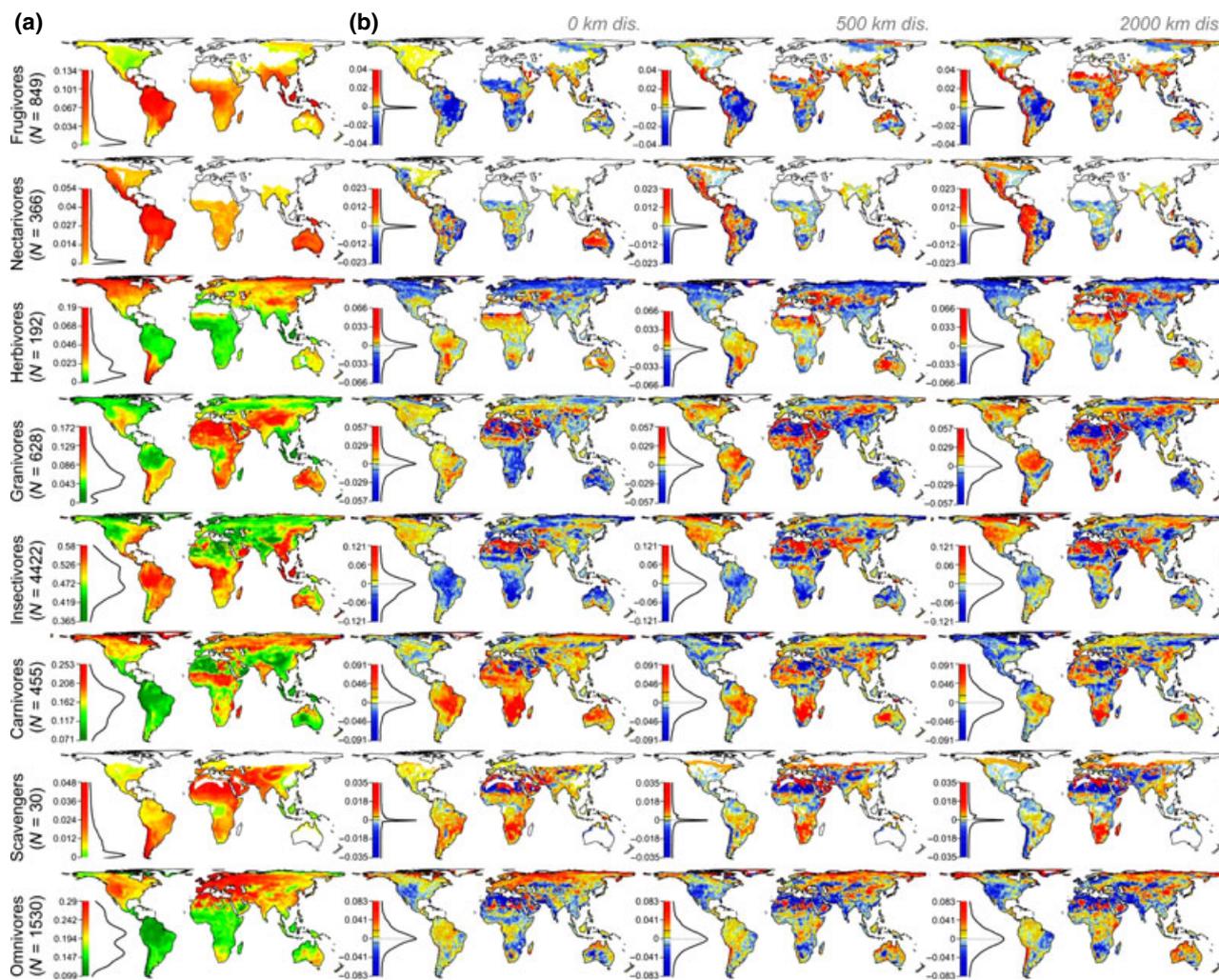


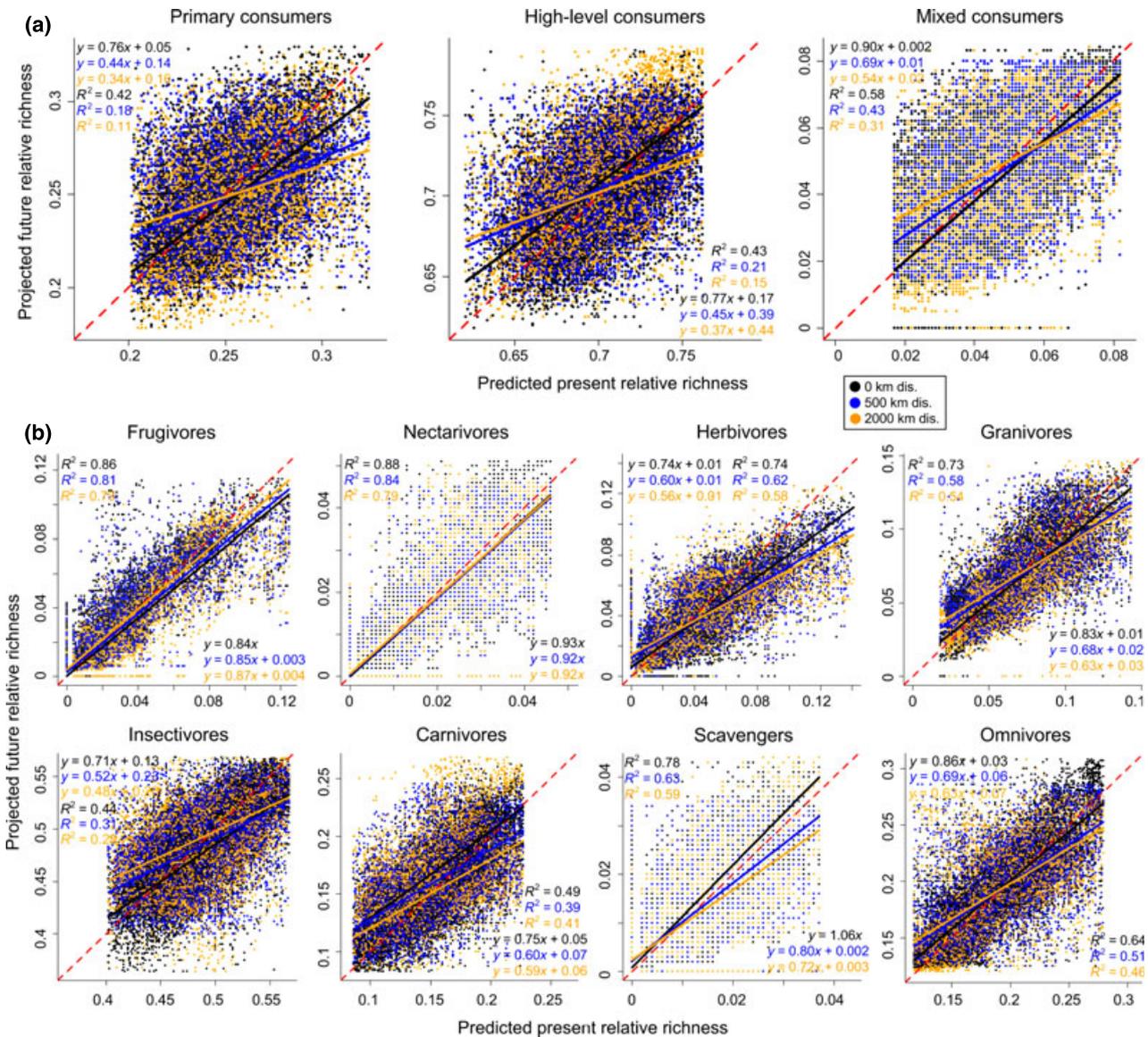
Fig. 2 Relative richness (proportions of total) and its changes for eight fine dietary guilds predicted for the present (2000) and projected for the future (by 2100). For other details see Fig. 1.

scenario (i.e., 0 km dispersal) that only estimates potential local extinctions without range expansion or migration into new assemblages. In the future and depending on the region, primary and higher level consumers may constitute up to 10% additional or fewer species than in today's assemblages (Fig. 1b). For instance, due to a concomitant decrease in primary consumers (see below) many extratropical Africa and eastern South America stand to gain assemblage richness of high-level consumer bird species. In contrast, due to local losses mostly in high-level consumers, primary consumers are projected to strongly increase in relative richness in northwestern South America, northeastern Africa, and central Asia.

At the fine ecological resolution, many assemblage changes in relative richness are expected to be relatively small (Fig. 2b). However, particularly strong losses in relative richness are projected for herbivores

in the Northern Hemisphere (up to 7%) and insectivores (up to 12%) in much of the Southern Hemisphere. This in turn would increase the relative richness of carnivores and omnivores, which are projected to see relatively little local extinction, by up to 8–9% in the Southern and Northern Hemisphere, respectively. Overall, the projected assemblage relative richness of guilds showed a relationship with their current-day values (Fig. 3) that was moderately strong for both major coarse dietary guilds ( $R^2 = 0.42$  and  $0.43$ ) and also insectivores ( $R^2 = 0.44$ ), which had both dramatic projected increases and decreases. Relative richness values were most similar between present and future in frugivores and nectarivores ( $R^2 = 0.86$  and  $0.88$ ).

In a summary view combining change patterns in relative richness for all fine dietary guilds, projected climate change significantly affected the expected relative richness for much of the globe (proportional



**Fig. 3** Relationships between predicted present (2000) and projected future (by 2100) relative richness (proportions of total) of three coarse (a) and eight fine (b) dietary guilds. Each point represents relative guild richness projected for dispersal scenarios of 0 km (i.e., stationary ranges, black circles), 500 km (blue triangles), and 2000 km (orange crosses). The points within 5–95% quantiles are used to calculate the regression results and estimated  $R^2$  values. Solid lines show the best regression fit under different dispersal scenarios (0 km, black; 500 km, blue; 2000 km, orange). Assemblages with projected increases in relative guild richness are above, and those with decreases below the dotted red lines indicate a 1 : 1 relationship.

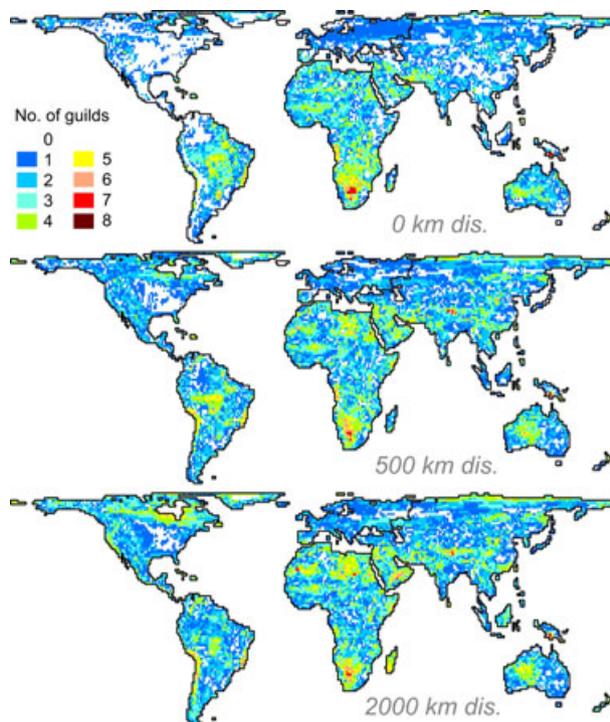
changes compared to present relative richness of each fine dietary guild >30%), with the number of such impacted guilds varying from zero to eight in southern Africa and New Guinea (Fig. 4).

#### Effects of dispersal

Assumed dispersal distance had significant effects on projected changes to the dietary assemblage structure and affected geographic patterns substantially. First, as local invasions added to the aforementioned

extirpations, more assemblages showed significant decreases or increases in relative guild richness. This is evident from the larger variance in the probability density curves of change values (see legends Figs 1 and 2). Second, these larger net changes broadly resulted in assemblage relative guild richness that was more dissimilar with the present than those under a nondispersal scenario (Fig 3).

The coefficient of determination (i.e.,  $R^2$  values) describing the relationship between predicted present and projected future relative guild richness decreased



**Fig. 4** Geographic variation in number of fine dietary guilds with particularly significant projected changes in relative richness for the three dispersal scenarios. Guild is counted as significantly affected in an assemblage, if relative change exceeds 30%, calculated as  $(\text{Guild Proportion}_{\text{future}} - \text{Guild Proportion}_{\text{current}}) / \text{Guild Proportion}_{\text{current}} \times 100$ .

with increasing dispersal distances. Except for frugivores and nectarivores, which appeared environmentally more strongly constrained, for all coarse and fine dietary guilds the relationship with present-day relative richness was substantially weaker for 500 or 2000 km-dispersal scenarios compared to a 0 km-dispersal scenario (differences in  $R^2$  of 0.10–0.30, Fig. 3). This implies that, with increased potential for dispersal, guild structure in all geographic locations becomes increasingly different from current conditions and less predictable. Third, larger dispersal distances tended to homogenize dietary guild structure of assemblages by disproportionately adding to currently low and subtracting from currently high relative guild richness, as illustrated by the slightly shallower slopes between predicted present and projected future relative guild richness (Fig. 3). Finally, larger dispersal had significant consequences for the specific geographic patterns of dietary reassembly. For example, larger dispersal distances tended to lead to larger increases in primary in lieu of high-level consumers in northern South America; tropical decreases and high-latitude increases relative insectivore richness were smaller when greater dispersal was assumed. In sum, species dispersal has

the potential to alter the geographic patterns of relative richness for all fine dietary guilds in northern Africa, southern Arabian Peninsula, Madagascar, and central South America (Fig. 4).

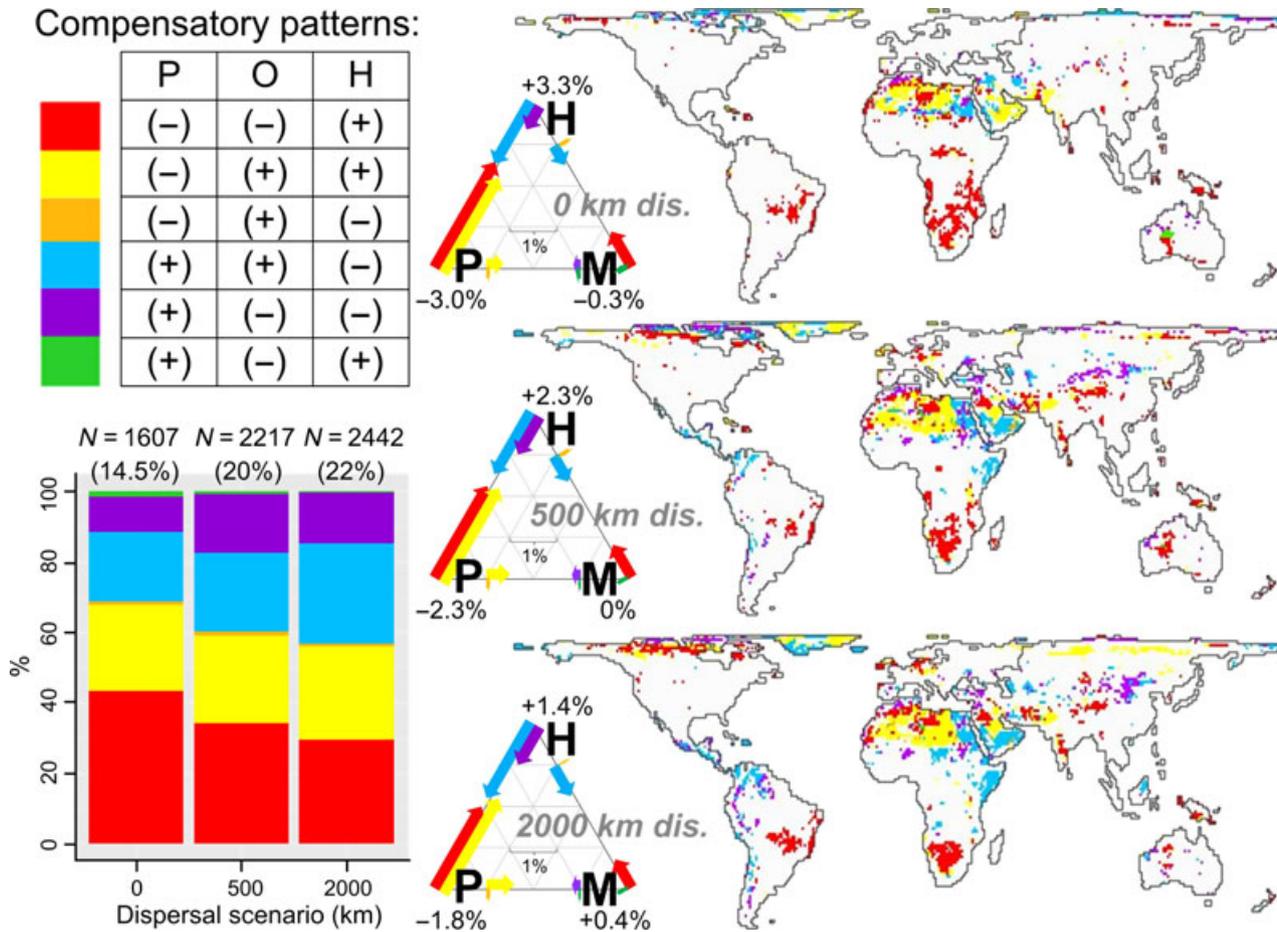
#### *Patterns of interguild compensation*

We performed additional analyses to better understand the patterns and magnitudes of directional changes among coarse dietary guilds in terms of changes in species numbers in the most impacted assemblages (those with a projected proportional change in all species greater than 10%; Fig. 5).

Under a nondispersal scenario, the highest proportions (43.4%) of highly impacted grid cells showed that high-level consumers are expected to increase in relative richness at the expense of primary and mixed consumers (red bars in Fig. 5). As dispersal distances increased, a greater propensity for primary and mixed consumers would increase in relative richness at the expense of high-level consumers (19.7%, 22.3%, up to 28.4% under 0 km-, 500 km-, and 2000 km-dispersal scenarios, respectively; blue bars in Fig. 5). These compensatory patterns are expected to be geographically concentrated in northern and southern Africa, central South America, and southern Arabian Peninsula, and area expansion in northern North America and central Asia. When calculating the compensatory balance among three coarse dietary guilds across the highly impacted grid cells under a nondispersal scenario, the projected average increase in high-level consumers is 3.3% while projected average decreases in primary and mixed consumers are 3% and 0.3%, respectively. The compensation primarily occurs between high-level and primary consumers. Toward longer dispersal, magnitudes of increases and decreases in the compensation among the three coarse guilds become smaller.

#### **Discussion**

Our goal was to examine how projected climate change would alter avian assemblages worldwide. We examined this issue using dietary guilds of species, rather than the typical practice of examining all species collectively or on a species-by-species basis. Our rationale is that species co-occurrence in dietary guilds has functional implications for communities and ecosystems. Hence, the disassembly of communities in terms of altered dietary guild structure may have more profound ecological consequences than species-level disassembly alone. Our results indicate that under future climate change, considerable disassembly of guild structure and reassembly in different geographic locations is expected across the globe. With increasing potential



**Fig. 5** Frequency (bar plots, left), magnitudes, and directionality (triangle plots) and spatial patterns (maps) of projected interguild compensation among the three coarse dietary guilds for 2100 compared to 2000. Only the assemblages ( $N$ , proportion of total grid cells) projected to experience strong changes ( $>10\%$  change over all guilds) are included in this analysis. For these assemblages, we show the frequency (percentage of total assemblages in that category) of each possible compensatory pattern, for all three dispersal scenarios. Each guild may increase/maintain (+) or decrease (-) in proportion, in response to changes in the other two guilds. Colors connect compensatory patterns to the magnitudes of directional changes (triangle plots) and maps. Arrows indicate decreases in one dietary guild that compensate for increases in another dietary guild. Length of arrows represents magnitude of the compensation, with small triangle side lengths equal to 1% change. For example, under a nondispersal scenario, a decrease of 2.6% in primary consumers (longer red arrow) and a decrease of 0.9% in mixed consumers (shorter red arrow) compensate for an increase of 3.5% in high-level consumers. Percentages on triangle plots represent overall projected average increases/decreases to each dietary guild under each dispersal scenario. Abbreviations of the dietary guilds: P, primary consumers; H, high-level consumers; M, mixed consumers.

dispersal distances, increased dietary homogenization of assemblages is expected and our ability to predict likely outcomes decreases significantly.

We expect to find the greatest changes in higher latitude areas (i.e., Greenland, northern Asia, and southern Africa) because species within guilds are expected to shift their geographic ranges poleward, as has been already observed over the past decade (Schneider & Root, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Chen *et al.*, 2011). Indeed, southern Africa is projected to experience the most dramatic changes across all dietary guilds, and careful regional ecosystem assessments and management strategies may be required to

understand and maintain ecological function in this biogeographic region. On the other hand, in currently species-poor regions such as the Arabian Peninsula, even few immigrating species will cause substantial changes to the current dietary structure. Moreover, compensatory and relative impact patterns among tropical and subtropical guilds indicate that the functional structure of global avian communities might have greater changes in the tropics than in extratropical regions.

Resolving the mechanisms of community disassembly and reassembly, such as alteration of guild structure, is not only interesting in itself but also crucial for an understanding of how communities will behave

under future climatic/environmental scenarios (Götzenberger *et al.*, 2012; Zarnetske *et al.*, 2012). For instance, with the increasing temperature and climatic changes, frugivores and insectivores showed a negative effect of relative richness which might be mainly caused by sequential changes in the high productivity and seasonal resource availability of tropical ecosystems (Jetz & Rahbek, 2002; Kissling *et al.*, 2012). Although classic biotic interaction-based ideas about guild assembly in communities maintain that if environmental conditions cause a decrease in the number of species within or among guilds, resources may become available to support new colonizing species leading to intraguild species compensation (Root, 1973). Alternatively, increased colonization attempts by species that do not belong to a local guild could lead to local extinction of resident guild members because of the inability of species to competitively coexist through resource partitioning (MacArthur & Wilson, 1967). Our analysis merely examined abiotic effects on assemblages and did not incorporate explicit mechanisms describing the nature of biotic interactions among species. However, we saw the same qualitative kinds of outcome for guild structure, thus revealing another potential mechanism for compensatory patterns in guild and community structures.

Dispersal especially is a key mechanism determining the likelihood of guild compensation (Goheen *et al.*, 2005). Our analysis showed that the nature of geographic guild composition and the degree of changes in the compensatory patterns increased with dispersal distance. We found a projected greater propensity for primary and mixed consumers at the expense of high-level consumers in areas with low present guild species richness (e.g., northern Africa and the Arabian Peninsula; Kissling *et al.*, 2012). This implies that presently unsuitable abiotic niche conditions might become more suitable under future climatic conditions leading to new abiotically based niche assemblages.

A limitation of our examinations of climate change on guild structure is that we only examine the effects of abiotic conditions, and use a conventional coarse  $110 \times 110$  km grain size (Jetz *et al.*, 2009; Belmaker & Jetz, 2011; Kissling *et al.*, 2012). We did not consider contemporary landscape modifications that may confound or conflate climate change effects, such as agricultural development, urbanization, and forestry practices that also occur at altogether different spatial grain sizes (MA, 2005). Consequently, our analysis may over- or underestimate the degree of likely change in guild compositions, especially if human land modifications impede dispersal (Schloss *et al.*, 2012). Future work aimed at understanding the interplay between human land-use change and climate change on guild composition would strengthen understanding of the

potential for guilds and their contributions to ecosystem functioning to persist on landscapes. The formidable challenge in future research is to align the spatial grain of human effects with the spatial grain and data resolution of avian range distribution information.

Interestingly, all metrics indicated a very strong predictive accuracy of our models: median values of AUC, sensitivity, and specificity: 0.96, 0.92, and 0.90, respectively (Figure S1). As with almost all studies of this sort, the evaluation datasets are not fully spatially independent from the training data and the metrics are thus potentially inflated. Broadly, our measures of accuracy were higher than usually seen for studies using similar validation approaches. We suggest two main potential explanations. First, a generally strong role of climate in affecting avian distributions at this spatial grain and extent of analysis has been suggested elsewhere (Jetz *et al.*, 2009; Pigot *et al.*, 2010; Barbet-Massin *et al.*, 2011; Jiménez-Valverde *et al.*, 2011; Kissling *et al.*, 2012), and the observed strong climatic model performance supports this. Second, and potentially more importantly, different to typical SDM-based studies using point data which rely on 'pseudo-absences' and often incur a high 'false' absence rate (Jetz *et al.*, 2012), species absences in this study were selected from areas of 'true/realized' absences as indicated by expert range maps which are expected to reliably avoid false absences at this grain (Hurlbert & Jetz, 2007). We note that additional work considering the effect of quality and geographic distances of species presences and absences on SDM results is a fruitful area of future work to advance both strength of predictions and opportunities for biological inference.

To the extent that guild structure determines ecosystem functions and services, our analyses demonstrating the potential for global-scale disassembly and compensatory reassembly hint that important ecosystem services may become highly altered under climate change, but these too need to be examined more mechanistically. For example, plant-eating birds (i.e., primary consumers in the coarse dietary guilds and frugivores, nectarivores, herbivores, and granivores in the fine dietary guilds) function as important seed dispersers, pollinators, and nutrient depositors in ecosystems (Sekercioglu, 2006), climate change may alter plant pollination and growth as well as colonization and succession of forests and hence to the spread and regeneration of certain plants (Ernst, 1908; Whittaker & Jones, 1994). In the Amazonian rainforest, granivorous birds are especially prevalent in pioneer or early stages of the ecological succession, where plants are selected for high and rapid reproductive rates, thus, producing large seed crops (Diaz & Telleria, 1996). Projected increases in relative richness of granivorous birds in this region

might enhance early ecological succession, but phenological changes caused by climate change (i.e., potentially slower or faster reproduction rates during rapid warming; Frenot *et al.*, 2005; Visser & Both, 2005; Rosenzweig *et al.*, 2007) may further limit the possible relocation of native species. Relative richness of herbivores, particularly, was projected to be lower by 2100 than present in most regions worldwide. Herbivory is a rare strategy in birds as only about 3% of extant birds exploit plants material exclusively as an energy source (Lopez-Calleja & Bozinovic, 2000). Although such species may be of important conservation concern in their own right, their potential loss under climate warming may have the least impact on ecosystems. Animal-eating birds (i.e., high-level consumers in the coarse dietary guilds and insectivores, carnivores, and scavengers in the fine dietary guilds), on the other hand, may exert important top-down control in ecosystems, such as through the biological control of insect pests (Sekercioglu, 2006) that further protects the insects' plants from extensive damage (Van Bael *et al.*, 2008). Guilds of these species are the least likely to change globally with environmental warming as is their contribution to ecosystem functioning. Any expected changes should be realized most in western South America and northeastern Africa. The importance and influence of omnivorous birds on ecosystem are not as clear as species belong to other dietary guilds.

With regard to the guild classification, complex needs of food sources and limited information of feeding habits and materials of species make it difficult to simply capture species dietary guilds in one single classification. Our results showed that different levels of 'ecological resolution' of the dietary guilds affected results of predictions and interpolations slightly. For example, different relative richness of species feeding both plant and animal materials (i.e., mixed consumers in the coarse dietary guilds and omnivores in the fine dietary guilds) was projected between the coarse (ranges in proportion varied from 0 to 0.1) and fine (ranges in proportion varied from 0.1 to 0.3) dietary guilds. All mixed consumers in the coarse dietary guilds were omnivores in the fine dietary guilds, but 50% and 38% of omnivores in the fine dietary guilds were classified into the primary and high-level consumers in the coarse dietary guilds, respectively, which led to trends of omnivores in the fine dietary guilds that were similar to primary consumers in the coarse dietary guilds.

## Conclusions

Given that guild structure determines community and ecosystem functions, our analyses suggest considerable potential for functional changes through projected dis-

and reassembly of avian guild assemblages worldwide. Species dispersal ability will be an important modulator of these climate change-induced effects, yet remains little understood. We suggest that future studies will be enhanced by extending species-level perspectives of climate change impacts and threats and broadening the study of climatic forcing and biotic components at the community or ecosystem level to include analyses of functional groups.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** (a) AUC, (b) sensitivity, and (c) specificity values of species distribution modeling (SDM) algorithms as selected for final species predictions for 7755 species with at least 10 occurrence grid cells. (d) Frequency of different SDMs as selected by the jack-knife procedure for 717 species with less than 10 occurrence grid cells. (e) Frequency of different SDMs for all 8472 species that are used in the final predictions.

**Figure S2.** Observed relative richness (proportions of total) for three coarse (a) and eight fine (b) dietary guilds. Number of species (N) classified in a guild is shown behind the dietary guild classification. White colors represent absences of guilds and black curves represent the frequency histogram.