



The limits of direct community modeling approaches for broad-scale predictions of ecological assemblage structure



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ABSTRACT

Two distinct modeling approaches are often used when predicting biodiversity patterns: stacking of species models (predict first, assemble later), and directly modeling a characteristic of a community such as species richness (assemble first, predict later). The relative utility of these two approaches for biogeographic, macroecological and global change analyses is uncertain. Here we compared the two approaches by predicting current-day avian dietary guild structure of assemblages worldwide. We found that the stacked-species modeling approach consistently predicted the geographic distribution of observed dietary guilds better than a direct community modeling approach. The exception was for plant-eating birds, especially frugivores, which are expected to have particularly strong climatic constraints on their diversity and distributions. Assemblage-level biodiversity patterns predicted by community-based modeling approaches, such as the stacked-species and direct community modeling approaches in this study, offer a means to help guide conservation decisions for determining environmental suitability and analyzing diversity hotspots. However, our results generally caution against the widespread use of direct community modeling approach at the large spatial extents for predicting species assemblages.

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1. Introduction

A major focus in biogeography and macroecology is to accurately model and predict geographic variation in the composition and attributes of biological communities. This pursuit is particularly relevant for projecting how communities and their many functions may be perturbed under impending climate change (Jetz et al., 2007; Dawson et al., 2011; Bellard et al., 2012). The potential constraints shown on community structure arising from assembly rules limiting species' coexistence have long been realized (Weiher and Keddy, 1999; Ackerly and Cornwell, 2007). But, how such constraints impinge on our ability to predict community structure and ecosystem functioning and how consistently they are shown at different spatial scales, especially in a broad-scale climate change future, still remain uncertain (Thuiller et al., 2003; Baselga and Araújo, 2009; Belmaker and Jetz, 2013). If prevalent,

assembly rules may under human-driven global change significantly affect the re-aggregation of communities and thus change the individual responses of species. Such community-level constraints on future species distributions would have significant consequences for the appropriate modeling approaches (Araújo and Luoto, 2007; Heikkinen et al., 2007; Baselga and Araújo, 2009).

Communities and their attributes (such as total species richness, functional indices or prevalence of a given group) are commonly modeled using a *stacked-species* community modeling approach that first models the spatial distributions of each species and then derives community attributes at different locations by aggregating the predicted individual species distributions (Guisan and Zimmermann, 2000; Ferrier and Guisan, 2006; Dubuis et al., 2011). This kind of approach offers detailed information on the exact identity of the species in the predicted assemblages and has often led to accurate predictions of community attributes for small and spatially restricted datasets (Leathwick et al., 2006; Elith and Leathwick, 2007; Algar et al., 2009; Baselga and Araújo, 2009; Chapman and Purse, 2011; Dubuis et al., 2011). However, by assuming that species assemble independently of each other, this approach ignores potential interrelationships among species comprising a community. One simple alternative is a *direct community* modeling

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approach that statistically associates aggregate community attributes with environmental variables (Ferrier and Guisan, 2006; Baselga and Araújo, 2009; Dubuis et al., 2011). Following in the footsteps of macroecological models of species richness (Brown, 1981; Jetz and Rahbek, 2002), this approach is straightforward to use with large, multi-species datasets and putatively able to accommodate species interdependencies within communities because it accommodates spatial co-occurrences of species to infer community-level patterns (Baselga and Araújo, 2009; Chapman and Purse, 2011). These factors combined with the approach's ability to quickly synthesize complex data for conservation applications have led to notable popularity (Ferrier and Guisan, 2006; Algar et al., 2009; Chapman and Purse, 2011).

An increasing number of studies are considering community attributes such as total species richness, proportional richness or community functional attributes as a response variable for current-day predictions and projections under climate change (Lemoine and Böhning-Gaese, 2003; Kissling et al., 2007; Steinmann et al., 2009; Kissling et al., 2010; Sommer et al., 2010; Chown et al., 2012; Dubuis et al., 2013; Venevskaia et al., 2013; D'Amen et al., 2015; Distler et al., 2015). One specific suggestion is that geographic patterns of energetic “capacity constraints”, the limits on species richness imposed by available energy, may be re-arranged under climate change and affect future community assemblages (Sommer et al., 2010; Chown et al., 2012). Biotic associations between taxonomic groups show sensitivity when forecasting future biodiversity (Kissling et al., 2007; Kissling et al., 2010). Accounting for trait data through an emerging trait biogeographic perspective reveals heterogeneous taxonomic partitioning of assemblages (Kissling et al., 2012; Ko et al., 2014). So far, community-based models are increasingly used to examine attributes of communities.

Despite this popularity, the appeal of potentially addressing biotic constraints in projecting communities under climate change, and an already existing debate about the choice of the *stacked-species* versus *direct community* modeling approach (Ferrier and Guisan, 2006; Leathwick et al., 2006; Baselga and Araújo, 2009; Chapman and Purse, 2011; Dubuis et al., 2011; Guisan and Rahbek, 2011; Distler et al., 2015), empirical evaluations are rare. Algar et al. (2009) found good performance of *direct community* compared to *stacked-species* modeling approaches for predicting changes in butterfly diversity in Canada. And for a study along a Swiss elevational gradient, Dubuis et al. (2011) showed that, while having slightly less predictive ability, only *direct community* modeling approaches were able to recover the specific shape of the elevation–richness relationship (Bonthoux et al., 2013). More recently, Distler et al. (2015) found that *direct community* modeling approaches could provide more accurate estimates of North American bird species richness than *stacked-species* modeling approaches, particularly during the summer season. However, apart from these case studies, the general suitability and performance of the community-level modeling approaches for broader spatial scales and for ecologically partitioned groups remain unclear.

The goal of our study is to provide such a general assessment and resolve the relative appropriateness of different methodologies for modeling patterns of functional community attributes over a broad geographic extent (and the typically concomitant coarse spatial grain) and a large range of species and communities. We use a global dataset of bird dietary preferences and geographic distributions to compare model performance of the *stacked-species* modeling approach with two types of *direct community* modeling approaches, one with total and the other with relative (or proportional) richness of different dietary species groups as response variable. Relative guild species richness, or guild prevalence, is a community attribute with important functional implications and has previously been shown to exhibit strong environmental associations (Kissling et al., 2012). We here ask whether the two types of *direct community* modeling approaches are indeed able to predict the variation in guild assemblage along climatic gradients and, by extension, are suited to address their potential perturbation under

climate change. If weak environmental associations of the response variable or overall limited predictive performance constrain the *direct community* modeling approach, is the *stacked-species* modeling approach able to successfully capture the aggregate response and predict its spatial variation? We here assess this for a range of guild groupings that vary in the respective environmental associations. Given the direct consequences of such changes for the functioning and services of ecosystems (Schmitz et al., 2003; Mooney et al., 2009; Kardol et al., 2010), identifying suitable approaches for modeling these and other community attributes is of strong applied importance and useful for biodiversity conservation and management.

2. Methods

2.1. Species data and environmental predictors

We used a comprehensive database of recent expert-based breeding distributions of all 9993 bird species in the world, spanning a latitudinal range of 60°S to 85°N (see Jetz et al., 2012) and mol.org for sources, taxonomic treatment and individual maps). Marine and pelagic species as well as species with less than four occurrence grid cells were excluded from the analysis, leaving a total of 8472 bird species. We intersected these distributions with a global 110 × 110 km equal area grid (approximately 1° near equator), a spatial resolution that according to recent validation of these sorts of expert-based maps offers sufficiently low false presence rates (Hurlbert and Jetz, 2007). This resulted in 11,079 grid cell assemblages for analysis.

We obtained estimates of the proportional use of each of seven food categories (fruits, nectar, plants, seeds, invertebrates, vertebrates, and carcasses) for each bird species from Wilman et al. (2014) to assign each species to a dietary guild. In a “coarse” dietary classification all species were classified as either primary consumers or high-level consumers based on their main proportional use of summed plant (i.e. fruits, nectar, plants, and seeds) and summed animal (i.e. invertebrates, vertebrates, and scavengers) diets. “Fine” dietary guilds were identified by highest proportional use as frugivores, nectarivores, herbivores, granivores, insectivores, carnivores, or scavengers. Those species exhibiting equal use of multiple summed or individual diets were classified as omnivores (named mixed consumers in the coarse dietary guilds and omnivores in the fine dietary guilds). For similar treatment and additional details see also Ko et al. (2014).

We extracted nine environmental predictor variables (all \log_{10} -transformed) including one topographic and eight climatic predictors over the same 110 km grid. All selected variables are known to exert a strong influence on the distributions of individual species as well as overall and guild species richness (Jetz and Rahbek, 2002; Field et al., 2009; Kissling et al., 2012; Ko et al., 2014). Elevational range was derived from GTOPO30 at 30-arc seconds (approximately 1 km), produced by the USGS (<http://eors.usgs.gov/>). Additionally, mean annual temperature, temperature seasonality (standard deviation of monthly means), mean temperatures of the coldest and warmest months, total annual precipitation, seasonality of precipitation (coefficient of variation of monthly precipitation), and total precipitation in the driest and wettest months were obtained for the 1975–2001 period (representing current conditions, i.e. 2000, in this study) from CRU TS 2.1 (Mitchell and Jones, 2005) with an original spatial resolution of 30-arc minutes (approximately 50 km). All environmental predictor variables at the coarse scale of 110 km grid cells (i.e. the spatial resolution of species distributions) were expressed by the area-weighted average values of fine scale data (i.e. topographic and climatic predictors in approximately 1 km and 50 km resolutions, respectively).

2.2. Models

Considering the success of ensembles of models in reducing both false negative and positive errors in predictions of species

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