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Future geographic patterns of novel and disappearing assemblages across three dimensions of diversity: A case study with Ecuadorian hummingbirds

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Abstract

Aim: Under climate change, it is likely that as species reshuffle based on their environmental tolerances, novel assemblages will form and some current assemblages will disappear. It is important for future monitoring and conservation that we understand where these novel and disappearing assemblages occur and how they differ among dimensions (taxonomic, phylogenetic and functional) of diversity. Here we investigate the geographical and environmental patterns of novel and disappearing assemblages; whether these patterns hold across dimensions of diversity; and how these assemblages are characterized in trait space.

Location: Ecuador.

Methods: We used ensemble species distribution modelling to estimate the distributions of 151 hummingbird species into the projected climate for 2070. Using standard beta diversity measures, we identified novel and disappearing taxonomic, phylogenetic and functional assemblages.

Results: We found that novel and disappearing hummingbird assemblages are likely under climate change, particularly in extreme environments and with novel assemblages replacing disappearing assemblages. Although the patterns of novel and disappearing assemblages were similar among dimensions of diversity, we found that there were fewest novel and disappearing functional assemblages. The future assemblages were characterized by an increase in functional space, which is counter to typical predictions of trait homogenization under climate change.

Main conclusions: Novel and disappearing assemblages are likely to pose management challenges for future conservation. Here we present an approach to identify such assemblages. By considering the geographic and environmental context of novel and disappearing assemblages for different dimensions of diversity, we can start to identify the mechanisms behind these patterns.

KEYWORDS

beta diversity, climate change, disappearing assemblages, ensemble modelling, hummingbirds, no-analogue assemblages, novel assemblages, species distribution modelling

1 | INTRODUCTION

Climate conditions are projected to change over the coming decades. Novel climatic conditions, referred to as no-analogue climates, are combinations of climatic factors that do not currently exist but are predicted to exist in the future. Throughout this study, we define “current” as climatic conditions measured in the 20th Century and “future” as projections for 2070 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Disappearing climates may also be a consequence of climate change; these are current climatic combinations that will not occur in the future (Williams et al., 2007). It is likely that as climatic space changes novel assemblages (future assemblages with no current analogue) will form due to differences in species' preadaptation to novel climates, the spatial change in climate variables and species' ability to adjust their ranges (Ackerly et al., 2010; Jackson & Overpeck, 2000; Ordonez, Williams, & Svenning, 2016; Williams & Jackson, 2007). In our study, we focus on the first two mechanisms. As with climate space, assemblages may also disappear (current assemblages with no future analogue). Historical assemblages with no current analogues (disappearing) have been identified from palaeoecological data (Veloz et al., 2012; Williams, Shuman, & Webb, 2001), and future assemblages with no current analogue (novel) have been predicted using species distribution modelling based on a correlative (Stralberg et al., 2009) or mechanistic (Reu et al., 2014; Urban, Tewksbury, & Sheldon, 2012) understanding of species relationships to climate. These studies have largely concentrated on taxonomic measures of diversity; however, changes in assemblage composition may alter other dimensions of biodiversity (Devictor et al., 2010; Swenson, 2011). Phylogenetic diversity highlights shared evolutionary history (Faith, 1992; Mace et al., 2003), and functional diversity provides insight into ecosystem services (Díaz & Cabido, 2001). Here, we present a framework for predicting how the reshuffling of species in response to climate

change may lead to novel and disappearing assemblages. We analyse the geographic and environmental patterns in the degree of novelty and disappearance, whether taxonomic, phylogenetic and functional dimensions display similar degrees of novelty and disappearance, and the morphological characteristics associated with novel and disappearing assemblages of Ecuadorian hummingbirds.

Identification of the geographic regions where novel and disappearing assemblages might occur can guide ecological research focused on novel species interactions, as well as conservation efforts aimed at maintaining different dimensions of diversity (Reu et al., 2014; Stralberg et al., 2009; Urban et al., 2012). No-analogue climates are often projected at the top or bottom of environmental gradients, with novel climate spaces mainly concentrated in tropical regions, and disappearing climate spaces at high latitudes and in tropical mountain regions (Williams et al., 2007). In a regional study of novel and disappearing climates, novel climates were found in the hot temperature extreme, and disappearing climates in the cold extreme at high elevations (Ackerly et al., 2010). Likewise, bird community turnover was highest at very low and very high elevations in response to recent climate change in Sierra Nevada, USA (Tingley & Beissinger, 2013). In contrast, in a comparison of current and late Quaternary plant communities, novel assemblages emerged in response to novel seasonality (Williams et al., 2001). These results suggest that no-analogue communities can emerge in different parts of climate space and often occur because of environmental extremes. Climate change scenarios for this century in our study region of Ecuador project an increase in temperature; variable changes in precipitation with both increases and decreases in precipitation; and high uncertainty in predicted precipitation trends (Marengo et al., 2010; Urrutia & Vuille, 2009). In our study, we expect disappearing assemblages in areas that are currently colder and wetter, and novel assemblages in areas that are currently warmer and drier, as species track their preferred climate regimes.

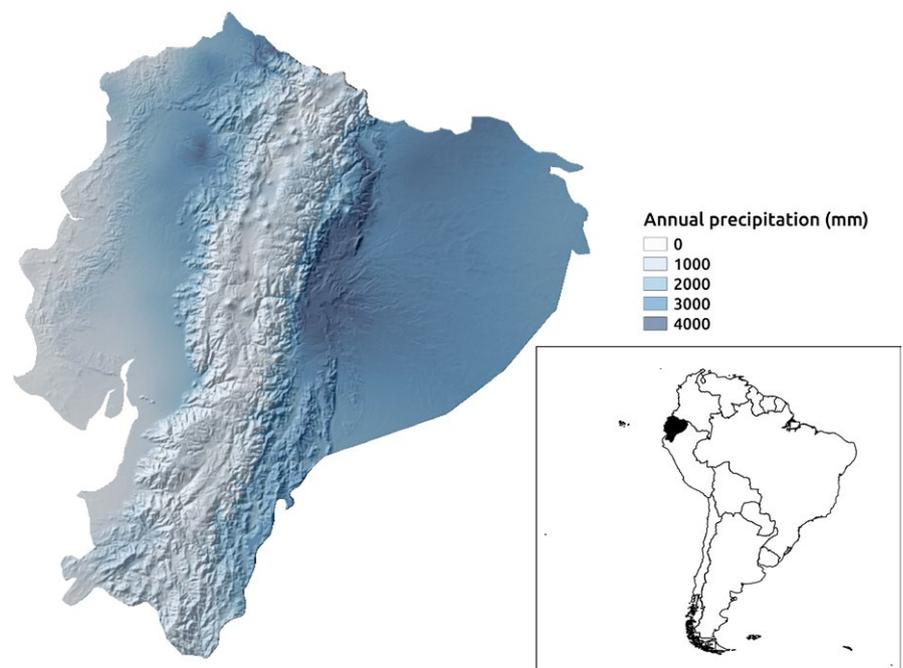


FIGURE 1 Study area of Ecuador showing two strong environmental gradients: precipitation (www.worldclim.org, Hijmans et al., 2005) and elevation (GTOPO30 data available from the U.S. Geological Survey; <https://usgs.gov>)

Considering changes in composition across the different dimensions of diversity should provide insight into potential novel interactions. These dimensions can be differentially influenced by historical and climatic factors. For example, if traits are conserved within phylogenetic lineages, we expect a comparable number of functional and phylogenetic assemblages to be analogous. This is because species with shared evolutionary histories would also have shared traits, and therefore, two assemblages would have the same dissimilarity whether they are measured using phylogenetic or functional diversity. However, if functional traits are labile, two distinct patterns could emerge: (1) if functional traits are associated with particular environmental conditions and are variable within lineages, there would be relatively more phylogenetic than functional novel and disappearing assemblages due to environmental filtering on species traits, or (2) if species with particular functional traits are unable to track novel environments and phylogenetic diversity is high, there would be relatively more functional than phylogenetic novel and disappearing assemblages.

Predicting shifts in trait space is important because traits influence ecosystem services (Cadotte, Carscadden, & Mirotnick, 2011; Díaz & Cabido, 2001; Haines-Young & Potschin, 2010) and ecological resilience (Oliver et al., 2015). Functional diversity can change in three ways when novel taxonomic assemblages form: (1) no change in functional space if new assemblages contain species with similar trait combinations as the current assemblage; (2) expansion in functional space if novel conditions favour traits with more extreme values; and (3) contraction and homogenization of functional space if novel conditions favour species with more generalist traits. Findings in the climate change literature suggest that functional homogenization will predominate under predicted environmental/climate change (Clavel, Julliard, & Devictor, 2011; Davey, Chamberlain, Newson, Noble, & Johnston, 2012).

We use hummingbird assemblages from Ecuador (Figure 1) to evaluate the prevalence and geographic patterning of the degree of novelty and disappearance in three dimensions of species assemblage diversity (taxonomic, phylogenetic and functional) under projected climate change to 2070. Hummingbirds are a diverse clade with well-studied traits, high local richness and high beta diversity along strong elevation and precipitation gradients (Graham, Parra, & Tinoco, 2012; Stiles, 2008; Weinstein et al., 2014). Species richness and geographic ranges of hummingbirds are correlated with environmental features such as temperature and precipitation due to their mutualistic association with floral resources and their tight physiological constraints (Graham, Parra, Rahbek, & McGuire, 2009; Rahbek & Graves, 2000). Ecuador is a particularly suitable study region because analyses of future climate scenarios highlight the tropics and subtropics as potential hotspots of no-analogue climate space (Williams et al., 2007). Using current and projected future distributions of hummingbirds in Ecuador, we address the following questions: (1) Where, in the terms of geography and environmental gradients, are novel and disappearing assemblages? (2) How does the degree of novelty and disappearance vary when measured using phylogenetic and functional diversity? and (3) How does the trait space change in areas with novel and disappearing assemblages?

2 | METHODS

2.1 | Biological data

We obtained presence-only data for 151 hummingbird species (see Table S1) across an extent of 88.65°W to 51.94°W and 23.52°S to 17.77°N. Although our modelling efforts were focused on Ecuador, we used occurrences from across the range of a species to best estimate the climate conditions where a particular species occurs. Occurrences outside Ecuador were obtained from the BIOMAP Database which houses data for Colombia (<http://www.biomap.net/>), and the Phelps Ornithological Collection (<http://www.fundacionwhphelps.org/>). Data were cleaned based on published elevation ranges and local gazetteers (Ridgely and Greenfield 2001). We removed occurrence records from sites with a high density of hummingbird feeders to minimize any bias in environmental tolerances due to artificially increased resources. Localities were also cross-referenced with citizen science databases to ensure presences were distributed across species ranges (Sullivan et al., 2009).

We obtained data on phylogenetic relationships from McGuire et al. (2014). We pruned the tree to only include species within the study area, resulting in a phylogeny for 132 of the 151 species.

We obtained data on three traits that influence species distributions and resource use: wing chord length (wrist to body in mm), body mass (g) and bill length (exposed culmen in mm) from Graham et al. (2012). Wing chord and body mass are associated with the competitive and functional role that each species plays within its assemblage (Altshuler, 2006; Feinsinger & Colwell, 1978; Stiles, 2008; Stiles, Altshuler, & Dudley, 2005). In addition, body mass scales positively with thermoregulatory ability in cold environments (Welch & Suarez, 2008). Bill length varies greatly among species (7.67–79.45 mm in our data) and influences floral resource use (Dalsgaard et al., 2009; Temeles, Koulouris, Sander, & Kress, 2009). Traits were measured on male hummingbirds. Including male-only measurements does not change the mean value for the species, but reduces the variance in body mass because females vary more in mass given reproductive activities. For species with multiple observations, we used the mean value and standardized the data across species to obtain a z-score for each of the traits. While there is within-species variation, the between-species variation is larger (body mass, within-species mean $SD = 0.58$, between-species $SD = 2.61$; bill length, within-species mean $SD = 1.01$, between-species $SD = 8.64$; wing chord length, within-species mean $SD = 2.29$, between-species $SD = 13.71$). We had complete information on the three traits for 109 of the 151 modelled species.

2.2 | Environmental data

We selected three variables from the WORLDCLIM database (www.worldclim.org, Hijmans et al., 2005): annual mean temperature, annual precipitation and precipitation seasonality. These variables encompass much of the climatic variation in Ecuador, are relatively uncorrelated and are biologically meaningful for hummingbirds (Parra, McGuire,

& Graham, 2010). We downloaded climate data at the 5-arcminute resolution. It should be noted that WORLDCLIM data are interpolated from available climate stations and therefore may not capture all of the climate variation, particularly for precipitation in topographically complex regions (Hijmans et al., 2005). We have greater confidence in the accuracy of the temperature data because elevation was used as a covariate in the interpolation; the known relationship between elevation and temperature allows more variation to be captured than for interpolated precipitation data.

We used the same three variables for 2070 based on seven general circulation models frequently used for species distribution modelling (CCSM4, CRNM-CM5, GISS-E2-R, HadGEM2-CC, IPSL-CM5A-LR, MIROC5, MPI-ESM-LR) and three emissions scenarios (Representative Concentration Pathways 2.6, 4.5 and 8.5; henceforward RCPs) resulting in a total of 21 future climate scenarios (IPCC CMIP5; www.worldclim.org). The RCPs are radiative forcing scenarios that can be matched to scenarios of greenhouse gas emissions and concentrations (Taylor, Stouffer, & Meehl, 2012). Under RCP 2.6, strong emissions reductions mitigate climate change and limit global temperature rises to below 2°C before 2100. Under RCP 4.5, there is a slight improvement and stabilization of current emissions by 2100, and under RCP 8.5, greenhouse gas emissions continue to increase unchanged into the future (van Vuuren et al., 2011).

2.3 | Species distribution modelling

To project species distributions into future climates, we used an ensemble species distribution modelling (SDM) approach. This approach minimizes idiosyncratic challenges of individual models (Araújo & New, 2007). However, the SDM approach can pose some difficulties for predicting into novel climates. For example, Feeley and Silman (2010) found that SDMs can over predict biotic attrition in novel climates; and Maguire, Nieto-Lugilde, Fitzpatrick, Williams, and Blois (2015) found that they can be over-fit to current climates, limiting their predictive capacity. However, there are few practical alternatives to SDMs available for predicting species distributions (Elith & Leathwick, 2009) and they have been found to successfully predict observed range shifts in mobile taxa (Ackerly et al., 2010). Acknowledging these issues, we interpret our results in terms of trends and patterns and not quantitative values.

We generated 2000 pseudo-absence points for each species from presence points for all other species in the dataset following Phillips et al. (2009) but excluding points where the focal species was recorded. We computed SDMs using three methods: generalized linear models (GLM; McCullagh & Nelder, 1989), generalized boosting model (GBM; Friedman, Hastie, & Tibshirani, 2000) and maximum entropy (MAXENT; Phillips, Anderson, & Schapire, 2006). These methods represent parametric and machine-learning approaches, ranging from the simpler GLM to the flexible machine-learning techniques of MAXENT, which is based on optimizing regression model structures and GBM, which is based on cross-validation of regression trees. We used data from across the species' ranges to ensure we included all climate conditions in which a species could occur, an essential aspect

for projection into future climate spaces. All SDMs were developed in R (R Core Team, 2015) using the package BIOMOD2 (Thuiller, Georges, & Engler, 2014). The code can be found on GITHUB (<https://github.com/bw4sz/FutureAnalog>).

We used the default settings in the BIOMOD2 package to parameterize the models (for details, see Thuiller et al., 2014), and used an 80/20 split on the data to calibrate (80%) and test (20%) the models. We evaluated model performance for each species based on the area under the curve of the receiver operating characteristic (ROC) and true skill statistic (TSS) scores. Ensemble models were generated by taking the ROC-weighted median of the GLM, GBM and MAXENT models for which ROC > 0.75 (ROC and TSS were strongly correlated in our models, Pearson's $r = .95$, see Fig. S2).

For each species, the resulting ensemble model was used to project presence into the future based on projected climate for each of the 21 future scenarios. Ensemble SDMs return a probability value of suitability for each cell. To define projected suitable areas, we converted this probability into a binary statement of presence/absence using a probability threshold. Taking a fixed probability threshold across all species would likely bias presence towards common species because the presence of common species is overestimated and rare species is underestimated (Jiménez-Valverde & Lobo, 2007; Liu, Berry, Dawson, & Pearson, 2005). Therefore, we set a threshold based on the probability of suitability where 95% of the known presences were predicted present (Gutiérrez, Boria, & Anderson, 2014; Liu et al., 2005; Pearson, Dawson, & Liu, 2004). Species' occurrences were projected into cells within the extent of Ecuador only because this was the focus of our study. Current and future species assemblage composition for each cell was generated by stacking the presences from the individual species distribution models.

2.4 | Calculating beta diversity across time

To quantify taxonomic, phylogenetic and functional assemblage shifts between the projections under current conditions and each of the 21 future scenarios, we calculated assemblage dissimilarity metrics based on the current and future species lists (Swenson et al., 2012). For each cell, we calculated taxonomic, phylogenetic and functional beta diversity indices between the current and future climate. For each measure, this resulted in an $m \times n$ matrix where m represents the cells in the future data and n the cells in the current data, and where each entry β_{mn} is the measure of beta diversity between cells m and n (because we used the same extent for both current and future, $m = n$).

For taxonomic beta diversity, we use the Sørensen dissimilarity measure (package ANALOGUE; Simpson & Oksanen, 2014):

$$\beta_{mn} = 1 - \frac{2A}{2A + B + C}$$

where m and n are two grid cells (where $m =$ current cell and $n =$ future cell), A is the number of shared species, B is the number of species unique to cell m , and C is the number of species unique to cell n . Sørensen dissimilarity is a measure of the proportion of shared species

between grid cells where 0 represents assemblages that share all species and 1 represents assemblages with no shared species.

For phylogenetic beta diversity, we used the PhyloSor metric (Bryant et al., 2008; Swenson et al., 2012) which accounts for the proportion of shared branch lengths between species lists. This is calculated similarly to the Sørensen dissimilarity measure but where A is the sum of the shared branch lengths, B is the sum of the branch lengths unique to cell m , and C is the sum of the branch lengths unique to cell n .

For trait beta diversity, we used mean nearest neighbour distance (MNND; Swenson et al., 2012). We calculated the Euclidean distance between each species across the three standardized trait values to generate a species-by-species matrix. Between each pair of sites m , n , we took the mean of the Euclidean distance between every species in assemblage m and their closest species in assemblage n based on the species-by-species Euclidean distance matrix and vice versa.

2.5 | Defining novel and disappearing assemblages

Novel assemblages are future assemblages with no current analogue, and disappearing assemblages are current assemblages with no future analogue. We defined analogue taxonomic, phylogenetic and functional assemblages as two assemblages where their respective dissimilarity measure was lower than 0.2. For each grid cell, we calculated how many current and future analogue assemblages it had. To determine the location of novel assemblages, we compared the projected future assemblage to all current assemblages. We assigned each pair as analogue or not and calculated the total number of future assemblages that had a current analogue. Those future cells with a total of zero current analogues are novel assemblages. To determine the location of disappearing assemblages, we carried out the same

steps but comparing the current assemblage to all projected future assemblages. The current cells with a total of zero future analogues are disappearing assemblages.

Specifically, for each dimension of diversity, we calculated the total number of current and future analogues for each assemblage using the following three steps. (1) We calculated the measure of taxonomic, functional or phylogenetic beta diversity (see Section “2.4” for details) between all pairwise combinations of current and future grid cells (Figure 2a). (2) We identified a given current and future assemblage pair as analogous if the beta diversity value between assemblages was below an arbitrary dissimilarity threshold of 0.2 (Figure 2b). This degree of difference is somewhat arbitrary, and we therefore tested multiple dissimilarity thresholds (0.05, 0.1, 0.2, 0.5). We determined that using a dissimilarity threshold of 0.2 was conservative, in that it did not mean every pair of assemblages was identified as different, but still sensitive enough to identify analogue assemblages. (3) We summed the number of current and future analogues for each assemblage and plotted them back into geographical space. Calculating the total number of current and future analogue assemblages gives us a measure of how close to novel or disappearing, respectively, the assemblage in a given grid cell is (e.g., few current analogue assemblages implies that the assemblage is close to being considered novel). The assemblages with no current analogues are novel, and those with no future analogue disappearing.

To control for aerial representation bias—that there are fewer high elevation cells and therefore fewer potential analogues—we also created null expectations based on current-to-current and future-to-future analogues. We calculated these in the same way as above, except that we compared each current cell to all other current cells, and each future cell to all other future cells. We then calculated the ratio between the predicted and expected number of analogues.

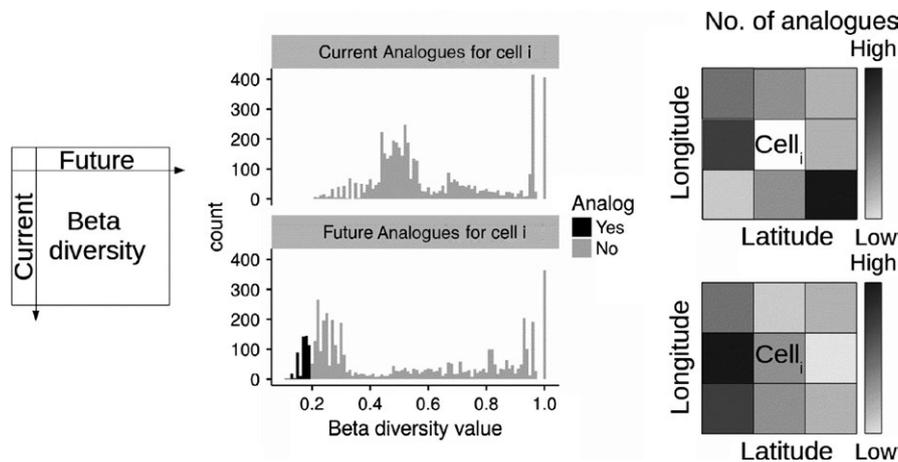


FIGURE 2 Methods to calculate number of analogue cells. First beta diversity is calculated between all current and future cells (we calculated taxonomic, phylogenetic and functional beta diversity: see Section “2” for details). To calculate the number of future analogues, we counted the number of cells for each current cell which were more than 20% dissimilar to the future cells. Any cell with zero future analogues is a disappearing assemblage. To calculate the number of current analogues, we counted the number of cells for each future cell which were more than 20% dissimilar to the current cells. Any cell with zero current analogues is a novel assemblage. The total number of analogue cells was then mapped back into geographical space, and from this, we can gain information about the degree to which an assemblage is novel or disappearing. For cell i in this example, there are no current analogues, meaning that this is a disappearing assemblage; there are some future analogues, and therefore, it is not a novel assemblage

A value below one means there are fewer analogues than expected and a value above one means there are more analogues than expected.

For each emissions scenario, we calculated the mean predicted-to-expected ratio across all GCMs. We present the results for the most extreme emissions scenario (RCP 8.5) and for the analogue threshold of 20% dissimilarity. We calculated the variation in the number of analogues between GCMs using the coefficient of variation ($c_v = \sigma/\mu$). For the other scenarios and analogue thresholds, the qualitative conclusions were similar in terms of spatial distribution of the number of analogue assemblages (for results from RCP 2.6 and RCP 4.5, see Figs S4 and S5; for results from the 5%, 10% and 50% thresholds, see Figs S6–S8).

2.6 | Identifying changes in trait space across time

We calculated overall trait space for each assemblage with a hypervolume method, using the default (Silverman) estimator and all default settings (R package `HYPERVOLUME`; Blonder, 2015). For each grid cell, we calculated the volume difference between the projected current and future assemblages. For future assemblages in each emissions scenario, the trait volume was calculated as the mean volume across GCMs. We also calculated the actual differences for each individual trait measure (mean wing chord, bill length and body mass) between each current and future grid cell to investigate the changes to individual traits.

3 | RESULTS

3.1 | Species distribution models

Model performance was above an AUC threshold of 0.75 for most model types and species. For GBM, AUC was greater than or equal to 0.84 for all species. For GLM and MAXENT, it was slightly lower: based on the AUC threshold of 0.75, 135 and 143 species could be included in the ensemble, respectively (for full evaluation statistics, see Fig. S1). Annual mean temperature was the most important climatic variable for determining the distribution of the majority of species (Fig. S3).

3.2 | Where are the novel and disappearing assemblages?

Novel and disappearing assemblages, or those that are close to novel or disappearing (fewer current or future analogues than expected), were concentrated in the Andes and the western dry lowlands of Ecuador (Figure 3a,c). This pattern was repeated across all three dimensions of diversity, although there were no fully disappearing phylogenetic or functional assemblages (those assemblages with no current or future analogue assemblages, respectively). In the eastern slopes of the Andes, there were more phylogenetic and functional analogues than expected. The wet lowlands to the east consistently had

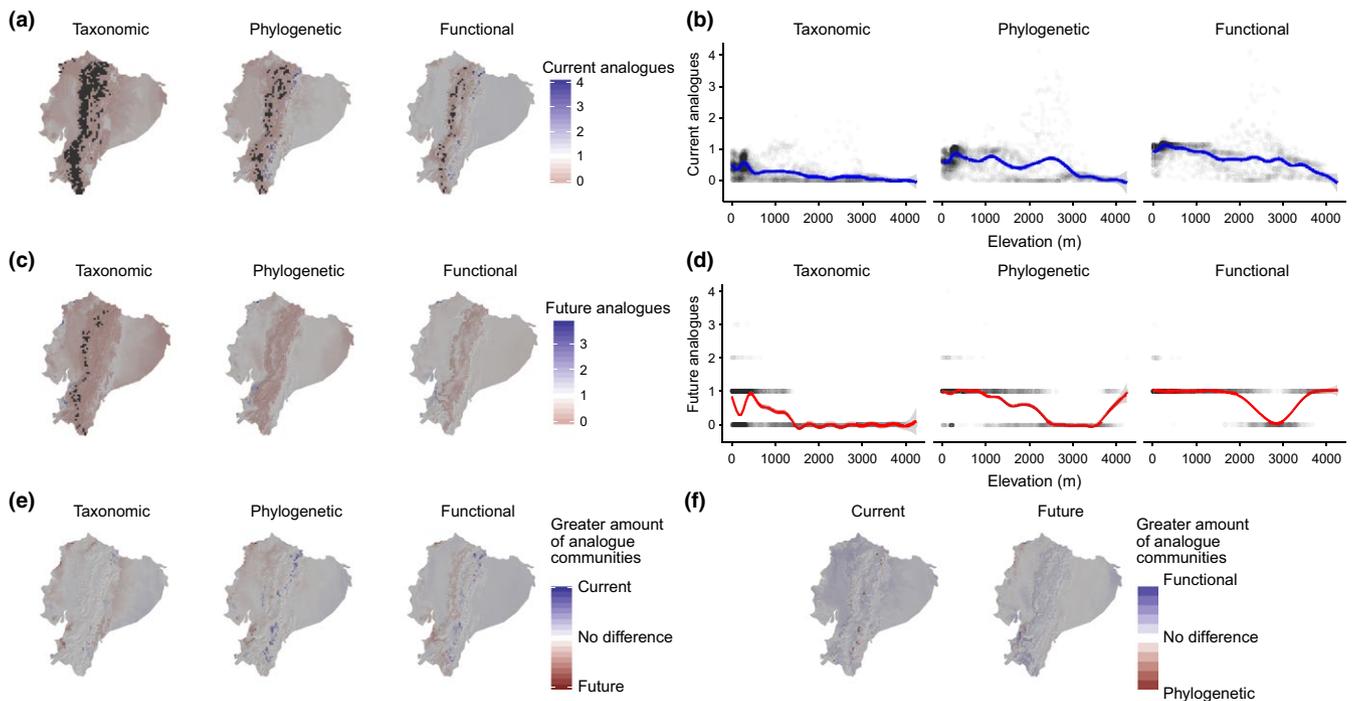


FIGURE 3 Plots showing (a) ratio of predicted number of current analogues for each cell to the expected number of analogues, with novel assemblages shown by black cells; (b) ratio of predicted number of current analogues to expected number of analogues plotted against elevation; (c) ratio of predicted number of future analogues for each cell to the expected number of analogues, with disappearing assemblages shown by black cells; (d) ratio of predicted number of future analogues to the expected number of analogues plotted against elevation; (e) difference between the number of current and future analogues; (f) difference between the number of phylogenetic and functional analogues. For each, we averaged the ratio of predicted number of analogues to expected number of analogues across the GCMs within the RCP 8.5 emission scenario. In (b) and (d), solid lines represent a fitted GAM model and the shaded area the 95% confidence limits

the expected number of current and future analogous assemblages for all dimensions of diversity (Figure 3a,c).

The total number of current or future analogues for a given assemblage revealed a nonlinear trend with elevation (Figure 3b,d). The number of taxonomic and functional analogues had a nonlinear negative relationship with elevation, and the assemblages predicted to have the most current analogues were concentrated around 300 m elevation. The number of phylogenetic analogues also had a second peak around 2,700 m elevation. The number of taxonomic analogues decreased quickly from 300 m elevation; however, the number of functional analogues decreased more slowly until around 3,000 m elevation. For all three dimensions of diversity, almost all novel assemblages were located at these high elevations (above 1,000 m), with the exception of some novel taxonomic assemblages that were located at low elevations. Future taxonomic analogues displayed a qualitatively similar pattern to current taxonomic analogues. Future phylogenetic and functional analogues, however, both were predicted to have a similar number of analogues to the null expectation at high elevations (~4,000 m). Similar to novel assemblages, nearly all disappearing assemblages were located at high elevations.

Assemblages in the Andes (for all three dimensions of diversity) and the western lowlands (for taxonomic diversity) were predicted to be both novel and disappearing (or close to), perhaps with disappearing assemblages making way for new species combinations (Figure 3e). But, predicted assemblages in the Andean slopes had more future than current analogues, suggesting a greater degree of novelty than disappearance. This was also the case for phylogenetic and functional assemblages in the wet lowlands. In contrast, assemblages in the eastern slopes and eastern dry lowlands, which had highest number of analogue assemblages overall, had a greater degree of disappearance than novelty (Figure 3e).

3.3 | How do the novel and disappearing assemblages vary among the dimensions of diversity?

Overall, there was a greater degree of phylogenetic than functional novelty and disappearance; each assemblage had a greater number of functional than phylogenetic current and future analogues (Figure 3f). Each assemblage had, as expected, fewer taxonomic than phylogenetic or functional analogues (Figure 3a,c). The number of novel and disappearing assemblages was similar for all dimensions of diversity in the Andes with very few of the 4,866 grid cells being analogues for cells in the highest elevations. The decoupling between degree of similarity predicted for the three dimensions of diversity mainly occurred in the slopes of the Andes and the eastern and western wet lowlands. Assemblages in these areas had fewer phylogenetic than functional analogues and the fewest taxonomic analogues.

3.4 | How does the trait space change in areas with novel and disappearing assemblages?

The assemblage-level trait space increased between current and future assemblages in the same areas as those where very few analogue

assemblages were predicted (Figure 4a) suggesting an expansion of trait space in novel assemblages. Hypervolume is measured in SD^n (standard deviations, where n is the number of dimensions: in our case 3 for each of the traits). Hypervolume values ranged from 7.6–359.9 SD^3 and from 8.5–166.4 SD^3 under current and future environmental conditions, respectively. The median hypervolume values were 37.5 SD^3 and 39.1 SD^3 for current and future environmental conditions, respectively. The maximum increase in hypervolume from current to future was 16.3 SD^3 to 166.4 SD^3 , and the maximum decrease in hypervolume was 359.9 SD^3 to 91.5 SD^3 .

The mean trait values for the assemblages when comparing current and future cells exhibit distinct differences among high elevations versus the lowlands (Figure 4b). There is a strong distinction in mean wing chord length across the elevational gradient, with decreasing wing chord length observed at high elevations (largest decrease from 77.4 mm to 19.2 mm), and increasing wing chord length observed in the lowlands (largest increase from 54.3 mm to 68.3 mm) in the future scenarios. The same general pattern was seen for body mass, with decreasing body sizes in higher elevations (largest decrease from 8.4 g to 5.8 g) and increasing body sizes in lower elevations (largest increase from 5.3 g to 7.3 g). Here, the magnitude of the difference in body size is smaller than for wing chord length, even when considering scaled values. In future scenarios, the mean bill length was predicted to be longer for the assemblages in higher elevations (largest increase from 17.4 mm to 24.3 mm) and shorter in the lowlands (largest decrease from 32.3 mm to 24.0 mm) compared to current cells. The novel assemblages that we identified as mainly being at higher elevations are therefore likely to be characterized by an increased functional trait space in the future, due to species with shorter wing chords, smaller body mass and longer bill length moving into the higher elevations.

3.5 | Uncertainty analysis

There was most uncertainty in the number of current and future analogues for taxonomic analogues (c_v up to ~ 2.5, Fig. S5) compared to functional or phylogenetic analogues. Generally, the highest values for c_v are at higher elevations, which is where the fewest analogue assemblages are predicted (Fig. S9).

We also examined variation between GCMs in the climate variables used as predictors in the ecological niche models. Mean annual temperature, which was the most important predictor for most species (Fig. S3) displayed very little variation between GCMs (Fig. S10).

4 | DISCUSSION

Increasingly, biologists are tasked with understanding the ecological implications of climate change. Evaluating the presence of novel and disappearing assemblages and the mechanisms generating them represents one way to consider these implications. Novel and disappearing hummingbird assemblages are likely to form under climate change, particularly in locations which are currently at the extreme ends of an environmental gradient such as high elevations and dry regions. In

our projections, disappearing assemblages were generally replaced by novel assemblages, suggesting species reshuffling rather than entire species assemblages shifting their geographic ranges to track environment simultaneously. We found that while there were novel assemblages for all dimensions of diversity, there were no disappearing phylogenetic or functional assemblages.

Identifying the geographic and environmental patterning of novel and disappearing assemblages should allow researchers to focus monitoring and conservation efforts. The degree to which taxonomic, phylogenetic and functional assemblages are novel or disappearing displayed qualitatively similar geographical and environmental patterns to each other. However, there were clear differences in the total number of analogues among the diversity dimensions, with the greatest number of functional analogues and the fewest taxonomic analogues. The novel assemblages were generally characterized by increasing functional space relative to current assemblages, counter to our prediction of trait homogenization,

suggesting that ecosystem function might be robust to climate changes, at least for this system.

Under climate change, a large proportion of our study area would have future assemblages with altered species composition, a result consistent with evaluation of no-analogue climates and assemblages obtained from fossil evidence (e.g., Veloz et al., 2012) as well as similar modelling efforts (e.g., Stralberg et al., 2009). We found that novel assemblages generally replace disappearing assemblages. It is likely that this is caused by the existing high elevation communities expanding as new species move upslope. Based on our data and modelling, there were no regional extinctions of species; in cases where species do go regionally extinct (e.g., at the high elevations) it may be that the novel assemblages are at low elevations and disappearing assemblages at high elevations as everything moves upslope. There was a nonlinear relationship between the number of analogue assemblages and elevation, with assemblages with the fewest analogues occurring from ~1,000 to 2,000 m and higher, and those with the most analogues at low-to-mid

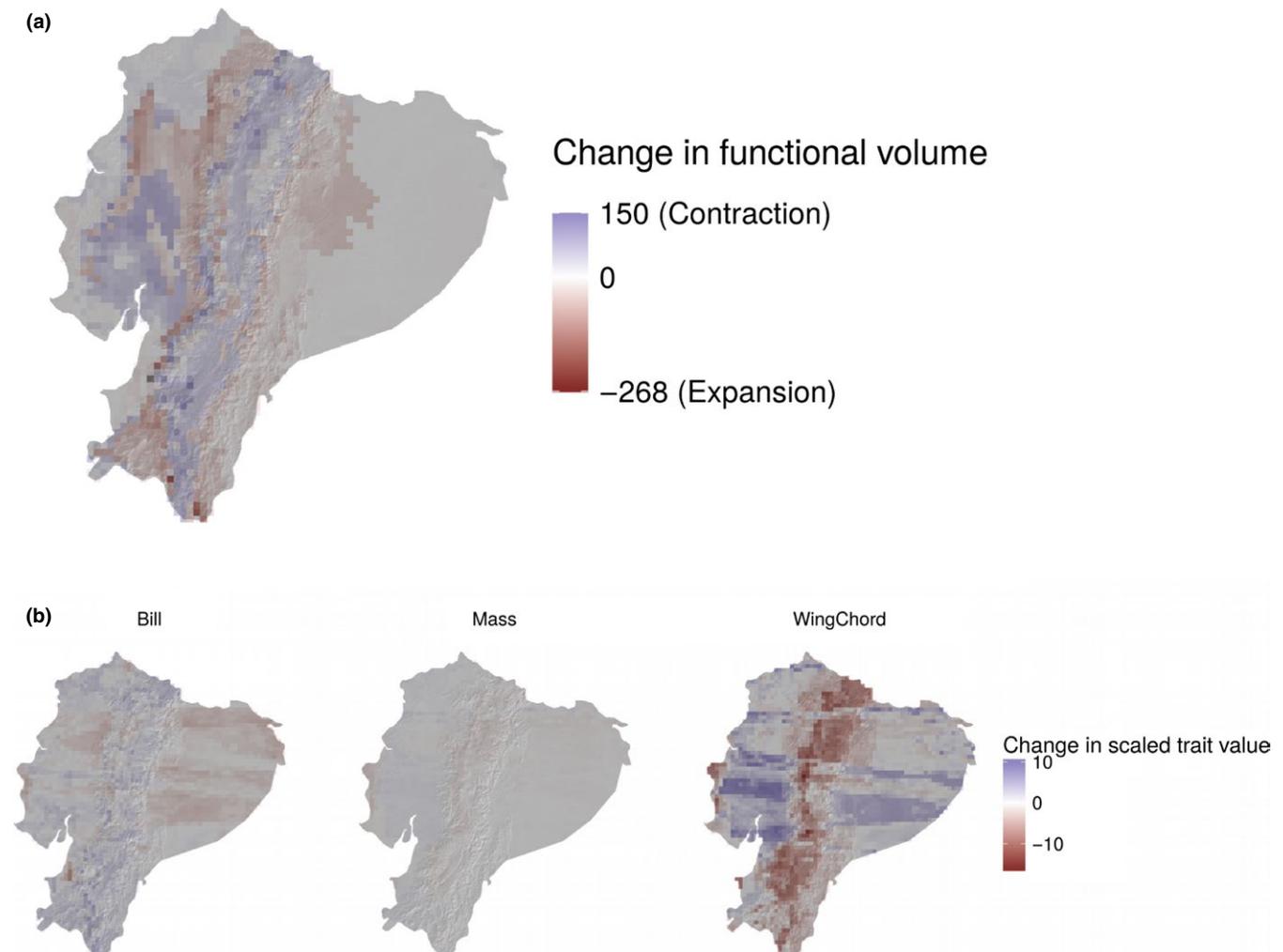


FIGURE 4 (a) Difference in total trait space between current and future (mean of all GCMs in the RCP 8.5 scenario) assemblages calculated using hypervolume. Blue suggests a contraction of trait space and red an expansion. Units are in SD^3 . (b) Change in the assemblage mean for each trait value. For each cell, we calculated the difference between the mean trait value for the current assemblage and the mean trait value across GCMs for the projected future assemblage for the RCP 8.5 scenario. Cells that are darker blue have higher values in the future compared to the current assemblage and cells that are darker red have lower values in the future compared to the current assemblage

elevations in wet conditions. Assemblages occurring from 1,000 m upward have few or no analogues between current and future climate projections. This means that fewer than 20% of species are shared between the current and projected time periods. This relationship with elevation is more pronounced from ~2,000 m upwards, with the pattern holding even when a threshold of 50% shared species is set.

Our finding of fewer analogues at the extremes of the environmental gradient may be a result of reduced environmental filtering as these extremes become warmer, and as a result, suitable for a greater number of species. The relationship we found between novel and disappearing assemblages and elevation contrasts with the findings of Stralberg et al. (2009) who found that the mountains of California were not generally predicted to contain novel assemblages. However, our results are consistent with recent empirical studies that find that species within an assemblage are not necessarily moving in synchrony, but that they are uniquely sensitive to changes in temperature and precipitation (Serra-Diaz et al., 2014; Tingley et al., 2012).

The geographical and environmental patterns of novel and disappearing assemblages were consistent across taxonomic, phylogenetic and functional dimensions. There was, however, a marked difference in the total number of taxonomic, phylogenetic and functional analogues. Because taxonomic diversity is the finest resolution of biodiversity we evaluated, we expected our model to predict fewer taxonomic than phylogenetic or functional analogues. However, different mechanisms likely influence the number and spatial pattern of phylogenetic and functional analogues compared to taxonomic. We expected that if functional traits are strictly conserved across a phylogeny, we would observe similar numbers of phylogenetic and functional analogues. Hummingbirds' traits are moderately and significantly conserved with a Blomberg's $K \sim 1$ (Graham et al., 2012); however, we found fewer phylogenetic than functional analogues (both current and future) for over 90% of grid cells. The difference between the number of phylogenetic and functional analogues is most pronounced in the slopes on either side of the Andes. The smaller number of phylogenetic analogues may be the result of historical isolation during the uplift of the Andes Mountains where the assemblages are in similar environments but with limited gene flow (Kattan, Franco, Rojas, & Morales, 2004; Weinstein et al., 2014).

Homogenization of functional space is expected under climate change (Clavel et al., 2011). Our results, however, suggest that it is the assemblages with greatest similarity between current and future climates which have the smallest functional volume and not the novel assemblages. In the areas with the fewest analogue assemblages, there were more extreme trait values and greater functional space. This suggests that novel assemblages are characterized by an increase in variation of morphological trait values. When examining the change in individual traits between current and future assemblages, the patterns indicate that if hummingbird species are tracking climate, those with smaller bodies and shorter wing chords will move into higher elevations as the temperatures become more suitable. This could be problematic if species are moving into areas where the air density and oxygen levels are not suitable (Buermann et al., 2011). The changes predicted in bill length could have conservation implications

if specialist species are moving into new areas more quickly than their resource plants.

In our study, and in previous studies of the potential for novel and disappearing assemblages under climate change, a correlative SDM approach was used. This approach has been criticized when used to extrapolate into novel environments; however, there are few practical alternatives (Elith & Leathwick, 2009). Given this limitation, we applied an ensemble forecasting approach (Araújo & New, 2007) which reduces some of the issues and uncertainties associated with extrapolation and potentially provides the most robust predictions afforded by SDM. By combining the results of three different model types (generalized linear models, generalized boosting models and maximum entropy), we likely minimized the bias in any given model. We also attempted to reduce the uncertainty in future climate projections by creating an ensemble of seven different GCMs. Finally, we interpreted geographical and environmental patterns, rather than quantitative estimates, of novel and disappearing assemblages. Climate change studies provide insights into the overall patterns of diversity (Araújo, Thuiller, & Pearson, 2006; Parida, Hoffmann, & Hill, 2015), and they can be useful for guiding future monitoring (Velasquez-Tibata, Salaman, & Graham, 2013). An alternative to SDMs are mechanistic models that incorporate species' interactions, dispersal capabilities and physiological constraints. These models may be better positioned to extrapolate species distributions into novel climates; however, they require data that are generally unknown for most species. As a result, they are not yet practical for predicting the distribution of a large number of species (Dormann et al., 2012; Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). Despite the difficulties that using correlative SDMs to extrapolate into no-analogue climates may present, we have made significant attempts to overcome these and our approach offers a logical and methodical way to think about novel and disappearing assemblages.

We show that by considering novel and disappearing assemblages in terms of geography and environment, correspondence between dimensions of diversity and change in functional trait space, we can start to identify some of the mechanisms behind these patterns and their implications. For example, both the relationship between the number of novel and disappearing assemblages and environment, and the expansion of functional trait space in areas with high numbers of novel assemblages suggest that a reduction in environmental filtering under climate change will result in co-occurrence of species that currently do not coexist. Additionally, by considering the geographical patterns in the differences between phylogenetic and functional analogues, we see that historical isolation can influence where decoupling in the different dimensions occurs. We have presented our framework using the case study of hummingbirds in Ecuador. Further research on other taxonomic groups and geographical areas will determine whether our results are generalizable.

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AUTHOR CONTRIBUTIONS

C.H.G. and B.G.W. conceived the ideas, L.J.G., B.G.W. and S.R.S. developed the analyses and all authors wrote the manuscript.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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