Received: 17 July 2018 | Revised: 28 March 2019 | Accepted: 7 May 2019

EDITOR'S CHOICE

DOI: 10.1111/ddi.12946

BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Projecting consequences of global warming for the functional diversity of fleshy-fruited plants and frugivorous birds along a tropical elevational gradient

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Funding information
German Research Foundation, Grant/Award Number: DE 2754/1-1

Editor: Kenneth Feeley

Abstract

Aim: Species in ecological communities are linked by biotic interactions. It is therefore important to simultaneously study the impacts of global warming on interdependent taxa from different trophic levels. Here, we quantify current and potential future associations of functional diversity (based on multiple traits) and functional identity (based on individual traits) between interacting taxa using projection models under climate change.

Location: A tropical elevational gradient (500–3,500 m a.s.l.) in the Manú biosphere reserve, south-east Peru.

Methods: We investigated different scenarios of how species' elevational ranges might change under climate change based on projected future increases in mean annual temperature and current associations of species' elevational ranges with temperature. We computed the functional diversity and identity of current and potential future plant and bird communities based on morphological traits that have been shown to be important for plant–frugivore interactions. Finally, we tested for changes in the associations between projected functional diversity and identity of future plant and bird communities.

Results: Projected functional diversity of plants and birds decreased under range contraction and range shift scenarios at low elevations. At mid- and high elevations, functional diversity of both species groups increased most strongly under range expansion. Correspondence between plant and bird functional diversity was weakest under range contraction, while it remained strong under range expansion and shift. Similarly, the correspondence of projected plant and bird functional identity was weakest under a range contraction scenario.

Main conclusions: Our findings suggest that a scenario in which species are dispersal-limited and sensitive to increasing temperatures is likely to cause a functional mismatch between plant and bird communities along this tropical elevational gradient. This implies that certain functional types of plants could miss avian seed dispersers in

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the future. Our approach of studying functional diversity of interacting taxa could be more widely applied to identify potential future mismatches between trophic levels.

KEYWORDS
biotic interactions, climate change, ecological communities, functional correspondence, global change, seed dispersal, trait matching, trophic interactions

1 | INTRODUCTION

Current climate change happens rapidly and alters patterns of biodiversity (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). In response to increasing temperatures, various plant and animal taxa have shifted their ranges poleward or upslope (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Feeley et al., 2011; Forero-Medina, Terborgh, Socolar, & Pimm, 2011; Parmesan et al., 1999). Such range shifts might explain observed changes in the composition of ecological communities towards more warm-adapted species (Bowler & Böhning-Gaese, 2017). Projecting changes in ecological communities is complex, as species differ in their vulnerability to climate change (Bowler, Heldbjerg, Fox, O'Hara, & Böhning-Gaese, 2018; Voigt et al., 2003). For instance, species from different trophic levels have been reported to show distinct responses to global warming (Kharouba et al., 2018; Post & Forchhammer, 2008). It is therefore important to investigate the effects of climate change on taxa from different trophic levels simultaneously (Schleuning et al., 2016).

Species in ecological communities are linked by biotic interactions, such as trophic interactions between plants and animals (Bascompte & Jordano, 2007). Independent species' range shifts could cause spatial mismatches between interacting species if the interdependent species shift their ranges differently due to differences in their thermal tolerances or dispersal abilities (Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008). Future spatial mismatches between currently interacting species might trigger secondary range contractions and extinctions if lost interaction partners cannot be replaced (Schleuning et al., 2016; Schweiger et al., 2008). Such indirect, interaction-mediated consequences of climate change have often been overlooked and should be considered when studying the potential impacts of climate change on biodiversity (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013).

According to the concept of ecological fitting (Janzen, 1985), trait matching between species determines who interacts with whom in ecological communities (Bender et al., 2018; Garibaldi et al., 2015). A widely documented example is the matching of bill length and corolla length in plant–hummingbird interactions (Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2014; Weinstein & Graham, 2017). In plant–frugivore interactions, bill width and fruit width are closely related (Dehling, Töpfer, et al., 2014; Moermond & Denslow, 1985; Wheelwright, 1985). At the community level, the variation and dominant value of such functional traits can be estimated by metrics of the functional diversity of multiple traits and the functional identity of single traits (Díaz et al., 2007; Gagic et al., 2015). Both, functional diversity and identity, have been shown to correspond between communities of interacting species. For instance, community means of the mouth length of pollinators and the nectar accessibility of their feeding plants improve predictions of plant reproduction (Garibaldi et al., 2015). Similarly, communities of fleshy-fruited plants and frugivorous birds show a high correspondence in their functional diversity and functional identity along elevational gradients (Dehling, Töpfer, et al., 2014; Vollstädt et al., 2017). However, potential future range shifts of species in response to climate change might alter the composition of ecological communities (Graham, Weinstein, Supp, & Graham, 2017). Associated changes in the functional diversity and functional identity of ecological communities may trigger a disruption in the functional correspondence between interacting taxa. Therefore, integrative functional analyses are needed to identify ecological systems and regions that are prone to disruptions of functional correspondence between interacting taxa (Figure 1).

Mountains are global biodiversity hot spots (Antonelli et al., 2018; Jetz, Rahbek, & Colwell, 2004) and are well suited to study functional associations between interacting taxa (Albrecht et al., 2018). Upslope range shifts of species in response to increasing temperatures might alter mountain biodiversity in distinct ways. The number of lowland species emigrating or going extinct from low elevations might exceed the number of persisting, warm-adapted species, resulting in a decline of diversity at low elevations (i.e., lowland biotic attrition; Colwell, Brehm, Cardelús, Gilman, & Longino, 2008). Mid-elevations might experience elevated species turnover, due to immigrating lowland species and upslope shifts of species from mid-elevations (Corlett, 2011). At high elevations, diversity might accumulate as species from lower elevations immigrate to high elevations (Steinbauer et al., 2018), but high-elevation species might also face an increased extinction risk if their suitable environment contracts towards the mountaintop (Peters & Darling, 1985). So far, there is empirical evidence for upslope shifts of the lower and/or the upper elevational range limits for a variety of plant and animal taxa across the globe (Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018; Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018). Consequences of elevational range shifts for biodiversity may be particularly severe in the tropics, where latitudinal temperature gradients are shallow and elevational range shifts more likely (Colwell et al., 2008). Tropical mountains are, therefore, particularly suitable for studying the effect of climate change on interacting species.

Here, we propose a new integrative analysis of functional diversity and projection models (Figure 1) to study potential future changes in the functional diversity of fleshy-fruited plant and frugivorous bird

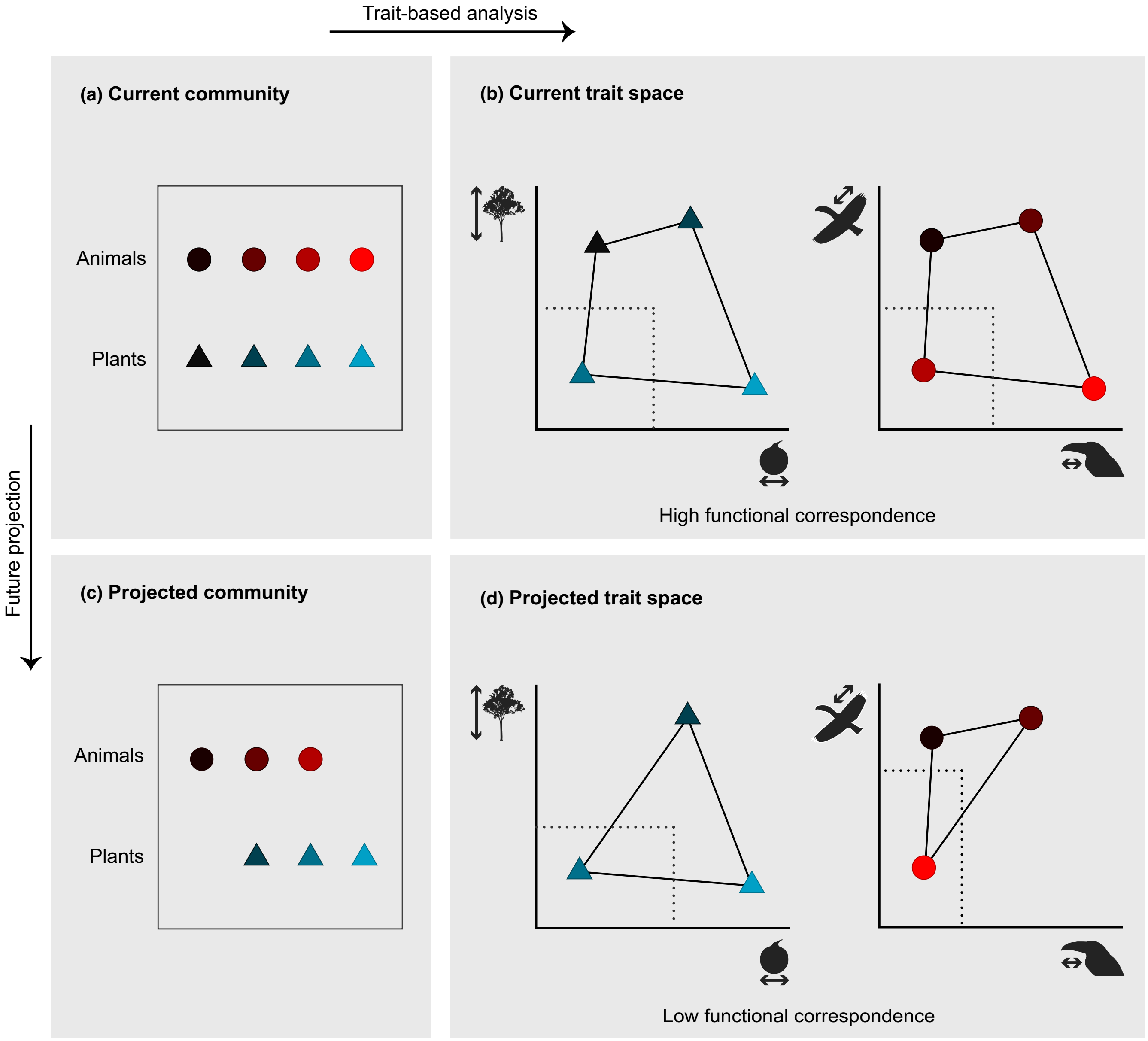

FIGURE 1 Projections of functional correspondence between interacting taxa from different trophic levels applying trait-based analyses. Shown are (a) hypothetical animal species (circles) and plant species (triangles) that co-occur in an ecological community. (b) Each species is defined by a set of functional traits that influence plant–animal interactions (e.g., fruit size and plant height and bill size and wing shape). Functional diversity is defined by the volume of the occupied multidimensional trait space (polygons in trait space) and the functional identity by community mean values of the respective traits (dashed lines to the individual axes). A high functional correspondence between plants and animals is indicated by similar values of functional diversity and identity. (c) A projection model, based on a future scenario, predicts different compositions of plant and animal communities. (d) Associated changes in functional diversity and identity of projected plant and animal communities could lead to a decrease in functional correspondence between plants and animals

communities along an elevational gradient in the tropical Andes of southeast Peru. We investigate multi-trait functional diversity and single-trait functional identity of plant communities based on fruit dimensions, plant height and crop mass and those of bird communities based on bill dimensions, wing pointedness and body mass. These species characteristics are relevant for trait matching in plant–frugivore networks (Bender et al., 2018; Dehling, Töpfer, et al., 2014; see further details in methods). We consider three previously reported scenarios of how species might alter their elevational ranges under increasing temperatures (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018; Figure 2a–c) and investigate changes in the projected functional correspondence of the two interacting species groups. We expect a decrease in functional diversity at low elevations under scenarios in which species shift their lower elevational range limit upslope (Colwell et al., 2008). Under scenarios in which species shift their upper elevational range limits upslope, we expect an increase in functional diversity at mid- and high elevations, because functionally more diverse species from low elevations might immigrate to mid- and high-elevation communities (Colwell

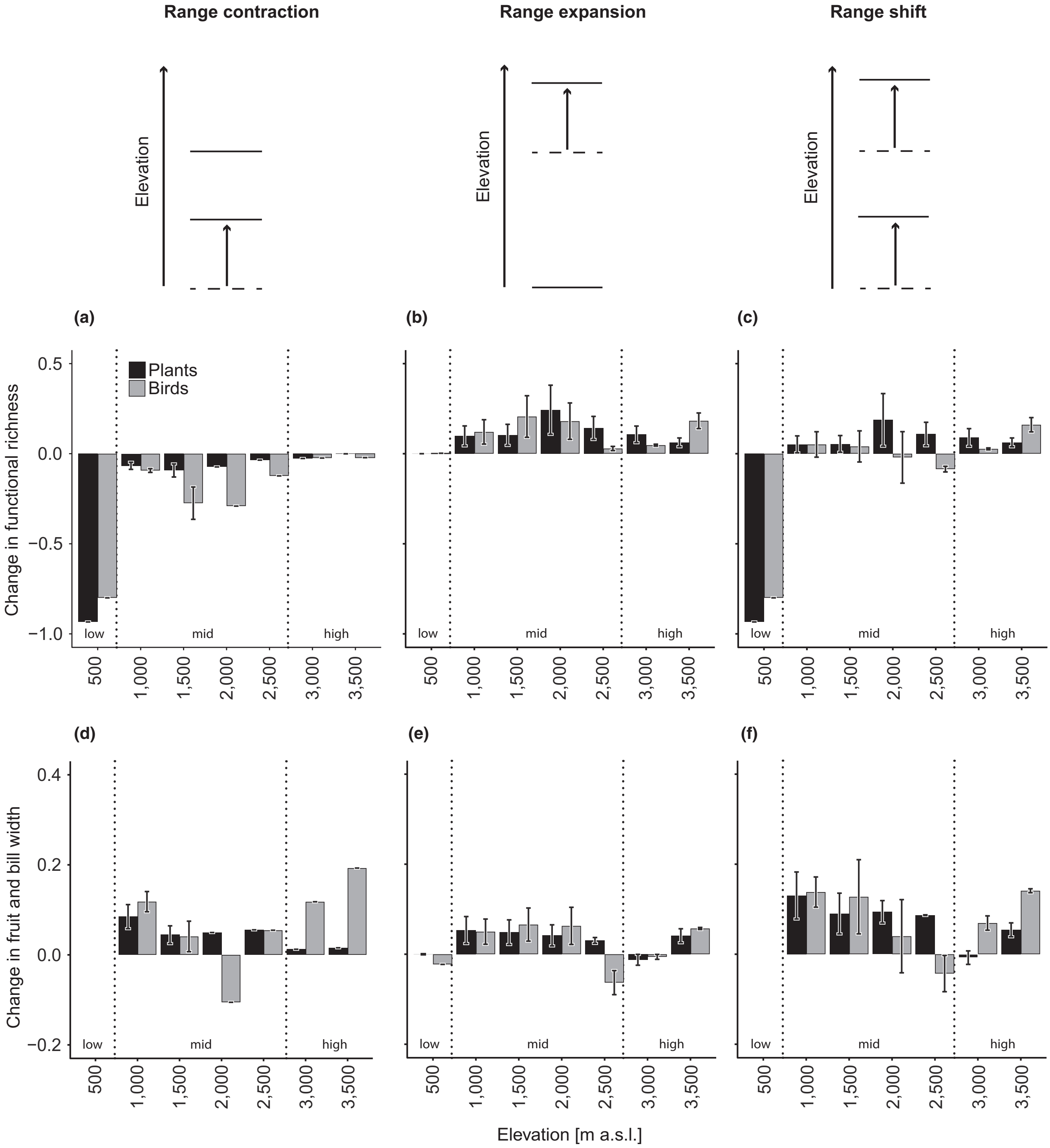

FIGURE 2 Projected changes in (a–c) functional richness and (d–f) mean fruit and bill width for fleshy-fruited plant (dark grey) and frugivorous bird (medium grey) communities under RCP 8.5 for the year 2080. We applied three vertical dispersal scenarios for future projections of plant and bird communities along the Manú gradient, that is, range contraction, range expansion and range shift. Changes were computed as future functional richness minus current functional richness and future fruit and bill width minus current fruit and bill width, respectively. Given are mean values and standard deviation (error bars) over five general circulation models (CCSM4, HadGEM2-ES, MIROC 5, MRI-CGCM and NorESM). Dashed lines indicate low, mid- and high elevations. Functional identity of lowland communities could not be quantified under range contraction and shift scenarios because projected species richness was zero

et al., 2008; Dehling, Töpfer, et al., 2014). We expect particularly pronounced changes in functional diversity of bird communities at mid-elevations because species turnover between neighbouring frugivorous bird communities is high at these elevations along the Manú gradient (Dehling, Fritz, et al., 2014). This might lead to a decoupling of plant and bird functional diversity and identity under future scenarios.

2 | METHODS

2.1 | Study system

We studied communities of fleshy-fruited plants and frugivorous birds at seven elevations located every 500 m from 500 to 3,500 m a.s.l. in the Kosñipata valley in the Manú biosphere reserve in south-east Peru (hereafter "Manú gradient"). The entire study region ranges from approximately 250 to 3,750 m a.s.l. The forest along the Manú gradient comprises four main vegetation types (Patterson, Stotz, Solarit, Fitzpatrick, & Pacheco, 1998). Lowland rainforest (≤500 m a.s.l.) is characterized by canopy trees up to 50 m high. Montane rainforest (~500–1,500 m a.s.l.) lacks such tall trees and is characterized by denser understory vegetation. Cloud forest (~1,500–2,500 m a.s.l.) is intermittently covered in slowly rising clouds and typically hosts a high number of epiphytes and bryophyte layers on tree branches. Elfin forest (>2,500 m a.s.l.) consists of compact, densely branched trees and shrubs. Around the treeline (~3,500 m a.s.l.), elfin forest turns into an irregular mosaic of forest and Puna grassland (Patterson et al., 1998). All forest types are characterized by high precipitation, while temperature declines with increasing elevation from 24.3°C at 500 m a.s.l. to 7.3°C at 3,500 m a.s.l. (Girardin et al., 2010, 2013; Rapp & Silman, 2012).

2.2 | Plant and bird communities

To identify fleshy-fruited plant species co-occurring along the Manú gradient, we sampled an area of 1 ha (divided into 10 plots of 20 m × 50 m) every 500 m from 500 to 3,500 m a.s.l. and recorded all plants with ripe fleshy fruits. Plants were identified as morphospecies, and samples of each species were taken. These samples were identified to species level in comparison with specimens from local herbaria. Each site was sampled once in the rainy season (December to March) and once in the dry season (June to September) between December 2009 and September 2011. This resulted in representative samples of the trait diversity of the fleshy-fruited plant communities along the Manú gradient (Dehling, Töpfer, et al., 2014) although rarely fruiting species may not have been covered by our sampling. Information on plant species' elevational distributions in Peru was taken from Brako and Zarucchi (1993), supplemented by data from Tropicos (2017; for about 3% of the analysed species). Because plant elevational ranges for entire Peru could overestimate local elevational ranges along the Manú gradient, we compared elevational range extents and functional diversity of current plant communities based on literature data and our own plot data (Figures S1 and S2). Functional diversity of plants, based on the two data sources, was positively correlated (Pearson $r = 0.81$, $p = 0.03$, $n = 7$ elevations; Figure S2). However, the plot data seemed to underestimate species' actual elevational range extents because about 80% of the analysed species were only recorded at a single elevation (Figure S1). Therefore, we decided to use the literature data that apparently provide a more comprehensive measure of the current elevational ranges of plants although this data source could slightly overestimate the current local ranges. We considered 392 plant species for which we had information on traits and elevational distribution in further analyses.

Information on co-occurring frugivorous bird species along the Manú gradient was compiled from local checklists (Merkord, 2010; Walker, Stotz, Pequeño, & Fitzpatrick, 2006) supplemented by field observations (Dehling, Fritz, et al., 2014; Dehling, Sevillano, & Morales, 2013). These occurrence data were compiled during repeated surveys along the Manú gradient over several years based on point counts, mist-netting or chance observations. If elevational ranges were derived from a country-wide guide book (Schulenberg, Stotz, Lane, O'Neill, & Parker, 2010), estimates of functional diversity of current bird communities were very similar to those obtained through the Manú checklist (Pearson $r = 0.98$, $p < 0.001$, $n = 7$ elevations; Figure S3). Because of its higher accuracy for the Manú gradient, we used range data from the Manú checklist. We considered all avian frugivore species that occur along the gradient, except ground-dwelling species (Tinamidae, Odontophoridae, Psophidae, Mitu). Ground-dwelling species have different fruit handling and foraging strategies than bird species that take fruit directly from the plant and their matching traits therefore differ compared to other guilds (Dehling, Töpfer, et al., 2014). Our final bird species pool included 217 frugivorous bird species.

We computed the current elevational range extent of each plant and bird species as the distance between its minimum and maximum elevational range limit (Tables A1 and A2 at DRYAD digital repository). Based on these data, we determined which plant and bird species occurred at each of the seven studied elevations (500–3,500 m a.s.l.) and on the lowest (250 m a.s.l.) and the highest elevations (3,750 m a.s.l.) of the Manú gradient. An elevational resolution of 500 m was appropriate for describing elevational turnover across this wide elevational gradient, as it corresponds to the resolution of the available distribution data and has been applied in previous work comparing patterns in plant and bird diversity along this gradient (Dehling, Töpfer, et al., 2014).

2.3 | Plant and bird traits

For all plant and bird species, we collected morphological traits that have been shown to determine interactions between plants and frugivores (Bender et al., 2018; Dehling, Töpfer, et al., 2014). Fruit width (mm) and fruit length (mm) of plants correspond to bill width (mm) and bill length (mm) of birds and relate to the size matching of bill and fruit (Dehling, Töpfer, et al., 2014; Moermond & Denslow, 1985; Wheelwright, 1985). Fruit crop mass (i.e., the fresh mass (g) of a single fruit multiplied by the number of ripe fruits per plant) corresponds to avian body mass (g) and represents the matching between food resource availability and avian energy requirements, that is, larger frugivores tend to feed on plants that offer a higher resource amount as this minimizes their foraging cost (Albrecht et al., 2018; Dehling, Töpfer, et al., 2014). Plant height (m) corresponds to avian wing pointedness (estimated as Kipp's index: the distance from the tip of the first secondary to the tip of the longest primary feather [mm] divided by wing length [mm]) and relates to trait matching of plant height at which fruits are offered and avian flight ability and manoeuvrability, that is, avian frugivores that forage in the canopy and fly long distances between fruiting plants have more pointed wings, while avian frugivores that forage in denser understory vegetation have more rounded wings which increases their manoeuvrability (Bender et al., 2018; Dehling, Töpfer, et al., 2014). Plant height and number of ripe fruits per tree were recorded in the field, while fruit dimensions and fresh fruit mass were measured on fruits collected during field surveys (on about 20 fruits per plant species). For 23 plant species (6% of the species pool), we used mean trait values at the genus level, as species-specific trait values were unavailable. Bill dimensions and wing pointedness were measured on museum specimens, following measurement protocols from Eck et al. (2011). Information on avian body mass was taken from the literature (Dunning, 2007). In our analyses, we used species means of all traits (see Tables A3 and A4 at DRYAD digital repository for trait values per plant and bird species and Appendix S1 for details on the museum collection and identity of bird specimens).

2.4 | Functional diversity and identity

We computed species richness, functional diversity and functional identity for each current and potential future plant and bird community. Species richness equals the number of species that occur in a community at a given elevation. Functional diversity was estimated as functional richness (Villéger, Mason, & Mouillot, 2008). To reduce the weight of species with extreme traits, we log-transformed all traits, except Kipp's index, prior to the functional richness computation. Kipp's index was normally distributed and therefore needed no transformation. To compute functional richness, we calculated Euclidean distances between the species of a community based on differences in the respective traits (bill dimensions, pointedness of the wing and body mass for birds and fruit dimensions, plant height and crop size for plants) and used principle coordinate analysis to project species into a multidimensional trait space. We calculated functional richness as the inner volume of a minimum convex hull spanning all species of a community in trait space (Villéger et al., 2008). Species richness and functional richness were standardized to range between zero and one by dividing the value of the community at a specific elevation by the value of the entire species pool (392 plants species and 217 bird species, respectively, see Tables A5 and A6 at DRYAD digital repository for current and future functional diversity of plant and bird communities at each elevation). Standardized values are comparable among communities at different elevations and between plants and birds.

To estimate the functional identity of each current and future plant and bird community, we standardized plant and bird traits to zero mean and unit variance across the entire species pool of plants and birds, respectively. We then computed functional identity as the mean value of each trait across all species in a community, yielding directly comparable measures of functional identity for plant and bird communities (see Tables A7 and A8 at DRYAD digital repository for current and future functional identity of plant and bird communities at each elevation).

2.5 | Temperature projections, tropospheric lapse rate and vertical distances

We calculated the projected temperature increase along the Manú gradient based on current and projected annual mean temperature downloaded from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; details given in Appendix S2). We used projected data for the year 2080 (averaged over 2061–2080), according to five general circulation models (CCSM4, HadGEM2-ES, MIROC 5, MRI-CGCM and NorESM) and the representative concentration pathway (RCP) 8.5. This baseline scenario assumes continuing human population growth, little economic and technological developments, high energy demands and high greenhouse gas emissions (radiative forcing of 8.5 W/m^2 at the end of the century; Riahi et al., 2011). We chose this scenario because CO_2 emissions have tracked the high end of emission scenarios until 2012 (Peters et al., 2012) and atmospheric CO_2 concentration further continues to rise (Le Quéré et al., 2018).

We then used the tropospheric lapse rate (i.e., the rate at which temperature decreases with increasing elevation, Mokhov & Akperov, 2006; details given in Appendix S2) to compute projected vertical distances (i.e., the distance a certain surface temperature will shift upslope under future conditions) for the Manú gradient (La Sorte & Jetz, 2010). We calculated the projected vertical distance for each elevation by dividing the projected anomaly in annual mean temperature of an elevation by the tropospheric lapse rate of that elevation (temperature anomaly [°C]/tropospheric lapse rate [°C/km] = vertical distance [km]).

2.6 | Projections of species' elevational ranges

We approximated the current realized temperature niche of a species by its current elevational range and considered three scenarios of how the current elevational ranges of species could change under global warming (i.e., future temperature increases). We assumed that projected changes in species' elevational ranges are primarily driven by projected changes in temperature. Observed elevational range shifts of Andean species in response to recent (Feeley et al., 2011; Forero-Medina et al., 2011) and historic climate change (Hansen, Seltzer, & Wright, 1994) support this assumption. At the Manú gradient, precipitation might be a less limiting factor for species' occurrences, as precipitation is currently high (Girardin et al., 2010, 2013; Rapp & Silman, 2012) and projected to increase (Hijmans et al., 2005; Stocker et al., 2014). We further assumed that plant and bird species shift their elevational ranges only upslope because the Manú gradient is entirely covered by rainforest (Patterson et al., 1998).

We computed species-specific vertical distances as the mean vertical distance across all of the studied elevations at which a species currently occurs (La Sorte & Jetz, 2010). The species-specific vertical distance approximates the distance a species would have to move upslope in order to track its current realized temperature niche under future global warming. In this computation, we considered vertical distances from nine grid cells at a resolution of 2.5 min that capture the entire elevational range of the Manú gradient

(250–3,750 m a.s.l.; see Tables A1 and A2 at DRYAD digital repository for current elevational ranges and species-specific vertical distances of plant and bird species).

We implemented three vertical dispersal scenarios corresponding to observed changes in species’ ranges on mountains (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018). First, under the range contraction scenario (Figure 2a), we assumed that species cannot persist under temperatures that exceed their current realized temperature niche (i.e., species cannot tolerate or adapt to higher temperatures) and that species are unable to shift their ranges upslope. Therefore, species' lower elevational range limits shift upslope, while species' upper elevational range limits remain unchanged. For this scenario, we added the species-specific vertical distance to the lower limit of each species' current elevational range. Second, under the range expansion scenario (Figure 2b), we assumed that species can tolerate or adapt to temperatures that exceed their current realized temperature niche, but also that species are able to shift their elevational ranges upslope to track their current realized temperature niche. Therefore, species' lower elevational range limits remain unchanged, while species' upper elevational range limits shift upslope. For this scenario, we added the species-specific vertical distance to the upper limit of each species' current elevational range. Third, under the range shift scenario (Figure 2c), we assumed that species cannot persist under temperatures beyond their current realized temperature niche, but are able to shift their ranges upslope. Therefore, species' lower and upper elevational range limits shift upslope and species fully track their current realized temperature niche. For this scenario, we added the species-specific vertical distance to both the lower and the upper limits of each species’ current elevational range.

We applied the vertical dispersal scenarios to all plant and bird species, which resulted in one potential plant and one potential bird community at each elevation for each vertical dispersal scenario and for each general circulation model. We compared projected future functional diversity and functional identity values of plant and bird communities only between corresponding dispersal scenarios because we have no prior knowledge on how dispersal scenarios may differ between plants and birds. We also did not vary dispersal scenarios among individual species within the two groups as this would require a quantification of the dispersal ability of each individual species. Our projections do not aim to mimic reality, but to provide insights into how plant and bird communities and their functional relationships could differ under different hypothetical scenarios.

2.7 | Statistical analyses

We quantified projected changes in plant and bird functional diversity by subtracting the current functional diversity of a community from its projected functional diversity. We compared these projections to analogous projections of plant and bird species richness. Furthermore, we computed projected changes in the functional identity of plant and bird communities by subtracting the current mean trait value of a community from its projected mean trait value. Projected changes were computed separately for each global circulation model.

To test for a correspondence between the functional diversity and functional identity of plant and bird communities along elevation (Dehling, Töpfer, et al., 2014), we fitted linear regression models with the functional diversity or functional identity of the plant communities as predictor and the functional diversity or functional identity of the corresponding bird communities as response. We did this for the current situation and for the three dispersal scenarios. These models were based on functional diversity and identity values that were averaged across the five general circulation models.

All computations were performed using R version 3.3.2 (R Core Team, 2016) and the packages “FD” (Laliberté & Legendre, 2010; Laliberté, Legendre, & Shipley, 2014) and “raster” (Hijmans, 2016).

3 | RESULTS

3.1 | Current patterns of functional diversity and identity

Current plant species richness ranged from 276 (see Table A5 at DRYAD digital repository for species richness and functional diversity of plant communities at each elevation) at low elevations (500 m a.s.l.) to 76 species around the treeline (3,500 m a.s.l.). The current bird species richness decreased from 126 species (see Table A6 at DRYAD digital repository) at low elevations to 19 species around the treeline. The current functional richness of plants (standardized relative to the full species pool) declined from 0.93 at low elevations to 0.09 around the treeline. The current standardized functional richness of bird species varied between 0.8 at low elevations and 0.12 around the treeline. Functional richness (Figure 3a) and species richness (Figure S6a) of current plant and bird communities were significantly positively related. Similarly, fruit width and bill width of current plant and bird communities were positively associated (Figure 4a). The other matching traits of plants and birds (mean fruit and bill length, plant height and Kipp's index, crop and body mass) showed largely similar patterns (Figures S7–S9a).

3.2 | Projected elevational ranges and resulting changes in functional diversity

Average projected increase in annual mean temperature across the Manú gradient varied between 3.0°C (*SD* = ±0.1, *n* = 9 elevations; MRI-CGCM) and 4.3°C (*SD* = ±0.1, *n* = 9 elevations; HadGEM2-ES) among the five global circulation models, with a mean temperature increase of 3.5 ± 0.44°C across elevations and general circulation models. The average species-specific vertical distance that a species had to shift to stay within its current realized temperature niche until 2080 ranged between 486.6 m (*SD* = ±12.6 m, *n* = 392 plant species; MRI-CGCM) and 681.9 m (*SD* = ±9.6 m; HadGEM2-ES) for plants. For birds, it varied from 483.8 m (*SD* = ±13.1 m, *n* = 217 bird species; MRI-CGCM) to 679.8 m (*SD* = ±9.6 m; HadGEM2-ES).

Plant and bird functional diversity changed under all vertical dispersal scenarios. At low elevations, functional richness

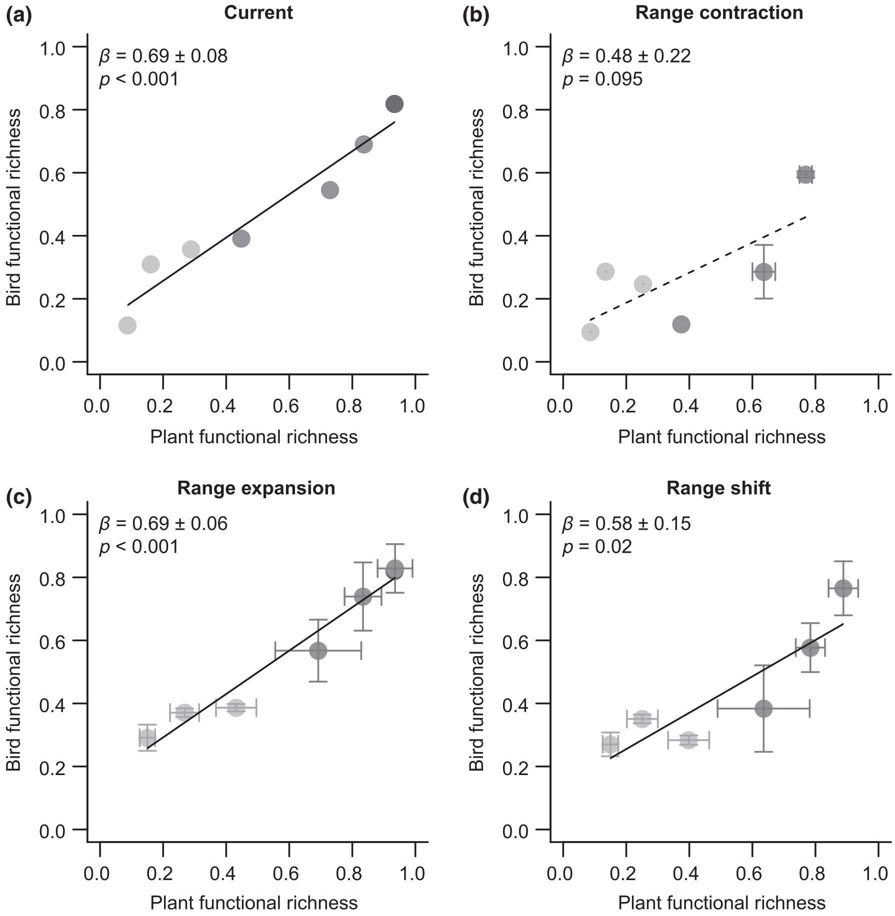

FIGURE 3 Associations between plant and bird functional richness under (a) current conditions and under scenarios of (b) range contraction, (c) range expansion and (d) range shift. Dots indicate the mean value and error bars the standard deviation across five GCMs (CCSM4, HadGEM2-ES, MIROC 5, MRI-CGCM and NorESM). Horizontal error bars refer to plants, vertical error bars refer to birds. Given are slope estimates (β) ± standard errors and the p-values of linear models of bird functional richness against plant functional richness. Regression lines are represented as solid lines (for $p < 0.05$) and dashed lines (for $0.05 < p < 0.1$). Low, mid- and high elevations are coloured in dark, medium and light grey, respectively

decreased strongly under range contraction and range shift scenarios (Figure 2a,c). At mid- and high elevations, functional richness increased under the range expansion scenario and, to a much lesser extent, under the range shift scenario. Increases were mostly weaker at high than at mid-elevations (Figure 2b,c). Projected changes in plant and bird species richness were overall similar to changes in functional richness, but were generally weaker (Figure S4). Mean fruit and bill width mostly increased at mid- and high elevations independent of the vertical dispersal scenarios (Figure 2d–f). Similarly, the mean values of fruit and bill length, plant height, wing pointedness, plant crop mass and avian body mass mostly increased under the different dispersal scenarios (Figure S5).

Projected future plant and bird functional richness corresponded least under the range contraction scenario (Figure 3b). This discrepancy between plant and bird functional richness resulted mostly from a stronger decrease in projected bird than plant functional richness at mid-elevations (Figure 2a). In contrast, under the range expansion and the range shift scenario, projected plant and bird functional richness was significantly positively associated (Figure 3c,d). Projected plant and bird species richness was significantly positively associated under each dispersal scenario (Figure S6).

In line with the findings for functional richness, the correspondence of projected plant and bird functional identity was weakest under a range contraction (Figure 4b) and highest under a range expansion scenario (Figure 4c). In addition, the correspondence of projected plant and bird functional identity was also weak under a range shift scenario (Figure 4d, Figures S7–S9).

4 | DISCUSSION

Our study simulated how different scenarios of temperature-driven range changes may influence the functional diversity of fleshy-fruited plants and frugivorous birds along a tropical elevational gradient. Under a scenario in which species' elevational ranges contract in response to increasing temperatures, the projected correspondence of functional diversity and functional identity between plant and bird communities was lowest, while under range expansion functional associations persisted. Our results show how integrative analyses of functional diversity and projection models can be a powerful tool to explore scenarios under which disruptions of functional relationships between interacting species are most likely.

4.1 | Projected changes in plant and bird functional richness

At low elevations, plant and bird functional diversity were projected to decrease under range contraction and range shift scenarios. If temperature increases by about 3–4°C, all fleshy-fruited plant and frugivorous bird species were projected to be lost from low elevations.

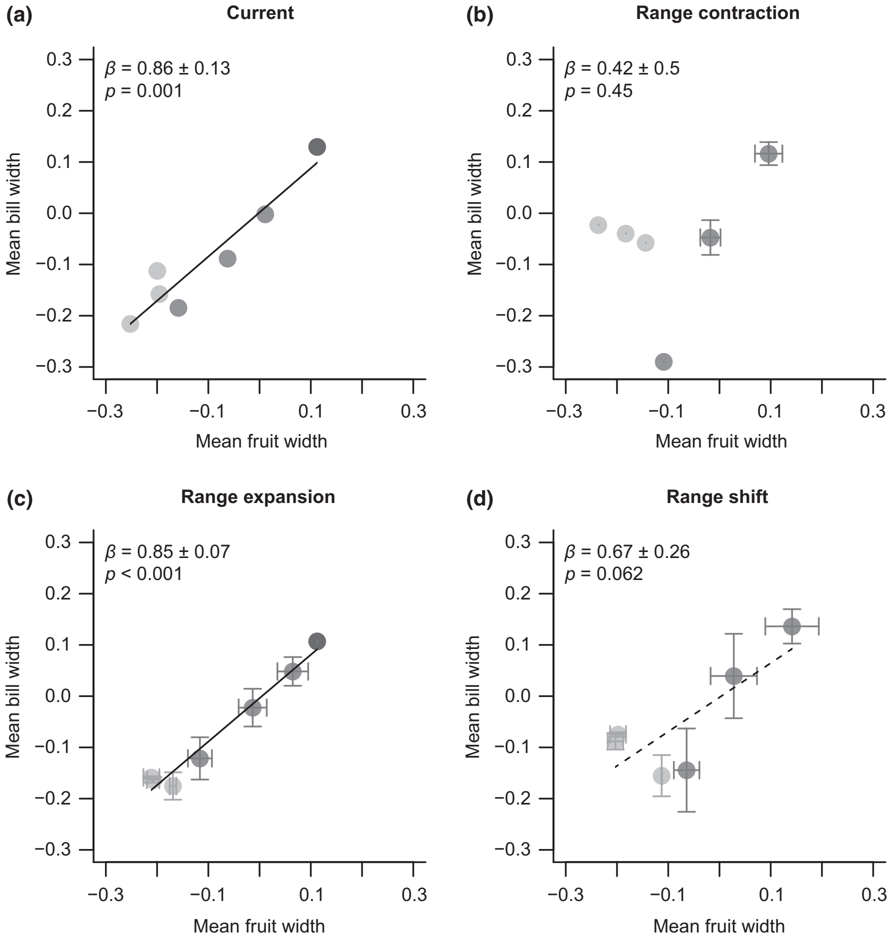

FIGURE 4 Associations between mean fruit width and mean bill width under (a) current conditions and under scenarios of (b) range contraction, (c) range expansion and (d) range shift. Dots indicate the mean value and error bars the standard deviation across five GCMs (CCSM4, HadGEM2-ES, MIROC 5, MRI-CGCM and NorESM). Horizontal error bars refer to plants, and vertical error bars refer to birds. Regression lines are represented as solid lines (for $p < 0.05$) and dashed lines (for $0.05 < p < 0.1$). Low, mid- and high elevations are coloured in dark, medium and light grey, respectively

Such a projected decline is in line with the hypothesis of lowland biotic attrition (Colwell et al., 2008). However, lowland biotic attrition might be mitigated by species from warmer regions that immigrate to lowland communities (Anderson et al., 2012). This requires the existence of such warm-adapted species (Colwell et al., 2008) and their ability to disperse to the respective regions (Anderson et al., 2012). The strength of lowland biotic attrition will further depend on species' thermal tolerances (Feeley & Silman, 2010). Occurrence-derived thermal tolerances of tropical lowland species might underestimate thermal tolerances as species possibly tolerate higher temperatures than currently realized (Feeley & Silman, 2010). A global meta-analysis on past distributional changes in vascular plants and endo- and ectothermic animals indeed shows that most lowland species rather extend their ranges upslope than emigrating away from low elevations (Freeman, Lee-Yaw, et al., 2018). Furthermore, changes in the composition of lowland plant communities in France lag behind observed temperature increases between 1965 and 2008 (Bertrand et al., 2011). Nevertheless, a decrease in plant species richness was recently reported at low elevations in the Alps (Scherrer, Massy, Meier, Vittoz, & Guisan, 2017), suggesting that lowland biotic attrition is happening in some mountain areas.

At mid-elevations, functional richness increased under range expansion and, to a lesser extent, under range shift, indicating that species with functionally more extreme trait combinations were projected to immigrate to higher elevations. The current decline in functional richness with elevation suggests a filtering of species with extreme trait values, for example, large-billed and large-fruited species, towards high elevations (Dehling, Fritz, et al., 2014; Dehling, Töpfer, et al., 2014). Our projections of upslope dispersal suggest that communities at high elevations might become functionally more diverse in the future. Empirical studies indeed report increasing plant species richness at mid- and high elevations under climate change in North America (Savage & Vellend, 2015; Sproull, Quigley, Sher, & González, 2015) and Europe (Steinbauer et al., 2018). If global warming continues, a likely scenario would be a gradual increase in functional diversity of plant and bird communities at mid- and high elevations of the Manú gradient and on other tropical mountains.

4.2 | Potential future differences between plant and bird functional diversity and identity

Projected plant and bird functional richness and identity corresponded least under the range contraction scenario. Low functional correspondence resulted from a stronger projected decline in bird than plant functional richness at mid-elevations and from a mismatch in mean trait values between plants and birds at mid- and high elevations. The high taxonomic and functional turnover between neighbouring bird communities at mid-elevations (Dehling, Fritz, et al., 2014; Jankowski et al., 2013) might explain the strong effect of range contraction on these bird communities. Accordingly, many montane bird species are projected to be threatened if they are vulnerable to increasing temperatures and limited in their vertical dispersal (La Sorte & Jetz, 2010). In current plant–frugivore communities across the Andes, certain functional types of frugivorous birds interact with certain functional types of fleshy-fruited plants (Bender et al., 2018). For instance, large-beaked bird species mostly feed on large fruits, species with pointed wings tend to forage in the canopy and species with a large body mass prefer plants with a large crop mass (Dehling, Töpfer, et al., 2014; Wheelwright, 1985). A higher plant than bird functional richness, as found at mid-elevations under the range contraction scenario, suggests that certain functional types of plants might lack seed dispersers with matching functional traits in future communities (Bender et al., 2018; Dehling, Töpfer, et al., 2014). This is in line with the projected mismatch between fruit and bill width at 2,000 m, where mean bill width was projected to decrease in the future. At this elevation, the dispersal of particular plant species might decrease because the loss of large-bodied frugivores reduces, particularly, the dispersal of large-fruited plant species (Markl et al., 2012). The projected increase in avian bill width at high elevations might have less severe consequences as broad-billed bird species tend to be flexible in their fruit choice (Bender et al., 2017; Moermond & Denslow, 1985; Wheelwright, 1985). Generally, avian flexibility to switch to other fruit resources could mitigate the risk to lose seed-dispersal functions under climate change. In the long run, however, a mismatch between plant and bird traits would likely trigger evolutionary changes in plant communities, for example, at the expense of large-fruited plant species (Onstein et al., 2018).

Under range expansion, projected differences between plant and bird functional richness and identity were smallest. This suggests that losing seed-dispersal functions under climate change is less likely if species are able to shift their upper elevational range limits upslope. Accordingly, the projected range loss of montane bird species under climate change was least severe if species were able to disperse vertically (La Sorte & Jetz, 2010). Indeed, many species across the globe already shifted their upper elevational range limits upslope (Freeman, Lee-Yaw, et al., 2018; Freeman, Scholer, et al., 2018). Projected changes were less conclusive under a range shift scenario. Associations between functional richness and, in particular, individual functional traits were projected to decrease under range shift. However, variation in projections was also highest under this scenario, indicating that future correspondence between plant and bird communities was most difficult to project if both lower and upper elevational ranges of species were assumed to change.

4.3 | Integrative analysis of functional diversity under climate change

Our approach provides a new way to integrate species' occurrences, functional traits and projection models to assess consequences of global warming for the functional correspondence between interacting taxa (Figure 1). The proposed approach can yield new information on how functional associations between taxa are likely to change under future climate change and is useful to identify under which scenarios functional mismatches between taxa are most likely to happen. Such analyses could be applied to a wide range of other taxa that are linked by trophic interactions and only require occurrence data for both taxa as well as information on the functional traits that mediate their interactions, such as traits that determine the probability of plant–pollinator or predator–prey interactions (Webb & Shine, 1993; Weinstein & Graham, 2017). Such trait-based approaches are timely as more and better trait data are increasingly becoming available (Kissling et al., 2018). Ultimately, a formal integration of such trait-based approaches into projection models is desirable and could improve how biotic interactions are accounted for in species distribution models (Dormann et al., 2018).

Our study is a first step towards comparative analyses of interacting taxa under climate change. We particularly encourage future studies that use more fine-scale occurrence data than those that are available for our study system. Moreover, the future projection models we apply rely on many assumptions and a better integration of species-specific responses in terms of physiological thermal tolerances (Khaliq, Hof, Prinzinger, Böhning-Gaese, & Pfenninger, 2014; Londoño, Chappell, Jankowski, & Robinson, 2017) and different dispersal capacities of species (Grewe, Hof, Dehling, Brandl, & Brändle, 2013) could improve model projections. A promising way forward could also be the use of time-series data that document how occurrences of interacting taxa have changed over time (Burkle, Marlin, & Knight, 2013), in order to quantify temporal variation in the functional associations between taxa.

5 | CONCLUSIONS

To our knowledge, this is the first study that simultaneously investigates how projected range change might influence the functional diversity of interacting taxa under climate change. Our results suggest that under a scenario in which species are sensitive to increasing temperatures and dispersal-limited, the potential for future functional mismatches between fleshy-fruited plants and frugivorous birds is highest. For conserving tropical mountain biodiversity, it might therefore be important to enable species to shift their ranges upslope and to plan for movement corridors along elevational gradients (Moore, Robinson, Lovette, & Robinson, 2008). Our approach of integrating functional diversity analyses and projection models can be widely applied to a range of interacting taxa linked by trophic interactions and could help to identify future scenarios under which biotic interactions between taxa are most vulnerable.

ACKNOWLEDGEMENTS

R. van den Elzen (ZFMK Bonn), R. Prŷs-Jones and M. P. Adams (NHM Tring), G. Mayr (SMF Frankfurt) and R. Winkler (NMB Basel) provided access to bird collections. M. Hennen, J. Bates and D. Willard (FMNH

Chicago) sent specimens, and J. V. Remsen and S. W. Cardiff (LSUZM Baton Rouge) and D. Willard (FMNH Chicago) provided additional measurements. We thank R. Diesener, S. Frahnert, C. Bracker, P.-R. Becker, J. Fjeldså, N. Krabbe and J. Mlíkovsky for information about collection holdings. We are grateful to Jörg Albrecht, Susanne Fritz, Christian Hof, Thomas Müller, Eike-Lena Neuschulz, Marjorie Sorensen and Diana Bowler for valuable comments on the research ideas and the development of the modelling approach. W.D.K. acknowledges a University of Amsterdam starting grant. D.M.D. was supported by a grant from the German Research Foundation (DE 2754/1-1). Field work at Manú was conducted under the permits 041-2010-AG-DGFFSDGEFFS, 008-2011-AG-DGFFS-DGEFFS, 01-C/C-2010SERNANP-JPNM, and 01-2011-SERNANP-PNM-JEF. Finally, we want to thank Kenneth Feeley and four anonymous reviewers for giving us valuable advice to improve the manuscript.

DATA ACCESSIBILITY

Species' current elevational ranges and species-specific vertical distances (Tables A1 and A2), morphological trait data of plants and birds (Tables A3 and A4) as well as current and projected species richness, functional richness (Tables A5 and A6) and functional identity (Tables A7 and A8) of plant and bird communities are provided at the DRYAD data repository (https://doi.org/10.5061/dryad.c0n737b).

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BIOSKETCH

Larissa Nowak is interested in how functional traits shape biotic interactions and in how functional diversity of ecological communities might change under climate change in tropical ecosystems. This study is part of her dissertation at SBiK-F and Goethe University and has resulted from an ongoing collaboration between SBiK-F, IBED and ZFMK.

Author contributions: L.N., W.D.K., I.M.A.B. and M.S. developed the research ideas; L.N., W.D.K., I.M.A.B. and M.S. conceived the modelling approach with input from D.M.D. and K.B.G.; L.N., I.M.A.B., D.M.D. and T.T. compiled distribution and trait data; L.N. analysed the data and wrote the first draft of the manuscript, and all authors commented on the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Nowak L, Kissling WD, Bender IMA, et al. Projecting consequences of global warming for the functional diversity of fleshy-fruited plants and frugivorous birds along a tropical elevational gradient. *Divers Distrib*. 2019;25:1362–1374. https://doi.org/10.1111/ddi.12946