



Contrasting drivers of diversity in hosts and parasites across the tropical Andes

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Edited by Pablo A. Marquet, Pontificia Universidad del Chile, Santiago, Chile, and approved January 6, 2021 (received for review May 26, 2020)

Geographic turnover in community composition is created and maintained by eco-evolutionary forces that limit the ranges of species. One such force may be antagonistic interactions among hosts and parasites, but its general importance is unknown. Understanding the processes that underpin turnover requires distinguishing the contributions of key abiotic and biotic drivers over a range of spatial and temporal scales. Here, we address these challenges using flexible, nonlinear models to identify the factors that underlie richness (alpha diversity) and turnover (beta diversity) patterns of interacting host and parasite communities in a global biodiversity hot spot. We sampled 18 communities in the Peruvian Andes, encompassing ~1,350 bird species and ~400 hemosporidian parasite lineages, and spanning broad ranges of elevation, climate, primary productivity, and species richness. Turnover in both parasite and host communities was most strongly predicted by variation in precipitation, but secondary predictors differed between parasites and hosts, and between contemporary and phylogenetic timescales. Host communities shaped parasite diversity patterns, but there was little evidence for reciprocal effects. The results for parasite communities contradicted the prevailing view that biotic interactions filter communities at local scales while environmental filtering and dispersal barriers shape regional communities. Rather, subtle differences in precipitation had strong, fine-scale effects on parasite turnover while host–community effects only manifested at broad scales. We used these models to map bird and parasite turnover onto the ecological gradients of the Andean landscape, illustrating beta-diversity hot spots and their mechanistic underpinnings.

generalized dissimilarity modeling | Neotropics | mountains | phylobetadiversity | community composition

Turnover in community composition across space, or “beta diversity,” reflects eco-evolutionary processes that determine range limits of species (1–3). These processes include adaptive specialization on particular habitats, barriers to dispersal, and interactions among species (4–6). Antagonistic interactions between hosts and parasites may have an underappreciated effect on turnover (7), as evidenced by the sensitivity of host populations to novel parasites. For example, introductions of avian malaria (*Plasmodium relictum*) and avian pox (*Avipoxvirus*) led to extinctions or range contractions for dozens of endemic Hawaiian honeycreeper species (8). Introduced parasites have also driven shifts in community composition when competing hosts differ in susceptibility to infection (9). While these cases highlight extreme impacts of parasites on host communities, it remains unclear whether host–parasite interactions generally drive turnover in continental faunas, whether such effects are reciprocal or unidirectional, and whether these interactions also impact diversity patterns at regional scales or over evolutionary time.

A persistent challenge in studying the factors that underlie community assembly is that turnover is dynamic and exhibits nonlinear variation over space and time (10). As a result, different processes may underlie turnover, depending on the scale at which the community is defined (11–13). For instance, numerous studies have asserted that adaptive specialization on abiotic conditions and barriers to dispersal drive regional turnover patterns while biotic interactions filter communities locally (2, 14). Still, the spatial scales of these various processes are uncertain (11, 15, 16), and empirical tests are complicated by the fact that potential drivers of turnover tend to be spatially autocorrelated (17).

To determine the drivers and scale of community turnover in complex systems, we need appropriate, nonlinear analytical tools. Generalized dissimilarity models (GDMs) are an extension of matrix regression that provides two notable innovations: 1) GDMs can incorporate various biotic and abiotic predictors into a single model, and 2) GDMs explicitly model the curvilinear relationship between community dissimilarity and ecological or

Significance

Interactions between hosts and parasites can reciprocally limit the ranges of individual species. But to what extent do they affect composition of communities? In the Andean biodiversity hot spot, we tested why host and parasite communities vary over spatial and temporal scales. Variation in rainfall was the predominant predictor of turnover for both hosts and parasites. However, the effects of species interactions were asymmetric: Parasite communities were strongly predicted by host communities, but not vice versa. Against conventional wisdom, climatic effects on parasite turnover were primarily local while biotic effects predominated regionally. Using our predictive models, we mapped faunal dissimilarity, illustrating hot spots of turnover that can guide conservation of host and parasite biodiversity.

Author contributions: S.M.M., L.N.B., J.L.W., T.V., and C.C.W. designed research; S.M.M., L.N.B., J.L.W., S.C.G., H.R.S., S.G.D., A.M.G., A.B.J., E.B., P.O., C.J.S., A.S., T.V., J.M.B., S.J.H., and C.C.W. performed research; S.M.M. analyzed data; and S.M.M. and C.C.W. wrote the paper with input from all authors.

The authors declare no competing interest.

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This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2010714118/-DCSupplemental>.

Published March 17, 2021.

geographic distance (4, 10, 18). This modeling framework is better suited than linear matrix regression to identifying key factors underlying turnover in complex environments (19–21). In addition, by incorporating phylogenetic measures of community diversity and similarity, we can use GDMs to test how drivers of turnover have varied over evolutionary time (22). Comparing “phylogenetic turnover” to species turnover allows us to distinguish deep-time processes that may restrict the ranges of clades from contemporary processes that may constrain the range limits of individual species (2). For example, evolutionary conservation of traits may exclude entire clades from certain habitats, leading to strong phylogenetic turnover over ecological gradients (3). Alternatively, if traits that underpin environmental associations are evolutionarily labile, species turnover will be higher than phylogenetic turnover and better predicted by ecological variation.

The tropical Andes provide an ideal natural laboratory for investigating community turnover in response to biotic and abiotic changes in the environment. Habitable elevational gradients spanning more than 5,000 vertical meters encompass rapid changes in vegetation structure, temperature, atmospheric pressure, ultraviolet (UV) exposure, and precipitation (23, 24). The Andean cordillera generates broad orographic precipitation, but its complex topography also creates a patchwork of rain shadows. Rain-shadowed slopes and valleys fragment the ranges of humid and dry-adapted species, particularly those occurring at higher elevations (25–29). Environmental change across elevational gradients of the Andes is exceptionally rapid compared to change along axes parallel to the cordillera. As a result, spatial distance and environmental difference are decoupled. Pairs of communities separated by the same geographic distance may have similar or contrasting environments. In this way, this landscape provides the opportunity to pinpoint environmental effects on community turnover and distinguish them from the effects of dispersal limitation.

The Andes are a global hot spot for species richness and turnover, evolutionary distinctness, and small-ranged species (30–33). Species interactions are thought to be particularly important in shaping Andean community turnover: For example, Andean birds are often highly specialized on particular habitats and resources (13, 34), and competitive exclusion is thought to further limit and reinforce range boundaries (7, 35–37). However, parasitism has received less attention as a driver of turnover compared to competition (35, 37) and bird–plant mutualisms (36, 38, 39). One important group that could affect bird turnover is the hemsporidians (Apicomplexa: Haemosporida), a diverse clade of vector-borne parasites in the genera *Haemoproteus*, *Parahaemoproteus*, *Plasmodium*, and *Leucocytozoon* (40, 41). These parasites can reduce the fitness of their hosts, even in low-level chronic infections (42), and are thought to have the potential to shape avian biogeographic patterns (40, 43). Hemsporidian communities in turn are thought to be influenced to varying degrees by host community, climate, and barriers to dispersal (44–51), but improved modeling frameworks with new data are needed to reciprocally test the causes of host and parasite turnover across biodiverse, tropical landscapes.

In this study, we identified and compared the drivers of diversity in interacting bird and hemsporidian communities of the Peruvian Andes. First, we tested whether similar or different drivers affect host and parasite turnover; second, we tested how drivers of turnover vary with spatial scale; and third, we tested how drivers of turnover have changed over evolutionary time. Then, we used a complementary modeling approach to identify sources of variation in species richness among host and parasite communities, respectively. We used these models to map host and parasite turnover and richness to identify hot spots for faunal overlap and transition, critical zones for biodiversity study and protection.

Results and Discussion

We analyzed host and parasite richness and turnover among 18 communities spanning 7° of latitude, 4,000 m of elevation, and

2 m of annual precipitation (Fig. 1 and *SI Appendix*, Table S1). We compiled lists of host and parasite species in each community using specimen-based field surveys, bird species range maps, and PCR screening and sequencing of host tissues for hemsporidian parasite infections (*Methods*). We approximated hemsporidian species limits using a conservative haplotype clustering approach (52–54). Our complete dataset comprised 1,345 bird species (526 of which we screened for parasites) and 400 parasite species. We then modeled turnover and richness across communities using a suite of ecoclimatic (temperature, precipitation, net primary productivity [NPP], and elevation) and biotic (host and parasite species turnover and richness) predictor variables.

Drivers of Host and Parasite Turnover. Precipitation was the strongest predictor of both host and parasite species turnover (Fig. 2*A* and *B*). The greater the difference in precipitation regimes, the fewer bird and hemsporidian species were shared between any two localities. The principal effect of precipitation on community composition in two such different groups of organisms

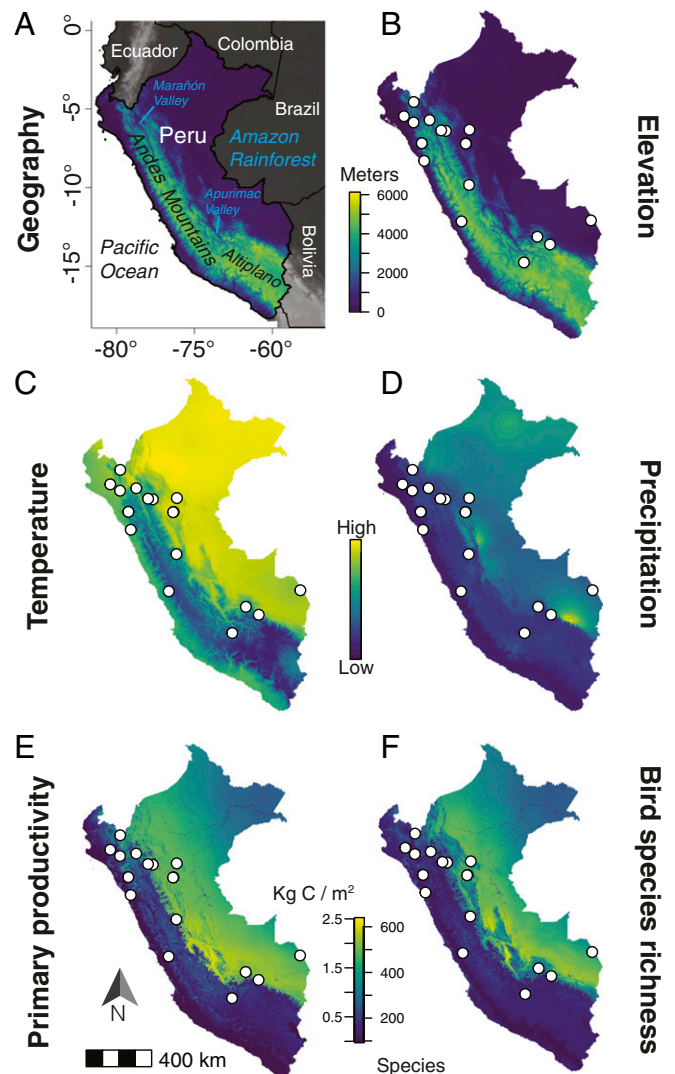


Fig. 1. Geography of the Peruvian Andes (A) and variables used to predict community turnover: (B) elevation; (C) temperature (PC1 accounting for 82% of variation in 11 WorldClim temperature variables) (93); (D) precipitation (PC1, accounting for 84% of variation in nine WorldClim precipitation variables); (E) net primary productivity (94); (F) bird species richness from GAM model. White circles in B–F represent locations of 18 communities in this study. Some points overlap; see *SI Appendix*, Fig. S2 for detail.

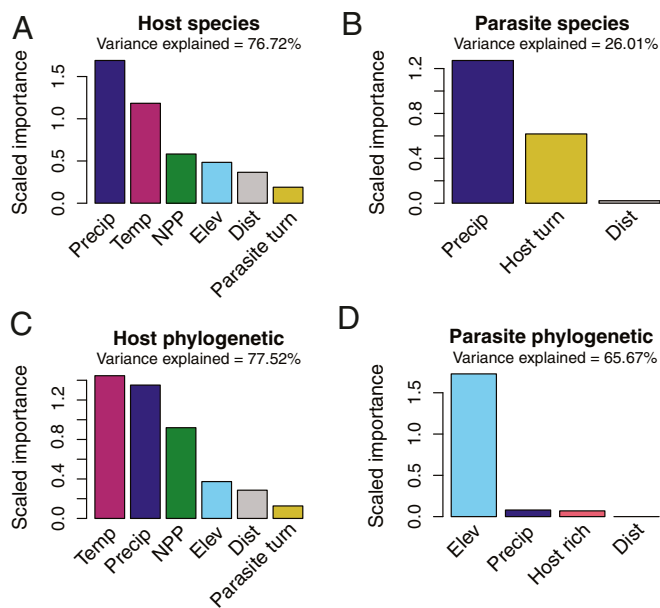


Fig. 2. Best predictors of host and parasite community turnover. Predictor importance is the change in total variance explained by the model when that predictor is randomized (10). Importance is scaled for comparison across models. Separate models were run to predict host and parasite species turnover (A and B) and host and parasite phylogenetic turnover (C and D). Predictors are abbreviated as follows: dist, distance; elev, elevation; host rich, host richness; host turn, host turnover; NPP, net primary productivity; parasite turn, parasite turnover; precip, precipitation; temp, temperature.

underscores how the Andean cordillera shapes biodiversity by creating rainfall variability. In the Peruvian Andes, local heating and westward transport of Amazonian moisture fuel deep convective storms, and the network of valleys and ridges creates local rain-shadow effects and alternating bands of humid, hyperhumid, and semiarid conditions (55). High precipitation sites in this region exceed 4,000 mm/y, with spatial variability reaching 190 mm/km (56). Our results suggest that these exceptional precipitation gradients underpin beta diversity in the tropical Andes across diverse taxa.

After accounting for precipitation, drivers of host and parasite turnover were strikingly different. Temperature, NPP, elevation, and geographic distance were all important predictors of host turnover (Fig. 2). However, parasite turnover explained very little variation in host species turnover, and parasite richness explained none (Fig. 24). These results suggest that bird species' ranges are constrained principally by a suite of environmental characteristics and far less, if at all, by physical dispersal limits or hemosporean parasites.

In contrast, host species turnover was a strong predictor of parasite species turnover, only exceeded by precipitation in its proportion of variance explained (Fig. 2B). Hemosporeans are not strict specialists and often can infect sets of phylogenetically clustered host species (50, 54, 57, 58). Although hemosporeans are known to use related hosts in different communities (58), our results emphasize that availability of compatible hosts does constrain parasite ranges. The importance of precipitation and host turnover in driving parasite turnover suggests that deterministic processes of host and environmental specialization structure hemosporean ranges. The strong contribution of rainfall to parasite turnover seemed paradoxical, given that these organisms have no free-living stage and thus have limited interaction with the external environment. Range sensitivity to precipitation likely reflects the distribution of the various dipteran vectors, all of which undergo aquatic or

moisture-dependent developmental stages (40). However, there is evidence that the abiotic environment can also directly constrain endoparasite ranges via unknown mechanisms (59, 60). Although similarity between parasite communities typically decays with increasing distance (50, 61), geographic distance had a minimal effect on parasite turnover in our models (Fig. 2B), suggesting that dispersal limitation is far less important than environmental and host effects on parasite species' range limits. In separate models for each genus of parasites, different environmental factors contributed to turnover; however, aspects of the host community were important in each model (SI Appendix, Fig. S1).

Our results corroborate an important role for antagonistic host–parasite coevolution in structuring parasite communities (43, 48, 62), but the effects were not reciprocal (Fig. 2A and B). The stronger effect of biotic interactions on parasite turnover versus host turnover was consistent with the unidirectional dependence of parasites upon their hosts. Indeed, our results are consistent with previous evidence in supporting the higher sensitivity of parasite communities to changes in host communities than vice versa (21, 51). The minor, but significant, contribution of parasite turnover to host turnover (Fig. 2A and C) suggests that we should not yet rule out a peripheral role for parasites and pathogens in limiting host distributions. It is possible that other unmodeled biotic interactions (e.g., other parasites, pathogens, interspecific competition, etc.) would explain residual variation in bird species turnover. However, our models, relying principally on environmental variables, explain most (>75%) of the observed variation. Our results therefore support the hypothesis that environmental filtering is the primary process driving turnover in tropical Andean bird communities.

Spatial Scale-Dependent Processes. Host species turnover increased nearly linearly over ecological gradients of temperature, precipitation, and NPP (Fig. 3B, C, and G). Thus, both minor (i.e., between neighboring communities) and more substantial ecological differences (between communities on opposite sides of the Andes) were associated with turnover in the host community. Climate and habitat characteristics reliably emerge as drivers of bird turnover both locally (13, 63–65) as well as over broader spatial scales (51, 66–69); however, it has been unclear whether turnover is gradual or abrupt over ecological gradients. Our analyses showed that bird communities in the Peruvian Andes change predictably, and additively with changes in habitat and climate. This result reinforces the idea that at least some of the processes that constrain species ranges operate along spatial continua (15, 70).

In contrast to climatic variables and primary productivity, the effect of elevation on bird species turnover occurred primarily at local scales. Once communities were separated by more than ~2,000 m (half the span of the total elevational gradient), the effects of elevation on turnover appeared to saturate (Fig. 3D). The inclusion of elevation in models likely reflects a degree of specialization by bird species on abiotic variables that are directly linked to elevation: partial pressure of oxygen, air density, and/or UV radiation (71). However, as communities become more separated along elevational gradients, the effects of those variables are likely overshadowed by aspects of the environment that have stronger effects on habitat structure and resource availability: e.g., temperature, precipitation, and NPP. Similarly, turnover associated with geographic distance occurred almost exclusively over the first ~300 km, a distance ~20% of the size of the region (Fig. 3A). This pattern suggests that the effects of dispersal limitation on communities, such as the abrupt differences observed on either side of rivers or mountain passes, were primarily local; however, among communities separated by larger geographic distances, differences in environment alone were sufficient to explain variation in bird community composition (6). Overall, the distance effect was relatively minor (Fig. 2A and C), further emphasizing that

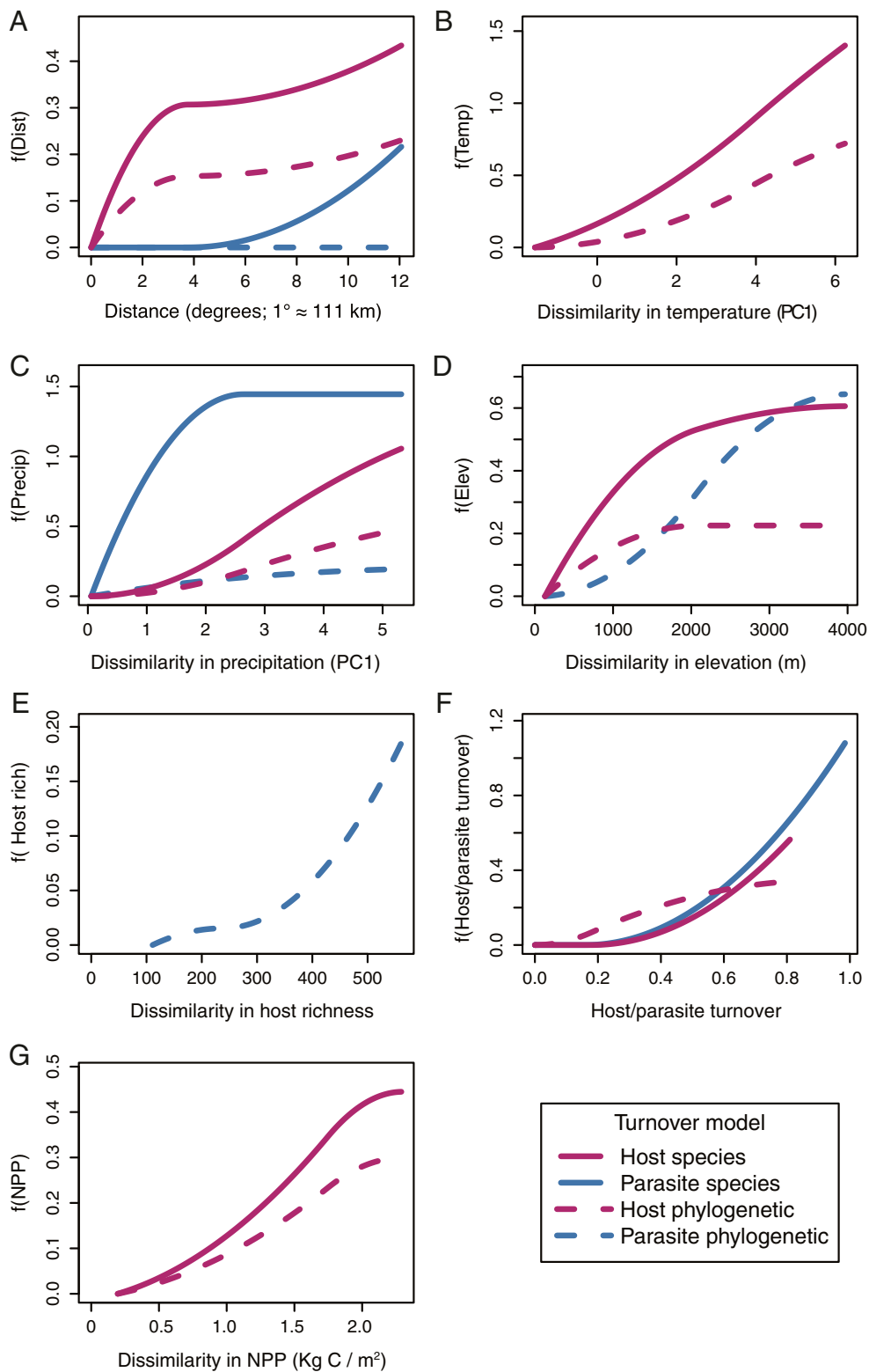


Fig. 3. I-splines showing the fitted relationship between GDM predictor variables and different measures of host and parasite community dissimilarity. Each panel shows how turnover increases between pairs of communities with increasing (A) geographic distance and increasing dissimilarity in (B) temperature; (C) precipitation; (D) elevation; (E) host richness; (F) host or parasite community composition; and (G) net primary productivity. The maximum height of each spline indicates the total degree of community turnover predicted by that variable while holding the others constant. The shape of the spline corresponds to how the rate of turnover changes over the ecological gradient. "Host/parasite turnover" refers to the effects of parasite turnover on host turnover and vice versa. Splines are only shown for factors included in the best model for each measure of turnover.

environmental filtering has been far more important than physical isolation in driving community assembly, especially at the regional scale.

The parasite community was structured by aspects of the host community and abiotic environment; however, these processes occurred over distinct scales. For parasite turnover, effects of precipitation were primarily local, indicating that slight differences in precipitation affected community composition (Fig. 3C). By contrast, minor changes to the host community did not result in much parasite turnover. Instead, the effects of host species richness and host turnover on parasite turnover were strong only after exceeding an apparent threshold of host community differentiation (Fig. 3E and F). Notably, the effects of parasite turnover on host turnover followed a similar spatial pattern although the total importance of biotic interactions in driving turnover was lower for hosts (Fig. 3F). These results contrast with previous assertions that habitat filtering and dispersal generate regional differences in community composition while biotic interactions shape community assembly locally (3, 15, 72). In the parasite communities that we studied, local adaptation to the abiotic environment was the primary predictor of parasite ranges. Within their ranges, parasites tended to exploit a subset of hosts that was somewhat flexible. However, once the host community changed sufficiently, availability of suitable hosts became the predominant factor restricting parasite ranges, leading to turnover.

Variation in Drivers of Host and Parasite Turnover over Time. A parallel suite of factors predicted the turnover of bird species and bird lineages (phylogenetic turnover), and these factors manifested at similar spatial scales across ecological gradients (Figs. 2 and 3). The general symmetry between species turnover and phylogenetic turnover indicates that the ecological factors that structure bird communities have tended to be phylogenetically conserved, operating uniformly over evolutionary time. We initially expected elevation would drive species turnover because, in the tropics, closely related species tend to replace one another across elevational contours (71, 73, 74), and species tend to evolve toward having narrow elevational ranges (75) where they undergo predictable genetic adaptation to local atmospheric pressure (76). We also expected that phylogenetic turnover would be driven by elevation because some large Neotropical bird clades are almost entirely lowland restricted (e.g., antbirds), and there is deep phylogenetic signal in elevational ranges: for example, in hummingbirds (77). Contrary to expectations, we found that elevation was a relatively minor contributor to both species and phylogenetic models of turnover, in each case superseded by precipitation, temperature, and primary productivity (Fig. 2A and C).

Different factors drove parasite species and phylogenetic turnover, in contrast to the congruence between host species and phylogenetic turnover (Fig. 2). Elevation was the most important predictor of parasite phylogenetic turnover (Fig. 2D). This result reflects the elevational segregation of the three major genera of hemosporidians: *Haemoproteus* species span the elevational gradient, but *Leucocytozoon* species are found predominately at high elevations, and *Plasmodium* species at low elevations (54, 78). The distinct zonation of parasite clades is visible in the sigmoidal shape of turnover over the elevational gradient (Fig. 3D). Phylogenetic turnover increases sharply between communities separated by 2,000 m, corresponding to the distinct transition from *Plasmodium*-dominated to *Leucocytozoon*-dominated communities. Niche conservatism is expected to improve the fit of phylogenetic turnover models relative to species turnover models (22). Indeed, the GDM of parasite phylogenetic turnover explained more variance (66%) than the best model of parasite species turnover (26%). The latter value was also low because most parasite species were rare, and we often observed near-complete species turnover between pairs of communities (SI Appendix, Fig. S2). With such uniformly high turnover over the study area, the model had a limited ability to

identify underlying drivers. However, incorporating phylogenetic information into models of turnover greatly improves our ability to understand the processes structuring parasite diversity. Because species may be replaced by close relatives in neighboring communities, phylogenetic turnover between pairs of communities was lower and more variable, compared to species turnover (SI Appendix, Fig. S2). This greater amount of variation over the study area provided more power to test hypothesized drivers of turnover among parasite clades.

Differences in the factors that predict species and phylogenetic turnover suggest that the processes that structure hemosporidian distributions have varied over evolutionary time (2, 22). While the importance of elevation to parasite phylogenetic turnover implicates phylogenetic conservation of vectors, the effects of the bird community on parasite species turnover suggest that traits related to avian host compatibility are more labile. Birds have more complex immune systems than those of dipteran vectors (79); correspondingly, hemosporidians are thought to be able to exploit a wide range of dipteran hosts while compatibility of avian hosts is likely more restricted (80, 81). Selection on parasites to evade host immune defenses likely underlies the complex and shifting associations between bird and hemosporidian species (82, 83). The constraints of host compatibility likely generated the association between parasite species turnover and host species turnover; however, the evolutionary lability of parasite counter adaptations and associated host switches may explain why the host effects were not important in predicting parasite phylogenetic turnover.

Predictors of Host and Parasite Species Richness. We modeled variation in species richness of birds and hemosporidians in our communities using generalized additive models (GAMs), including the same suite of predictor variables as we used to model turnover. Net primary productivity and elevation explained a high proportion (78%) of variation in bird species richness among our communities (Fig. 1A and SI Appendix, Fig. S3 and Table S2). The strong positive relationship between primary productivity and species richness (SI Appendix, Fig. S3F and Table S2) is consistent with the hypothesis that tropical communities are hyperdiverse because greater resource availability promotes species coexistence (84, 85). Our model results for avian turnover complement models of richness and provide a plausible mechanism for heightened species diversity at the regional scale: Higher primary productivity facilitates greater species coexistence within communities while local adaptive specialization within an ecologically heterogeneous landscape creates strong community turnover over short distances, reinforced in some cases by local barriers to dispersal. The only significant predictor of hemosporidian species richness was the diversity of hosts that we sampled at that community, which explained 43% of deviance (SI Appendix, Fig. S4 and Table S3). This result suggests that more intensive sampling of this diverse community is needed to adequately model drivers of parasite species richness.

Model Limitations. The diversity and distribution of birds in the Peruvian Andes are better understood than those of their parasites. Correspondingly, our best models explained more variation in species turnover for birds compared to parasites (76% vs. 26%) and more variation in species richness (78% vs. 43%). Although our survey encompassed 400 hemosporidian lineages, the relatively low amount of variance explained by the parasite species model indicates that much of the hemosporidian diversity in Peru remains to be documented. Many, if not most, of the species expected to be driven extinct by climate change and habitat conversion will be parasites, adding urgency to the need for more intensive sampling and study of parasite and other symbiont communities, particularly in biodiversity hot spots (86, 87).

Our models did not include predictors relating to the dipteran hosts (vectors) of the parasite community. Each of the three parasite genera we studied is transmitted by a different dipteran family that has its own habitat and climatic niche (40, 88). Variation in the distribution of these vectors likely underlies the elevational segregation that we see among hemsporidian genera and may affect turnover within each genus (*SI Appendix*). Most available evidence suggests hemsporidian distributions are less constrained by vector compatibility than by vertebrate host compatibility (80, 89). Nevertheless, the role of vector availability and diversity in shaping hemsporidian distribution requires further study.

Map Projections of Turnover and Richness across the Region. We mapped our best models of host and parasite diversity onto the landscape of Peru using high-resolution topographic and environmental data (Figs. 1A and 4). To do this, we made a raster object created from transforming predictor variables using model-estimated coefficients. The map of bird species richness (Fig. 1A) corresponds closely to maps of NPP and elevation (Fig. 1B and E), the two strongest predictors in that model. For turnover models, because predicted values are dissimilarities between two points, we used a principal components analysis to reduce dimensionality of predictors and assigned the first three principal components (PCs) to the red, green, and blue channels on the maps. Areas with similar colors on each turnover map are expected to have similar communities; however, individual colors are composites of predictor variables and therefore do not represent any particular value (see *SI Appendix*, Tables S4–S7 for PC loadings of predictors). Spatial rasters of these maps are available for download and further study at https://github.com/smcnew/Peru_GDM.

Map projections of turnover highlighted known topographic features, ecotones, and major areas of biotic endemism. The maps clearly delineated the Andes, rain-shadowed valleys such as that of the Marañón River, and the well-known axis of community differentiation between the dry west slope of the Andes and the humid east-facing slopes (26, 29, 90). The map of bird species turnover (Fig. 4A) identified subtle differences between ecologically similar regions such as the northern and southern Amazon and more substantial differences between communities of the northern Peruvian Andean highlands and the cooler southern Altiplano plateau. In contrast, the map of bird phylogenetic turnover (Fig. 4C) showed less differentiation over latitudinal gradients, reflecting that avian clades at the genus level and above tend to be broadly distributed across the study area. The covariance of key environmental predictors generated broad geographic congruence among host and parasite maps. However, different combinations of predictor variables in each model resulted in the contrasting color schemes within each of the four turnover maps. While one caveat of model projections is that extrapolating to areas beyond the geographic extent of sampled localities may introduce errors, we believe our projections across the extent of Peru are appropriate because our sampling design encompasses a broad range of parameters for each of the important environmental variables (*SI Appendix*, Table S1).

Maps of turnover are needed to anticipate and mitigate threats to biodiversity. Areas of high turnover, such as where contrasting colors adjoin on the eastern and western flanks of the Andes (Fig. 4A–D), are expected to retain biodiversity under climate warming or shifts in rainfall regimes. Populations in heterogeneous regions, such as tropical mountains, may not need to move far to track climate niches, increasing their likelihood of persistence under changing environments (91, 92). Moreover, in areas with high beta diversity, small extensions of protected areas can greatly expand the number of conserved species (13). In this way, modeling the processes that underlie turnover and visualizing those processes at a regional scale illustrate how the evolutionary mechanisms that generate and maintain diversity are

necessary and useful foundations for setting habitat protection and restoration priorities.

Methods

Sampling and Specimen Data. Birds were sampled in the wild following protocols approved by the University of New Mexico Institutional Care and Use Committee (Protocol 08UNM033-TR-100117; Animal Welfare Assurance number A4023-01). Collections were authorized by permits issued by management authorities of Peru (004-2007-INRENA-IFFS-DCB, 135-2009-AG-DGFFS-DGEFFS, 0377-2010-AG-DGFFS-DGEFFS, 0199-2012-AG-DGFFS-DGEFFS, and 006-2013-MINAGRI-DGFFS/DGEFFS). Specimen data are available in the ARCTOS (<https://arctosdb.org>) and iDigBio (<https://www.idigbio.org>) databases and in *Dataset S1*. Specimens and tissues are primarily housed at the Museum of Southwestern Biology, the Field Museum of Natural History, and the Centro de Ornitología y Biodiversidad.

Community Geography and Abiotic Variables. Sampling localities were clustered into 18 communities based on geographic and elevational proximity (*Dataset S1* and *SI Appendix*, Fig. S5). We extracted the median elevation, latitude, and longitude for samples collected in each community and used those points as the geographic centers of each community (*SI Appendix*, Table S1). To characterize climatic variation among communities, we used 19 bioclimatic variables from the WorldClim database (93). We downloaded rasters of each of the bioclim variables using the “raster” package in R (version 3.5.1) at 2.5-arc minute resolution and cropped them to our study area (Peru). Then, we ran principle components analyses on the temperature variables (bioclim variables 1 to 11) and precipitation variables (12–19) to create composite measures of temperature and precipitation across Peru. PC1 of the temperature variables (hereafter “temperature”) explained 82% of variation in those variables. PC1 of the precipitation variables (“precipitation”) explained 84% of variation (Fig. 1C and D). Finally, we extracted temperature and precipitation values for each of our communities based on their median latitude and longitude.

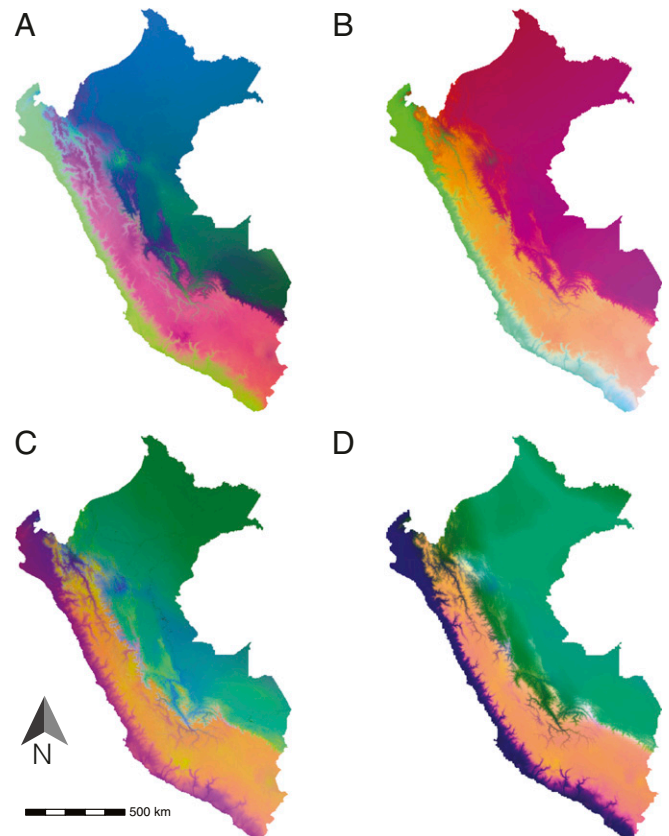


Fig. 4. Maps depicting turnover in (A) host species, (B) parasite species, (C) host phylogeny, and (D) parasite phylogeny. Maps were created by transforming and predicting top-ranked GDM models (Fig. 2) onto raster of predictor variables (10). Regions with similar colors within each map are expected to have similar communities.

We accessed NPP data using products created and maintained by the Numerical Terradynamic Simulation Group at the University of Montana (94). NPP is a measure derived from satellite imagery of the net amount of carbon fixed by plants in an ecosystem (95). NPP integrates the effects of sunlight, temperature, and precipitation on resource availability at the base of the food chain. Resource availability is a long-standing hypothesized driver of biodiversity gradients (96, 97). We used GeoTiff rasters of mean NPP from 2000 to 2015, cropped to our study area, and extracted values for each of our communities using the R package “raster.” Our environmental predictor variables (temperature, precipitation, NPP, and elevation) were not strongly correlated ($|r| < 0.7$) (98), with the exception of temperature and elevation ($r = 0.86$) (SI Appendix, Fig. S6). We tested whether including either temperature or elevation in models (and not both) would qualitatively change results: Removing one of the two predictors generally reduced explained variance (SI Appendix, Fig. S7). In addition, explained variance decreased substantially when the dropped predictor was particularly important (e.g., temperature from models of host turnover and elevation from parasite phylogenetic turnover), indicating that, although correlated, these two variables are imperfect proxies for one another (SI Appendix, Fig. S7). We opted to keep both temperature and elevation in the model because temperature is a direct measure of climatic conditions, and elevation is associated with other important environmental gradients, such as UV exposure and atmospheric pressure, and because GDMs are considered fairly robust to collinearity (99).

Parasite Community Data. We used molecular screening to detect infections of *Haemoproteus* (including *Parahaemoproteus*), *Leucocytozoon*, and *Plasmodium* parasites. In total, we screened 3,754 individual hosts from 526 species for hemosporidian infection. We extracted DNA from avian tissue or blood using QIAGEN kits and used three nested PCRs to amplify a 478-base pair (bp) fragment of the parasite cytochrome-b (*cyt b*) mitochondrial gene (100–102). Positive infections were visualized on agarose gels and then sequenced in both directions. We identified hemosporidian infections to genus through comparison with sequences published on the GenBank and MalAvi databases (103). Species limits are not well understood in hemosporidian parasites; however, slow rates of evolution suggest that even slightly diverged lineages may represent distinct evolutionary entities (52). We followed previous studies (53, 54) in clustering haplotypes into distinct lineages (i.e., species) if they were $\leq 0.5\%$ divergent (up to 2-bp substitutions) and recovered from similar hosts and/or similar ranges. Despite recent work suggesting that screening of *cyt b* barcodes may fail to detect low-intensity hemosporidian infections when a host is coinfecting with multiple parasite lineages (104), use of *cyt b* barcodes remains an effective and standardized method to screen for hemosporidian parasites (103).

In total, we detected and sequenced 1,694 infections, representing 514 unique haplotypes, which we clustered into 400 distinct parasite “species” (Dataset S1) (105–108). Estimated parasite species richness ranged from 22 to 263 per community (SI Appendix, Table S1). The most common parasites were *Haemoproteus* (51.5% of infections), followed by *Leucocytozoon* (27.2%) and *Plasmodium* (21.3%). Individual birds were infected with up to five distinct parasite species; the median number per infected host was one.

Estimating Parasite Richness and Community Dissimilarity. We estimated parasite species richness of each community using the R package “iNext,” which rarefies data to account for differences in sampling effort and then provides asymptotic diversity estimates (109). We rarefied infections per community to the minimum detected across communities ($n = 44$) and calculated Bray–Curtis dissimilarity using the “vegan” package to characterize parasite species turnover (110). We used generalized UniFrac distance to characterize parasite phylogenetic turnover, which weights distances by species abundance (111). UniFrac distance estimates dissimilarity using a phylogenetic tree of all taxa present in two communities. We estimated the parasite phylogeny using Bayesian inference in BEAST (v.1.10.0) (112, 113) using the broad-platform evolutionary analysis general likelihood evaluator (BEAGLE) library (114). We used the generalized time reversible (GTR) nucleotide substitution model and rooted the tree with *Leucocytozoon* (115). To avoid subsampling artifacts, we rarefied and calculated Bray–Curtis and UniFrac dissimilarities 1,000 times and used the mean dissimilarities for GDM analyses (SI Appendix, Fig. S2). We tested whether model fit could be improved by excluding rare parasite species. When we included only the 75 parasite species that were detected at least five times, we found that the dissimilarity matrix was visually similar (SI Appendix, Fig. S8 A and B) and drivers of turnover were unchanged (SI Appendix, Fig. S8 C and D).

We additionally calculated Bray–Curtis and generalized UniFrac dissimilarities separately for each of the three major hemosporidian genera (*Haemoproteus*,

Leucocytozoon, and *Plasmodium*). For each genus, we only included communities in which we detected at least 20 infections of that genus and then rarefied to the minimum number of infections detected across communities 1,000 times (SI Appendix).

Host Community Data. We compiled a fine-scale list of host species that were predicted to be present at each community based on BirdLife International distribution data (116) and museum specimen records. To do this, we intersected bird distribution shapefiles with the geographic center points of each of our 18 communities. Then, we filtered this subset of hosts using data on species elevational ranges (90, 117) to include only those species whose elevational ranges overlapped the elevational range of the community. Finally, we combined that list with specimen records from the Museum of Southwestern Biology that included any bird species collected within 0.001° of each community center point (<https://arctosdb.org>). The resulting host list included 1,345 species across our 18 communities (Dataset S2). To map model projections generated from GDMs, we created a raster of bird species richness across Peru using BirdLife species distributions and the R package “letsR” at a resolution of 0.01° (~ 100 m) (118).

To quantify host species turnover, we calculated Jaccard dissimilarity (based on presence/absence of species) between pairs of communities using the R package “vegan” (110) (SI Appendix, Fig. S2). Bray–Curtis and Jaccard dissimilarities are rank-order similar and relatively robust to taxonomic error and undersampling (119). Phylogenetic community turnover was characterized with unweighted UniFrac dissimilarity. We generated a host phylogeny by using the phylogeny subsets tool from BirdTree.org (31, 32). BirdTree.org uses a calibrated backbone tree of well-supported avian clades and generates trees for all bird species by partially constraining them to their respective clade. We arbitrarily chose the posterior distribution of 100 likely trees using the Hackett et al. (120) backbone.

GDMs. We tested the relative contributions of biotic and abiotic factors in predicting parasite and host community turnover using GDMs in the R package “gdm” (10, 22). For each environmental predictor variable, the model fits an l-spline function using maximum likelihood estimation. l-splines have a series of “knots” where polynomial pieces connect and thus can model variable rates of turnover along the environmental gradient. The height of each spline reflects the degree of compositional turnover between communities.

We fit separate models predicting host species turnover (Jaccard dissimilarity), host phylogenetic turnover (unweighted UniFrac dissimilarity), parasite species turnover (Bray–Curtis dissimilarity), and parasite phylogenetic turnover (generalized UniFrac dissimilarity). We first fit full models containing a suite of environmental predictor variables we hypothesized could drive turnover: distance, temperature, precipitation, elevation, and NPP. The full models of host turnover also included parasite species richness and parasite community dissimilarity as predictors. The full models of parasite turnover included host species richness, host community dissimilarity, and the Shannon diversity index of the hosts sampled at each community (to account for differences in sampling effort). The body size distributions of sampled hosts were similar across communities (SI Appendix, Fig. S9). After fitting full models, we performed backward-elimination model selection following Ferrier et al. (10) to choose models that explained the greatest amount of variance with the fewest predictors. We created maps of host and parasite turnover using best GDMs which we projected back onto rasters of predictor variables following Ferrier et al. (10). We subsequently created separate models of species and phylogenetic turnover for each genus of parasites (*Haemoproteus*, *Leucocytozoon*, and *Plasmodium*) (SI Appendix, Fig. S1).

GAMs. We used generalized additive models (GAMs) to identify factors that affect host and parasite species richness across our sampling sites. GAMs are an extension of generalized linear modeling that, like GDMs, incorporate smoothing functions to better model nonlinear data (121). Host and parasite species richness were separately modeled with a negative binomial error structure using the same suite of predictor variables as used in the GDMs. Instead of “geographic distance” as a predictor variable, we used latitude. Best fitting models were chosen through backward elimination of nonsignificant variables. We used the “raster” package to project model predictions onto maps and visualize estimated host species richness across Peru (Fig. 1F). For GAM models of parasite richness, only the Shannon diversity index of sampled hosts at that community was a significant predictor so we did not create a projected richness map.

Data Availability. Specimen information is available from the Arctos (<https://arctosdb.org>), iDigBio (<https://www.idigbio.org>), MalAvi (<http://130.235.244.92/Malavi/index.html>), and GenBank databases (JQ988105–JQ988751 and

MN458565–MN459658) and in Dataset S1. Data and code used for analyses are available at GitHub, https://github.com/smnew/Peru_GDM.

ACKNOWLEDGMENTS. We are grateful for our coauthor and friend, Paloma, who passed away tragically before this paper was completed. We thank Iris Olivas, Benjamin Winger, Matthew Graus, Laura Pagès Barceló, Alessandra Quiñonez, Jano Nuñez, Robert Driver, William Talbot, Daniel Lane, Chris Merkord, Dora Susanibar, Gregory Schmitt, Donna Schmitt, Walter Vargas, Jorge Tiravanti, Matthew Jones, Phred Benham, Elizabeth Beckman, Natalie Wright, Monica Flores, Karen Verde, José Huaroto, Mariela Combe, Abraham Urbay (deceased), Fernando Angulo, Jennifer Clark, Peter Yaworsky,

Matthew Fitzpatrick, and the Fuller Evolutionary Biology Laboratory. We thank Servicio Nacional Forestal y de Fauna Silvestre and the local communities throughout Peru who permitted and facilitated our fieldwork. We thank the editor and two anonymous reviewers. This work was supported by NSF Grant DEB-1146491, NSF Grant PRFB-1611710, a Rose Postdoctoral Fellowship (to S.M.M.), Center for Evolutionary and Theoretical Immunology Seed Grant NCRN-NIH P20RR018754, the Davee Foundation, the Faulk Medical Research Trust, and the Pritzker DNA Laboratory. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

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