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Ecology, not distance, explains community composition in parasites of sky-island Audubon's Warblers ☆

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ABSTRACT

Haemosporidian parasites of birds are ubiquitous in terrestrial ecosystems, but their coevolutionary dynamics remain poorly understood. If species turnover in parasites occurs at a finer scale than turnover in hosts, widespread hosts would encounter diverse parasites, potentially diversifying as a result. Previous studies have shown that some wide-ranging hosts encounter varied haemosporidian communities throughout their range, and vice-versa. More surveys are needed to elucidate mechanisms that underpin spatial patterns of diversity in this complex multi-host multi-parasite system. We sought to understand how and why a community of avian haemosporidian parasites varies in abundance and composition across elevational transects in eight sky islands in southwestern North America. We tested whether bird community composition, environment, or geographic distance explain haemosporidian parasite species turnover in a widespread host that harbors a diverse haemosporidian community, the Audubon's Warbler (*Setophaga auduboni*). We tested predictors of infection using generalized linear models, and predictors of bird and parasite community dissimilarity using generalized dissimilarity modeling. Predictors of infection differed by parasite genus: *Parahaemoproteus* was predicted by elevation and climate, *Leucocytozoon* varied idiosyncratically among mountains, and *Plasmodium* was unpredictable, but rare. Parasite turnover was nearly three-fold higher than bird turnover and was predicted by elevation, climate, and bird community composition, but not geographic distance. Haemosporidian communities vary strikingly at fine spatial scales (hundreds of kilometers), across which the bird community varies only subtly. The finer scale of turnover among parasites implies that their ranges may be smaller than those of their hosts. Avian host species should encounter different parasite species in different parts of their ranges, resulting in spatially varying selection on host immune systems. The fact that parasite turnover was predicted by bird turnover, even when considering environmental characteristics, implies that host species or their phylogenetic history plays a role in determining which parasite species will be present in a community.

1. Introduction

Spatial variation among parasite communities provides a critical window into ecology and evolution of host–parasite dynamics. Studies in a variety of host–parasite systems have tested possible mechanisms of parasite community assembly (e.g. Brooks and Hoberg, 2007; Poulin, 2011; Huang et al., 2014; Krasnov et al., 2016; Clark et al., 2017). These studies have shown that parasite community composition can be affected by climate, dispersal barriers, the host community, or host phylogenetic community structure, to varying degrees. For example, in a study of haemosporidian parasites of birds across Australasia, Clark et al. (2017) found evidence that each of these drivers affects parasite

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☆ Note: Data reported in this paper are available in GenBank (Accession numbers **MF752555–MF752704**), MalAvi and ARCTOS.

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community structure. These mechanisms need to be tested at smaller spatial scales, in various geographic settings, and with various taxa in order to reveal general principles of the host–parasite community dynamics over space and time, particularly in light of climate change (Brooks and Hoberg, 2007).

Community similarity generally declines with distance, referred to as the 'distance-decay' relationship (Nekola and White, 1999; Poulin, 2003), and it is thought that these relationships and their underlying predictors differ between micro-organisms such as parasites, and macro-organisms such as hosts (Astorga et al., 2012; Nemergut et al., 2013). Turnover, or change in community composition across space, might be closely linked for host and parasite communities due to the total dependence of parasites on hosts. This has been demonstrated previously for haemosporidian parasites of birds, for both non-phylogenetic (Ishtiaq et al., 2010; Svensson-Coelho and Ricklefs, 2011) and phylogenetic turnover (Clark and Clegg, 2017). Phylogenetic measures of turnover, or phylogenetic beta diversity, can provide insights on the evolutionary implications of various patterns of host and parasite turnover (Fountain-Jones et al., 2018). Turnover for hosts or parasites can be affected by ecological variables including biotic and/or abiotic variables, which can potentially decouple turnover from distance (Warburton et al., 2016).

There are several possible reasons to expect mismatches between host and parasite turnover. Species traits such as dispersal ability or niche breadth should affect rates of turnover, and these traits could differ systematically between hosts and parasites. Parasite dispersal potential is often believed to be greater than that of hosts, because potential for dispersal at different life stages or in different host species is possible (Njabo et al., 2011; Carlson et al., 2015). Additionally, host-generalist parasites may have opportunities to expand their geographic ranges beyond individual host species, whose ranges are constrained by forces that may not affect the parasite (Poulin, 2003). These mechanisms would predict lower parasite turnover relative to host turnover. On the other hand, there are several reasons why parasite species turnover could be higher than that of hosts: (i) Parasite dispersal may be reduced because they are sensitive to environmental clines, as when conditions for parasite transmission or reproduction (e.g. vectors) are limited spatially or seasonally (Njabo et al., 2011); (ii) particular reproductive modes (e.g. longer times in the free-living stages, or shorter generation times) could facilitate faster diversification in parasites (Mazé-Guilmo et al., 2016); and (iii) parasites can become physically isolated by host-switching within geographic regions, causing accumulation of parasite diversity at a smaller spatial scale than in hosts (Galen and Witt, 2014). Disentangling potential drivers of parasite community composition will provide insights into the evolutionary stability of host–parasite relationships and the extent to which host and parasite communities will respond similarly to climate change.

Haemosporidians (Apicomplexa: Haemosporida) are a cosmopolitan clade of intracellular blood parasites that includes at least three genera that infect songbirds: *Parahaemoproteus*, *Plasmodium*, and *Leucocytozoon* (Galen et al., 2018). These parasites can affect hosts by diminishing survival and condition (Marzal et al., 2008; Asghar et al., 2015), reducing reproductive success (Marzal et al., 2005; Knowles et al., 2010), and potentially accelerating diversification of allopatric or parapatric populations that are exposed to different parasite faunas (Ricklefs, 2010; Thornhill and Fincher, 2013). Haemosporidians are thought to diversify rapidly via host switching (Ricklefs and Outlaw, 2010; Galen and Witt, 2014; Ricklefs et al., 2014), but the roles of geography and physical isolation in diversification remain poorly understood. Some haemosporidian parasites are closely associated with a single host species, while others appear to be broadly distributed generalists (Moens and Pérez-Tris, 2016; Soares et al., 2017). In at least some cases, the distributions of haemosporidians are thought to depend on avian host species distributions (Reullier et al., 2006), vector abundance (Kimura et al., 2006), or climate (Sehgal et al., 2010). Although over 3000 unique lineages of avian haemosporidians have been documented (Bensch et al., 2009), it remains difficult to compare host and parasite richness because the vast majority of haemosporidian-host interactions remain undescribed. One repeated finding from previous studies in both tropical and temperate zones is that there are differences among the three haemosporidian genera in their biogeographic tendencies: *Plasmodium* lineages tend to be broadly distributed host generalists (e.g. Walther et al., 2016), *Parahaemoproteus* lineages tend to be more host-specialized (e.g. Moens and Pérez-Tris, 2016), and *Leucocytozoon* lineages tend to be sensitive to climate (e.g. Galen and Witt, 2014).

The spatial scale and potential drivers of haemosporidian turnover have been tested in both island and continental systems, with variable results (Svensson-Coelho and Ricklefs, 2011; Scordato and Kardish, 2014; Ellis et al., 2015; Fecchio et al., 2017b; Soares et al., 2017). In certain island systems, the distance-decay effect has been found to vary across haemosporidian genera (Ishtiaq et al., 2010) and across host species (Svensson-Coelho and Ricklefs, 2011). In continental systems, there is evidence of geographic distance effects on parasite community turnover in some studies (Fecchio et al., 2017a), but not in others (Ellis et al., 2015; Fecchio et al., 2017b). Variation in the host community often predicts variation in the parasite community; for example, host turnover explains parasite turnover in Melanesian (Clark and Clegg, 2017), Caribbean (Ricklefs et al., 2011), and eastern North American (Ellis et al., 2015) haemosporidian communities. Interestingly, haemosporidian lineages infecting Northern Cardinals (*Cardinalis cardinalis*) in eastern North America were found to vary from locality to locality more than expected based on turnover in the whole haemosporidian community, suggesting coevolution with different parasite lineages in different parts of the host range (Ellis et al., 2015). In sum, previous studies show that the spatial scale of haemosporidian turnover and its causes remain poorly understood.

The sky islands of the arid southwestern United States are a setting in which the causes of turnover among parasite communities can be tested at a relatively fine spatial scale with well-defined dispersal barriers. The term 'sky island' refers to high elevation forests that are geographically isolated by expanses of low, arid habitats (McCormack et al., 2009). Southwestern sky islands were most recently connected during the Last Glacial Maximum (LGM; ~18–9 kilo-annum (ka) although some sky-island clades diversified during earlier divergence events, >1 million years ago (Mya) (McCormack et al., 2008). It is not known whether parasite community variation among sky islands tracks host community variation or is governed by other factors.

Here we address patterns and drivers of haemosporidian turnover among sky islands separated by tens to hundreds of kilometers using generalized dissimilarity modeling (GDM). GDM, a form of non-linear matrix regression, permits analysis of spatial patterns of community dissimilarity as a function of environmental dissimilarity and geographic distance (Ferrier et al., 2007; Fitzpatrick et al., 2013). It is an appropriate method to understand turnover because it accounts for expected non-linear relationships of dissimilarity with distance, and it is robust to collinearity (Fitzpatrick et al., 2013; Warren et al., 2014; Glassman et al., 2017). As a first step toward understanding community turnover among sites, we sought to describe variation in haemosporidian abundance and test its potential drivers; therefore, we used generalized linear models (GLMs) to ask: What, if anything, predicts avian haemosporidian infection in an array of southwestern sky islands? We then used GDM to ask: Do climate, host community, and/or geographic distance explain turnover of haemosporidian lineages among these sky islands?

As a consistent and practical way of sampling sky-island haemosporidian communities, we surveyed parasites from a widespread and abundant host, the Audubon's Warbler (*Setophaga auduboni; Aves:* Parulidae). This species breeds above ~2100 m elevation in forests of southwestern North America, becoming more abundant at higher elevations (Hunt, P.D. and Flaspohler, D.J., 1998). Yellow-rumped Warbler (*Setophaga coronata*), Birds of North America Online, https://doi.org/10.2173/bna.376). *Setophaga auduboni* exhibits little to no phenotypic variation (Milá et al., 2007) or population genomic differentiation (Toews et al., 2016) across the geographic extent of our study area. Given the tendency of haemosporidian parasites to infect multiple host species (Moens et al., 2016), we expect that *S. auduboni* shares a large proportion of its haemosporidian lineages with other hosts. Infection rates in a single host species might differ from infection rates in the greater host community (Hellgren et al., 2011). However, studying haemosporidian parasites of a widespread, abundant host species can provide accurate insights on patterns and processes that typify the whole haemosporidian community (Svensson-Coelho and Ricklefs, 2011), as well as a direct test of spatial variation in parasitism experienced by a single host.

2. Materials and methods

2.1. Field sampling

We collected 178 *S. auduboni* specimens along elevational transects (~2200–3500 m) in eight sky island mountain ranges in New Mexico and Arizona, USA (Fig. 1; Table 1) in compliance with animal care regulations and federal, state, and tribal collecting permits. Specimens were collected during the breeding season in 2004 (1.6% of samples), 2012 (15.7%), 2013 (78.6%), and 2016 (3.9%; Supplementary Table S1). Specimens, together with frozen tissues and data, were deposited in the Museum of Southwestern Biology and are searchable via the open-access Arctos database (arctosdb.org; Supplementary Table S1).

2.2. Parasite genetic analysis

We extracted DNA from pectoral muscle with a QIAGEN kit. We used three nested PCRs to amplify a 478 bp fragment of mitochondrial *cyt b* (Hellgren et al., 2004; Waldenström et al., 2004; see Supplementary Data S1). Haplotypes differing by one or more base pairs (~0.2%) from published sequences on GenBank or MalAvi (Bensch et al., 2009) were considered novel (not found previously). Co-infections were phased with existing haplotypes when possible (Supplementary Data S1). Novel haplotypes were named following MalAvi conventions, and sequences were uploaded to GenBank and MalAvi.

There is evidence that haemosporidian sequences that differ by as little as a single nucleotide may be different species (Bensch et al., 2009). Nonetheless, classifying lineages based on a 1 bp *cyt b* difference could potentially lead to overestimates of parasite diversity. To minimize the chance of sequencing error, we sequenced both forward and reverse *cyt b* strands for each parasite (see Supplementary Data S1 for details). Additionally, we analyzed all haplotypes as independent lineages and adopted a haplotype classification approach that allowed us to test our predictions under a more conservative set of criteria, defined below, and modeled after Svensson-Coelho et al. (2013) (Supplementary Data S1). We collapsed all haplotypes into 'haplogroups', following a two-level scheme: (i) haplotypes were collapsed if they co-occurred in the same individual and differed by 1 bp; and/or (ii) haplotypes were collapsed if they overlapped in distribution (defined as co-occurrence in one or more sky islands) and differed by 1 bp (Supplementary Fig. S1; Supplementary Tables S1 and S2). We conducted all analyses for both haplotypes and haplogroups.

2.3. Modeling haemosporidian infection status

To determine causes of infection status, we constructed a set of binomial GLMs for each haemosporidian genus. We defined 'infection status' as whether or not an individual host was infected (e.g. presence/absence of infection; 1 if infected, 0 if uninfected). Each

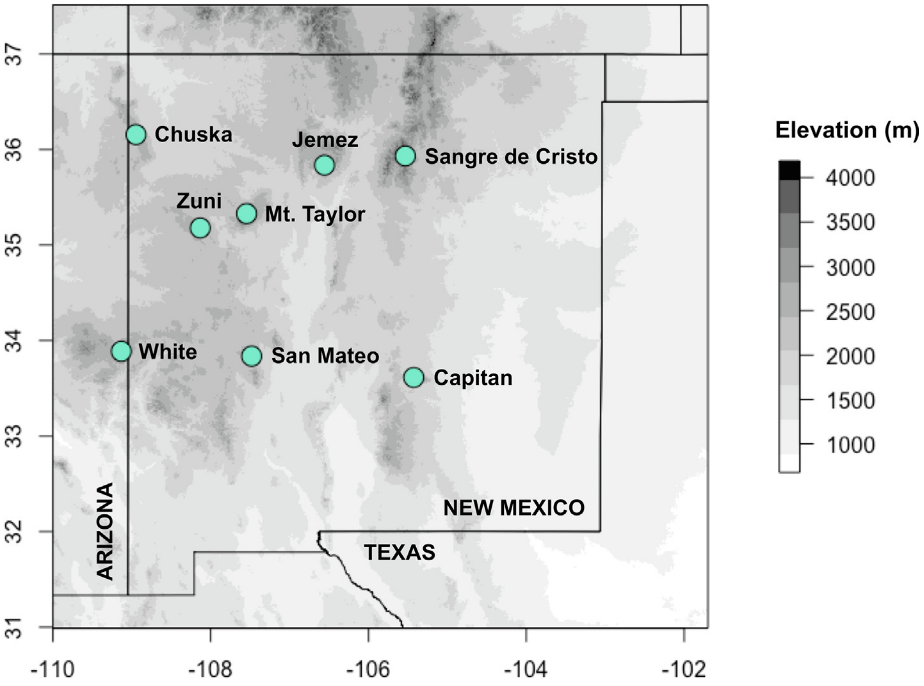


Fig. 1. Map of sampled southwestern sky islands in New Mexico and Arizona, USA, with higher elevations shaded darker. Map data from Jarvis et al. (2008), Hole-filled SRTM for the globe, version 4.

Table 1

Summary of sky island study site locations in New Mexico and Arizona, USA and elevational ranges. For each site we report the total number of birds sampled, infections recovered, haplotypes recovered and haplogroups recovered.

Site	Mean latitude and longitude	Elevational range of samples (m)	Birds sampled	Total infections	Number of haplotypes	Number of haplogroups
Capitan	33°36′50.40″ N, 105°25′37.20″ W	2286–3103	14	7	6	5
Chuska	36°09′27.37″ N, 108°56′47.62″ W	2223–2812	45	46	16	10
Jemez	35°50′13.20″ N, 106°33′ 28.80″ W	2489–3372	17	17	13	10
Mt. Taylor	35°19′44.04″ N, 107°32′45.60″ W	2404–3321	26	32	16	13
Sangre de Cristo	35°55′58.80″ N, 105°31′ 58.80″W	2283–3504	16	8	4	4
San Mateo	33°50′13.20″ N, 107°28′51.60″ W	2354–3064	18	15	9	7
White	33°53′16.80″ N, 109°07′58.44″ W	2382–3060	25	16	9	8
Zuni	35°10′44.40″ N, 108°07′55.20″ W	2303–2766	17	17	9	8

model set included infection status as the response variable, and all possible additive combinations of five predictor variables: site, elevation, latitude, temperature-aridity index, and seasonality index. The latter two variables were derived from the Principal Components Analysis (PCA) described below. We did not consider quadratic variables or interactions. Input variables were centered and scaled following Gelman (2008). Each model set included an intercept-only (null) model. We evaluated goodness-of-fit by examining residual deviance statistics for the global model in each set and evaluated overdispersion, or whether the variance was larger than expected, using the overdispersion metric, $\hat{c}$. Values of $\hat{c} > 1$ indicate overdispersion, and values much higher than one (i.e., >4) indicate a lack of fit. We used Akaike Information Criterion for small sample sizes (AICc) and Akaike weights (w_i) to compare models. When $\hat{c}$ was >1, quasi-AICc (QAICc) was used (Richards, 2008). We eliminated models with uninformative parameters, defined as having a higher AICc or QAICc score than a nested version (i.e. a subset) of the same model (Richards, 2008; Arnold, 2010; Table 2). We tested 32 candidate models for each model set and retained the null model in all candidate model sets. Final models are presented in Table 2. All models were built in R, v3.3.2 (R Core Team, 2016).

The effect of each predictor was estimated by calculating model-averaged regression coefficients (Table 3). We then used standardized model-averaged regression coefficients to calculate the average probability of infection when all scaled covariates were at the mean. Estimated probabilities of infection take into account the underlying uncertainty of estimates better than raw probabilities and provide a useful way to compare the magnitude of effect sizes. We used the inverse logit and model-averaged regression coefficients to calculate the proportions of change in estimated probability of infection for elevation and latitude for *Parahaemoproteus*.

We used PCA to characterize climate variability among sky islands. Climate data were obtained from WorldClim (version 1.4), which contains data on precipitation and temperature from 1950 to 2000, summarized as 19 bioclimatic variables (Hijmans et al., 2005). We transformed three non-normally distributed WorldClim variables and substituted transformed for original variables in the PCA, which incorporated all 19 climate variables. The first two PCA axes (PC1 and PC2) explained 83% of climate variation and were subsequently used as predictor variables in models. Loadings indicated that PC1 represented increased temperature and decreased precipitation, which we refer to as the "temperature-aridity index". PC2 represented increased temperature seasonality and decreased precipitation, which we henceforth refer to as the "seasonality index" (Supplementary Table S3).

We excluded age and sex from our models because we found no significant differences between sexes or ages in Chi-square tests. This negative result for all data combined was consistent when we separately analyzed infection status for *Parahaemoproteus*, *Plasmodium*, and *Leucocytozoon*, respectively.

2.4. Diversity analyses

We estimated the haemosporidian phylogeny using maximum likelihood (ML) in RAxML, v8.2.10 (Stamatakis, 2014). We used the GTR+G model of nucleotide substitution and conducted a rapid bootstrap analysis with 1000 replicates, after which we searched for the best scoring ML tree. We rooted the tree with *Leucocytozoon* (Borner et al., 2016; Galen et al., 2018).

Table 2

Comparison of three sets of candidate models describing predictors of *Parahaemoproteus*, *Plasmodium* and *Leucocytozoon* infection status. Models are ranked in ascending order by their delta quasi-AICc (ΔQAICc) or ΔAICc scores relative to model with the lowest QAICc or AICc score in the set. *Parahaemoproteus* models were evaluated using QAICc and ΔQAICc; and *Plasmodium* and *Leucocytozoon* models with AICc and ΔAICc. Akaike weights (w_i) quantify the probability that a particular model is the best model in the set, given the data. K indicates the number of parameters. Model sets included models with single main effects and additive (+) effects of five explanatory variables: study site, elevation, latitude, temperature-aridity index (PC1), and seasonality index (PC2). Candidate sets were selected from full model sets by eliminating any model with a higher QAICc or AICc score than a nested version of the same model.

Model Set	Model	K	QAICc or AICc	ΔQAICc or ΔAICc	*wi*
Parahaemoproteus	Elevation + PC2	4	181.28	0.00	0.43
	PC1 + PC2	4	182.59	1.31	0.22
	PC1	3	183.57	2.29	0.14
	Elevation + latitude	4	183.86	2.58	0.12
	Elevation	3	185.61	4.33	0.05
	Latitude	3	187.94	6.66	0.02
	Site + PC2	10	188.04	6.76	0.01
	PC2	3	189.63	8.35	0.01
	Site	9	190.27	8.99	0.00
	Intercept only	2	190.94	9.66	0.00
Plasmodium	Intercept only	1	89.020	0.00	1.00
Leucocytozoon	Site	8	154.83	0.00	0.98
	Elevation	2	164.68	9.85	0.01
	PC1	2	165.00	10.17	0.01
	Intercept only	1	166.64	11.82	0.00

Table 3
Standardized model-averaged regression coefficients (β and 95% confidence limits (CL) used to estimate effects of predictors and precision of effects across three candidate model sets. Dashes indicate that a parameter was not present in a final model set. NA values indicate that a parameter was not tested due to the absence of certain haemosporidian genera from sites. For all models, Site: Capitan was the reference category. Sky island study sites were located in New Mexico and Arizona, USA.

Parameter	Model-averaged estimate and 95% CL								
	Parahaemoproteus models			*Plasmodium* models			*Leucocytozoon* models		
	β	Lower CL	Upper CL	β	Lower CL	Upper CL	β	Lower CL	Upper CL
Intercept	−0.12	−1.17	0.93	−2.63	−3.21	−2.04	−1.30	−2.57	−0.03
Elevation	−1.13	−1.93	−0.33	–	–	–	0.77	0.02	1.53
Latitude	0.72	0.00	1.43	–	–	–	–	–	–
Temperature-aridity Index	1.10	0.36	1.85	–	–	–	−0.75	−1.52	0.02
Seasonality Index	0.77	−0.42	1.96	–	–	–	–	–	–
Site: Chuska	4.23	0.24	8.22	NA	NA	NA	−1.34	−3.07	0.39
Site: Jemez	4.21	0.02	8.41	NA	NA	NA	0.42	−1.22	2.07
Site: Mt. Taylor	4.06	0.38	7.74	NA	NA	NA	1.15	−0.35	2.64
Site: Sangre de Cristo	2.99	−0.46	6.44	–	–	–	−1.41	−3.80	0.98
Site: San Mateo	1.79	−0.39	3.97	–	–	–	0.05	−1.65	1.74
Site: White	2.14	−0.33	4.61	–	–	–	−0.69	−2.45	1.06
Site: Zuni	5.14	1.48	8.81	–	–	–	NA	NA	NA

We calculated parasite alpha diversity (within-site haplotype diversity) with rarefaction and the Chao1 index using EstimateS (Colwell, R. K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.1.0; Supplementary Data S1). Using a loop of the function rrarefy() in the package 'vegan' (Oksanen et al., 2017. Vegan: Community Ecology Package. R package version 2.4-3), we rarefied our site-by-species parasite haplotype abundance matrix 1000 times based on the lowest number of infections per mountain range site (see Table 1). This enabled us to replicate expected species richness in a random subsample of a specified size from the parasite haplotype community as a way to account for uneven sampling effort across study sites. We used the Jaccard index, a presence-absence-based dissimilarity metric (Magurran, 2004), to evaluate non-phylogenetic (taxonomic) diversity using the 'vegdist()' function in the R package 'vegan' (Oksanen et al., 2017), and we used unweighted UniFrac to assess phylogenetic diversity, which measures the fraction of unshared branch lengths between two communities (Lozupone et al., 2010), using the function 'GUniFrac' in the R package 'GUniFrac' (Chen, J., 2018. GUniFrac: Generalized UniFrac distances. R Package version 1.1). For both Jaccard and Unifrac calculations, we used site-by-species parasite haplotype matrix rarefaction runs to generate 1000 dissimilarity matrix outputs, and took the mean of all output matrices to represent phylogenetic (UniFrac) and non-phylogenetic (Jaccard) beta-diversity for parasite haplotype, parasite haplogroup, and bird communities (Table 4; Supplementary Table S4).

To characterize host turnover, we used eBird data (eBird.org) and expert knowledge (see Supplementary Data S1) to generate bird community lists comprised of the breeding bird species occurring >2100 m elevation in each sky island (Supplementary Table S5); we then selected one phylogenetic tree for the sky-island breeding bird community from the posterior distribution of likely trees using BirdTree.org, with the 'Hackett All Species' option (Hackett et al., 2008; Jetz et al., 2012). 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 (Jetz et al., 2012, 2014). Presence/absence scores were used to calculate Jaccard index values, and unweighted UniFrac was used to assess phylogenetic beta diversity of the breeding bird community. We tested the sensitivity of phylogenetic beta diversity estimates to phylogenetic uncertainty; alternative trees from the posterior set produced highly similar estimates (see Supplementary Fig. S2).

2.5. Geographic structure and turnover of parasite communities

We characterized parasite and bird community composition using non-metric multidimensional scaling (NMDS), based on unweighted UniFrac distance matrices, in R (Oksanen et al.,

Table 4
Measures of non-phylogenetic (taxonomic) and phylogenetic community dissimilarity among the haemosporidian haplotype community ('Parasites') and the breeding bird community ('Birds'). Italicized values: Jaccard index pairwise beta diversity estimates (below the diagonal). Unitalicized values: unweighted UniFrac pairwise beta diversity estimates (above the diagonals). Larger numbers indicate greater differences in community structure (i.e. greater turnover). Sky island study sites were located in New Mexico and Arizona, USA.

Clade	Sky island	Capitan	Chuska	Jemez	Mt. Taylor	Sangre de Cristo	San Mateo	White	Zuni
Parasites	Capitan	–	0.64	0.53	0.66	0.44	0.48	0.53	0.73
	Chuska	*0.88*	–	0.64	0.74	0.59	0.67	0.73	0.69
	Jemez	*0.78*	*0.83*	–	0.58	0.41	0.49	0.65	0.72
	Mt. Taylor	*0.83*	*0.89*	*0.83*	–	0.62	0.67	0.66	0.77
	Sangre de Cristo	*0.62*	*0.74*	*0.68*	*0.83*	–	0.49	0.64	0.72
	San Mateo	*0.74*	*0.91*	*0.81*	*0.90*	*0.70*	–	0.57	0.67
	White	*0.83*	*0.92*	*0.87*	*0.87*	*0.81*	*0.80*	–	0.70
	Zuni	*0.87*	*0.85*	*0.86*	*0.89*	*0.78*	*0.79*	*0.87*	–
Birds	Capitan	–	0.04	0.13	0.03	0.14	0.04	0.11	0.04
	Chuska	*0.11*	–	0.11	0.02	0.12	0.08	0.09	0.03
	Jemez	*0.20*	*0.14*	–	0.12	0.01	0.16	0.11	0.14
	Mt. Taylor	*0.08*	*0.05*	*0.15*	–	0.13	0.07	0.10	0.02
	Sangre de Cristo	*0.23*	*0.16*	*0.04*	*0.18*		0.17	0.11	0.15
	San Mateo	*0.07*	*0.15*	*0.23*	*0.12*	*0.26*	–	0.06	0.05
	White	*0.19*	*0.15*	*0.12*	*0.16*	*0.16*	*0.13*	–	0.09
	Zuni	*0.07*	*0.08*	*0.17*	*0.03*	*0.21*	*0.10*	*0.16*	–

2017). NMDS was chosen because it uses rank orders to account for large differences in count data and does not assume linear relationships (Winter et al., 2017). Communities were more similar when phylogeny was taken into account (Table 4), so we used only unweighted UniFrac distance matrices as inputs for NMDS analyses. See Supplementary Figs. S3–S5 for reporting of NMDS stability assessment, stress values, and dimensions.

To quantify the best environmental and geographic predictors of parasite and bird community composition, we used GDM. In GDM, predictor variables are transformed using a series of I-spline functions with a high degree of smoothness at places where polynomial pieces connect ("knots"), and models are fitted using ML estimation (Ferrier et al., 2007; (Glassman et al., 2017). The sum of three coefficients for each variable describes the proportion of turnover explained by that variable, reflected in the maximum height of its I-spline (Ferrier et al., 2007; Fitzpatrick et al., 2013). The I-spline slope indicates the rate of turnover along that particular environmental or geographic gradient (Fitzpatrick et al., 2013; Glassman et al., 2017). The difference in height between any two points along the I-spline corresponds to the modelled contribution of that predictor variable to the difference between those sites; in this way, I-splines indicate the importance of each variable for community composition.

We fit GDMs for the parasite haplotype community and bird community in the R package 'gdm' (Manion et al., 2018. gdm: Generalized Dissimilarity Modeling. R package version 1.3.8). For both models we used bioFormat=3 in the formatsitepair() function to specify that our response variable was a site-by-site dissimilarity matrix, calculated from phylogenetic UniFrac values described above. We started with a full model with the following predictor variables: pairwise geographic distance, elevation, temperature-aridity index (PC1), and seasonality index (PC2); for the parasite models we also included the mean values of bird community composition (MDS1 and MDS2), and for bird models we used parasite community composition (MDS1 and MDS2). We used backward elimination to arrive at a best-fit model: beginning with the full model, we removed the variable with the lowest sum of coefficients at each step, and calculated the change in deviance explained (Ferrier et al., 2007). For each GDM analysis, results included: (i) a set of best predictor variables, (ii) a fitted I-spline for each predictor variable describing its relationship with turnover, and (iii) percent deviance explained by the model (used to assess GDM model fit).

2.6. Data accessibility

Specimen and parasite data are available in Supplemental Tables S1–S2. Parasite sequences are archived in ARCTOS, MalAvi, and GenBank (Accession numbers MF752555–MF752704). Voucher specimens and frozen tissue samples are archived at the Museum of Southwestern Biology Division of Birds and Division of Genomic Resources, respectively, where they are available for further study (https://msb.unm.edu/).

3. Results

3.1. Haemosporidian abundance and diversity

We recovered 46 haemosporidian mtDNA haplotypes from 178 birds (Fig. 2; Supplementary Table S2). A total of 109 birds (61.2%) had at least one haemosporidian infection. We identified 158 infections, and 67% of the mtDNA haplotypes (31 of 46) were novel (Supplementary Tables S6–S7). *Parahaemoproteus* was the most abundant and diverse genus, followed by *Leucocytozoon*; *Plasmodium* was relatively rare. There were no significant differences in haplotype or haplogroup richness among sky islands (Supplementary Fig. S6).

To account for the possibility that some haplotypes were within-species variants, we collapsed haplotypes into 30 haplogroups. Consolidation reduced diversity by ~1/3, with similar effects on each genus (Supplementary Fig. S1; Supplementary Table S7). All results for haplotypes and haplogroups were qualitatively similar, so henceforth we emphasize the haplotype results.

3.2. Haemosporidian communities in sky-island Audubon's warblers

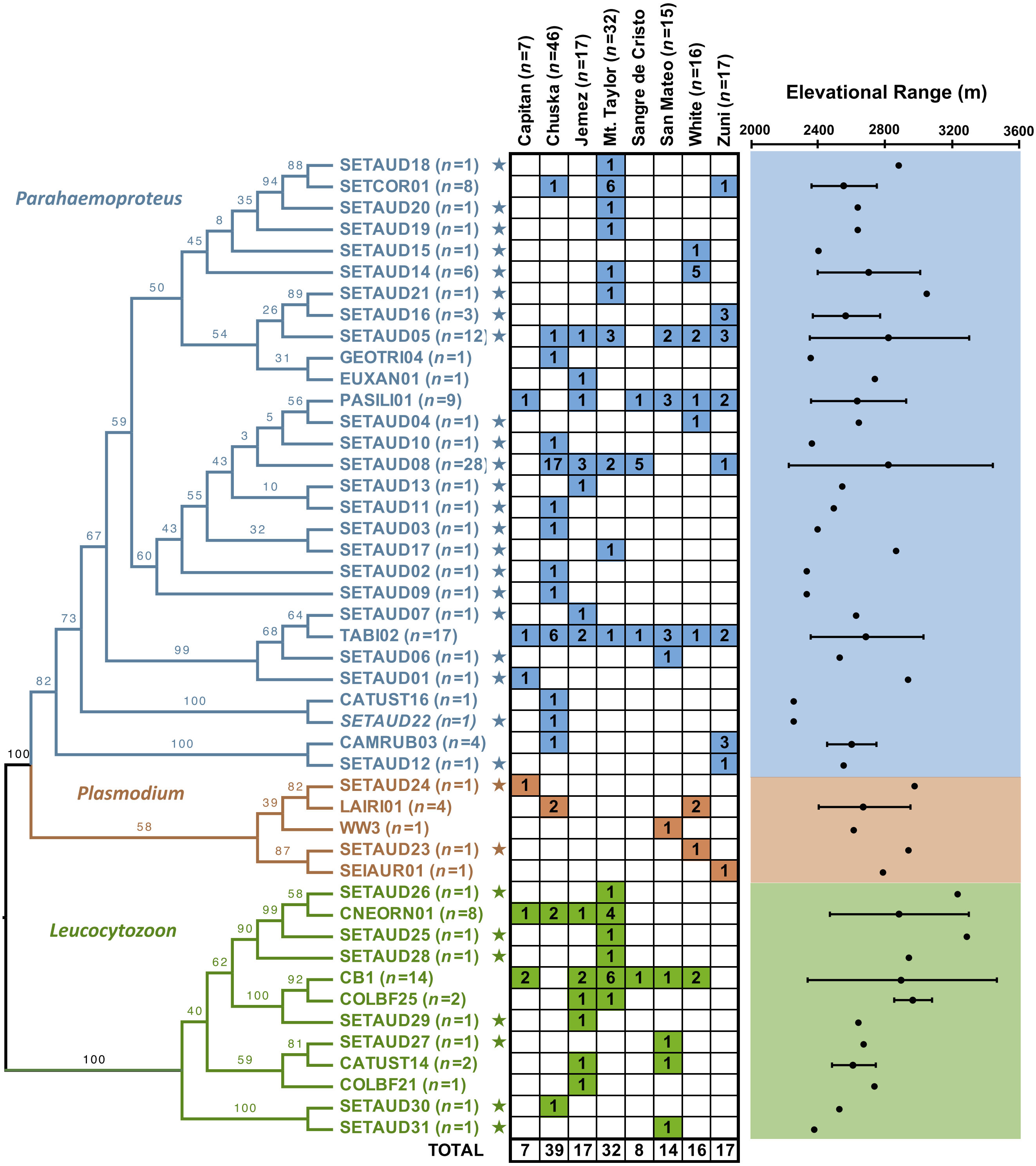
The levels of diversity and novelty in the haemosporidian parasites of sky-island *S. auduboni* were notably high. The total number of haemosporidian haplotypes identified in the Yellow-rumped Warbler complex (*Setophaga coronata* and *S. auduboni*) is now 64, making it the world's second most parasite-rich host, after only *Parus major* (66 haplotypes), according to the MalAvi database (Bensch et al., 2009). Some of this diversity was attributable to parasite community differences among sky islands, highlighting the need to understand the spatial scale and drivers of parasite species turnover.

The haemosporidian parasite lineages infecting *S. auduboni* included a mix of widespread host generalists and range-restricted host specialists (Supplementary Data S2). Of the 15 previously published haplotypes we recovered, five spanned multiple continents, and three were found in >15 host species (Supplementary Table S2). Only one of these widespread and host generalist lineages was abundant in our survey, CB1 (*Leucocytozoon*), which is known from eight host species, three countries, and two continents (Supplementary Table S2). The *Plasmodium* haplotypes we identified were already known to be widespread host generalists, consistent with previous studies (Sehgal et al., 2010; Supplementary Table S2). By contrast, four of the 15 previously described haplotypes are known to infect only two host species, and two others are only known from *S. auduboni* (Supplementary Table S2).

We found that the most abundant parasite lineages in the community appear to be host-specialized. Our two most frequent haplotypes were TABI02 and SETAUD08 (both *Parahaemoproteus*). TABI02 is known only from five species of warblers (Parulidae) in Arizona, Missouri, USA, and New Mexico, whereas SETAUD08 is known only from *S. auduboni*. This is inconsistent with Hellgren et al. (2009) who showed that host-generalist parasites tended to also be more abundant in any particular host. It is partly consistent with Drovetski et al. (2014), who found that the most abundant lineages in Europe included both generalist and specialists.

3.3. What factors explain haemosporidian infection status?

Predictors of infection status differed among haemosporidian genera. The estimated probability of infection was highest for *Parahaemoproteus* (47.0%), followed by *Leucocytozoon* (21.4%), and was lowest for *Plasmodium* (6.7%). The probability of *Parahaemoproteus* infection decreased by ~25% for every 50 m increase in elevation, and it increased by ~35% for every one degree increase in latitude. The probability of *Parahaemoproteus* infection also increased with a decreasing temperature-aridity index (PC1) and seasonality index (PC2; Tables 2–3). *Plasmodium* infection status was unpredictable, although its relative rarity likely limited statistical power. *Leucocytozoon* infection status varied strongly by mountain range but was not predicted by environmental characteristics (Table 2). For *Parahaemoproteus* and *Leucocytozoon*, best-fit models performed substantially better than the null, intercept-only model (Table 2).



Haplotype	Capitan (*n*=7)	Chuska (*n*=46)	Jemez (*n*=17)	Mt. Taylor (*n*=32)	Sangre de Cristo	San Mateo (*n*=15)	White (*n*=16)	Zuni (*n*=17)
SETAUD18 (*n*=1) ★				1				
SETCOR01 (*n*=8)		1		6				1
SETAUD20 (*n*=1) ★				1				
SETAUD19 (*n*=1) ★				1				
SETAUD15 (*n*=1) ★							1	
SETAUD14 (*n*=6) ★				1			5	
SETAUD21 (*n*=1) ★				1				
SETAUD16 (*n*=3) ★								3
SETAUD05 (*n*=12) ★		1	1	3		2	2	3
GEOTRI04 (*n*=1)		1						
EUXAN01 (*n*=1)			1					
PASILI01 (*n*=9)	1		1		1	3	1	2
SETAUD04 (*n*=1) ★							1	
SETAUD10 (*n*=1) ★		1						
SETAUD08 (*n*=28) ★		17	3	2	5			1
SETAUD13 (*n*=1) ★			1					
SETAUD11 (*n*=1) ★		1						
SETAUD03 (*n*=1) ★		1						
SETAUD17 (*n*=1) ★				1				
SETAUD02 (*n*=1) ★		1						
SETAUD09 (*n*=1) ★		1						
SETAUD07 (*n*=1) ★			1					
TABI02 (*n*=17)	1	6	2	1	1	3	1	2
SETAUD06 (*n*=1) ★						1		
SETAUD01 (*n*=1) ★	1							
CATUST16 (*n*=1)		1						
SETAUD22 (n=1) ★		1						
CAMRUB03 (*n*=4)		1						3
SETAUD12 (*n*=1) ★								1
SETAUD24 (*n*=1) ★	1							
LAIRI01 (*n*=4)		2					2	
WW3 (*n*=1)						1		
SETAUD23 (*n*=1) ★							1	
SEIAUR01 (*n*=1)								1
SETAUD26 (*n*=1) ★				1				
CNEORN01 (*n*=8)	1	2	1	4				
SETAUD25 (*n*=1) ★				1				
SETAUD28 (*n*=1) ★				1				
CB1 (*n*=14)	2		2	6	1	1	2	
COLBF25 (*n*=2)			1	1				
SETAUD29 (*n*=1) ★			1					
SETAUD27 (*n*=1) ★						1		
CATUST14 (*n*=2)			1			1		
COLBF21 (*n*=1)			1					
SETAUD30 (*n*=1) ★		1						
SETAUD31 (*n*=1) ★						1		
TOTAL	7	39	17	32	8	14	16	17

Fig. 2. Phylogeny of 46 haemosporidian *cyt b* haplotypes and elevational ranges over which each was encountered in *Setophaga auduboni* from sampled sky islands. We rooted the tree with *Leucocytozoon* (Borner et al., 2016; Galen et al., 2018). Branch labels indicate bootstrap values. Shading corresponds to parasite genera (see online for color figure). The number of infections is indicated by *n*, and numbers in the shaded cells indicate the number of infections with each haplotype per mountain range. Stars indicate novel haplotypes. The observed elevational range of each haplotype is represented by shaded areas; a single dot represents a single elevation.

3.4. Host and parasite turnover

We found strikingly high rates of parasite turnover among sky islands, far higher than the rates of bird turnover (Table 4). This was consistent for phylogenetic and non-phylogenetic measures of turnover, respectively (Table 4 and Supplementary Table S4). Mountain ranges were generally widely dispersed in NMDS parasite community ordinations (Supplementary Figs. S3–S4), while mountain ranges were tightly clustered in bird community ordinations (Supplementary Fig. S5), consistent with observed high dissimilarity of parasite communities and lower dissimilarity of bird communities (Table 4).

GDM disentangled the effects of geographic and environmental predictors on parasite turnover and bird turnover, respectively (Fig. 3). The GDM model for parasite community turnover explained a moderate proportion of the variance among parasite communities (deviance explained = 53%; Table 5). The full and reduced parasite community models were consistent, so we present the full model. Elevation and bird community composition (Bird MDS2) were the best predictors of parasite community composition (Table 5; Fig. 3C and 3E). The pairwise geographic distance between sky islands explained very little variation in parasite community composition.

The GDM model of bird community composition explained a large proportion of the variance among the bird community (deviance explained = 75%; Table 5). The full and reduced bird community models were consistent, so we present the full model. Elevation and geographic distance were the best predictors of bird community composition, while parasite community composition (MDS2) and seasonality index (PC2) explained a lesser degree of the variation in the bird community (Table 5; Fig. 3D and 3F).

4. Discussion

The factors that predicted the probability of infection differed among haemosporidian genera. *Parahaemoproteus* was the most common and abundant genus encountered in the sky-island forests, consistent with previous findings that it is associated with woodland habitats (Clark et al., 2016; Illera et al., 2017) and mountains (Lutz et al., 2015). The fact that elevation was an important predictor of *Parahaemoproteus* infection suggests a mechanism that could potentially contribute to high host species turnover along these gradients (Fig. 2). We observed that *Parahaemoproteus* infection increased with increased temperatures and decreased precipitation (temperature-aridity index; Table 3), although our study was restricted to montane woodlands that are relatively cool and wet. Zamora-Vilchis et al. (2012) also found that *Parahaemoproteus* was strongly positively correlated to temperature in the Australian Wet Tropics bioregion, where mean annual temperatures of sampled localities ranged between 16.4 °C and 21.8 °C. Illera et al. (2017) found that temperature was negatively correlated with *Parahaemoproteus* prevalence in one mountain range in northern Spain, where the mean annual temperature was ~15 °C. Recently, Pulgarín-R et al. (2018) found no association between *Parahaemoproteus* prevalence and climatic variables along a tropical aridity gradient in Colombia.

Our finding that *Plasmodium* infection status was unpredictable was likely due to its low frequency in our survey. The relative rarity of *Plasmodium* is consistent with previous studies in the southwestern United States (Marroquin-Flores et al., 2017) and other arid environments (Zamora-Vilchis et al., 2012).

Leucocytozoon varied idiosyncratically by mountain range (Table 2). Although environmental variables were not included in the top models, there was a trend toward *Leucocytozoon* infection increasing at higher elevations and with cooler, wetter conditions (i.e. temperature-aridity index; Table 3). These effects may have been modest because the entirety of our survey took place in relatively cool and forested montane habitats, but they are consistent with studies from across the globe: Lutz et al. (2015) found that rates of *Leucocytozoon* infection decreased at drier, low elevation sites in Malawi; Galen and Witt (2014) and González et al. (2014) found more *Leucocytozoon* in wetter conditions and at higher elevations in the Andes; and Merino et al. (2008) found that *Leucocytozoon* prevalence increased with latitude in Chile. It is also likely that *Leucocytozoon* variation among sky-island mountain ranges is partly attributable to unmodeled aspects of the environment such as proximity to water, which could affect local abundance of simulid vectors.

We found that parasite communities exhibited striking turnover, far greater than that of bird communities (Fig. 3A, B; Table 4). Previous studies have demonstrated marked haemosporidian parasite community turnover at much larger spatial scales, ranging from ~750 km (Ellis et al., 2015) to ~2400 km (Scordato and Kardish, 2014); and one study at a large spatial scale (~2100 km) found only subtle turnover (Fecchio et al., 2017b). Here we describe turnover of host and parasite communities at relatively fine spatial scales of a few hundred kilometers. The fact that haemosporidian parasite turnover is high at this fine scale, across which avian host communities are relatively constant, suggests that haemosporidian communities exhibit turnover patterns closer to the 'micro-scale' expected of microbial communities (Astorga et al., 2012; Nemergut et al., 2013). Rather than parasite turnover mirroring host turnover, it was far greater (Fig. 3A, B; Table 4). This is consistent with a study of Caribbean islands in which there was greater inter-island variation in haemosporidians compared with avian hosts (Ricklefs et al., 2016). These patterns suggest that there are fundamentally different processes causing turnover for micro- (parasite) and macro-organisms (hosts). For example, parasite communities might turn over faster than host communities due to higher sensitivity to climate variation, faster evolutionary rates, or host switch-driven speciation. The finer spatial scale of turnover in parasites could exert spatially varying selective pressure on host immune systems, promoting host genetic diversity and potentially accelerating host diversification (Laine and Tellier, 2008; Thornhill and Fincher, 2013; Betts et al., 2018).

We found that parasite turnover is predicted by host turnover. This finding, consistent with previous studies that encompassed equivalent and/or larger spatial scales (Ishtiaq et al., 2010; Svensson-Coelho and Ricklefs, 2011; Ellis et al., 2015; Clark and Clegg, 2017; Fecchio et al., 2017b), suggests that at least some of the geographic variation in host communities is a cause or consequence of heterogeneity of parasite communities. It further implies that the identity of specific species in a multi-host, multi-parasite system can be important for the persistence (or lack of persistence) of potential symbiont species. This is consistent with indirect antagonistic effects among bird or parasite species, respectively, mediated by symbiont species. Such effects could limit ranges and ultimately accelerate diversification for hosts or parasites.

Although differences among sky-island parasite communities were somewhat idiosyncratic, turnover was partly explained by abiotic environmental variables and biotic ecological variables (Fig. 3). A distance-decay relationship is expected to exist among parasite communities at large spatial scales (Nekola and White, 1999; Poulin, 2003), but we found that geographic distance did not explain parasite turnover among sky islands. This negative finding is consistent with Fecchio et al. (2017b), who found no effect of geographic distance on haemosporidian community turnover in manakins across the Amazon basin; however, Fecchio et al. (2017a) did find a latitude effect on turnover among Amazonian areas of endemism in a broader community survey. The lack of a distance effect at this scale suggests that dispersal distance (and colonization potential) of parasites does not constrain the island biogeographic cycle by which sky island communities are assembled; rather, environmental filters are dominant drivers of parasite community composition. This fits with the idea that vagile, migratory hosts such as *S. auduboni* provide long-distance dispersal capability for parasites, even if the potential is seldom realized due to ecological constraints on colonization.

In our study, we sampled haemosporidian parasites from a single, widespread host, *S. auduboni*, which shares many parasite haplotypes with other New Mexico breeding bird species (Marroquin-Flores et al., 2017). It is plausible that the patterns observed in *S.*

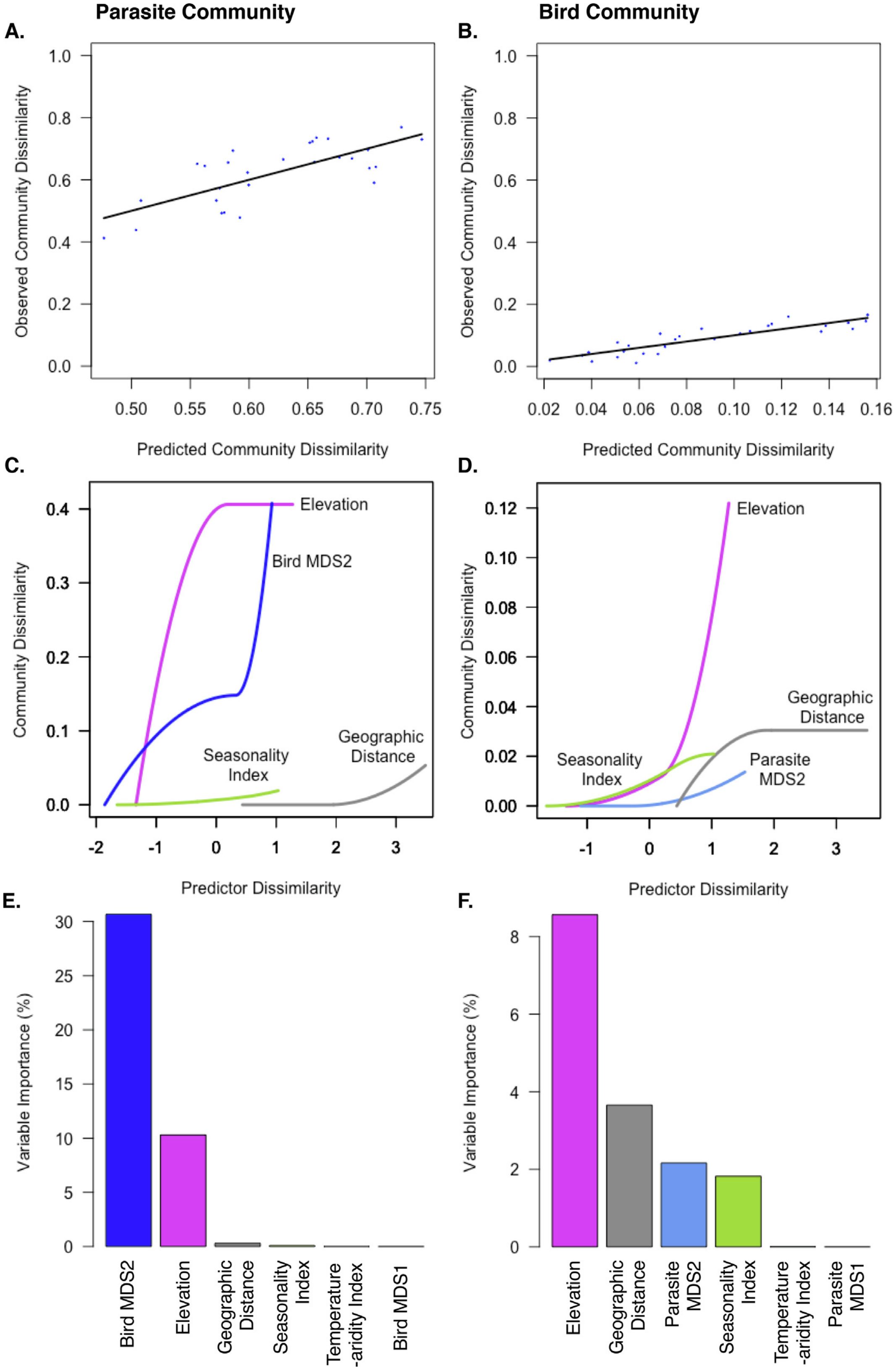


Fig. 3. Relationships between observed and predicted community dissimilarity for (A) the haemosporidian parasite haplotype community and (B) the bird community, based on generalized dissimilarity modeling analysis. For generalized dissimilarity modeling-fitted I-splines (partial regression fits) for variables associated with (C) parasite beta diversity and (D) bird beta diversity, the maximum height reached by each curve indicates the total amount of community turnover associated with that variable (i.e., its relative contribution to explaining beta diversity). The shape of each I-spline indicates how the rate of community turnover varies with increasing differences in a given predictor variable between sites. Predictor values are taken from *x*-values of fitted I-splines; these indicate the rate of turnover among mountain ranges for each of the predictors plotted. Variable importance, or percent change in deviance explained by the full model and the deviance explained by a model fit with that variable permuted, is shown for (E) the parasite community model and (F) the bird community model. All predictors depicted are from full bird and parasite generalized dissimilarity modeling models. MDS values indicate mean values for bird and/or parasite community composition, derived from non-metric multidimensional scaling ordinations.

Table 5

Outputs of generalized dissimilarity modeling for parasite haplotype (deviance explained = 53%) and bird community dissimilarity (deviance explained = 75%). Predictors and standardized coefficients from the full generalized dissimilarity modeling models for parasite and bird communities are reported. All predictors were standardized prior to input in models. We calculated coefficient values by taking the sum of the three I-spline coefficients, equivalent to the maximum height on the I-spline curve for each predictor. NA values indicate that a predictor was not tested in a model set. MDS indicates mean values for bird and/or parasite community composition, derived from non-metric multidimensional scaling ordinations.

Predictor	Coefficients	
	Parasite Dissimilarity Model	Bird Dissimilarity Model
Elevation	0.41	0.12
Geographic Distance	0.05	0.03
Temperature-aridity Index	0.00	0.00
Seasonality Index	0.02	0.02
Parasite Community Composition (MDS1)	NA	0.00
Parasite Community Composition (MDS2)	NA	0.01
Bird Community Composition (MDS1)	0.00	NA
Bird Community Composition (MDS2)	0.42	NA

auduboni reflect those of the whole bird community. This rationale is supported by Svensson-Coelho and Ricklefs (2011), who found that a single host species, the Black-faced Grassquit (*Tiaris bicolor*), reflected diversity and turnover patterns observed within the whole haemosporidian community. The high parasite turnover we observed within a single host species might remain the same or become greater if the entire breeding bird community were sampled. On the other hand, variation in Northern Cardinal haemosporidians from place to place (Ellis et al., 2015) was greater than expected based on a variation among a suite of sampled host species, suggesting that a single host species approach could result in inflated measures of turnover. It is also possible that *S. auduboni* might be a 'key host', similar to the Eurasian Blackbirds (*Turdus merula*) of the Hellgren et al. (2011) community level survey on mid-Atlantic islands, due to the fact that *S. auduboni* has a higher parasite burden than most co-occurring breeding bird species (Marroquin-Flores et al., 2017). Another possibility is that absolute values of parasite turnover estimates could be inflated by the modest level of sampling within each sky-island; deeper sampling would be expected to change absolute values, but we think it is unlikely that our explanatory statistical models could be biased by under-sampling. Future studies should examine whole bird communities. There are few such surveys at present, particularly in continental systems, due to the large scale of the sampling efforts that would be required. Among other challenges, to facilitate spatial comparisons, the timing of sampling would need to be unbiased by seasonal or inter-annual variation.

Our application of GDM yielded new insights regarding predictors of community turnover (Fig. 3; Table 5), and this method seems ideally suited for the further study of avian haemosporidians. The advantages of using GDM included adequately accounting for collinearity among predictors and the expected non-linear relationships of geographic and environmental distance. By simultaneously accounting for environmental characteristics and host and parasite community composition, our GDM results explained substantial variation in parasite (53%) and bird communities (75%), respectively.

This study revealed causes of abundance and turnover for haemosporidian parasite communities across an array of sky islands in southwestern North America. Infection status was predicted by environmental characteristics, but sky islands also showed idiosyncratic variation. Using our single host-species approach, parasite turnover was approximately three-fold higher than bird turnover among sky islands separated by no more than a few hundred kilometers. GDM revealed that variation in parasite community composition among sky islands could be explained by abiotic and biotic ecological variables, but not by geographic distance. Importantly, we found that parasite turnover and host turnover were linked. Although not unprecedented, this finding was surprising because both parasites and hosts tend to be generalized in these communities. This implies that the identities of specific host and parasite species matter to community composition, even in a complex multi-host, multi-parasite system.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2018.11.012.

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