Received: 9 March 2020 | Revised: 5 November 2020 | Accepted: 8 November 2020

DOI: 10.1111/ddi.13201

BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Host diversity outperforms climate as a global driver of symbiont diversity in the bird-feather mite system

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Funding information
Coordenação de Aperfeiçoamento de Pessoal de Nível Superior

Editor: Susan Cunningham

Abstract

Aim: The simultaneous influence of abiotic and biotic factors as main drivers of global species distributions remains poorly understood, especially in host-dependent groups. In this study, we diverge from traditional macroecological approaches by considering both biotic (avian species diversity) and abiotic (climatic) factors in determining the global distribution pattern of feather mite species richness, one of the most abundant and diverse bird ectosymbionts.

Location: Global.

Methods: We used a global dataset of feather mite–bird interactions published in 2016, complemented with an up-to-date literature survey. We created statistical models designed to explain the effect of abiotic (i.e., temperature, precipitation and energy-related variables) and biotic factors (bird species richness) on the species richness of feather mites. We used these models to predict global distribution patterns of mites and estimate each explanatory variable's relative importance in temperate and tropical regions.

Results: According to our models, bird species richness accounts for ~63% of the global distribution pattern of mites, which is ten times more relevant than climatic variables. Among abiotic drivers, precipitation intensity and seasonality were the most important variables, accounting for 10% of mite species richness. This figure is lower in tropical regions, where biotic factors are seven times more important than in temperate regions.

Main conclusions: We demonstrate that global mite diversity was primarily determined by biotic and, to a lesser extent, abiotic factors. The relative importance of the predictive variables, however, varied between tropical and temperate regions. The strong association between bird species richness and feather mite species diversity at a global scale raises concerns about the potential for future co-extinctions.

KEYWORDS
avian, co-evolution, host–symbiont, interaction, macroecology, symbiosis

1 | INTRODUCTION

Over the last century, several studies have reported the ecological and evolutionary processes behind the heterogeneity of global patterns of aquatic and terrestrial species, from animals to plants (Jetz et al., 2012; Tisseuil et al., 2013). Spatial and temporal variation in climate and productivity affect species diversification and extinction, altering current patterns of diversity (Gaston, 2000; Rangel et al., 2018). For instance, abiotic factors such as temperature and precipitation affect plant species composition, plant biomass and productivity, cascading up to species interacting across the food web (Gaston, 2000). In particular, there is an extensive literature showing a core set of ecological rules such as abundance–occupancy, species–area and distance–decay relationships of free-living organisms that can be mediated by abiotic factors (Shade et al., 2018). However, there is a prevalence of using abiotic factors as predictors of macroecological patterns, whereas relatively few studies included species interactions that may have both a direct effect on species distribution and even an indirect effect mediated by the abiotic variables. Thus, assessing how biotic interactions affect macroecological patterns is needed to advance macroecological theory (Dallas et al., 2018; Early & Keith, 2019).

Biotic factors (intra- and interspecific interactions between species) may also be regulated by abiotic factors such as climate. Climate may alter species abundance (Naka et al., 2020) or modify the power of biotic interactions (Early & Keith, 2019; Romero et al., 2018). For example, climate might affect the ability of vertebrates to capture their prey (Woodroffe et al., 2017), or the strength of predation by arthropods (Romero et al., 2018), which potentially could alter the outcomes of interspecific interactions and cause spatial or temporal mismatches between interacting species (Early & Keith, 2019; HilleRisLambers et al., 2012). Several studies have used latitudinal or altitudinal variation to demonstrate that the outcome and strength of biotic interactions may change across stress gradients, resulting in higher predation levels towards the tropics (Romero et al., 2018; Sanford et al., 2003). For instance, herbivory rates may increase in sites with extreme temperatures due to a lack of natural predators, which, in turn, may limit plant range limits (Rodríguez-Castaneda et al., 2016). Conversely, in regions with low or moderate temperatures, ants are known to reduce herbivory on plants, allowing plant range expansion (Rodríguez-Castaneda et al., 2016). This phenomenon is known as the "effect per interactor" mechanism (sensu Louthan et al., 2015), where the stress gradient determines the effect of an individual interactor on a focal individual. Therefore, the explanatory power of biotic and abiotic factors to species distributions may be different across the globe (Louthan et al., 2015; Romero et al., 2018).

Several studies have shown that climatic changes characterize the Anthropocene, including the rise of global temperatures and extreme changes in precipitation (Fischer & Knutti, 2015). These changes may lead to a decline in species diversity of several taxonomic groups and a consequent homogenization of biotic communities (Hautier et al., 2015). Moreover, some authors argue that these effects may be worsened by affecting biotic interactions, leading to further species declines (Koh et al., 2004). However, little is known about the direct and indirect consequences of the loss of host species on dependent species (Colwell, Dunn, et al., 2012), and thus, the role of climate change on biotic interactions is often neglected.

The lack of knowledge is particularly acute for host–symbiont systems, in which most macroecological patterns are yet to be investigated (Hortal et al., 2015). Despite these uncertainties, some macroecological patterns have emerged and are well supported by different empirical data (Dallas et al., 2018; Hechinger, 2015). For instance, more diverse host communities tend to be associated with more diverse symbiont communities (Wood & Johnson, 2016). Accordingly, losing a species in a more diverse host community will lead to the loss of a higher number of symbiont species. Another pattern is the existence of latitude–diversity relationships, with tropical areas usually supporting more symbiont species (Dallas et al., 2018; but see Clark, 2018; Fecchio, Tkach, et al., 2019). Importantly, the tropics have been considered the most threatened regions in a global extinction crisis, mainly due to the loss of different interactions (e.g., Stork, 2010 and Romero et al., 2018). However, simultaneous assessments of abiotic and biotic factors' influence in explaining symbiont macroecological patterns are virtually absent.

In host–symbiont systems, climate change is expected to affect interaction dynamics in different ways: (1) the new environmental conditions may directly impact symbionts' survival (Carlson et al., 2020; Cizauskas et al., 2017). (2) The extinction of a host species may drive a symbiont species to extinction in a phenomenon known as co-extinction (Carlson et al., 2020; Dunn et al., 2009). These two aspects may be affected by ecological and evolutionary factors, such as species dispersal capabilities (Cizauskas et al., 2017; Doña & Johnson, 2020), level of specialization (Strona & Fattorini, 2016), host specificity (Fecchio, Wells, et al., 2019; Koh et al., 2004), host characteristics (e.g., evolutionary history: Colwell, Dunn, et al., 2012) and community characteristics, such as species richness (Koh et al., 2004). Among these factors, host-switching dynamics has received considerable attention because it can aid some symbionts to avoid extinction (Brooks & Hoberg, 2007; Carlson et al., 2017; Cizauskas et al., 2017; Doña & Johnson, 2020). Specifically, symbionts with higher colonization capabilities tend to be more generalist and may be less impacted by climate conditions changes because they may escape unsuitable conditions by reaching new hosts (Doña & Johnson, 2020). However, symbionts with lower dispersal capabilities have lower opportunities to reach new hosts, tend to be less generalist, and thus most of their attempts to switch hosts fail (Doña & Johnson, 2020; Poulin, 2011). In addition, these specialist symbionts might be particularly sensitive to certain abiotic factors (e.g., humidity), and if so, climate change may reduce even further the possibilities of successful colonization and thus increase symbiont extinction rates (Bush et al., 2013). Therefore, studies on the relevance of climate on symbiont associations at a global scale

would improve our understanding of symbiont macroecology and inform conservation practices (Carlson et al., 2017).

Feather mites (Acariformes: Astigmata: Analgoidea and Pterolichoidea) represent a good system to simultaneously assess the role of abiotic and biotic factors on host-dependent organisms, with high levels of host specificity and specialization, well-curated global databases, and for which studies on co-evolutionary history are available (Doña et al., 2016, 2017a; Proctor, 2003). At a global scale, studies on population properties of feather mites (e.g., prevalence and abundance) have found influence of climate (Diaz-Real et al., 2014). Moreover, studies at local scales found that feather mites are affected by environmental conditions in several ways, such as presenting reduced abundances in drier and colder environments (Meléndez et al., 2014), and being affected by desiccation and temperature. At global scale, in the temperate regions, stressful conditions due to climate seasonality and extreme values might force host switching, which indicates abiotic factors may perform better in predicting mite diversity. Conversely, in the tropics, non-stressful conditions might favour host specificity and the relative importance of biotic factors These results suggest that diversity patterns of feather mites might be influenced by climate (Proctor, 2003), but it is necessary to include direct and indirect effects mediated by host diversity.

Despite their tight association with their avian hosts, feather mites are known to switch hosts at an ecological and evolutionary scale (±100 generations, 200 to 400 years), a process that has been found to be the main driver of diversification in this group (Doña, Proctor, et al., 2017; Doña, Sweet, et al., 2017; Matthews et al., 2018). Nevertheless, attempts to colonize new hosts are often unsuccessful because of feather mites' high level of specialization to the habitat (host) conditions (Doña et al., 2019). In addition, climate change may further reduce the possibilities of feather mite species to reach new host species (Brooks & Hoberg, 2007; Carlson et al., 2017). Thus, knowing how dependent on climate mite diversity patterns are could provide insights into how affected their likelihood of colonizing new hosts will be in a climate change scenario. Also, because host switching (i.e., and not cospeciation) is the main driver of speciation, and their limited dispersal capabilities (i.e., that may prevent colonizing available hosts; Johnson et al., 2016), it may be that high host diversity levels do not correspond with high levels of symbiont diversity as for other groups of symbionts.

In this study, we investigated how abiotic (climate and energy) and biotic factors (bird species richness) determine the α-diversity of feather mites on a global scale. We used an updated version of an extensive global dataset of feather mite species associated with bird hosts (Doña et al., 2016). We hypothesized that (i) mite diversity is affected by both biotic and abiotic factors. Given the high levels of host specificity between feather mites and birds, we expect to find a stronger effect of biotic than abiotic factors determining global mite diversity patterns. We also hypothesized that (ii) the effect of both biotic and abiotic factors might differ between tropical and temperate regions. We predict that biotic factors might be relatively more important in tropical regions, while abiotic factors may be more important in temperate regions with more variable climatic conditions.

2 | METHODS

2.1 | Datasets

We used a published global dataset containing records of feather mites (hereafter referred to as mites) interactions in 147 countries (Doña et al., 2016). This dataset includes 12,036 records published between 1882 and 2015 that document the association of 1,887 species of mites to 2,234 species of birds. To minimize contamination, identification issues and sampling mistakes, we only used records that: (i) included well established mite–bird associations and were considered of high quality by Doña et al. (2016); and (ii) studies that presented sampling effort (number of sampled birds and their associated feather mites) and location (geographical coordinates).

Because this dataset was published in 2016, we complemented it by carrying out an additional search in two bibliographic databases (Scopus and Web of Science®) with articles published in 2016 and 2017. For this new search, we used the following keywords: “feather mite” AND “bird”, “mite” AND “bird”, “ectoparasite” AND “bird” (Appendix S1). We also filtered these results by only selecting papers that followed the criteria mentioned above. The expanded database's localities include both polar circles (68°S to 78°N, covering ~16,750 km of latitude) and four continents (179°W to 179°E, covering ~18,060 km of longitude).

The historical mean of climatic and productivity variables was obtained from WordClim v. 2.0 (Fick & Hijmans, 2017) and ENVIREM (Title & Bemmels, 2018) for each site in our dataset based on latitude and longitude. In addition, we defined grids with a spatial resolution of 0.5° (~55 km in the equatorial region) to obtain the global climatic data from the grid centroid. Climatic data were categorized into three groups: temperature, precipitation and energy (see Table S1 in Supporting Information). Because the dataset from WordClim and ENVIREM has different raster resolutions, we adjusted them to the same spatial resolution (i.e., 0.5°) and used it as the analytical unit in the predictive models (see below). Therefore, our final dataset comprises two different scales: (1) site scale, points encompasses sampled birds and their associated feather mites; and (2) global scale, grids with a resolution of 0.5° covering every terrestrial ecosystem where bird species richness and climatic data were obtained for predicting global patterns of feather mites based on models produced at the site scale. At the global scale, climatic data were obtained from each cell in 25,200 cells. Global avian richness was extracted from BirdLife International (http://www.birdlife.org) using the sum of overlapped shapefiles of all species within each 0.5° grid, which generates a global bird richness map (Supporting Information Figure S1). The climatic data were used as predictors of the abiotic model, while bird richness as the predictor of the biotic model (details below).

2.2 | Potential biases

The use of any dataset carries some intrinsic biases, such as issues with species identification and heterogeneity of sampling efforts

(Doña, Proctor, et al., 2017). We believe our dataset is robust to avoid misidentifications, due to the expected low number of cryptic species in feather mites (Doña et al., 2015, 2016). On the other hand, the predominance of migratory birds would generate bias because of the seasonal habit of these species. However, our dataset comprises 65% and 35% of residents and migratory birds, respectively (BirdLife International; http://www.birdlife.org). Therefore, we believe this percentage will not affect the global pattern of bird species richness. Finally, to avoid biased conclusions due to heterogeneity of sampling effort we compared species richness data using rarefaction techniques, such as interpolation and extrapolation (see below).

2.3 | Data analysis

We used a principal component analysis (PCA) to reduce the multicollinearity of abiotic factors (temperature, precipitation and energy). We used the first and second PCA axes and made separate analyses to different sets of climatic variables: temperature axes tPC1 and tPC2 explained 71% and 13% of the observed variation; precipitation axes, pPC1 and pPC2, explained 60% and 24%; and energy axes, ePC1 and ePC2 explained 41% and 26%, respectively. The first (tPC1) and second (tPC2) axes of temperature represented mainly the annual mean value and max temperature of the warmest month at each location, respectively; the two axes of precipitation represented annual precipitation (pPC1) and seasonality (pPC2); and the axes of energy represented annual potential evapotranspiration (ePC1) and monthly variability in potential evapotranspiration (ePC2) (Table S2).

To test the relative importance of both bird species richness and abiotic factors on mite diversity, we first performed an individual-based rarefaction to control the effect of sampling effort (i.e., the number of collected birds) on mite richness (dependent variable: the number of mite species sampled on each individual bird) and bird richness (predictor variable). Species richness is a metric sensitive to differences in sampling effort (Gotelli & Colwell, 2001) and therefore comparing intensely with weakly sampled sites might bias richness comparisons. We obtained standardized values of species richness based on Hill numbers (order $q = 0$) using bird sampling effort (number of individuals) and the presence/absence of feather mites (Chao et al., 2014). The method proposed by Colwell, Chao, et al. (2012) and Chao et al. (2014) unified the classic rarefaction approach to predict the interpolated richness with theoretical extrapolation using the same rarefaction curve. This new method compares sites based on the lowest sampling effort (the interpolation procedure), but it also extrapolates species richness allowing comparisons based on the highest sampling effort (the extrapolation procedure). Therefore, to control for the sampling effort (i.e., the number of sampled birds), we obtained the interpolated (predicted richness for the location based in the lowest sampling effort; rarefied richness) and extrapolated values (predicted richness for the location based in the highest sampling effort; hereafter extrapolated richness) (Chao et al., 2014). To produce a comparable measure of mite diversity, considering that the number of sampled birds varied between sites, we treated each bird individual as a sample where the mites were collected. By doing so, the sampling effort by location was added in a sampled-based incidence rarefaction (using a Bernoulli product model) to estimate mite rarefied and extrapolated richness (Colwell, Chao, et al., 2012). Likewise, to produce an unbiased measure of bird richness, we also controlled for the effects of the number of individual birds collected on species richness by location. Thus, the sampling effort (the number of individual birds) was added in an individual-based rarefaction using the number of bird individuals to estimate the rarefied and extrapolated bird richness per site. The rarefied richness was estimated with a sampling effort of 35 individuals and the extrapolated richness with sampling effort of 2.615 individuals.

We used generalized additive mixed models (GAMM) (Wood, 2001; Zuur et al., 2010) with Gaussian distribution to test the effect of abiotic (PC1 and PC2 from temperature, precipitation and energy) and the biotic factors (either rarefied or extrapolated richness of hosts) on species richness of mites (the response variables were the rarefied and extrapolated richness of mites). Thus, we performed one GAMM model for each response variable. We used GAMM because we expected a nonlinear relationship between mite diversity and some independent variables. The GAMM function has the argument "s()" (from GAMM package in R—Wood, 2001) that wrap the independent variables and specify a smoothing spline fit. Importantly, we can specify all linear relationships in the same model removing the term "s()" in these predictor variables. We used exponential correlation with the formula: corExp(1, form = ~longitude + latitude) to consider spatial autocorrelation. We simplified models removing those insignificant variables ($p > .05$) to improve model fitting (Zuur et al., 2010). In addition, we used a log-likelihood approach (with the function loglik from the MASS package) to obtain the most likely model, that is, with a lower loglik value (models were detailed in Table S3). Because GAMM models support the inclusion of linear predictors, we were able to test whether bird richness had a positive effect on mite diversity and whether this effect was stronger than those from abiotic factors in the same model (Table S3). In addition, we performed a variance partitioning analysis to identify the relative importance of each significant predictor variable on mite richness. This analysis partitions the variance explained by abiotic factors (temperature, precipitation and energy), space (latitude and longitude) and biotic factor (bird richness), identifying the variable with the highest effect on mite richness.

2.4 | Predictive models

Based on the models created to explain mite richness at the site scale, we performed a predictive model to estimate the global number of feather mite species. This model allowed us to evaluate whether bird species richness has a stronger positive effect on mite diversity in tropical regions, and climate has a stronger role in temperate regions. For this, we obtained global values of climate and bird species richness using 0.5° grids. Before analyses, we standardized

the predictor variables (abiotic and biotic factors) to mean = 0 and standard deviation = 1.

We used the best GAMM models (M4 for rarefied and M1 for extrapolated richness, Table S3) to estimate global mite richness by grid with the "predict" function (e.g., Jetz et al., 2012). After obtaining the global model, we generated two new simplified models: (1) biotic model, containing only bird richness, but with climatic variables equal to the mean value ($\mu = 0$, as values were standardized: see above); and (2) abiotic model, containing climatic variables with bird species richness equal to the mean value ($\mu = 0$).

After obtaining global and simplified models (biotic and abiotic), we calculated the difference between the adjustment of the two simplified models (i.e., global—simplified model) and performed the subtraction between the models of adjustment (formula: |Adjustment of abiotic model| - | Adjustment of biotic model|) as a measure of model importance. This measure of model importance varied as follows: (i) grids with positive values indicated the abiotic model (i.e., climatic variables) had a better predictive power, meaning that the predicted mite richness of the abiotic model was more similar to the global model, (ii) whereas negative values indicated bird species richness represented a better predictive power. When elaborating the maps, the variation in the response variable was standardized between zero and one, where zero represented the lowest strength and 1 the highest strength of bird richness in determining mite diversity.

We performed an h-block cross-validation method to analyse global model's predictive power in estimating feather mite richness. Because both climatic and bird species richness data have a clear spatial structure, nearby sites might have similar values, which, in turn, can generate a bias in the predictive model. Therefore, we accounted for spatial autocorrelation, creating a matrix of distance between sites and choosing a cut-off value of 500 km selecting data subsets for the cross-validation method. Then, we randomly split our dataset in a nested subset that only included those sites that were at least 500 km from one another. This subset was defined as the training data in the leave-one-out cross-validation procedure (Tallavaara et al., 2018). For each subset of the training data, we performed the global model to train data and predict target values (site test). Then, we calculated the prediction root mean squared error (RMSE) and R^2 that were 1.30 and 0.32, respectively. Thus, this approach revealed that our global model was suitable to predict global mite richness (e.g., Tallavaara et al., 2018). All analyses were performed in the R environment (R Core Team, 2020) with the iNEXT (Hsieh et al., 2016) and mgvc packages (Wood, 2001).

3 | RESULTS

Our filtered and expanded dataset included 769 individual mite/bird interactions from 42 locations, distributed in four continents, with 376 bird species occurrences and 292 feather mite species occurrences (Figure 1). We found an unequal distribution of studies among continents, 57% were performed in Europe, 24% in the Americas, 14% in Asia and 5% in Oceania. Likewise, most studies

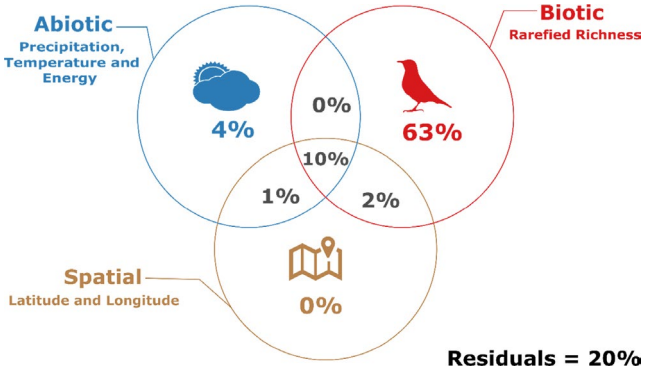

FIGURE 1 Percentage of variance explained by spatial, climatic and bird richness factors that determine the global diversity pattern of feather mites

(75%) were conducted in the temperate region and only 25% in the tropics. Rarefied and extrapolated bird richness varied from 1 to 5 (mean sample coverage = 0.13) and 2 to 71 species (mean sample coverage = 0.92), respectively. On the other hand, rarefied and extrapolated mite richness varied from 1 to 7 (mean sample coverage = 0.08) and 2 to 98 species (mean sample coverage = 0.92), respectively. The average rarefied mite richness was 1.3 species in the temperate region and 1.1 in the tropics.

Abiotic factors, such as mean annual precipitation and precipitation seasonality explained approximately 4% of the variation in the species richness of mites (Figure 1). Temperature was also an important variable for the richness of mites. Regions with higher mean temperature, such as the tropics, presented higher mite richness than colder areas (tPC1, $F = 2.86$, $p = .05$, Figure 2a). On the other hand, regions with extremely low precipitation, such as deserts and polar regions, tended to have a lower mite diversity than humid areas, such as tropical and subtropical regions (pPC1, $F = 22.40$, $p = .01$, Figure 2b). In addition, regions with more precipitation seasonality conditions presented lower mite diversity, either for rarefied (pPC2, $F = 48.38$, $p < .01$, Figure 2c) or extrapolated richness (pPC2, $F = 10.00$, $p < .01$). However, the amount of energy available did not affect either rarefied or extrapolated mite richness (Table 1).

For the biotic factor, we found that for each species of bird, there are approximately two species of mites (for both rarefied and extrapolated richness) (Figure 2d). Bird species richness was the main driver of global mite species richness, which results in similar diversity patterns (Figure 4a and S1). This result is also evidenced at the local scale (Figure 3). Avian species richness was the most important explanatory variable for mite species richness, both for rarefied ($t = 47.82$, $p < .01$, Table 1) and extrapolated richness ($t = 10.50$, $p < .01$, Table 1). In fact, the effect of the biotic factors that we tested (bird species richness) was, on average, fifteen times more important than the effect all abiotic factors combined to account for mite richness, explaining approximately 63% of this variation (Figure 1).

The global predictive model presents a threefold higher mite richness in the tropics (for both rarefied and extrapolated data) than in temperate regions. Regions with higher bird species richness,

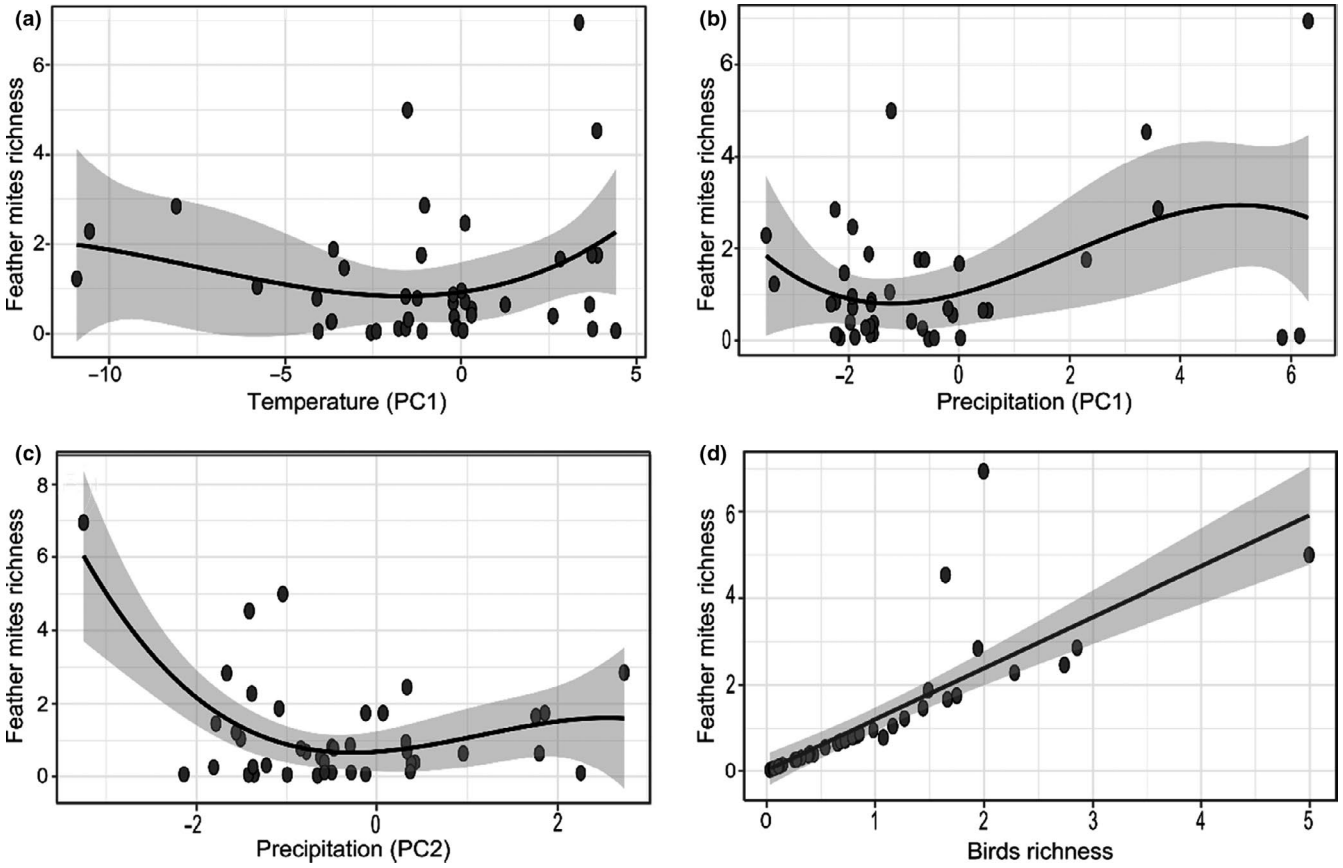

FIGURE 2 Feather mite's rarefied species richness based on the principal component analysis (PCA) axis. Values in the y-axis represent the rarefied richness of mites, values in the x-axis represent the PCA score and the rarefied richness of birds ($R_{adj} = 0.98$, $df = 10$, model 4-Table S3)

TABLE 1 Result of generalized additive mixed models (GAMM) with rarefied (model 4) and extrapolated (model 1) richness of mites (see methods)

Drives	Rarefied		Extrapolated	
Linear	***t***	***p***	***t***	***p***
$_{e}$PC2	–	–	0.85	.39
Richness of birds	47.82	<.01*	10.78	<.01*
Smooth	***F***	***p***	***F***	***p***
s($_{p}$PC1)	22.40	<.01*	0.36	0.54
s($_{p}$PC2)	48.38	<.01*	11.77	<.01*
s($_{t}$PC1)	2.86	.05*	3.24	.08
s($_{t}$PC2)	–	–	2.41	.12

precipitation and incidence of energy, as well as more energy and precipitation stability, yielded higher mite diversity (Figure 4a). However, we found that biotic and abiotic models predicted high feather mite diversity differently for distinct global regions. Specifically, biotic models indicate higher mite diversity in the tropics, and abiotic models point out diversity peaks in temperate hotspots (Figure 4b and c). According to both global and biotic models, avian diversity is the major limiting factor for feather mites, due to resemblance between the global and biotic models. Moreover, the biotic model had an adjustment ~15 times larger than the abiotic model. However, the biotic model had a distinct predictive power between tropical and temperate regions compared with abiotic models, having a ~7 times higher explanatory power in the tropics than in temperate regions (Figure 4d).

4 | DISCUSSION

The role played by biotic interactions, particularly symbiotic species, in species diversity and how climate sets up these interactions have been poorly studied in macroecology (Early & Keith, 2019). As far as we know, this represents the first study to evaluate the factors governing the global distribution patterns of feather mite diversity. More importantly, we presented evidence indicating that avian diversity is a relevant global predictor of mite diversity and that this biotic factor is a better predictor of mite diversity in tropical regions. In contrast, models including only abiotic factors (mainly climate) predict mite diversity relatively well in temperate regions, where conditions are more variable throughout the year and can reach extreme values during at least one season. Therefore, these results bring new insights for the macroecological theory, as it shows that the relative importance of biotic and abiotic factors may vary between tropical and temperate region. These findings are particularly important for

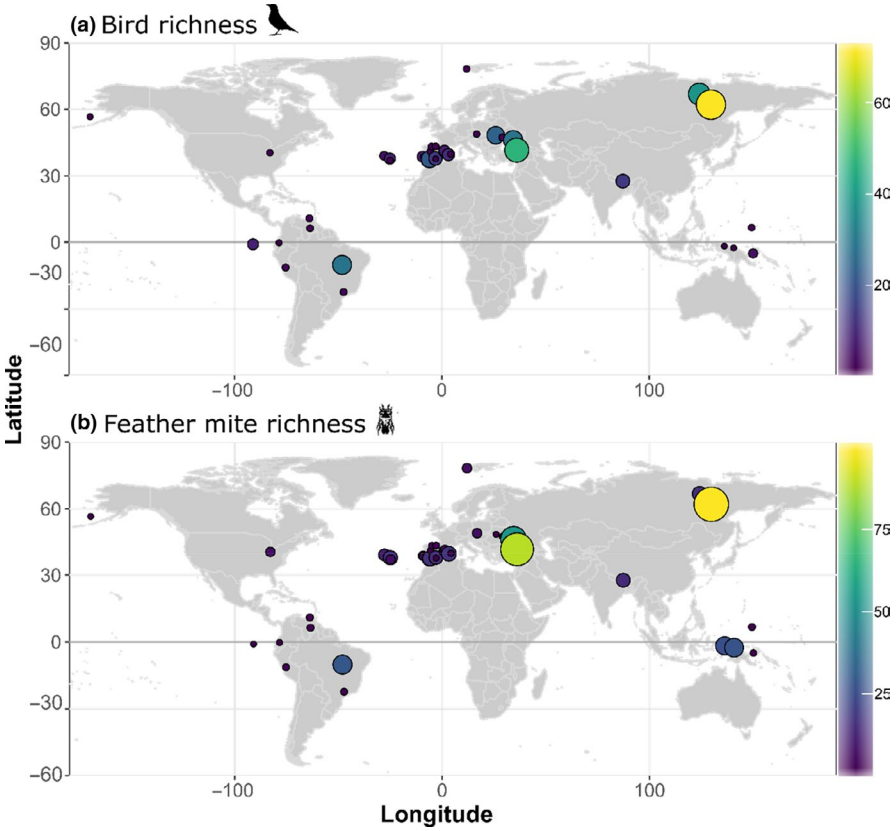

FIGURE 3 Birds and feather mite species richness per site. Site colours and sizes are shown according to the rarefied richness of birds and mites

the macroecological theory of symbionts, in which the correlation between host richness and symbiont diversity has been largely reported (Dallas et al., 2018; Wood & Johnson, 2016), but the relative contribution of host diversity versus abiotic factors in explaining symbiont diversity was still unknown. Our results strongly agree with this correlation and show that abiotic factors have a relatively smaller influence than host diversity in this group of symbionts.

Our results also show that biotic factors, such as avian diversity, are essential to determine feather mite species distribution in the tropics. The strong relationship between species richness patterns of different biological groups is a known phenomenon, especially for antagonistic relationships, such as herbivory, predation and competition (Early & Keith, 2019; Romero et al., 2018). Our findings reinforce a recent macroecological discovery, which postulates that species from tropical regions suffer stronger influence—which is indirect in this case—from biotic interactions than in temperate regions (Romero et al., 2018, but see Moles & Ollerton, 2016). Previous studies in host–parasite systems have found great intensity and prevalence of parasitism, and higher parasite richness in tropical regions (reviewed in Schemske et al., 2009). Here, we documented that part of this latitudinal effect might be assigned to climate (see below). However, our results reinforce a major impact of macroevolutionary history dictating the tight association between feather mites and birds. In fact, a previous study has shown that feather mites have high host specificity and usually inhabit closely related hosts (Doña, Proctor, et al., 2017). In addition, these authors demonstrated that host switching between distantly related host species was infrequent. Considering these results, we argue that understanding global patterns of host diversity is a pre-requisite to understanding the macroecology of symbionts.

This study reports that besides avian diversity, precipitation and temperature are major environmental drivers of mite species distribution. Hence, regions with intermediate precipitation (no extreme conditions) and limited seasonal distribution of rains (low seasonality) are pointed out as having higher mite diversity. This sensitivity is likely associated with the risk of desiccation of feather mites (direct effect), which is lower in more stable (lower range of climatic variation), more humid and hotter regions, such as rainforests (Proctor, 2003). Therefore, considering future climate change scenarios that indicate an increased occurrence of extreme precipitation values (including more frequent droughts) and rising temperature conditions may cause species extinction within this group (Carlson et al., 2017; Fischer & Knutti, 2015). In contrast, the small overall influence of abiotic factors on mite diversity suggests that the colonization of new hosts may not be hampered in the event of climate change (Doña & Johnson, 2020). However, our results also indicate that climate may play an important role, mainly in temperate regions. We suggest the need for further research on this topic because the extinction rate of symbionts with limited dispersal capabilities is expected to be twice that of those capable of dispersal (Carlson et al., 2017). Moreover, precipitation and temperature might also be major determinants of the redistribution of bird species, which may have an indirect negative effect on feather mite diversity (Gaston, 2000).

Lastly, and perhaps more troubling, the positive linear relationship between avian and mite diversity shown here, raises concerns

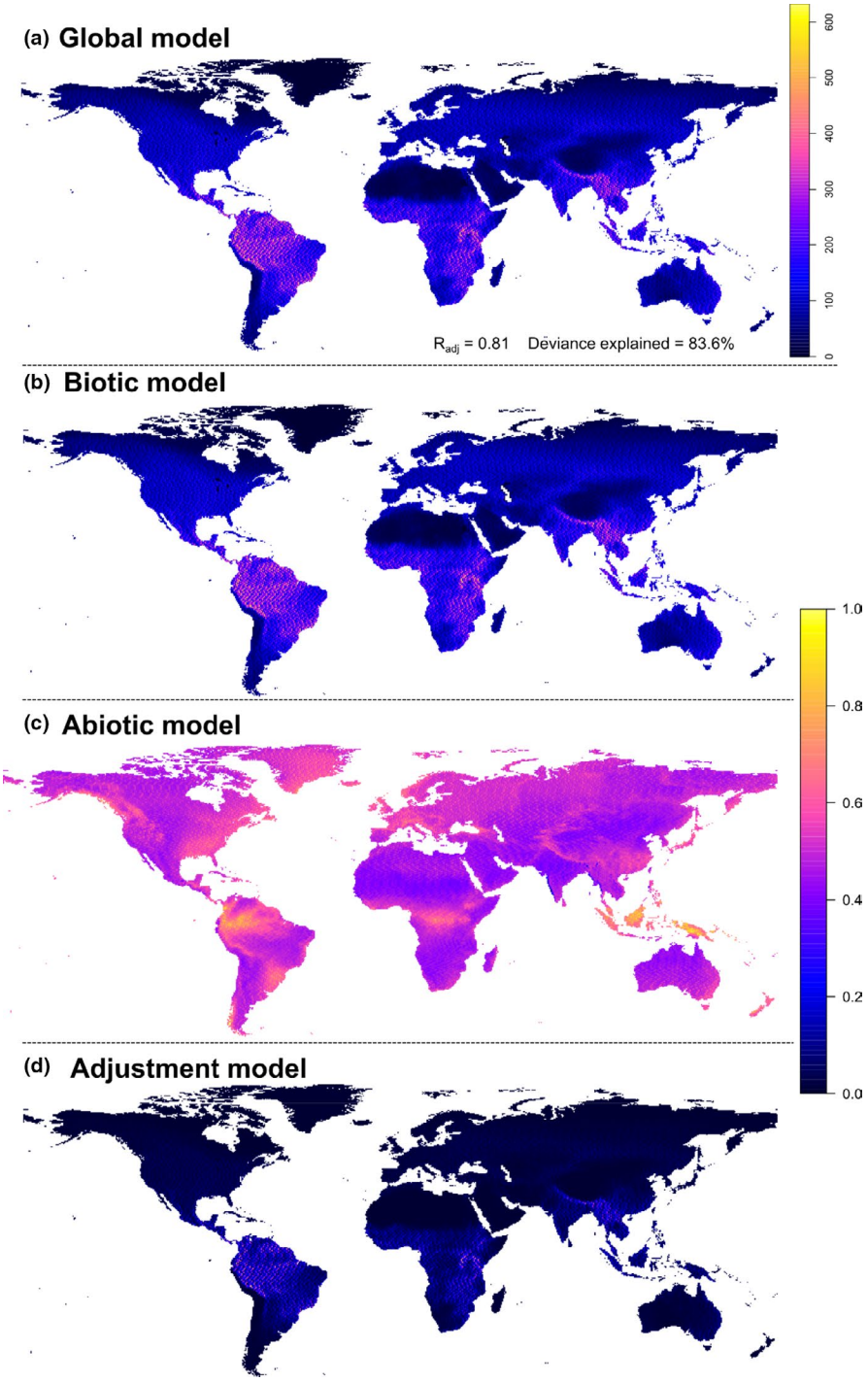

FIGURE 4 Global distribution of feather mite species richness calculated by different models. (a) Feather mite species richness distribution predicted by the global model, which includes abiotic and biotic factors; (b) Mite richness distribution predicted by the biotic model, which includes bird richness and keeps climate variables equal to the mean; (c) Mite richness predicted by the abiotic model containing climatic variables but fixing bird richness equal to the mean; (d) Adjustment differences of the abiotic and biotic models in relation to the global model

about co-extinctions. Recent studies predict that climate change and changes in land-use will result in the extinction of ~5% of the world's feather mite species (Carlson et al., 2017) and may impact negatively the range size of more than 50% of the global avian species by 2,100 (Jetz et al., 2007). These predictions suggest that feather mite diversity might drastically drop if climate change and reduced avian diversity are considered simultaneously, mainly in tropical regions (this study, Romero et al., 2018). Our results are in line with studies demonstrating that the forecasted climate changes may have stronger negative impacts on tropical species due to both the direct and mainly indirect effect of climate. For example, tropical insects have a projected fitness decline in warmer temperatures because they are live very close to their optimal temperature; also, they usually have less variation in temperature range (Deutsch et al., 2008). Likewise, predation pressure is expected to decline in the tropics due to climatic instability (Romero et al., 2018). By rearranging biotic interactions, climate change can erode biodiversity affecting ecosystem goods and services (Early & Keith, 2019; Wheeler & Braun, 2013). Therefore, we suggest that future studies seek to understand the potential response from these groups in future climatic scenarios and subsequent decrease in host diversity. For instance, to which

extent are feather mite species likely to become extinct after their hosts' extinction or if the extinction rate is associated with host vulnerability (Strona et al., 2013).

4.1 | Caveats and concluding remarks

We are aware that generalizing the effects of climate and host on feather mites as abiotic and biotic factors, respectively, might not be ideally suitable to some organisms such as deposit-feeding animals whose food is abiotic. Likewise, although ectosymbionts' interaction is clearly biotic, they also use their hosts as a physical "environment" to survive. Thus, by interpreting our findings about the interplay between abiotic and biotic factors driving macroecological patterns of symbionts, it is essential to consider such biological information about the studied organisms explicitly. In addition, although our methods estimate model performance (e.g., cross-validation), we cannot compare our model extrapolations with empirical data in unsampled sites, which indicates that future studies could improve our predictions by combining new empirical data at the macroecological scale.

Overall, our results emphasize the higher importance of biotic than abiotic factors (precipitation, energy and temperature) in the global distribution of a group of symbionts. Additionally, biotic and abiotic factors might predict the diversity of symbionts differently between regions (tropical and temperate). These results emphasize the need to include biotic interactions to better understand the predictive power of macroecological models (e.g., Louthan et al., 2015). Therefore, we argue that studies seeking to understand the effects of climate change on species' global distribution must also consider biotic interactions in the systems involved. Thus, we suggest that future studies aiming to understand the effects of climate change on symbiotic diversity, should also explore direct (via reduced diversity of any given animal/plant group) and indirect effects (via changes in interspecific interactions) to have better predictive power.

ACKNOWLEDGEMENTS

We are grateful to Dr. Felipe Melo and Ricardo Dobrovolski for comments that greatly improved earlier version of this manuscript. This study is part of the RAFG's master dissertation developed in the Graduate Program in Ethnobiology and Nature Conservation (PPGETNO). RAFG received a scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

DATA AVAILABILITY STATEMENT

We used a published global database of feather mites for Doña et al. (2016) (available at https://doi.org/10.1002/ecy.1528) and complemented this dataset with an additional search in two bibliographic databases (Scopus and Web of Science®) with articles published in 2016 and 2017 (see Supporting Information-Appendix S1). The complete dataset is going to deposit on Dryad as public repository for publication. Climatic data was downloaded from Fick and Hijmas (2017) (http://www.worldclim.org/data/worldclim21.html).

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Author contributions: R.A.F.G. and T.G.-S. conceived and designed the study. R.A.F.G., F.A.H, and M.H.V. did the data compilation of mite diversity and extracted environmental and bird diversity variable. R.A.F.G. and T.G.-S. performed models and other analyses. F.A.H, J. D., and L.N.N. contributed knowledge about the studied system. R.A.F.G. and T.G.-S. led the writing of the manuscript, with substantial contributions from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Gusmão RAF, Hernandes FA, Humberto Vancine M, Naka LN, Doña J, Gonçalves-Souza T. Host diversity outperforms climate as a global driver of symbiont diversity in the bird-feather mite system. *Divers Distrib.* 2021;27:416–426. https://doi.org/10.1111/ddi.13201