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15-Sep-2020  
  
Dear Mrs. de Angeli Dutra:  
  
I write to you regarding manuscript # ECOG-05343 entitled "Can migratory birds spread avian haemosporidian parasites?" which you have submitted to Ecography.  
  
In view of the criticisms of the reviewer(s) and the recommendation by the Subject Editor found at the bottom of this letter, I am sorry to report that your manuscript has been declined by Ecography.   I hope the enclosed comments may be of value for you.  
  
However, your paper is a candidate for transfer to another journal published by Wiley.  Please consider the journal options below and if you would like us to transfer your manuscript and associated reviews (if your paper received reviews), click the transfer link.  You will then be taken to the transfer portal site where you can select your preferred journal and initiate the transfer.  
  
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Thank you for considering Ecography.  
  
Sincerely,  
  
Prof. Miguel Araújo  
Editor-in-Chief, Ecography  
  
  
  
Recommendation by the Subject Editor (Dr. Susanne Akesson):  
I do not think this manuscript, and especially since it suffers from some methodological problems, is suitable for Ecography. After a major revision, it may however, be submitted to Ecology and Evolution.  
  
  
Reviewer(s)' Comments to Author:  
Reviewer: 1  
  
Comments to the Author  
This is a review of “Can migratory birds spread avian haemosporidian parasites?” (manuscript ID: ECOG-05343). The authors set out to test two hypotheses. The first is that “migratory birds spread parasite lineages along their migratory routes”. The second hypothesis is that the “prevalence and richness of haemosporidian lineages” at a locality will be positively related to the number of migratory routes that intersect that locality. The topic of how infectious disease spreads is of great importance in the fields of ecology, evolution, and public health. It is also difficult to study because pathogen dispersal is not as easily monitored as the dispersal of many free-living organisms. I therefore think that the authors have tackled a difficult, but important, topic.  
  
The description of the methods is difficult to follow (as explained below), which has made it difficult for me to interpret the results. I also am not sure that the statistical models (as I understand them) are accurate tests of the two hypotheses as they are currently stated. For example, the authors do not state whether migrants were sampled on their migratory routes or on their breeding or wintering grounds (just that they are migrants, l. 88-91), rendering the results of their test of the hypothesis of migrants spreading parasites along their migratory routes difficult to interpret. In fact, not identifying which sampled localities are part of migratory routes poses problems for the tests of the second hypothesis as well. Take l. 65-67 of the introduction as an example. Those lines state that to test the second hypothesis, the authors will compare parasite richness and prevalence to “the proportion of migratory birds passing through a locality”. I could not find a description of how the authors determined which birds were “passing through” and it seems like that may not have been part of the study. My opinion is that this manuscript should not be published as it is currently written. Nevertheless, there are really interesting aspects to this study. I have done my best to indicate to the authors where I think the main problems are and, in some cases, how they can be improved. I will give a more detailed review of sections of the manuscript below.  
  
Abstract  
“Hence, haemosporidian parasites…are likely dispersed thought [should read “through”] migration”. This is missing an argument. You should state that avian haemosporidians are found infecting migratory birds.  
  
“South America provides an ideal opportunity to investigate the role of migration and parasite dispersal as it holds the greatest richness of birds”. Species richness per se does not have to do with migration or transmission of parasites by migrants or at least the connection is not obvious. You should explain that there are many migrants birds in S. America that are infected with the parasites and/or (as is written in the introduction) that a large diversity of host species may mean that the chance of a parasite encountering a susceptible species goes up.  
  
  
Introduction  
l.10 “Conversely, the spread of pathogens might increase host richness by reducing local competition pressures and, therefore, preventing competitive exclusion”. This statement is difficult to understand.  
  
l.14-17 “studies have documented the influence of migratory birds on the spread of important pathogens with some of these able to infect humans (Alekseev et al. 2001, Morshed et al. 2005, Poupon et al. 2006, Hellgren et al. 2007, Lindeborg et al. 2012, Ricklefs et al. 2017)”. This makes it seem like the references document pathogens that can infect humans and are spread by migratory birds, so a few references should be moved to an earlier part the sentence.  
  
l.26-28 “Indeed, migratory species are known for their potential to connect distant habitats and transfer large amounts of biomass and nutrients between ecosystems”. How does transfer of biomass and nutrients relate to the transmission of parasites? More explanation here would be helpful.  
  
l.29-31 “migratory birds do not possess higher immune gene richness in wetter areas, which jointly with temperature is one of the main factors that influence haemosporidian prevalence (Illera et al. 2017).” Immune genes or wetter areas is one of the main factors?  
  
l.37-39 “Previous research has documented the prevalence of avian malaria in different regions of Brazil, and markedly different prevalence for Plasmodium spp, which is the most prevalent haemosporidian in this region, have been reported between these regions”. Unclear what this means. Consider rephrasing.  
  
l.58 It reads (i), (ii), (ii).  
  
l.59-62 “Due to the fact migrants can carry parasites from many sites and potentially infect resident birds, we predicted that parasite lineages using migratory birds should occur in a greater percentage of localities than those using only resident birds”. Alternatively, parasites that can infect multiple host species may have larger geographic distributions. I know that the authors try to account for this with by controlling for the number of host species each lineage infects, but number of host species only tells part of the story if parasites differ in the phylogenetic diversity of host species that they infect. Could the result that is eventually obtained of parasites that infect residents and migrants having greater geographic distributions than parasites that infect only migrants or only residents be indicative of the success of a generalist parasite? I think that is worth exploring (even to say it’s not the case), either here or in the discussion.  
  
  
Methods  
The dataset description is insufficient. First, the “new, previously unpublished data” require a section all to themselves with a complete description of where they are from, how they were collected, what protocols were used. Second, what data specifically were extracted from MalAvi? How were they combined with the rest of the data? Are the non-MalAvi data presented as a supplementary file (or in an online repository) separately from the MalAvi data? How did the authors guarantee that the MalAvi data did not include records from their dataset?  
  
l.83-84 Is there a table with the locality biome information? Could it be presented on the map in Figure 1? That would be helpful to the reader.  
  
l.95-96 Prevalence and richness could use explanations here. Were they calculated per host species within localities? Did you separate the parasite genera? Also, explain to the reader how Moran’s I varies (from -1 to 1, usually) and what it would mean for your variables and why you are calculating it. Otherwise the results will have no context.  
  
l.101-106 You downloaded a subset of full trees from birdtree.org then you randomly selected 100 trees, and then you randomly selected one tree from those 100? Why not just select one tree from the start? Define “phylo file”. It’s hard to justify writing that one tree would “account for phylogenetic uncertainty”. Typically phylogenetic uncertainty is accounted for by running an analysis on multiple trees or on a consensus tree.  
  
l.109 Cite Pagel (1999) Inferring the historical patterns of biological evolution. Nature, 401, 877-884.  
  
l.111-112 Phylogenetic signal could be defined here. Furthermore, describing lambda equal to one as “strong phylogenetic signal” should be changed. Lambda = 1 suggests that a trait has evolved in a way that is consistent with a Brownian motion (i.e., random walk) model of trait evolution. Phylogenetically close species will be more similar in trait values than species pulled randomly from the phylogeny under a Brownian motion model, but other models of evolution can describe traits that are more similar among phylogenetically close relatives than expected from a Brownian motion process (the latter could be described as stronger phylogenetic signal than Brownian motion).  
  
l.115 define “mean precipitation seasonality”. Why were those two variables chosen to represent climate?  
  
l.123 where are the results reported?  
  
l.124 delete “effect” and also explain what I = 0.15 means. Was this significantly different than the null expectation? Did it depend at all on sample size among localities? Again, is prevalence a species or locality measure? Examination of spatial autocorrelation among parasite communities across a region is a novel analysis and deserves detailed explanation and discussion.  
  
l.125 Why would adding biome as a random effect account for spatial autocorrelation? You do not mention the neighborhood size (the distance among points at which the autocorrelation is measured) so I cannot tell at what scale the autocorrelation occurs and whether biomes can account for it. Can that information be added in?  
  
l.127-128 “considerable phylogenetic signal” is signal that is significantly different than zero? Consider adding in P values of this test.  Was it calculated on all parasites together? Furthermore, what is the context? Why is it being reported in the methods? What is it setting up?  
  
What follows next is my understanding of the modeling, which I found difficult to follow, and some specific comments and questions. I hope that it helps the authors to identify areas that need clarification.  
  
The first hypothesis is tested by comparing the proportion (not “percentage” as written on l. 134 and 137; alternatively if it was percentage, the y axis of Fig. 2 should be changed, i.e., it’s important that figures present what’s in the models so as not to confuse the reader) of sampled localities that parasite lineages were found in as a function of the migratory status of the lineages’ host species. That is to say, the proportion of sampled localities that a lineage was found in was the response variable and the migratory status of the lineage’s host species was the explanatory variable in a model. The explanatory variable was categorical (six categories in total) and included the following categories: lineages that infect only resident host species, lineages that infect only migratory (either partial or full migrants or both) host species and lineages that infect both resident and migratory host species. This analysis also included lineage samples size (presumably the number of times a lineage was found in each locality) and number of host species of each lineage as covariates (the text states that lineage sample size and number of host species were controlled for in the model without explaining how, l. 143; I assume they were included as explanatory variables in the model). Priors were chosen automatically using an R function but not described (l.144; maybe they should be, even to say they are flat priors of some sort). It seems that the response variable has the same denominator for every parasite lineage which begs the question of why it’s being modeled as a proportion. Why not model it as the number of localities occupied? The results shouldn’t change, but it would make things clearer. Four chains were used, presumably for some kind of MCMC sampler to explore the parameter space of the model coefficients, although this is not stated (authors should consider adding it in). In most MCMC analyses, 2000 iterations/chain is lower than you would need to converge on accurate parameter estimates. Did the authors check convergence? Presumably the dataset used is the full data including the MalAvi data (authors should state explicitly).  
  
The first hypothesis is also tested with a model that includes prevalence as the response variable and the percentage of migratory bird species in a locality as the explanatory variable. Authors should explicitly state which dataset was used. It is written that prevalence refers to the “prevalence of infection in each bird species among localities” (l. 150-151) suggesting that there is a unique value for each bird species. However the explanatory variable is defined by locality and there is no mention of how a property of species within localities (i.e., prevalence) can be compared with a property of localities (i.e., the percentage of migratory bird species). Then I think that another set of models is created (l. 159), which related prevalence (again, unclear how prevalence is defined, unclear what dataset was used) with a number of explanatory variables. Then a statement is made regarding retaining some of the explanatory variables for another model (l. 164), but the authors could give a better justification and description here. This third (?) model incorporates a random effect of biome to “account for phylogenetic inference” (l. 165-166; at least that’s how I interpreted it; the authors may have meant that biome was a random variable and something else was used to control for phylogenetic inference, but that something else should be stated explicitly if that is the case. Either way I think the sentence needs clarification).  
  
To test the second hypothesis a generalized linear mixed model (GLMM) was created (it’s not explicitly stated that this is a GLMM, only that the R function used was “glmer”; many readers would probably appreciate a precise description of the models) with parasite lineage richness as the response variable and the percentage of migratory individuals per locality. I understand that parasite lineage richness is the number of lineages found in a locality when looking at all host species sampled at the locality. Then model selection was performed (l.183) on “previous models including variables that presented an effect on our dependent variable”. What models are those? Is there a table of them somewhere? Were they defined in the previous section testing the first hypothesis? That could use better explanation. Also, why is precipitation the only variable that isn’t log-transformed and scaled (l.188)?  
  
Results  
I could not find the figure legends in the manuscript. I used the supplementary figure legends as a guide since they are presumably the same.  
  
l.201 Are you sure that the number of occupied localities corresponds well to spatial distributions? Are there any examples of parasites that were found in only a few localities, but those localities were very far apart, say northern Colombia and Argentina? This highlights the fact that summary data are not shown in the manuscript, but could be helpful. What was the average number of localities, countries, biomes that each lineage occupied? What is the max distance between the localities that a single lineage occupied? Etc. The authors could present a number of summary statistics that would give the reader more context for interpreting the results and understanding the data.  
  
On a related note about understanding the data, Fig. 3 and the similar figures in the Supplementary materials should have data points and you might consider highlighting them by biome or country or something to help with understanding these data.  
  
I have not commented on the rest of the results or the discussion because of my confusion over the methods. But it seems that after the methods are clarified, the results could be simplified by presenting the Plasmodium and Haemoproteus results in the main text and removing the grouped genera results.  
  
Reviewer: 2  
  
Comments to the Author  
This study aims to test the role of migratory birds as spreaders of blood parasites through South American localities using two approaches. The first one is testing whether parasites shared by migratory and resident species are more widespread. The second approach is testing the correlation between proportion of migrants in the bird community and local parasite richness and prevalence. The authors show that parasites shared by residents and migrants show the greatest geographic range (estimated as the proportion of sampled localities with presence of the parasite). They fail to observe the expected relationship between proportion of migrants in the community and parasite prevalence or richness, but the analyses reveal a negative relationship between richness of migratory species and parasite richness.  
  
I liked reading the study and found the observed patterns interesting. However, I am not sure that they support the conclusions of the study due to various reasons. One potentially important problem with the study is the structure of the sampling. The study is certainly broad, but I am not that sure that each parasites has been sampled so exhaustively that their geographic distributions can be properly scored with these data, which may be influenced by singletons and intensively sampled sites typical of this kind of data (the study would benefit from a more comprehensive description of its sampling, for example in a supplementary appendix). Figure 2 suggests this may be an important problem (by the way, figure captions are missing in my copy for review): parasites not shared by migrants and residents are found in 1-2 sites on average (proportion of sites with presence of the parasite computed with n = 156 sites), meaning that according to the study they are most often local endemics or near endemic. This applies to parasites sampled in migrants alone, which one would expect to find in more places (at least those visited by their hosts). Parasites shared between residents and migrants are found in 2-3 sites, that is one more site on average. If the hosts sharing these parasites were not sampled in the same site as I worry it may be the most common occurrence, poorly sampled parasites (singletons) would greatly contribute to explain the whole figure, as parasites found in two hosts would be the only ones found in two sites. If most parasites are found in just one or two sites (Figure 2), how confident can we be that parasite geographic ranges are being analysed in this study? Intensively sampled sites are places where the networks of host-parasite interactions are more completely sampled, and such sites may have contributed many data of parasites shared by species of all kinds, thereby decreasing the average geographic spread of these parasites to just one in 156 sites. Perhaps the authors should think about restricting their analyses to parasites whose distribution can be estimated with some confidence, for example using lineages with a minimum number of observations. Using sites with a minimum sample size may also help to produce more informative results.  
  
Another important issue is where transmission takes place, which is relevant to understanding parasite spreading (see for example Hellgren et al 2007 cited in the paper) but is not considered in the study. Blood parasites may be found in birds' blood wherever the host is present, but this does not mean that they are transmitted in all places where they are found. Migratory hosts may carry parasites around the places they visit and this may increase the range of localities where their parasites are observed. But in order to parasites being spread by migrants, the parasites need not only be moved around by migratory hosts, but also be transmitted in the localities they visit. Therefore, that parasites shared with migrants are found in more localities is expected simply because migrants visit more places. If migrants truly contribute to spread parasites around (by definition: spilling parasites over birds from different areas), then their parasites should spread across more localities and this should be detected in the birds that can only acquire parasites locally (the residents). Therefore, a more appropriate approach for testing the hypothesis of the authors would be comparing the geographic range of parasites found in resident birds only or shared by resident and migratory species, but using only data of resident hosts to count localities with presence of each parasite (that is, localities where the parasite has truly established and is locally transmitted). If migrant birds are spreading parasites around, one would expect the parasites they can spread infecting residents all around the place, while parasites restricted in their movements (those that cannot move with migrants) would have more confined distributions. If migrants are included in the count, then it is not surprising that parasites of migrants are found in every place where migrants are found. Anyway, I believe this may become relevant once the dataset is restricted to parasites for which geographic ranges can be estimated with confidence, as I said before.  
  
The second prediction that proportion of migrants should increase prevalence and richness of parasites is not met. The authors claim that they "demonstrated that where the percentage of migrant species in a community is high, local haemosporidian richness is low, indicating the presence of migrant species can decrease parasite richness in bird communities". How possibly can this happen? Adding new host species (the migrants) to the list of sampled hosts may increase or leave as is the accumulated number of parasites found in one site, but by no means can it reduce it. Therefore, a better explanation for this pattern is that migrants tend to concentrate in areas where parasite richness is low. This is interesting in its own right, but in a different context. In this study, that result does not support the hypothesis that migrants are good spreaders (from a macroecological perspective), as they tend to avoid parasite-rich areas.