

# What controls the range of hosts a fish parasite infects?

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## **Abstract**

Host-parasite interactions are complex interactions capable of being influenced by a multitude of factors. Predicting what hosts a given parasite can infect is a central goal in parasite ecology. Here, we use concepts from niche modeling to develop predictive models capable of predicting host community composition of a given parasite. We do this using a large database of freshwater fish-parasite interactions (FishPest). For each of 238 parasite species that were recorded at least 20 times in the database, we trained boosted regression tree models on host trait variables, geographic variables, and parasite community variables in order to determine both the predictive capability of our models on hold-out data, and the relative influence of our three different variable classes on predictive accuracy. We found that models trained on parasite community variables had high predictive accuracy ( $\overline{AUC} = 0.89$ ) relative to models trained on geographic variables ( $\overline{AUC} = 0.79$ ), or host traits ( $\overline{AUC} = 0.66$ ). Taken together, our findings suggest that the parasite communities of host species contain valuable information on the likelihood of infection by a novel parasite, which has implications for predicting how introduced parasites will integrate themselves into natural communities.

## Keywords

FishPEST, species distribution model, boosted regression tree, parasite niche

## Introduction

Parasites are ubiquitous in nature, and are incredibly diverse in their life histories, transmission modes, and degree of host specificity (Poulin, 2011). The question of what constrains which hosts a parasite infects is a central question to disease ecology. On one hand, host-parasite relationships may be viewed as complex interactions determined by environment (Locke et al., 2013), geography Nieberding et al. (2008), co-evolutionary history Krasnov et al. (2012), or trait matching between host and parasite Rohr et al. (2013). On the other, host-parasite interactions may be viewed as random Kennedy (2009), or neutral interactions, such that predicting which hosts a parasite will infect is either impossible, or determined simply based on host abundance Canard et al. (2014). The degree to which host-parasite interactions are environmentally constrained, and therefore predictable, is unclear. Previous efforts to characterize parasite communities have largely focused on parasite richness (Arneberg, 2002; Nunn et al., 2003; Ezenwa et al., 2006; Poulin and Rohde, 1997) instead of parasite community composition. Further, studies examining parasite community composition have focused efforts on topological measures of host-parasite networks (Guégan and Hugueny, 1994; Canard et al., 2014; Krasnov et al., 2012; Poulin, 2010) or examined distance decay relationships in parasite community dissimilarity (Locke et al., 2012, 2013; Poulin, 2003). The ability to 1) discern if host-parasite interactions are simply neutral processes, and 2) predict the identity of the subset of hosts able to be infected by a particular parasite is a large knowledge gap in the study of parasite ecology. From an applied perspective, parasite host range prediction could be useful for forecasting potential parasite spillover events to novel hosts Colautti et al. (2004), including humans Daszak et al. (2000).

One of the largest factors holding predictive models of parasite distributions among

potential hosts is the relative paucity of data (but see ). However, this barrier is being overcome both by scientists Strona and Lafferty (2012a); Nunn and Altizer (2005) and museums (Gibson et al. (2005)). Studies utilizing these large datasets have largely asked questions about parasite co-occurrence patterns Strona et al. (2013), or the factors influencing parasite sharing Braga et al. (2014); Dallas and Presley (2014). These studies largely examine parasite community composition, and determine the influence of host traits or phylogenetic relationships on parasite community composition. However, few studies have attempted to predict which hosts a given parasite species will infect, despite the importance of this question to public health, and host-parasite network structure. Specifically, efforts predicting parasite spillover to humans may be essential for mitigation of zoonotic diseases. Further, the ability to predict which hosts an introduced parasite will infect in the native community can guide management decisions, and effectively predict change in host-parasite network structure. Previous efforts to predict parasite species host ranges have been hampered by the use of deprecated niche modeling algorithms, and conceptual differences in study goals (Strona and Lafferty, 2012a). Specifically, Strona and Lafferty (2012a) developed a framework, specifically PaNic (Strona and Lafferty, 2012b), that estimates parasite niche boundaries as defined by the host traits of known hosts, and then estimated which hosts *could* become parasitized by the given parasite species, given constraints (e.g., host family, geographic location) imposed by the user. Our goal is slightly different from this, in that we aimed to develop predictive, validated models that would allow for the determination of the relative importance of host traits, geographic variables, and other parasites that infect a given host species. This aim addresses a central gap in our understanding of host specificity in parasites; what constrains which hosts get infected by a given parasite species?

We address this knowledge gap by using a large database on freshwater fish parasites (Strona et al., 2013), in order to develop predictive parasite species distribution models for a number of parasite species. In doing so, we can address the predictive capability of models trained on different variable classes. Parasite occurrence is likely not a simple

function of host traits, as previous modeling efforts have assumed. Specifically, the number and identity of host species that a given parasite could infect may be constrained by geographic location, host trait variables (i.e. patch quality), or the existing parasite community of the given host species (i.e. parasite community structure). To address the relative importance of these variable classes, we trained boosted regression models on each of these three variable classes, and compared the accuracy obtained from each model in predicting the potential distributions of 238 parasite species. Parasite species distributions were most constrained by the existing parasite community, as this model allowed for highly accurate prediction of parasite occurrence likelihood. Models trained on host traits had poor predictive capabilities, and models trained on geographic variables had intermediate predictive accuracy. Taken together, our findings suggest that predicting the host distribution of a given parasite species requires information on the parasite communities of the potential hosts, and not necessarily any information on host traits.

## Methods

**Data and processing** We use an existing global database of fish-parasite associations (hereafter referred to as FishPest; (Strona et al., 2013)) consisting of over 38,000 helminth parasite records spanning a large diversity of parasites (Acanthocephala, Cestoda, Monogenea, Nematoda, Trematoda). Many of these entries represent isolated occurrences of parasites on hosts. In order to allow for cross-validation and accurate prediction, we constrained our analyses to parasites with a minimum of 20 host records. In other words, we only examined parasites that had been recorded more than 20 times, but these occurrences could be on fewer than 20 host species. The inclusion of duplicate occurrences was only permitted if the parasite was recorded on a host in a different geographic location, based on latitude and longitude values. This resulted in a total of 238 parasite species. Our response variable was parasite occurrence (binary), and was predicted using three classes of variables, representing host life history traits, geographic location, and parasite

community similarity (Table 1).

Values of predictor variables were obtained largely through the FishPest database Strona and Lafferty (2012a); Strona et al. (2013), supplemented by variables obtained from FishBase Froese and Pauly (2010). However, there were still some missing predictor variable values. Missing predictor variable values were imputed using the imputation procedure in the `randomForest` R package (Liaw and Wiener (2002)). Details of host trait and geographic variable determination are provided in Strona et al. (2013) and Table 1. Parasite community structure was considered as the first five principal components from a principal components analysis on the host-parasite matrix. This matrix contains information on all parasites infecting all host species, except with the parasite species of interest removed. Thus, the principal components represent a measure of parasite community structure among host species without any information about host range of the parasite species under consideration. Typically, the cumulative proportion of variance explained from the first five principal components was low, with a mean value of 0.28 cumulative proportion of variance explained. In addition, we included parasite species richness of a host as a predictor variable, as this may reflect the susceptibility of host species to parasitism.

**Predictive model formulation** Here, we used boosted regression trees to predict parasite occurrence among potential host species for each of our 238 parasite species. Regression tree analysis is an extremely powerful tool for prediction and feature selection, bypassing many of the issues of simple regression models (e.g. multicollinearity, nonlinear relationships) Elith et al. (2008); Dallas and Drake (2014). Boosting refers to the process of creating a large number of regression trees, and weighting them by their predictive power to extract general weak rules, which are then combined to enhance predictive ability. The optimal number of trees was determined using the out-of-bag (OOB) estimation procedure, with the upper limit set to 50000. Other pertinent parameters include the learning rate ( $l = 0.001$ ), which controls the degree each new tree contributes to the overall model, and interaction depth ( $id = 4$ ), which allows for up to four-way

interactions among predictor variables.

The absence of a recorded interaction between host and parasite does not mean that the parasite does not infect that host. Borrowing from the idea behind Maximum Entropy modeling, we sampled the data to obtain background interactions, which we define here as a set of possible interactions between host and parasites. This background set was not composed of the entire dataset, but rather a sample of five times the number of positive occurrence records for a given parasite. These data were subset into a training set, 70% of the data used to train the boosted regression tree model, and a test set, the remaining 30% of the data used to test the predictive accuracy of the trained model.

From the final boosted regression tree models, we are able to extract variable relative contribution ( $RC$ ) measures, which provide information about the importance of each variable to the final model predictions. Relative contribution values for each predictor variable was determined by permuting each predictor variable and quantifying the reduction in model performance, a method that is free of classical assumptions about normality and equal variance (Anderson 2001). Relative contribution estimates were then based on the number of times a given predictor variable was selected for splitting, weighted by the degree the split improves model performance, and scaled between 0 (no contribution) to 100 (maximum contribution).

All models were compared to a random null model, which randomized occurrence values in the test dataset, but kept them constrained to the total number of occurrences. Model performance was assessed using receiver operating characteristic curves, which relate true positive and false positive (type I error) rates graphically. The area between the curve generated by true and false positives and the 1:1 line from the origin gives a measure of predictive accuracy.

## Results

**Importance of host traits, geographic variables, and parasite community similarity** All models performed better than our null predictions (null model  $\overline{AUC} = 0.50$ ). With varying degrees of accuracy, models were able to predict parasite occurrence for the 238 parasite species examined using host traits ( $\overline{AUC} = 0.66$ ), geographic variables ( $\overline{AUC} = 0.79$ ), and parasite community similarity ( $\overline{AUC} = 0.88$ ). The full model containing all variables was able to successfully predict parasite occurrences in the hold-out test dataset with high accuracy ( $\overline{AUC} = 0.89$ ), only marginally more accurate than the model trained with only parasite community similarity variables (Figure 1). The relative contribution ( $RC$ ) values for each separate model, and the model trained on all available data are provided in Figure 2.

In the full model, variables of different classes were allowed to have different relative contributions, which allows for the determination of variables driving the predictive accuracy of the full model. For instance, relative contribution values were largest for the parasite community similarity values obtained from the principal components analysis on the host-parasite network with the parasite species of interest removed (Figure 2), with the five PCA vectors comprising around 52% of the relative contribution values, and four of the top five predictive variables. On the other side of the predictive spectrum, host trait variables, specifically host age at maturity, lifespan, and growth rate, contributed very little to model performance.

**Was predictive ability influence by parasite ecology?** The relative importance of variable classes, or the general predictive power of the trained model, may differ as a function of parasite taxonomic group or host specificity. We tested for variation in predictive power among parasite taxonomic group (Acanthocephalans, Cestodes, Monogeneans, Nematodes, and Trematodes) and as a function of the number of host specificity. Here, we defined parasite host specificity as the number of hosts a parasite infects. We failed to

184 detect evidence that parasite taxonomic group (Figure S1) influenced predictive power in  
185 any of our trained models. We did, however, observe an effect of host specificity (Figure  
186 S2), as predictive accuracy became more variable as host specificity increased (i.e. the  
187 number of hosts a given parasite infected became smaller). Despite this variability, the  
188 the mean predictive accuracy over a range of host specificity values remained constant  
189 (Figure S2).

## 190 Discussion

191 We provide evidence that host traits are not as important to determining which hosts a  
192 given parasite will infect relative to geographic location, or parasite community similarity.  
193 This suggests two things. First, the current paradigm that attempts to define a parasite's  
194 niche based on qualities of the host (e.g. body size) may need to be reconsidered. Second,  
195 it suggests that the parasite community infecting a given host species contains informa-  
196 tion that can either predict or preclude the occurrence of a novel parasite species on that  
197 host. Further, model predictive accuracy did not vary strongly as a function of parasite  
198 type or specificity, suggesting that our findings may be broadly applicable to parasites  
199 of different transmission modes, life histories, and degrees of specificity. Taken together,  
200 our analyses suggest that parasite communities of freshwater fish are not simply random  
201 assemblages, but are predictable with high accuracy given only information on coinfect-  
202 ing parasites. Further, our findings have implications to host community invasibility by  
203 novel parasites, parasite spillover, and host-parasite network structure.

204  
205 We found that host traits generally poorly predicted parasite occurrences, a striking  
206 finding given that a parasite's niche is often defined using information on host life history  
207 and phylogeny (Strona and Lafferty, 2012a; Rohde, 1993). It is possible that host traits  
208 are important in structuring a parasite niche, especially host traits related to the ability  
209 of a parasite to infect a given host species (e.g. immune defenses, diet breadth, or geo-  
210 graphic range) (Johnson et al., 2012). This would be the case if the host traits measured



here were not the traits that most constrain parasite occurrences, and if geographic and parasite community variables were highly correlated with unmeasured host traits. However, host traits examined here should have captured at least some information related to likelihood of parasite infection. Specifically, host population growth rate and host age at maturity are likely related to immune defenses (Zuk and Stoehr, 2002), as host trophic level is related to exposure (Price, 1990). Geographic variables predicted parasite occurrences more accurately, but the importance of individual geographic variables varied greatly among parasite species (Figure 2), suggesting either that parasite species are responding to different geographic variables, or that a methodological aspect of the analysis causes no single variable to dominate predictions. This could occur if geographic variables were highly correlated, or if interactions among variables were very important (i.e. the interaction between latitude or longitude with geographic region).

Parasites may be introduced with the addition of non-native host species to communities. The successful integration of the non-native host may be either enhanced if parasites of the non-native host “spillover” to the resident host community, or reduced by the sharing of parasites from the resident host community to the potential invader (the so-called biotic resistance hypothesis; Britton (2013)). The ability to predict the likelihood of both avenues of parasite sharing could allow for the prediction of invasion probability based on the parasite community of host species present. Based on our work, predicting what resident host species are likely to become infected by a novel parasite requires only information on the parasite communities of the resident host species. This means that pre-invasion prediction of parasite spillover may be possible.

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## References

- Arneberg, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* 25:88–94.
- Braga, M. P., E. Razzolini, and W. A. Boeger. 2014. Drivers of parasite sharing among neotropical freshwater fishes. *Journal of Animal Ecology* .
- Britton, J. R. 2013. Introduced parasites in food webs: new species, shifting structures? *Trends in Ecology & Evolution* 28:93–99.
- Canard, E., N. Mouquet, D. Mouillot, M. Stanko, D. Miklisova, and D. Gravel. 2014. Empirical evaluation of neutral interactions in host-parasite networks. *The American Naturalist* 183:468–479.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology letters* 7:721–733.
- Dallas, T., and J. M. Drake. 2014. Relative importance of environmental, geographic, and spatial variables on zooplankton metacommunities. *Ecosphere* 5:art104.
- Dallas, T., and S. J. Presley. 2014. Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. *Oikos* 123:866–874.
- Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287:443–449.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* 77:802–813.
- Ezenwa, V. O., S. A. Price, S. Altizer, N. D. Vitone, and K. C. Cook. 2006. Host traits and parasite species richness in even and odd-toed hoofed mammals, artiodactyla and perissodactyla. *Oikos* 115:526–536.

263 Froese, R., and D. Pauly. 2010. Fishbase.

264 Gibson, D., R. Bray, and E. Harris. 2005. Host-parasite database of the natural his-  
265 tory museum, london. URL [http://www.nhm.ac.uk/research-curation/scientific-](http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/index.jsp)  
266 resources/taxonomy-systematics/host-parasites/database/index.jsp .

267 Guégan, J.-F., and B. Hugueny. 1994. A nested parasite species subset pattern in trop-  
268 ical fish: host as major determinant of parasite infracommunity structure. *Oecologia*  
269 100:184–189.

270 Johnson, P. T., J. R. Rohr, J. T. Hoverman, E. Kellermanns, J. Bowerman, and K. B.  
271 Lunde. 2012. Living fast and dying of infection: host life history drives interspecific  
272 variation in infection and disease risk. *Ecology Letters* 15:235–242.

273 Kennedy, C. 2009. The ecology of parasites of freshwater fishes: the search for patterns.  
274 *Parasitology* 136:1653–1662.

275 Krasnov, B. R., M. A. Fortuna, D. Mouillot, I. S. Khokhlova, G. I. Shenbrot, and  
276 R. Poulin. 2012. Phylogenetic signal in module composition and species connectivity  
277 in compartmentalized host-parasite networks. *The American Naturalist* 179:501–511.

278 Liaw, A., and M. Wiener. 2002. Classification and regression by randomforest. *R News*  
279 2:18–22.

280 Locke, S. A., M. S. Levy, D. J. Marcogliese, S. Ackerman, and J. D. McLaughlin. 2012.  
281 The decay of parasite community similarity in ring-billed gulls *larus delawarensis* and  
282 other hosts. *Ecography* 35:530–538.

283 Locke, S. A., J. D. McLaughlin, and D. J. Marcogliese. 2013. Predicting the similarity of  
284 parasite communities in freshwater fishes using the phylogeny, ecology and proximity  
285 of hosts. *Oikos* 122:73–83.

286 Nieberding, C. M., M.-C. Durette-Desset, A. Vanderpoorten, J. C. Casanova, A. Ribas,  
287 V. Deffontaine, C. Feliu, S. Morand, R. Libois, and J. R. Michaux. 2008. Geography

and host biogeography matter for understanding the phylogeography of a parasite.  
Molecular phylogenetics and evolution 47:538–554.

Nunn, C. L., S. Altizer, K. E. Jones, and W. Sechrest. 2003. Comparative tests of parasite  
species richness in primates. *The American Naturalist* 162:597–614.

Nunn, C. L., and S. M. Altizer. 2005. The global mammal parasite database: an online  
resource for infectious disease records in wild primates. *Evolutionary Anthropology:  
Issues, News, and Reviews* 14:1–2.

Poulin, R. 2003. The decay of similarity with geographical distance in parasite commu-  
nities of vertebrate hosts. *Journal of Biogeography* 30:1609–1615.

———. 2010. Network analysis shining light on parasite ecology and diversity. *Trends  
in Parasitology* 26:492–498.

———. 2011. *Evolutionary ecology of parasites*. Princeton university press.

Poulin, R., and K. Rohde. 1997. Comparing the richness of metazoan ectoparasite com-  
munities of marine fishes: controlling for host phylogeny. *Oecologia* 110:278–283.

Price, P. W. 1990. Host populations as resources defining parasite community organiza-  
tion. Pages 21–40 *in* *Parasite communities: patterns and processes*. Springer.

Rohde, K. 1993. Niche restriction in parasites: Proximate and ultimate causes. *Para-  
sitology* 109:S69–84.

Rohr, R. P., R. E. Naisbit, C. Mazza, and L.-F. Bersier. 2013. Matching-centrality decom-  
position and the forecasting of new links in networks. *arXiv preprint arXiv:1310.4633*  
.

Strona, G., and K. D. Lafferty. 2012*a*. FishPEST: an innovative software suite for fish  
parasitologists. *Trends in parasitology* 28:123.

———. 2012*b*. How to catch a parasite: parasite niche modeler (panic) meets fishbase.  
*Ecography* 35:481–486.

- 313 Strona, G., M. L. D. Palomares, N. Bailly, P. Galli, and K. D. Lafferty. 2013. Host range,  
314 host ecology, and distribution of more than 11,800 fish parasite species: Ecological  
315 archives e094-045. *Ecology* 94:544–544.
- 316 Zuk, M., and A. M. Stoehr. 2002. Immune defense and host life history. *The American*  
317 *Naturalist* 160:S9–S22.

Table 1: Description and units of variables used to predict parasite occurrences.

Variable	Units	Description	Range
Age at maturity	years	Age at sexual maturity	0.1 – 34
Growth rate	years <sup>-1</sup>	Rate to approach asymptotic length	0.02 – 9.87
Life span	years	Estimated maximum age	0 – 145
Max length	cm	Maximum fish species length	1 – 2000
Trophic level	–	1 + mean trophic level of food	2 – 5
Area of occupancy	No. 1x1 ° cells	Global host distribution	1 – 1610
Geographic region	–	Biogeographic region	–
Latitude	max - min  degrees	Latitudinal distribution	1 – 148
Longitude	max - min  degrees	Longitudinal distribution	1 – 359
Parasite species richness	#	No. parasite species of host species	0 – 89
Principal components	–	PCA axes of host-parasite network	-11.7 – 9.8

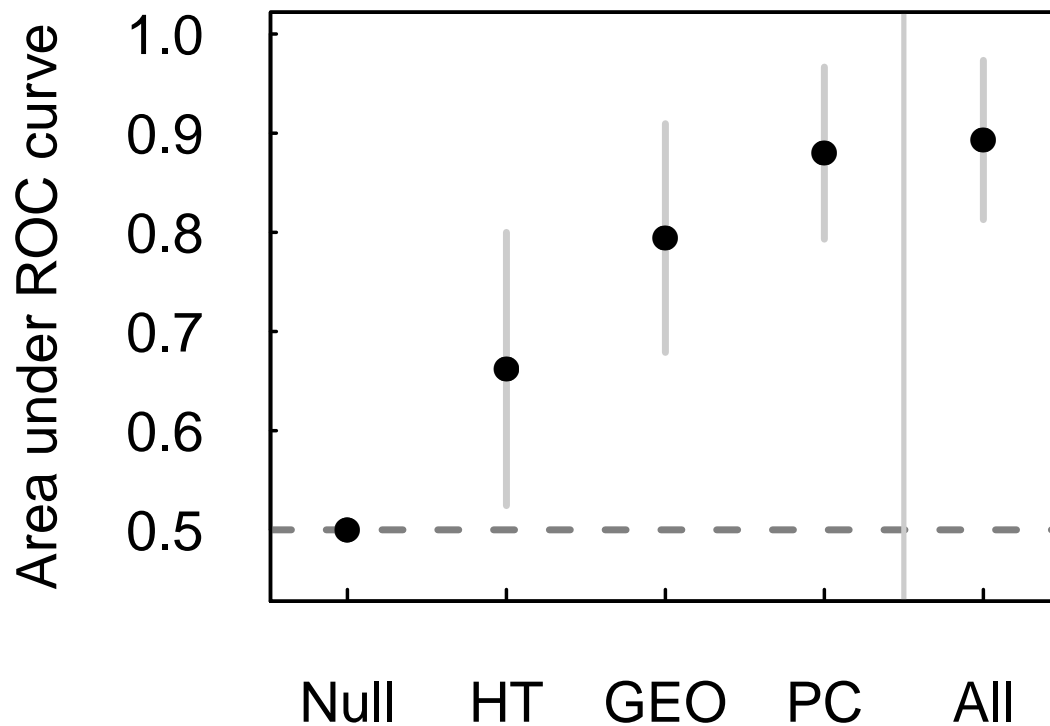


Figure 1: Accuracy, measured as the Area under Receiver operating characteristic (ROC) curves, for our predictive boosted regression tree models incorporating host traits (HT), geographic variables (GEO), parasite community information (PC), and the full model (ALL). These trained models were compared to a null model (Null) that maintained interaction number (number of occurrence records), but assigned occurrences equiprobably among potential interactors.

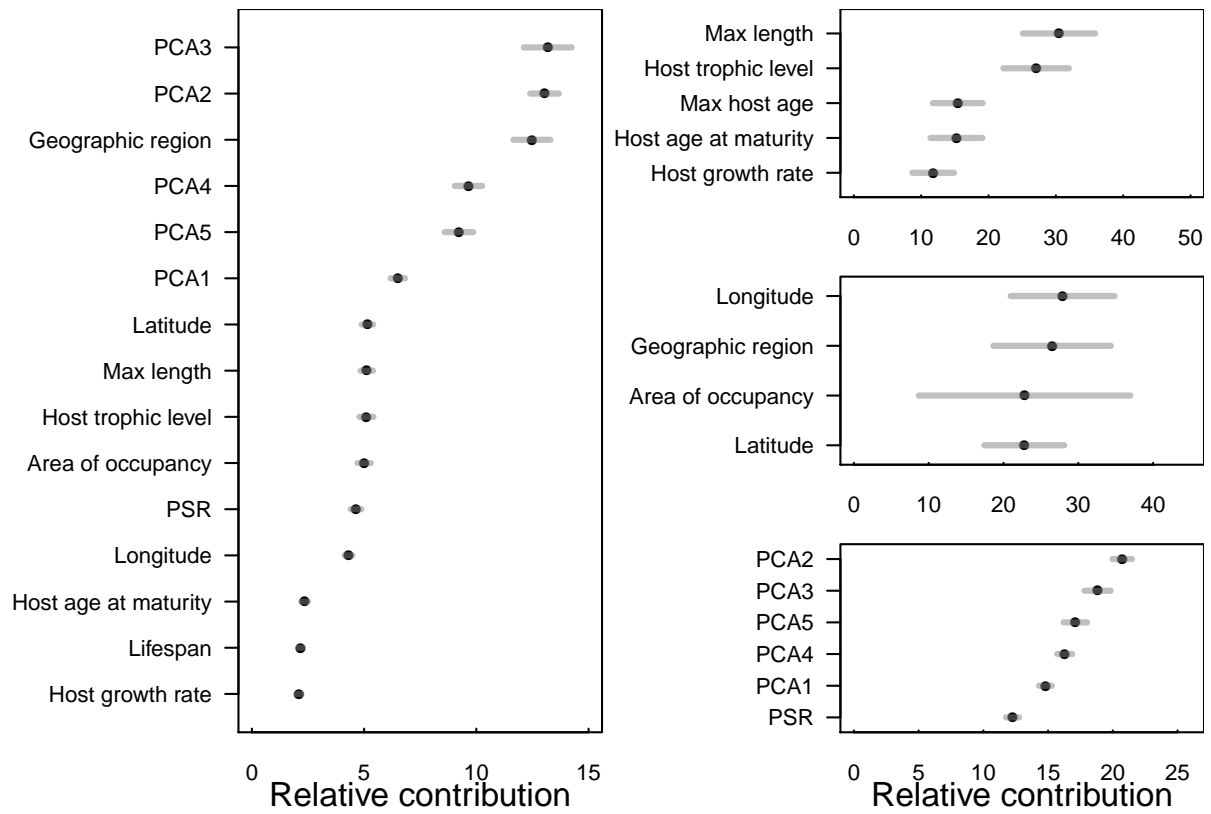


Figure 2: The average relative contribution values from the boosted regression tree models trained on all available data (left), host trait data (top right), geographic variables (middle right), and parasite community similarity (bottom right). Variables named “PCA” are principal components axes, and “PSR” refers to parasite species richness. Other variable definitions and units are available in Table 1.