Competition and environmental gradients structure Canidae assemblages across the planet

Distribution patterns in Canidae

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Abstract

Aim

The phylogenetic information of assemblages carries the signature of ecological and evolutionary processes that assembled these communities. Closely related species, under similar environmental conditions, are likely to present similar traits due to environmental filtering. However, if species are too similar, it is unlikely that they will co-occur because of competitive exclusion. Identifying the mechanisms that shape communities is not simple, as they can vary spatially. Here, we investigated how the phylogenetic structure of Canidae is affected across the globe by the environment and competition.

Location

Americas, Eurasia, and Africa.

Time period

Present.

Major taxa studied

Canidae.

Methods

We first identified phylogenetically clustered and overdispersed Canidae assemblages over the planet. Then, we apply Structural Equation Models in these communities in order to identify the effect that temperature, vegetation cover, human impact, and body size dissimilarity have on the global distribution of canids.

Results

South America and Asia present a high concentration of clustered communities, whereas Central America, Europe, and North America show phylogenetically overdispersed assemblages. Vegetation cover and human impact are the most important variables to explain the patterns of phylogenetic structure in overdispersed and clustered communities, respectively, followed by temperature and body size dissimilarity. Interestingly we found that more body size dissimilarity is associated with more clustering in clustered communities, but with more overdispersion in overdispersed communities.

Main conclusion

Canidae community composition across the world presents significant patterns of clustering and overdispersion, which vary following mainly the environmental gradient, suggesting habitat filtering as the main force acting on Canidae assemblages. We conjecture that competition may still have played an important role, because character displacement seems to have driven species to diverge in their body.

Key-words: Clustering, community assembly, habitat filtering, NRI, overdispersion, phylogenetics.

1. INTRODUCTION

The assembly of an ecological community is influenced by several biotic and abiotic factors (Webb, 2000; Webb *et al.*, 2002; Westoby, 2006), including competition and habitat filtering. On the one hand, the competitive exclusion principle predicts that ecologically similar species cannot coexist if resources are limiting, and under phylogenetic trait conservatism, this implies that communities will be phylogenetically overdispersed (Darwin, 1859; Elton, 1946; Leibold, 1998; Webb *et al.*, 2002). On the other hand, phylogenetically closely related species likely share traits that allow them to tolerate a specific environment (Jarvinen, 1982; Weiher *et al.*, 1998; Webb *et al.*, 2002; Di Marco & Santini, 2015), which implies phylogenetic clustering of species in an ecological community. Because this also applies to traits that are linked to competitive ability, competition may also lead to phylogenetic clustering (Mayfield & Levine, 2010; HilleRisLambers *et al.*, 2012). If one can rule out this possibility, patterns of phylogenetic overdispersion or clustering are indicative of competition and habitat filtering respectively if the relevant traits are phylogenetically conserved. If traits are not conserved, overdispersion may be due to trait convergence of distant species, and clustering could be a result of historical processes that limited species' dispersion from their ancestral ranges (Webb, 2000; Webb *et al.*, 2002; Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007).

Webb (2000) and Webb *et al.* (2002) described how communities can be tested for phylogenetic overdispersion or clustering by comparing the value of a community metric to that of a null distribution of randomized communities. One such metric is the net relatedness index (NRI), where negative values of NRI are indicative of overdispersion, while positive values indicate clustering (Webb, 2000; Webb *et al.*, 2002). They suggested that randomized communities can be obtained by permuting the presence-absence pattern on the phylogenetic tree. Pigot & Etienne (2015) argued that such a permutation approach does not yield a proper null distribution because it ignores speciation, colonization, and extinction dynamics. They developed a method that does take these processes into account and found that a null community (i.e. without habitat filtering or competition, but with speciation, colonization and extinction dynamics) would be overdispersed relative to the randomized community resulting from permutation. While absolute values for phylogenetic dispersions are therefore difficult to interpret, relative values are still informative: one can still compare dispersion patterns between communities and ask why some communities are more overdispersed or clustered than others. Many studies have used the phylogenetic approach described by Webb (2000) and Webb *et al.* (2002) to understand how the phylogenetic information of clades is structured through space (Cavender-Bares *et al.*, 2004; Helmus *et al.*, 2007; Kress *et al.*, 2009; Kraft & Ackerly, 2010; Goberna *et al.*, 2014; Yang *et al.*, 2014; Miazaki *et al.*, 2015; Cadotte & Tucker, 2017; Pérez-Valera *et al.*, 2017; Zhang *et al.*, 2018; Kusumoto *et al.*, 2019). The majority of these studies have shown that overdispersion dominates at small scales, while clustering explains the structure of communities better at large scales. These findings demonstrate that the interpretation of the mechanisms acting in a community is scale-dependent (Webb *et al.*, 2008). In this light, it is interesting to note that a large number of studies on phylogenetic structuring of communities are at small scales (see Cardillo, Gittleman, & Purvis, 2008).

Another difficulty in studies on the phylogenetic structure of communities relates to how abiotic and biotic factors are treated as independent forces acting on a community. Although habitat filtering and competition are contrasted in their effect on community structure, they occur together in natural communities (Ackerly, 2003; Cadotte & Tucker, 2017). Over the last decade, several studies have attempted to understand how much each mechanism influences communities (Kraft & Ackerly, 2010; Goberna *et al.*, 2014; Cadotte & Tucker, 2017; Pérez-Valera *et al.*, 2017; Zhang *et al.*, 2018; Kusumoto *et al.*, 2019). The results have been inconclusive. Cadotte & Tucker (2017) noted that "it is likely that most observational data reported as evidence for environmental filtering, in fact, reflect the combined effects of the environment and local competition." To overcome these issues, one needs a detailed analysis of whether traits are conserved or not on a phylogenetic tree and of how patterns of phylogenetic dispersion vary with environmental variables.

Here, we assess patterns of phylogenetic dispersion in the family Canidae across the world. As canids are present in all continents, except in Antarctica (Wang & Tedford, 2008; Wilson & Mittermeier, 2009), and have a well-resolved phylogenetic tree (Porto *et al.*, 2019), they are an ideal group to test how the phylogenetic structure of a whole clade is structured over the world by the influence of environmental and competition forces. The phylogeny of extant canids presents 36 species distributed in three distinct clades (Porto *et al.*, 2019) with a variety of patterns: multiple species of a single genus, multiple genera of only one species, species with continental distributions, and also geographically restricted species. We explore, using Structural Equation Models (SEM), how dispersion pattern relates to environmental variables and a measure of competition among canids (dissimilarity in body size).

2. MATERIAL AND METHODS

2.1 DATA COMPILATION

Canids' range maps were compiled from the IUCN Red List for all the 36 species (IUCN, 2019). We processed these maps using ArcGIS (ESRI, 2019) to generate a presence-absence matrix of species within defined grids cells of 300 x 300 km (hereafter, assemblages). From these grids, we extracted average values for three environmental variables (mean temperature, vegetation cover, and human footprint) (Center for International Earth Science Information Network, 2005; Fick & Hijmans, 2017; USGS, 2019). Temperature and vegetation cover are two of the most commonly used suites of variables in studies that evaluate species distribution (Porfirio *et al.*, 2014), while human footprint was included in the models following Di Marco & Santini (2015), who found that human impacts explain the distribution of terrestrial mammals better than biological traits. Canid body size were obtained from the Handbook of the Mammals of the World (Wilson & Mittermeier, 2009) and also from the Animal Diversity Web (ADW) (Myers *et al.*, 2018) (Table S1).

We then calculated for each grid cell the body size dissimilarity among the canids within each assemblage using the decoupled trait approach proposed by De Bello *et al.* (2017) (*dcFdist*). This approach calculates functional differences between species accounting for the shared evolutionary history. Thus, we can measure how different canids within communities are, based on their body size, while accounting for their ancestry. Body size dissimilarity was used as a measure of competition. We are assuming here that dissimilarity has resulted from past competition and has led to character displacement, as already suggested by Smith *et al.* (2004) and Lomolino (2005) for mammals. Therefore, the greater the body size dissimilarity within an assemblage, the greater was the competition in that assemblage. Analyses were performed in R 4.0-2. (R Development Core Team, 2020) using the raster package 3.3-13 (Hijmans & Etten, 2012).

2.2 PHYLOGENETIC DATA ANALYSES

We used the phylogeny presented by Porto *et al.* (2019) that includes all 36 extant canid species and one recently extinct. The phylogeny was constructed through Bayesian inference based on 23 genes and 68 osteological characters. We removed the extinct species *Dusicyon australis* from this tree because there is no environmental data available for the region where the species lived before the year of its extinction (1876). To investigate how body size is distributed over the phylogeny, we calculated its phylogenetic signal using the *K*-statistic (Blomberg & Garland, 2003) with the R package Phytools 0.7-47 (Revell, 2012). Values of $K < 1$ describe less phylogenetic signal than expected under a Brownian motion model of character evolution, while values of $K > 1$ describe data with greater phylogenetic signal than expected under Brownian motion.

To analyze phylogenetic dispersion patterns over the planet, we first calculated the standardized effect size of mean pairwise distances in communities (MPD) for each assemblage using the package Picante 1.8-2 (Kembel *et al.*, 2010). Expected MPD was obtained by 1000 randomizations (999 iterations for each). We then calculated the net relatedness index (NRI) from MPD as follows:

$$NRI = -1 \times \frac{Observed\ MPD - Expected\ MPD}{SD(Expected\ MPD)}$$

Larger (positive) NRI values imply a more phylogenetically clustered assemblage while smaller (negative) NRI values indicate more phylogenetic overdispersion.

2.3 STRUCTURAL EQUATION MODELS

To test the influence of biotic and abiotic variables on NRI patterns we used Structural Equation Models (SEM) (Mitchel, 1992; Wang *et al.*, 2013). SEM allow testing the contribution of different variables while accounting for potential correlations between them. We did not specify *a priori* whether any of these correlations had positive or negative effects. We tested four models (Figure 1). Our predictor variables were mean temperature, vegetation cover, human footprint, and body size dissimilarity. We assumed they all affect NRI values. The models differ as follows. Model 1 assumes that the human footprint has an impact on global temperature, which in turn affects vegetation cover. Model 2 is similar to model 1, but the human footprint affects vegetation cover, and the temperature is influenced by both variables. None of these two models have the influence of environmental variables on body size, but Models 3 and 4 do. In Model 3, body size is assumed to be influenced by vegetation and temperature, because higher values of these variables indicate more resources. Vegetation influences temperature in areas with high human density. Temperature influences vegetation cover, because in general, higher temperatures are associated with tropical forests. In Model 4, human footprint has an

effect on temperature and vegetation due to urbanization, and different from Model 3, there is no influence of vegetation on temperature.

Because SEM analyses on all assemblages (phylogenetically overdispersed and clustered) simultaneously could mask some effect related to the predictor variables, besides analyzing all data together, we also conducted the SEM analyses separately for assemblages with negative NRI values and assemblages with positive NRI values. We conducted these analyses through maximum-likelihood estimation using the R package lavaan 0.6-7 (Rosseel, 2012), and the models were compared using the Akaike information criterion (AIC) (Akaike, 1973). Spatial autocorrelation was taken into account during the analyses using the package semTools 0.5-3 (Jorgensen *et al.*, 2020).

Another way to identify the mechanisms acting in communities would be applying the null model of assembly proposed by Pigot & Etienne (2015), DAMOCLES. The model considers the historical effects of speciation, colonization, and local extinction acting over time to determine the present composition of the community. However, DAMOCLES needs more species than we usually have in our communities to reliably estimate parameters.

3. RESULTS

Phylogenetic signal in body size was high across the phylogeny of canids (K = 1.31, P < 0.01). The NRI values distributed over the world showed that there are phylogenetically overdispersed and underdispersed communities in different continents (Figure 2A). South America and Asia generally have high positive NRI values, whereas Central America, Europe, a large part of North America, and some regions in Asia show negative NRI values. Mean temperature, vegetation cover, human footprint, and body size dissimilarity also varied considerably across the world (Figures 2B, 2C, 2D, 2E).

Structural Equation Model 4 was selected as the best model for the three NRI analyses (negative, positive, and all data together), more than three AIC units better than the second-best model in all cases, model 3 (Table 1). The weights of model 4 were 0.832, 0.866, and 0.886 for negative, positive and all data together analyses, respectively. Model 3, on the other hand, presented weights of 0.167, 0.133, 0.113. Models 1 and 2, with no influence of environmental variables on body size dissimilarity, had a very poor performance in the model comparison. In Model 4, all predictor variables influence NRI values, but also the human footprint influences vegetation and temperature, which in turn influences vegetation cover and body size dissimilarity.

For all NRI data (Figure 3A), model 4 shows that the environmental variables temperature (P < 0.01, effect = 0.37) and vegetation (P < 0.01, effect = -0.19) were the most important to explain the phylogenetic distribution of canids (Table 2). Model 4 also shows that body size dissimilarity and human footprint had very weak and non-significant effects on NRI (-0.01 and 0.002, respectively).

For analyses on only the communities with positive NRI values, model 4 indicated that the environmental variables are still the most important to explain the phylogenetic composition within assemblages. Human footprint ($P < 0.01$, effect = 0.34) and temperature ($P < 0.01$, effect = 0.26) had the largest effects on canid assemblages (Figure 3B, Table 3). Body size dissimilarity also presented a significant effect on NRI (the more dissimilar the community in terms of body size, the more similar they are phylogenetically), smaller than the effect of human footprint, but close to that of temperature. Furthermore, temperature had a strong influence on body size ($P < 0.01$, effect = -0.57) (Figure 4B).

For analyses on only the negative NRI communities (Figure 3C), the environmental variables are still the ones with the largest influence on phylogenetic dispersion. Based on model 4, vegetation cover is the most important variable ($P < 0.01$, effect = 0.49), suggesting that as vegetation cover increases, species within these communities become phylogenetically closer. Temperature ($P < 0.01$, effect = -0.24) and body size dissimilarity ($P < 0.01$, effect = -0.23) also had a considerable negative effect on NRI (i.e., the less dissimilar the community in terms of body size, the more dissimilar they are phylogenetically). For the negative NRI analysis, correlations among the environmental variables, and the effect of the environment on body size dissimilarity were larger than in the analysis of all NRI values together (Table 4). In addition, vegetation cover presented a positive effect on body size ($P < 0.01$, effect = 0.59) (Figure 4A).

4. DISCUSSION

The composition of canid communities across the world shows both negative and positive values of NRI and is influenced by distinct factors in different continents. However, it seems that the environment plays a greater role than traits related to biotic factors to explain the phylogenetic composition of Canidae assemblages. This pattern was maintained when NRI was analyzed as a whole and separately, but the effects of variables were much stronger in the separate analyses (Figures 3A, 3B and 3C) which supports our idea that it is necessary to separate the phylogenetic information to have a better understanding on how these variables structure Canidae assemblages through space.

Body size dissimilarity among canids was not the main factor structuring assemblages with negative NRI values. In these communities, the vegetation cover has the greatest effect, where canids become less closely related as vegetation cover increases. However, the best model suggests that overdispersed communities are maintained due to the combined effect of temperature and body size dissimilarity (Figure 3C). Nevertheless, our model shows that the environmental variables have a larger effect on overdispersed communities than body size dissimilarity. We can observe on the map how overdispersed assemblages vary across the environmental gradient (Figures 2A and 2C), showing that these communities in the Northern hemisphere are associated with low vegetation cover.

Interestingly, the relationship between body size dissimilarity and NRI has a different direction in positive and negative NRI communities. In positive NRI communities more phylogenetic clustering is associated with more body size dissimilarity, while in negative NRI communities more phylogenetic overdispersion is associated with more body size dissimilarity. Note that body size dissimilarity has been corrected for phylogenetic signal, so this larger similarity in body size is more than can be expected from shared evolutionary history. Hence, this implies that species are much more dissimilar in their body sizes at very negative NRI values (highly overdispersed communities) and very positive NRI values (highly clustered communities) than at small positive and negative NRI values (communities with random phylogenetic structure). In clustered communities this may be explained by character displacement after speciation: competition may have driven phylogenetically related species to diverge in their body sizes. In overdispersed communities this may be explained by character displacement after secondary contact. These explanations assume that clustered communities undergo mostly sympatric speciation whereas overdispersed communities assemble through immigration after allopatric speciation. This seems to be in line with the results from Porto *et al.* (2021), on the origin and dispersal of the Canidae lineages. They show that highly clustered communities, such as South America, the Middle East and South Asia, present several lineages that originated within these regions. South America, for example, is inhabited only by species of a single clade — endemic to this continent. Furthermore, highly overdispersed regions, such as North America, Europe and South Africa, are inhabited by lineages of distinct clades, where many have their origins outside these regions.

The overdispersed pattern presented by assemblages of canids living in North America, Europe, and the northern part of Asia is probably due to a large number of distinct species of the genera *Vulpes*, *Canis*, and *Urocyon* that coexist within these areas and are very phylogenetically distant, being separated around 12 million years ago (Ma) (Porto *et al.*, 2019). Species from these three genera have very distinct diet, habitat type, and social behavior (Wang & Tedford, 2008; Wilson & Mittermeier, 2009).

For phylogenetically clustered assemblages, the combined effect that human footprint and temperature have on NRI values suggests that habitat filtering plays an important role within these communities. The effect of human impact suggests that as human population density increases, canids become phylogenetically closer (Figure 3B). This is in line with Di Marco & Santini (2015) who demonstrated that human impacts predict the geographical distribution of terrestrial mammals better than the biological traits of species. While past events shaped the current distribution of species (Davies *et al.*, 2007), current environmental forces influence the capacity for species to survive in different regions (Pearson & Dawson, 2003). Endemic canids of South America, like those from the genus *Lycalopex*, and also species from the Northern hemisphere, such as

Vulpes lagopus are constantly losing habitat and being killed by humans (Hoffmann *et al.*, 2011). By contrast, even though human activity in North America is large, this region still has a highly overdispersed pattern. This might be explained by the large number of species of the *Canis* genus that live within this region. Several species in this clade, such as the coyote (*Canis latrans*) (Poessel *et al.*, 2013), have shown high plasticity to co-exist with humans, being able to live and obtain resources near to urban areas.

Temperature also presented a positive effect in phylogenetically underdispersed assemblages, suggesting that warm regions on the planet, such as deserts and tropical forests, can impose a much greater environmental filter on canids than cold regions. Our finding is contrary to what was proposed by Dobzhansky (1950), who argued that biotic factors are more limiting in the tropics, while abiotic conditions are more important at higher latitudes. However, our finding may not be so surprising given that the first ancestors of the living canids were probably packing hunters with medium body sizes, around 70 cm (Wang & Tedford, 2008; Porto *et al.*, 2019). Deserts and tropical forests may act as a strong filter to canids with such a lifestyle because food is scarce in deserts and pack hunting is difficult inside dense forests. An alternative explanation may be differential diversification rates. Pigot & Etienne (2015) showed that allopatric speciation creates overdispersed patterns, suggesting that for canids speciation might be higher at higher latitudes. Extinction must then also be higher at high latitudes to explain the lower diversity at these communities (Weir & Schluter, 2007).

We emphasize the better performance that models with environmental variables influencing body size dissimilarity had compared to the ones that did not. This suggests environmental control of body size dissimilarity. For overdispersed assemblages, places with more vegetation cover probably influenced competition in a way that biotic interactions may have led to character displacement. In underdispersed communities, temperature strongly affects body size dissimilarity, showing that as temperature increases, species become similar in their sizes (less dissimilarity). As body size is well known to be a good proxy for species' ecological niches (De Roos *et al.*, 2003; Nakazawa *et al.*, 2010), this is strong evidence for habitat filtering in warmer places, which can generate ecologically similar Canidae assemblages.

Even though canids are not dispersal limited, because they can travel long distances (Wang & Tedford, 2008; Wilson & Mittermeier, 2009), they may still tend to be found in higher numbers near to their center of diversification than far from it. This can also help understand the phylogenetic structure of the Middle East + Northern Africa, and South America, which, based on the fossil records and biogeographical models, had major diversification events of foxes and South American canids, respectively (Wang & Tedford, 2008; Porto *et al.*, 2021). Ecological speciation within these regions might have generated species' phylogenetic clustering. In these areas the number of endemic species is high, and speciation tends to generate similar trait values (Gillespie, 2004).

The majority of studies of the phylogenetic structure within communities concerns plants or focus on small geographic scales. Nevertheless, some studies with vertebrates at large spatial scales have demonstrated contrasting patterns of phylogenetic composition. Cooper, Rodríguez, & Purvis, (2008) found a tendency of overdispersion in assemblages of New world monkeys, Australasian possums, and North American ground squirrels. Yan *et al.* (2016), however, found phylogenetic clustering for Mammalia, Aves, Reptilia, and Amphibia from China. And Cardillo (2011) demonstrated an unstructured phylogenetic pattern on African carnivore's assemblages. Here we presented a case where both patterns are important to understand community composition across the planet, depending on the region studied.

Larger geographical scales are expected to generate more phylogenetic clustering than overdispersion because the rate of speciation increases with more space available (Losos & Schluter, 2000) due to higher habitat heterogeneity (Kneitel & Chase, 2004), and thus sister species are more likely to co-occur at larger scales. Even though we found many areas with phylogenetic clustering (Figure 2A), there were also many areas with overdispersed patterns, indicating that the scale we used (300 km × 300 km) may still be too small for clustering to kick in. Therefore, we anticipate that using an even larger scale, e.g. the biome scale, will reveal clustering. Studying community structure at that scale, however, is no longer very informative, exactly because of the large expected biogeographic contribution to phylogenetic dispersion.

The results presented here agree with the ideas proposed by Mayfield & Levine (2010) about how competition can drive clustered patterns in specific situations, making it complicated to trust relatedness indices within communities to separate the real role of biotic and abiotic factors. Here we managed to show the distinct effects of each variable acting on assemblages, partitioning the phylogenetic structure of communities and applying structural equation models to them. Without this methodology, it could have led us to wrong conclusions as we would have only considered the effect that different variables have on dispersion patterns in communities, but not considering the effects they have on each other.

The mechanisms that influence the assembly of a community can act in complex ways (Ricklefs, 1987, 2015). In this study we used both a phylogenetic approach and an approach based on current environmental variables and traits. We demonstrated that canid community composition over the world presents significant patterns of clustering and overdispersion. These patterns follow mainly the environmental gradient, suggesting habitat filtering as the main force acting on Canidae assemblages, but competition may also have played a key role in shaping the communities through character displacement.

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DECLARATION SECTION

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

All data generated or analyzed during this study are included in this published article.

Competing interests

We have no competing interests.

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Authors' contributions

L.M.V.P. conceived and designed the study and analyses. L.M.V.P. performed the analyses. L.M.V.P. wrote the first draft of the manuscript. R.S.E. and R.M. commented on the methods and contributed to substantial revisions on the draft.

TABLE LIST

Table 1. Akaike information criterion ranking of the four models of Structural Equation Models tested for negative, positive, and total NRI values.

Models	df	Negative NRI			Positive NRI			Total NRI		
		AIC	ΔAIC	Weights	AIC	ΔAIC	Weights	AIC	ΔAIC	Weights
Model 4	13	3295.996	0	0.832	16755.383	0	0.866	27995.420	0	0.886
Model 3	14	3299.202	3.206	0.167	16759.117	3.734	0.133	27999.539	4.119	0.113
Model 2	10	3513.220	217.224	5.6E-53	17980.139	1224.756	9.66E-100	29029.366	1033.946	2.6E-132
Model 1	10	3525.275	229.279	1.3E-55	17997.486	1242.103	1.6E-127	29050.563	1055.143	6.7E-140

Table 2. Results of the best-fitting Structural Equation Model (model 4) for total NRI values indicating the effect size among biotic and abiotic variables.

Regressions:		**Estimate**	**Std Err**	**z-value**	***P***	**Effect**
NRI ~	Body size dissimilarity	-0.041	0.094	-0.436	0.663	-0.012
	Human footprint	0.000	0.002	0.061	0.951	0.002
	Temperature	0.017	0.001	12.829	< 0.01	0.374
	Vegetation cover	-0.003	0.000	-7.172	< 0.01	-0.186
Temperature ~	Human footprint	0.666	0.051	13.094	< 0.01	0.323
Vegetation cover ~	Human footprint	0.494	0.131	3.774	< 0.01	0.097
	Temperature	0.756	0.063	11.906	< 0.01	0.307
Body size dissimilarity ~	Temperature	-0.006	0.000	-16.927	< 0.01	-0.426
	Vegetation cover	0.000	0.000	1.480	0.139	0.037

** P of the model (<0.01)*

Table 3. Results of the best-fitting Structural Equation Model (model 4) for positive NRI values indicating the effect size among biotic and abiotic variables.

Regressions:		Estimate	Std Err	z-value	*P*	Effect
Positive NRI ~	Body size dissimilarity	0.446	0.069	6.479	< 0.01	0.238
	Human footprint	0.001	0.000	11.076	< 0.01	0.335
	Temperature	0.006	0.001	6.981	< 0.01	0.259
	Vegetation cover	-0.000	0.000	-1.281	0.20	-0.039
Temperature ~	Human footprint	0.047	0.004	10.610	< 0.01	0.318
Vegetation cover ~	Human footprint	0.027	0.010	2.686	< 0.01	0.086
	Temperature	0.473	0.069	6.902	< 0.01	0.222
Body size dissimilarity ~	Temperature	-0.007	0.000	-22.262	< 0.01	-0.565
	Vegetation cover	-0.001	0.000	-6.564	< 0.01	-0.167

** P of the model (<0.01)*

Table 4. Results of the best-fitting Structural Equation Model (model 4) for negative NRI values indicating the effect size among biotic and abiotic variables.

Regressions:		Estimate	Std Err	z-value	*P*	Effect
Negative NRI ~	Body size dissimilarity	-0.203	0.038	-5.309	< 0.01	-0.226
	Human footprint	0.037	0.017	2.214	0.03	0.096
	Temperature	-0.004	0.001	-4.026	< 0.01	-0.242
	Vegetation cover	0.519	0.064	8.091	< 0.01	0.485
Temperature ~	Human footprint	11.582	0.937	12.357	< 0.01	0.453
Vegetation cover ~	Human footprint	-0.012	0.012	-1.014	0.31	-0.033
	Temperature	0.010	0.000	22.149	< 0.01	0.722
Body size dissimilarity ~	Temperature	-0.006	0.001	-6.333	< 0.01	-0.334
	Vegetation cover	0.700	0.063	11.136	< 0.01	0.588

** P of the model (<0.01)*

FIGURE LIST

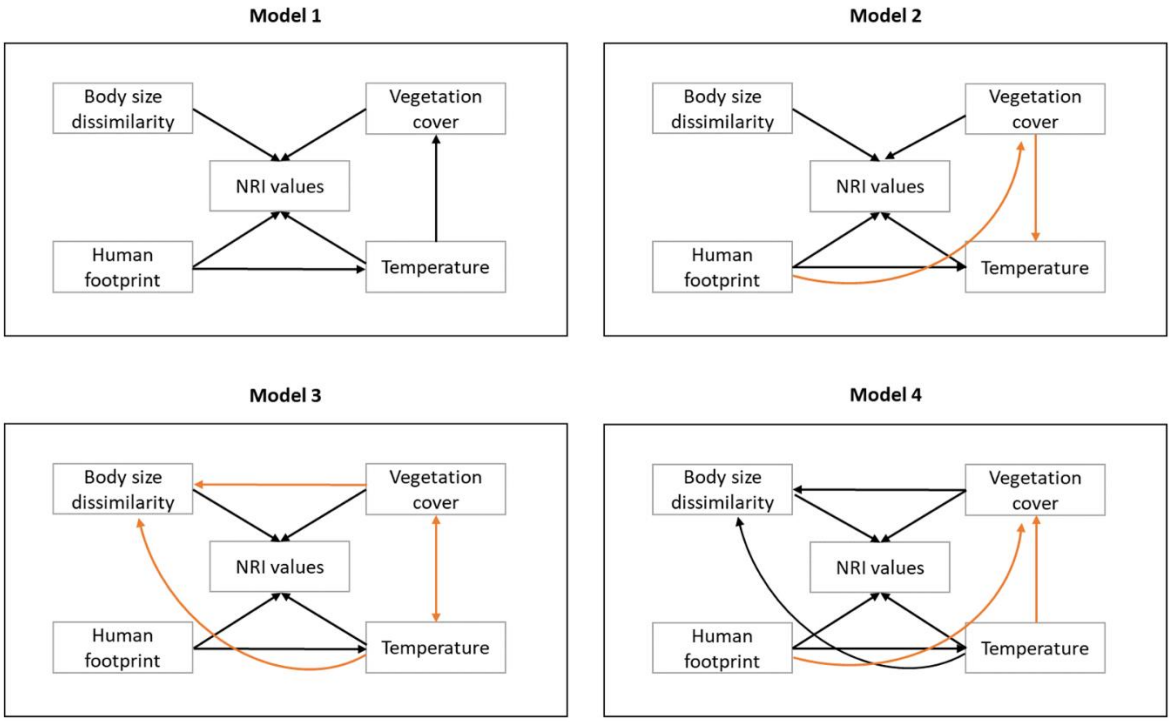

Figure 1. Schematic representations of the four Structural Equation Models tested in this study. The same models were used for negative, positive, and for all NRI values through separate analyses. Arrows indicate the direction of the variables' effects. Orange arrows indicate different effects added to the model compared to the previous model.

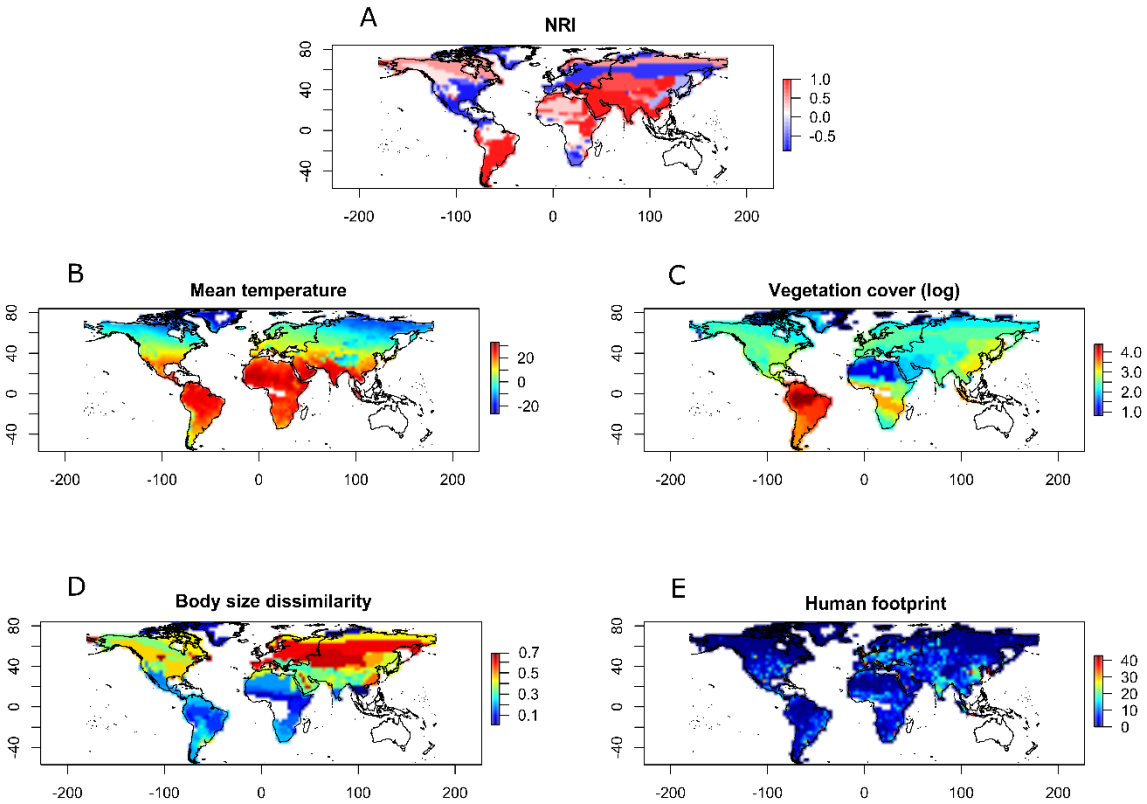

Figure 2. NRI and variables used in this study plotted over the world. (A) NRI values for each assemblage showing that phylogenetic dispersion of canids varies spatially. Assemblages colored in blue present negative NRI values indicating that species within these areas are phylogenetically more dissimilar. Assemblages colored in red represent positive NRI values, where species are phylogenetically more similar. (B) Values of the global average temperature used in this study measured in Celsius (°C). (C) Global pattern of log-transformed vegetation cover percentage. (D) Body size dissimilarity (cm) among canids for each pixel. (E) Values of the human footprint (people per square kilometer).

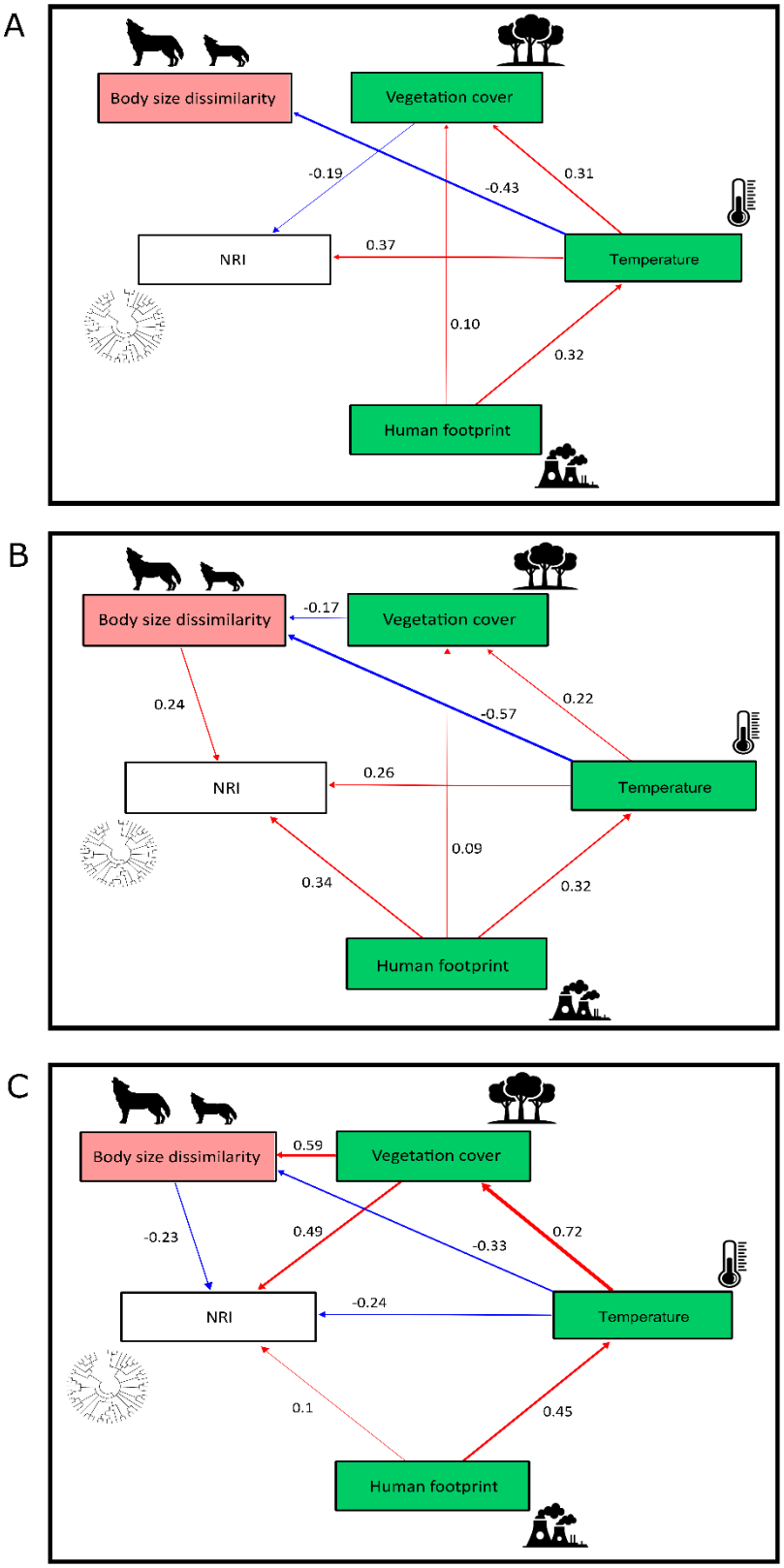

Figure 3. Best-fitting Structural Equation Model for the total NRI (A), clustered communities - positive NRI (B), and overdispersed communities - negative NRI (C) values. Positive and negative effects are indicated by red and blue arrows, respectively. Arrow thickness is scaled to illustrate the relative effect of each variable. Only significant effects (arrows) are shown ($P < 0.05$).

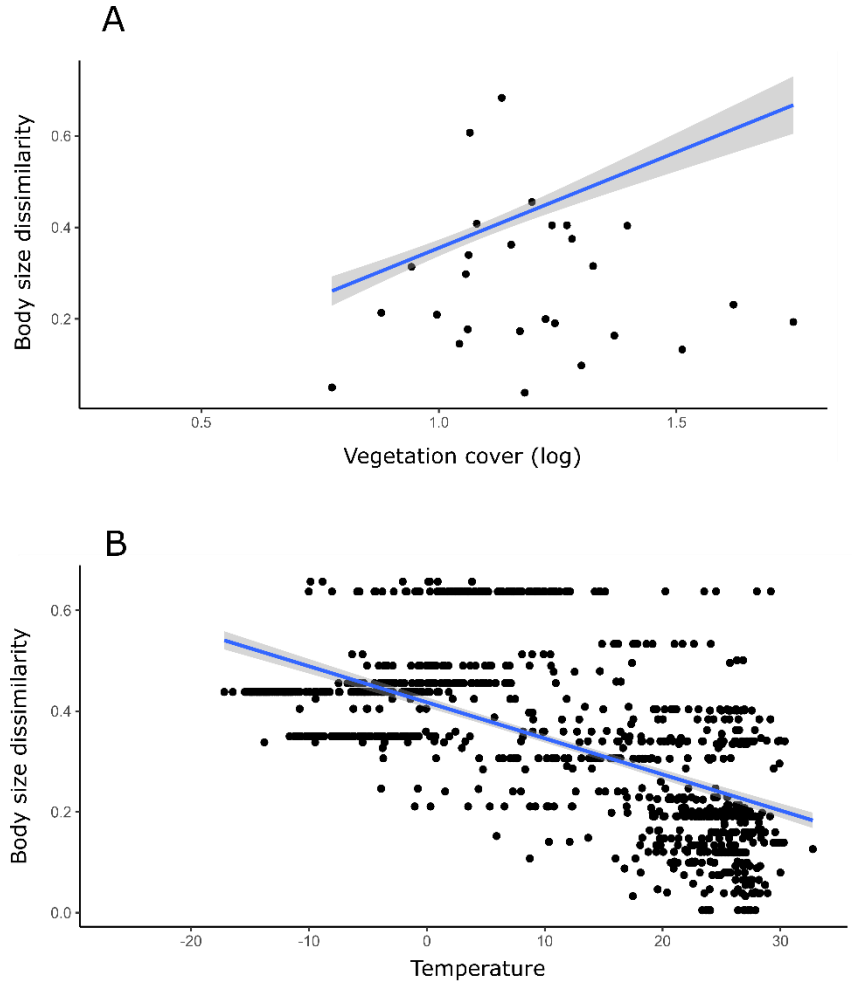

Figure 4. (A) Correlation between vegetation cover and body size dissimilarity within overdispersed communities ($R^2 = 0.12$, $P < 0.01$). (B) Correlation between temperature and body size dissimilarity within clustered Canidae assemblages ($R^2 = 0.37$, $P < 0.01$).

SUPPLEMENTARY MATERIAL

Table S1. Body size of the 36 species of canids used in this study.

Species	Body size (cm)
Atelocynus microtis	86
Canis adustus	85.5
Canis aureus	78
Canis anthus	78
Canis latrans	84
Canis lupus	108.5
Canis mesomelas	88
Canis rufus	112
Canis simensis	94.4
Cerdocyon thous	67.25
Chrysocyon brachyurus	105
Cuon alpinus	111.75
Lycaon pictus	115.75
Nyctereutes procyonoides	59.75
Otocyon megalotis	53.35
Lycalopex culpaeus	69
Lycalopex fulvipes	52.15
Lycalopex griseus	58.05
Lycalopex gymnocercus	65.85
Lycalopex sechurae	64
Lycalopex vetulus	58.5
Speothos venaticus	66.25
Urocyon cinereoargenteus	56.9
Urocyon littoralis	53
Vulpes bengalensis	47
Vulpes cana	57.35
Vulpes chama	57.35
Vulpes corsac	47.5
Vulpes ferrilata	56.25
Vulpes macrotis	50.25
Vulpes pallida	46.5
Vulpes rueppellii	47.5
Vulpes velox	52
Vulpes vulpes	63.5
Vulpes zerda	36.4
Vulpes lagopus	60

BIOSKETCH

Lucas Porto is a biologist interested in understanding the global patterns of Canidae distribution through time.