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Combining Geographic Distribution and Trait Information to Infer Predator–Prey Species-Level Interaction Properties

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Abstract: Biotic interactions are a key component of the proper functioning of ecosystems. However, information on biotic interactions is spatially and taxonomically biased and limited to several groups. The most efficient strategy to fill these gaps is to combine spatial information (species ranges) with different sources of information (functional and field data) to infer potential interactions. This approach is possible due to the fact that there is a correspondence between the traits of two trophic levels (e.g., predator and prey sizes are correlated). Therefore, our objective was to evaluate the performance of the joint use of spatial, functional and field data to infer properties of the predator–prey interaction for five neotropical cats. To do this, we used presence–absence matrices to obtain lists of potential prey species per grid-cell for each predator range. These lists were filtered according to different criteria (models), and for each model, an interaction property was estimated and compared with field observations. Our results show that the use of functional information and co-occurrence allows us to generate values similar to those observed in the field. We also observed that there were differences in model performance related to the intrinsic characteristics of the predator (body size) and the interaction property being evaluated.

Keywords: food web; carnivores; body size; functional traits; co-occurrence

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1. Introduction

One of the greatest challenges in ecology is filling the knowledge gap in our understanding of the role of species interactions in originating and maintaining biodiversity [1–3]. Despite the increasing number of studies and data available in recent years, information is still limited to answering questions about species interactions, such as the geographic variation of species diets or the effects of such interactions on individual survival and fitness of species [1,4]. In addition to the general lack of sampling in some regions, there is a dearth of spatiotemporal information on biotic interactions, which is also taxonomically biased for some species or groups of species [1]. Even in large studies on trophic networks [5], it is difficult to obtain representative and unbiased information on biotic interactions for most species due to both the stochastic nature of populations—i.e., if two species co-occur but one species is rare, they will hardly interact [3,6], and due to the characteristics of the species (e.g., activity period, migratory status). Therefore, filling this lack of information on biotic interactions requires finding new methods that allow us to infer interactions or their descriptors from existing information and thereby complement this information, improve our understanding of interactions and reduce their loss [7,8].

The use of geographic co-occurrence (i.e., the occupation of the same geographical space–sites—by two or more species) was one of the first strategies used to make inferences about relationships between species [9]. Considering that two species need to co-occur in the same place at the same time in order to interact and that these interactions affect the demography of such species, we would expect that they will mutually affect their co-occurrence (e.g., prey population crashes may lead to local predator extinction or migration [6]). However, species' co-occurrence can be affected by the particular species' response to the environment as well as by sampling effort (e.g., co-occurrence probabilities of two sympatric species with different climate tolerances will vary in geographic space, also affecting the co-occurrence detectability) [6]. Likewise, co-occurrence alone is unable to distinguish forbidden or improbable interactions, those interactions that, for mechanical, historical or ecological reasons, cannot occur in nature –an herbivore eating a carnivore—from potential interactions, those interactions that have not been reported but could be occurring in nature [6,10,11]. These problems with the use of co-occurrence to infer biotic interactions led to the development of methods based on the Eltonian niche concept, i.e., 'the place of an animal in a community, its relation to food and enemies' [12], in which the Eltonian niche of a species is defined by its position on the food web and according to its functional traits [3,13]. The main difference between the use of co-occurrence and functional traits is that the latter allows us to establish mechanisms by which species interact (e.g., correspondence between hummingbird beak size and flower size in pollination, if prey size falls within the predator's prey size range [3,10]). Therefore, if we want to infer interactions, we can use co-occurrence as a starting point and, by defining the Eltonian niche of species from functional traits crucial for the type of interaction evaluated, refine these inferences [3,13–15].

Functional traits (e.g., body mass, activity period) are more consistent with the local spatial scale in which interactions occur compared to environmental variables [16], which reflect broader characteristics of Grinnellian (instead of Eltonian) niches, i.e., 'all values of the scenopoetic variables for which the intrinsic growth rate is positive' [17]. In general, species with similar Eltonian niches tend to share functional traits, which increases functional redundancy and thereby reduces analysis complexity by allowing for the grouping of species with similar roles in the community [13,18]. Furthermore, the use of functional traits of species can be used to evaluate trait matching between interacting species, thus helping to discover interactions that have a greater probability of occurring or to define trait intervals within which species can interact [3,19]. The relevance of functional traits is particularly important in interactions such as predation, where the correspondence of functional traits between predator and prey (e.g., body mass) as well as the prey's presence or absence within the predator's feeding range largely determines the viability of an interaction [3,10,14].

In predator–prey interactions, body size is one of the most important traits, as the predator chooses its prey based on whether it satisfies its metabolic requirements [20–22]. Given that the distribution of mammalian body size is left-skewed, with small species being more common in most regions [23], if researchers only use co-occurrence data to infer potential interactions, there will be good inferences on small predators, as they tend to feed on small prey, but these inferences will be less accurate as predator size increases due to their need for larger and less common prey [20,22]. The relevance of using other functional traits, such as activity period or foraging strata, to infer descriptors of interactions will depend on predator requirements, as well as their size. For instance, while many top-predators are active all day, meso-predators tend to have reduced activity periods and to be restricted to certain strata due to the risk of being predated by carnivores of similar or larger sizes [24,25]. One of the most efficient strategies to infer trophic interactions and understand the spatial variation of food webs has been the use of observed feeding intervals; this is the extreme values of a trait (e.g., body mass) that determine that a species can be consumed by a predator [3,10,14]. Using feeding intervals allows us to reduce the number of potential preys based on existing knowledge about the prey species consumed by the predator and their size, so their performance is usually good for most species (e.g., [10]). Because the Eltonian niche of species is defined by species traits and their position on the food web [13], it is expected that combining prey functional traits with predator feeding intervals will result in a better representation of the Eltonian niche of the predator and, thus, better inferences of potential interactions and their descriptors.

In the present study, we proposed a new approach to infer predator–prey species-level interaction properties. Our approach is based on the combination of the Eltonian niches and the geographical distributions of species, focusing on a five-step procedure requiring data on species' geographic distributions, body sizes, feeding intervals and foraging traits. To evaluate our approach, we selected a set of five Neotropical predators with different Eltonian niches that include top predators (*Panthera onca*, *Puma concolor*) that forage all day, as well as species of mesopredators (*Leopardus pardalis* and *Herpailurus yagouaroundi*), and small predators (*Leopardus wiedii*), with variable activity periods and foraging strata that are distributed throughout the American continent. Our objective was to use the spatial co-occurrence and functional traits of predators and prey species to generate species-level properties of predator–prey interactions that can be contrasted against the empirical data of such properties descriptors as observed in the literature for different predators and data levels. (i) Species level: considering the complete geographic distribution of a predator and all of its prey and (ii) locality level: considering point/locality data observed in the field on the occurrence and interaction of both the predator and its prey. As such, this combined approach of geographic distributions with the Eltonian niche concept can be useful for integrating knowledge of species interactions across spatial scales, a recently recognized challenge in biogeography and macroecology [26].

2. Materials and Methods

2.1. Data Collection

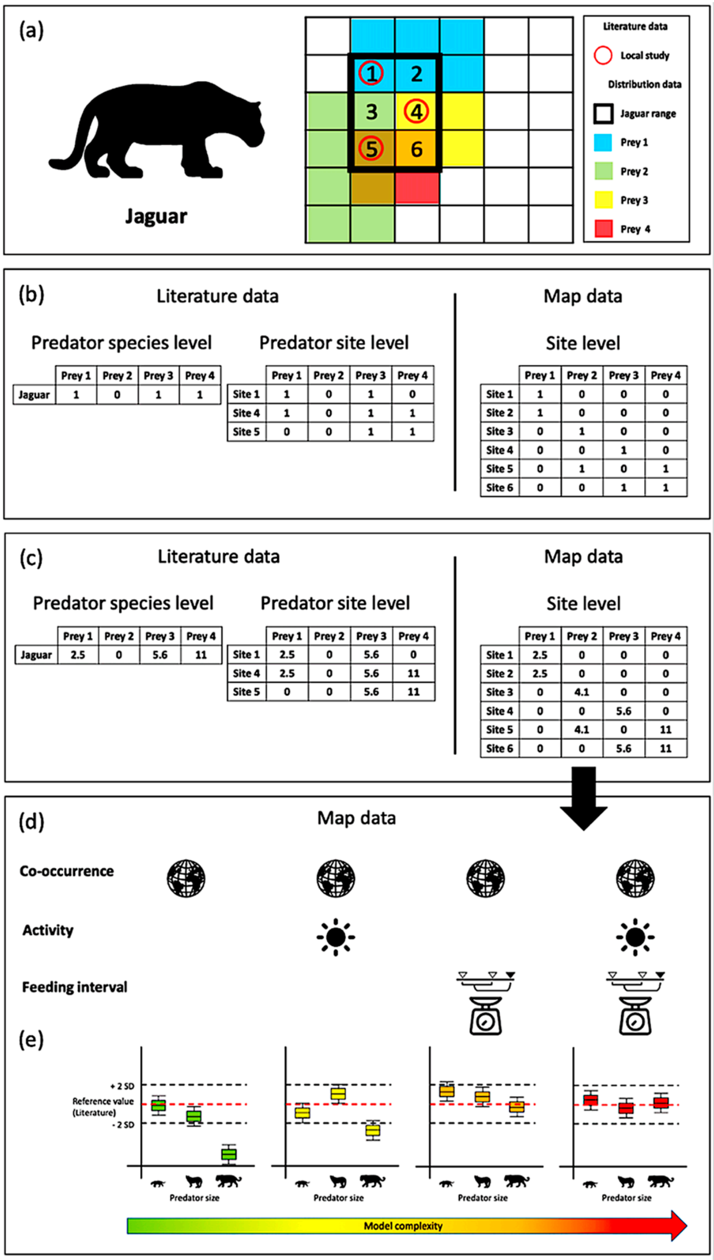
We collected species geographic ranges (i.e., extents of occurrence polygons), from the IUCN database (https://www.iucnredlist.org/; accessed on 29 August 2019), mean body mass across sexes (in grams) for mammalian species [27], life history traits, namely activity period and foraging strata that provide information about co-occurrence on finer scales, from the EltonTraits database, which was obtained through the standardization of field data or interpolations [25], and predator–prey interaction data (i.e., lists of prey species for different predators in different localities) from a literature review. Note that our considered traits represent either mean values of species (body size), as intraspecific variation is rarely available, or consensual values coming from standardization of descriptions on the use of strata or time period of activity. We considered as a predator–prey interaction only those cases in which direct evidence of consumption by the predator was found; that is, the prey species record was obtained from the predator's feces, stomach contents, or direct observations. We focused on five Neotropical predators for which the three types of data were available from a previous study [28]: margay (*Leopardus wiedii*), jaguarundi (*Herpailurus yagouaroundi*), ocelot (*Leopardus pardalis*), cougar (*Puma concolor*), and jaguar (*Panthera onca*). This dataset included a total of 77 publications for 13 countries across the Neotropics, from the southern United States to northern Argentina, with 202 prey species reported as part of the diet of these five predators (margay = 50, jaguarundi = 49, ocelot = 126, cougar = 87, jaguar = 87; see Sánchez-Barradas & Villalobos, 2020 for a detailed description of how the data were obtained).

We used literature data at two levels: (i) species level, as the total number and identity of mammal species reported as prey within the individual geographic range of each predator (i.e., considering the entire distribution of the predator as a single site) and (ii) locality level, as the observed localities with lists of prey (at least three species) reported for each predator (margay n = 6, jaguarundi n = 7, ocelot n = 21, cougar n = 9, and jaguar n = 5).

2.2. Interaction Properties: Summary of the Approach

Our approach for inferring interaction properties for predator species started by selecting predators for which there was available information on their observed predator–prey interactions and compiling geographic ranges for these predators and their potential prey (all other mammals excluding the focal predator) (Figure 1a). Based on these two types of information, interactions and geographic distributions, the second step consisted of obtaining three datasets for each predator (Figure 1b): (1) A "species-level" dataset that comprised the complete list of prey species reported to be consumed by the predator. We defined this dataset as the predator's "interaction field," in analogy to the species' phylogenetic field (i.e., the phylogenetic structure of co-occurrence within a focal species' range; [29,30]) this was done because by using the distribution area of a species as a unit of study, it was possible to understand the ecological information contained in the predator's coexistence pattern. Here, a predator's interaction field was a species-level property representing its complete Eltonian niche, from which we then obtained a single reference value for the focal species/predator (see below). (2) A "locality-level" dataset that compiled all the localities for which there was information (literature) on the prey consumed by the predator. This dataset considered only those localities with enough prey (i.e., three or more prey species) to calculate a reference value for each site. (3) A "cell-level" dataset was obtained from the range maps of the predator and its potential prey. Based on these range maps and their overlap within a gridded domain ($1^\circ \times 1^\circ$ resolution), we obtained a presence–absence matrix where rows represent the sites (grid-cells) occupied by the predator, columns represent the prey species present in at least one of the predator's sites, and the matrix elements denote presence (1) or absence (0) of those prey species. To ease illustration and calculation, we used this presence–absence matrix format to depict all three datasets. Note that the first two datasets were from the literature on predator–prey interactions; thus, we considered them as observed data and used them to derive reference values at the species and locality levels. Conversely, the third dataset, cell level, was simply based on range maps, and we used it to derive expected values on the interaction properties that could then be compared to the reference values from the two previous levels. To compare the locality with the cell-level data, we considered only those grid-cells in which there were observed locality data (Figure 1b).

The third step of the approach consisted of replacing the presence values (1s) in all three matrices with the corresponding body sizes (i.e., body mass in grams) of each species (Figure 1c). Then, the fourth step of our approach consisted of using the cell-level data to create different trait combinations (see below for a detailed description) that define the potential set of prey species belonging to the Eltonian niche of the predator (Figure 1d). Trait combinations included: (1) geographic co-occurrence between predator and preys, (2) same as (1) but also considering the species' activity periods and foraging strata, (3) same as (1) but also considering the feeding range of the predator and (4) same as (3) but also considering the species' activity periods and foraging strata. Finally, the fifth step consisted of contrasting the reference values at both the species and locality levels with those obtained from the different models on cell-level data to assess their accuracy in describing the interaction properties (Figure 1).



(b)

	Prey 1	Prey 2	Prey 3	Prey 4
Jaguar	1	0	1	1

	Prey 1	Prey 2	Prey 3	Prey 4
Site 1	1	0	1	0
Site 4	1	0	1	1
Site 5	0	0	1	1

	Prey 1	Prey 2	Prey 3	Prey 4
Site 1	1	0	0	0
Site 2	1	0	0	0
Site 3	0	1	0	0
Site 4	0	0	1	0
Site 5	0	1	0	1
Site 6	0	0	1	1

(c)

	Prey 1	Prey 2	Prey 3	Prey 4
Jaguar	2.5	0	5.6	11

	Prey 1	Prey 2	Prey 3	Prey 4
Site 1	2.5	0	5.6	0
Site 4	2.5	0	5.6	11
Site 5	0	0	5.6	11

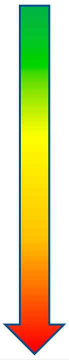
	Prey 1	Prey 2	Prey 3	Prey 4
Site 1	2.5	0	0	0
Site 2	2.5	0	0	0
Site 3	0	4.1	0	0
Site 4	0	0	5.6	0
Site 5	0	4.1	0	11
Site 6	0	0	5.6	11

Figure 1. General approach to infer predator–prey interaction properties at the predator level combining geographic co-occurrence and Eltonian niches. (**a**) Predators that have information on predator–prey interactions, as well as range maps were selected; (**b**) from the literature and distribution data; three datasets were obtained for each predator, depicted as presence-absence matrices. The first two datasets, species level (considering the complete predator's distribution and its reported prey) and locality level (considering only localities with literature data), were obtained from the literature and used later as reference values for interaction properties. The third dataset, the cell level, was obtained from range maps and their overlap. (**c**) The presence values (1s) are replaced by the body size of the mammal species in the three datasets. (**d**) Different trait combinations (geography: co-occurrence, life-history: activity, and morphology: feeding interval) were used to derive models of different complexities that define the potential set of prey species belonging to the Eltonian niche of the predator. (**e**) These models were used to derive descriptors of interaction properties for the predator based on the cell-level dataset, which were then contrasted against the reference values from the species- and locality-level datasets.

2.3. Trait Combinations and Interaction Models

Given that geographic co-occurrence is usually not sufficient to infer species interactions [10], we considered different trait combinations that reflect the match between the foraging characteristics of each predator and the vulnerability of each potential prey [3,10,13,14] to create nine interaction models. These models further represented different levels of complexity in data acquisition, ranging from simple models that use only distribution data (i.e., co-occurrence) to multifactor models that use distribution data combined with trait data and field observations of prey size intervals and prey size frequencies (Table 1). These models were classified as a purely geographic model: (I) Co-occurrence (COC), considering all prey species co-occurring with the focal predator species; two spatiotemporal models based on life-history traits; (II) Activity: same as co-occurrence but considering only those prey species that are active at the same time period as the focal predator species; (III) Strata: same as co-occurrence but considering only those prey species that forage in the same strata as the focal predator species; two body size models considering feeding intervals; (IV) NM: same as co-occurrence but considering only those prey species that fall within the feeding interval of the focal predator species obtained from the literature; (V) RNM: same as co-occurrence but considering only those prey species that fall within the restricted feeding interval of the focal predator species (i.e., ”Preference” in Table 1, describing preferred preys by size category as defined by a model considering the frequency of prey consumption per size category per predator; for a detailed description of this model see Supplementary Materials file S1–S3); and four saturated models combining life history and body size data; (VI) NMA: same as NM but considering only those prey species that are active at the same time period as the focal predator species; (VII) NMAS: same as NMA but considering only those prey species that forage on the same strata as the focal predator species; (VIII) RNMA: same as RNM but considering only those prey species that are active at the same time period as the focal predator species; and (IX) RNMAS: same as RNMA but considering only those prey species that are active at the same time period and that forage on the same strata as the focal predator.

Table 1. Species’ trait combinations used in the interaction models for inferring predator–prey interaction properties. Values of 1 imply the consideration of that trait in the corresponding model (row), 0 values otherwise. NM = Niche Model, RNM = Restricted Niche Model, NMA = Niche Model with Activity, NMAS = Niche Model with Activity and Strata, RNMA = Restricted Niche Model with Activity, and RNMAS = Restricted Niche Model with Activity and Strata (see text and Supplementary Materials File S1–S3 for detailed descriptions). Colors indicate model complexity following the scale depicted by the arrow at the right.

Models	Distribution	Traits				Model Complexity
		Activity Period	Foraging Strata	Prey Body Mass		
				Interval	Preference	
Co-occurrence	1	0	0	0	0	
Activity	1	1	0	0	0	
Strata	1	0	1	0	0	
NM	1	0	0	1	0	
RNM	1	0	0	1	1	
NMA	1	1	0	1	0	
NMAS	1	1	1	1	0	
RNMA	1	1	0	1	1	
RNMAS	1	1	1	1	1	

2.4. Model Performance

To evaluate the performance of the different interaction models, we selected and calculated two metrics describing the properties of predator–prey interaction at the level of the predator: the mean prey size (MPS) and the predator–prey ratio (PPR) for each predator. We chose the MPS, given that, in addition to being a central tendency measure, it is one of the easiest measures to obtain and calculate from local studies and has served as a basis for several studies and metrics, such as the PPR detailed below [20,22]. The PPR—the result of dividing the average mass of a predator by its average prey mass—is a measure that provides information on the metabolic balance of a predator–prey interaction [21,22]. We decided to use PPR because it has been proposed as a useful measure for assessing food web dynamics and complexity as it relates to species trophic efficiency, as well as food web stability [22]. For instance, in carnivores, it is common for large-sized predators (e.g., jaguar, cougar) to prey on species of similar size to them, thus showing a PPR close to unity. In contrast, medium- and small-sized predators' prey on species that are usually several times smaller than them [20], showing a PPR larger than 1. Moreover, the PPR has a negative correlation with the trophic level, so it can be used as a proxy for it [21,22].

Both metrics (MPS and PPR) were calculated for each predator at the species level, locality level, and cell level for each model, with the first two levels being used to derive reference values and the latter level for creating expected/predicted values. At the species level, the observed MPS and PPR for each predator species were calculated by considering all the prey species reported throughout its geographic range, thus creating a single reference value per predator for the MPS and PPR across its entire geographic distribution (i.e., all occupied grid-cells have the same metric value). Conversely, regarding the interaction models using the cell-level dataset (Table 1), each one generated a different predicted metric value per grid-cell, given that different species compositions influence model prediction. In short, because each interaction model has different conditions for determining whether or not a species is prey, each model generates a different species composition per grid-cell, so the values of the metrics vary both between models and between cells.

At the locality level, observed values of MPS and PPR for each predator were calculated for each of their local studies, considering only the prey species reported in that study (see supplementary material file S4). Therefore, in contrast to the species-level analysis, at the locality level, there were as many MPS and PPR values as there were local studies for each predator. In the same vein, each interaction model generated a predicted metric value only for those grid-cells occupied by predators that contained local data. Note that interaction models make the same metric predictions at both species level and locality level, as they are based on species compositions of grid-cells (i.e., co-occurrence), whereas the observed metric values differ between levels because they use different data (i.e., the set of different prey species reported for the same predator in all its localities at the species level, and point locality data at the locality level).

Following Williams and Martínez [31], we calculated normalized errors (NE) to compare the predictions of the interaction models with the reference values at both species and locality levels. First, we calculated the difference between the reference and predicted values, obtaining a "raw error" [RE] for each interaction metric (MPS and PPR). Then, these REs were divided by the standard deviation of the distribution of metric values across the considered occupied grid-cells. Such a procedure allowed us to put all predictions from the different models on a single axis (i.e., performance) based on their distance, in standard deviations, to the reference value (i.e., empirical observations). Accordingly, model predictions are better when closer to the reference value (i.e., NE = 0). We considered a model to be good when 95% or more of its normalized errors fell within the range of ±2 standard deviations [31]; that is, most of the model predictions were similar to the empirical observations of the predator diet.

3. Results

Interaction Models vs. Reference Values

According to our results, all interaction models performed better in predicting the predator–prey ratio (PPR) than for the mean prey size (MPS). In addition, MPS results were related to the size of the predator, with larger predators showing larger MPS. Conversely, the PPR values were low and very similar for all predator species. Regarding the levels of analysis, we observed better performance of the models for the locality level than for the species level.

At the predator species level for mean prey size (MPS; see supplementary material Figure S1), we observed that the co-occurrence model (Figure S1a) had predictions closer to the reference values in small species. For the margay, most of its observations were close to the reference value (Figure S1a), while models for the other predators underestimated the reference value and the discrepancy seems to increase as the size of the predator increased. The models that considered the activity period and the foraging strata (Figure S1b) had predictions closer to the reference values than the co-occurrence models (Figure S1a), especially for medium and small predators. In the models that consider the body size of prey (Figure S1c), we observed that the NM predictions for the MPS were lower than the reference values for all predator species but were closer to the reference values for the larger species (i.e., jaguar) compared to the co-occurrence model (Figure S1c vs. Figure S1a). The RNM had predictions closer to the reference values for four of the five predators and less underestimation than previous models for the largest one (Figure S1c). Regarding the saturated models (Figure S1d), we found that they had very good approximations to the MPS reference values in the two largest predators, whereas the rest of the predators had poor results, with predictions lower than the reference values.

At the locality level for mean prey size (MPS; see supplementary material Figure S2), the co-occurrence model (Figure S2a) had predictions closer to the reference values for all predators, except for the smallest, which was overestimated. The models that considered the activity period and foraging strata (Figure S2b) had predictions closer to the reference values, except for the Activity model for the margay, which overestimated its MPS. The models that considered the body size of prey (Figure S2c) had predictions closer to the reference values for all predator species, except for the RNM of the jaguarundi, which overestimated its MPS. Regarding the saturated models (Figure S2d), they had predictions closer to the reference values for the three largest predators but showed overestimated MPS in several models of the margay and the jaguarundi.

At the predator species level for the predator–prey ratio (PPR; Figure 2), we found that the co-occurrence model had predictions closer to the reference values for four of the five predators, except for the largest (Figure 2a). The models that considered the activity period and the foraging strata had predictions closer to the reference values for all predator species (Figure 2b), but there were two exceptions where the models overestimated the reference PPR value: the Activity model of the ocelot and the Strata model of the jaguar. The models that consider the body size of the prey (Figure 2c) had predictions closer to the reference values of the PPR for all predator species, except for the smallest (i.e., the margay). Finally, the four models that considered all the traits and the co-occurrence (Figure 2d) had predictions closer to the reference values of the PPR for the largest predators (i.e., cougar and jaguar), while for the rest of the predators, differences were observed among the four models.

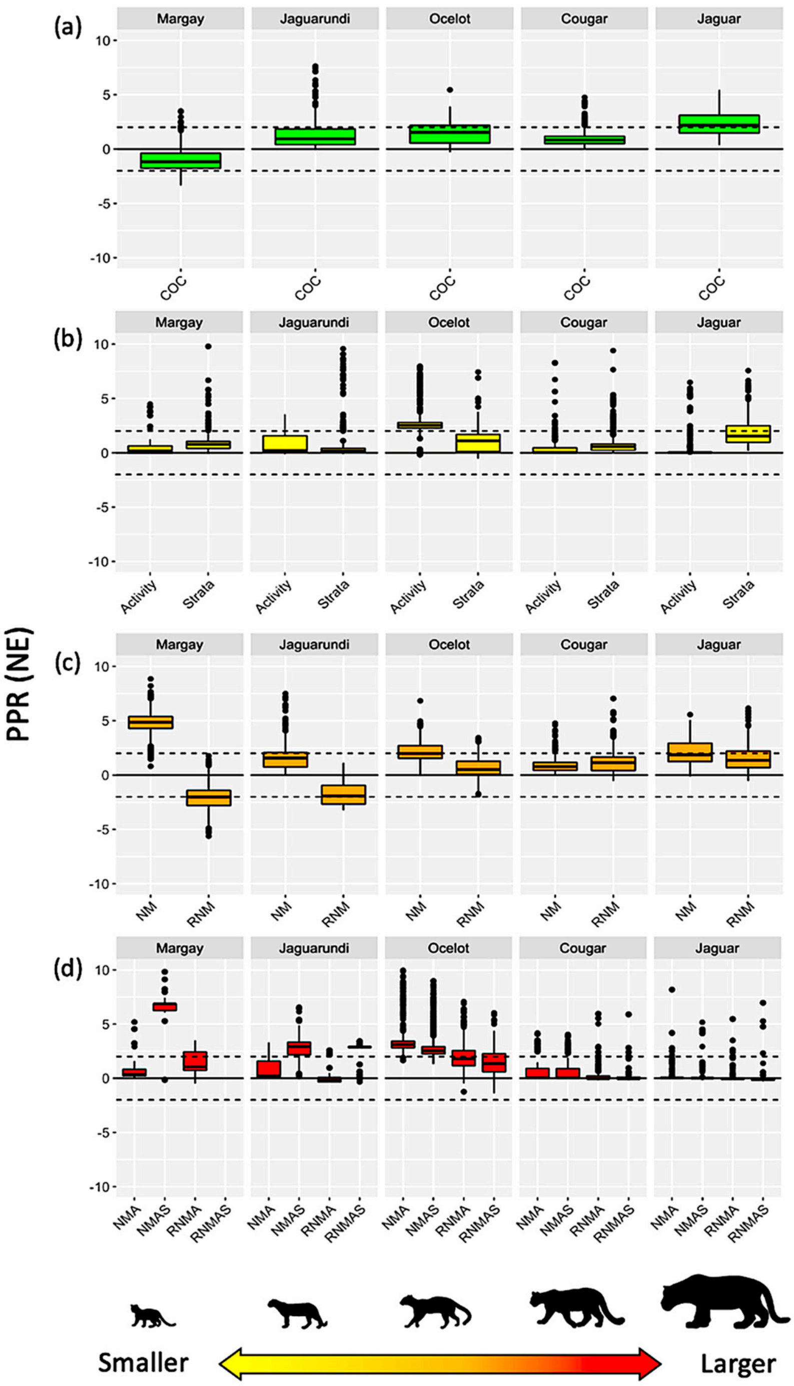


Figure 2. Normalized error (NE) of the predator–prey ratio for the nine models evaluated at the predator species level for each predator species, where the *x*-axis shows the different predator species and models and the *y*-axis shows the normalized errors for (**a**) co-occurrence model, (**b**) spatiotemporal models, (**c**) body size models and (**d**) saturated models. The upper horizontal dashed line indicates the reference value plus two standard deviations, while the lower horizontal dashed line indicates the reference value minus two standard deviations and the continuous horizontal line indicates the reference value. See Table 1 and the methods for the model definitions. Cat silhouettes are from PhyloPic (phylopic.org) and represent the evaluated species.

At the locality level for the predator–prey ratio (PPR; Figure 3), we found that the co-occurrence model (Figure 3a), the models that considered the activity period and the foraging strata (Figure 3b), and the models that considered body size (Figure 3c) had predictions closer to the reference values for all predator species. Finally, the saturated models (Figure 3d) had predictions closer to the reference values for all models except the NMA for the Ocelot (overestimated) and the RNMAS for the cougar and jaguar, which had underestimations.

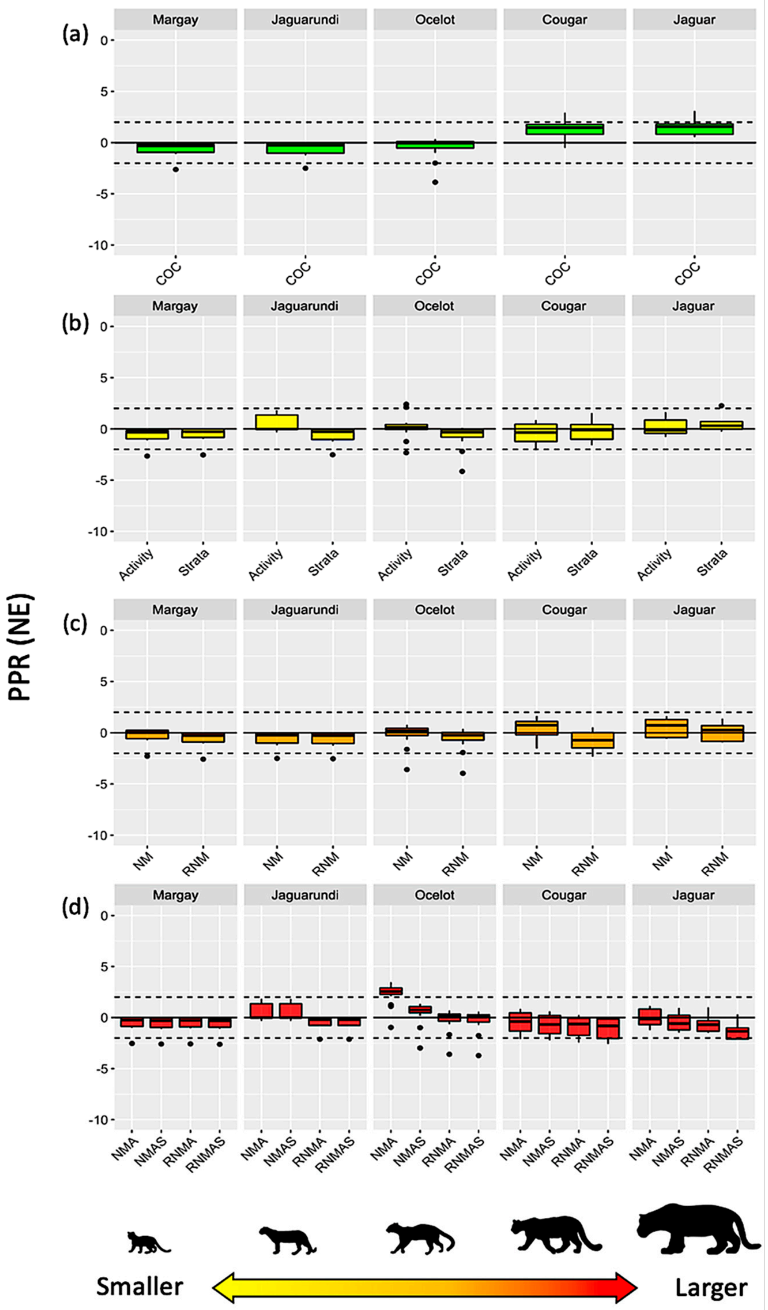


Figure 3. Normalized error (NE) of the predator–prey ratio for the nine models evaluated at the locality level for each predator species, where the *x*-axis shows the different predator species and models and the *y*-axis shows the normalized errors for (**a**) co-occurrence model, (**b**) Spatiotemporal models, (**c**) body size models and (**d**) saturated models. The upper horizontal dashed line indicates the reference value plus two standard deviations, while the lower horizontal dashed line indicates the reference value minus two standard deviations and the continuous horizontal line indicates the reference value. See Table 1 and the methods for model definitions.

4. Discussion

Here, we propose a new approach to infer predator–prey species-level interaction properties based on combining Eltonian niches and geographic distributions of species. We evaluated the potential of using morphological and functional traits to filter information obtained from geographic range maps (co-occurrence) and describe predator–prey interaction properties at the predator level, considering its complete distribution (species level) and local observations (locality level). We showed that combining such trait information at broad spatial scales generates good predictions of predator–prey interaction properties that agree, in general, with those derived from observations of empirical studies at the local spatial scale. Our results of the different models vary with the body size of predator species, with the simpler models (e.g., co-occurrence, COC) showing better predictions for medium and small predators and the more complex models (e.g., co-occurrence with activity and restricted feeding interval, RNM) showing better predictions of the empirical observations for larger predators (i.e., cougar and jaguar). Overall, our modeling framework based on geographic and Eltonian niche information can be a useful tool to generate information about predator–prey interactions in places where no local information is available, providing at the same time a tool for guiding field work.

According to our results, all interaction models had better performance for the predator–prey ratio (PPR) than for the mean prey size (MPS). Moreover, MPS results were related to the size of the predator, as expected, according to its metabolic needs [20]. This is because, although all predators evaluated are reported to be opportunistic and consume any available resource [32,33], larger predators consume larger prey more frequently, as they require larger amounts of meat [20], which makes their MPS higher than that of smaller predators. On the other hand, PPR values were low and very similar for all predator species, with larger predators not showing a body size similar to that of their prey, as expected [22]. The observed PPR values suggest that the predators evaluated, even the larger ones, frequently consume prey slightly smaller than themselves (PPR > 1), which is due to their hypercarnivorous diet that favors the consumption of any prey close to their optimal prey size opportunistically [33,34]. Our results show that the models can approximate well the descriptors of interactions observed in the literature, even for PPR, which is a highly informative descriptor, as it is related to the trophic level of species and energy flows in food webs [21,22]. This good model performance suggests that the combined use of distribution information and existing data on interactions allows us to fill knowledge gaps and contribute to the conservation of species and their interactions in the current context of global change [7], where interactions are lost at a faster rate than species that produce subsequent extinctions.

Regarding the data levels evaluated, all interaction models showed better performance at the locality level (considering as many values as localities with enough prey information) than at the species level (considering only a single value across the predator's entire distribution) for both metrics, the MPS and the PPR. However, this result should be taken with caution since the number of localities was very limited for most predator species, which, together with the variability of predator diets, can generate observations of similar MPS or PPR between species of very different sizes, such as the jaguar and the ocelot [35]. Likewise, at the locality level, medium or small predator species showed MPS similar to those of the larger predators, contrary to metabolic expectations [20] and to the observed at the species level. These differences between the MPS at the species level and at the locality level suggest that the diet patterns of these predators are more robust when we consider the totality of prey known to the predator (species level) because they behave as expected according to their metabolic needs (i.e., a positive correlation between prey size and their predators [20]). On the other hand, when analyzing only localities (i.e., diet fractions), species diets can become very similar due to the generalist behavior of predators and the limited number of observations for some predator species [33,35]. Regarding PPR, it was lower and constant between localities for larger predators and more variable for small predators. This suggests that the similarities between large and small predators are due more to variability in the diet of the latter, which is well known for species such as ocelots and jaguarundi [35]. In summary, our results show that at the locality level predator diet observations can be very similar due to the great variability observed in predators' diets, especially those of medium and small size, which favored that models such as co-occurrence had predictions closer to the observed values in large species.

Our analysis at the locality level, despite limitations in the number of samples, showed that local observations of predator–prey interaction properties (i.e., MPS, PPR), are highly variable as well as differences or biases in sampling among different species [1,35–37]. In our case, differences in sampling effort may increase bias in local observations most likely because felines are opportunistic and generalist predators [32,33,35]. Carnivores during the search for optimal prey tend to consume smaller species as a temporary source of food; thus, the size of the recorded prey in a particular study may not necessarily reflect the metabolic needs of the predator [33,35,36]. As such, if the number of samples and prey reported for a predator is small, smaller preys are more likely to be recorded, which could generate similar patterns among predators of different sizes. This was observed for our co-occurrence interaction model, which, despite only considering the species composition per grid-cell without any additional filtering, performed similarly well for all predators. The opportunistic nature of predator–prey interactions differs from other more tightly linked interactions, such as pollination, where the correspondence between the functional traits of interacting species allows for less intraspecific variation (e.g., [19]). Hence, our modeling framework could have better results in these kinds of more intimate interactions.

Our results at the species level confirm that functional traits such as body size, activity period and foraging strata are sufficient to generate accurate predictions of predator–prey interaction properties such as the mean prey size or de predator–prey ratio for most predator species. In our case, predators' body size was a relevant trait for inferring their interaction properties, given that it influences the selection of prey and is positively correlated with prey size [20,22,36]. Furthermore, our results also showed that traits that do not require field observations of interactions and that are available in databases—activity period and foraging strata—seem to have a similar or better performance than body size in predicting predator–prey interaction properties at both the species and locality levels, even in species whose knowledge about their diet is poor, such as the jaguarundi [35]. This is relevant considering the difficulty of studying predators in the field and that there are large differences in the sampling effort among species, particularly in felids [1,35,37]. In the case of co-occurrence models, our results showed good performance in small species of predators (i.e., margay, jaguarundi and ocelot). This is most likely due to the skewed distribution toward smaller body sizes in mammals [23], leading to a higher co-occurrence of small predators with smaller mammals but making imprecise predictions for larger predators in both levels. Therefore, while traits such as body size, activity period and foraging strata appear to be very useful in defining interactions, since their performance can be related to the niche of the species, the usefulness of the co-occurrence in the present study is related to the Grinnellian niche of species and not to the Eltonian, that is, co-occurrence reflects similar climatic tolerance of the species but not their functional trait matching. Such usefulness and better performance of an interaction model based on geographic co-occurrence could be specific to our considered interaction type and taxon (felids) and not necessarily for other interaction type/taxa. For instance, in other types of interaction, such as herbivory between ungulates and plants, the co-occurrence among trophic levels would not be as determinant for the interaction (beyond being the first condition) as their temporal coexistence and phenology of plants, which determine the actual possibilities for the interaction to occur such as the time of year that the plant resource (e.g., foliage) is available for the herbivore.

Considering functional traits in interaction studies has allowed the development of theoretical frameworks that integrate the climatic and trophic niches of species [3,13] and predict food web properties, such as trophic level and their spatial variation, when such information on trophic networks or interactions is limited or absent [10,14,15]. Here, we took advantage of two complementary characteristics of these theoretical frameworks:

first, using functional traits allows defining intervals within which an interaction can occur through trait matching [3,10,14,31], and second, species with a similar Eltonian niche usually share functional traits and belong to similar trophic levels [13]. These two characteristics allowed us to use functional traits (morphology and life history) to filter information based on geographic co-occurrence and obtain properties of predator–prey interactions from broad-scale data, which were similar to those observed in the literature at the local scale. This is particularly encouraging under current scenarios of global change that threaten species and their interactions, allowing us to provide a first description of interactions before we lose them without having to wait for local studies to be conducted [1,8,13,38]. Note, however, that using single trait values for species (e.g., mean body size, reported activity period) can be suboptimal given the known intraspecific variation for several (if not most) traits. For example, it is well known that species body size varies with latitude and temperature, with smaller individuals at hotter/lower latitudes and larger individuals at colder/higher latitudes (e.g., *Puma concolor* [39]), which could modify the species' feeding intervals at different locations. Similarly, the species period of activity could vary in response to climate or the presence of competitors (e.g., the ocelot modifies its activity period in response to the presence of humans or larger predators [40]).

Finally, our approach shows that by choosing traits that determine local coexistence and resource importance and combining them with the ranges of these species, it is possible to generate predictions close to the empirically observed data. This implies that this method can be used in other trait-mediated interactions, such as pollination, frugivory or parasitism, as long as data on the geographic distributions and traits of the evaluated species is available. For example, if we want to evaluate frugivory, we would need to know which plants produce fruits in our area of interest as well as their phenology (e.g., months when fruits are produced, immature, ripe and so on). We would also need data on their consumers (i.e., birds, mammals) along with their geographic distributions. Finally, we would require at least minimal field data (e.g., obtained from the literature) on the consumers and their diets to refine inferences (i.e., if a bird consumes only ripe fruits of certain plants even if the plant and bird co-occur in space, they will not interact until the fruit is ripe). If we wish to replicate this approach with other groups, it is necessary to consider data uncertainty. For example, if we have a database of functional traits at the species level, we must use field data at the same resolution to avoid introducing biases when changing the taxonomic resolution (e.g., recalculating such traits at the genus level when these may already be average data or imputations). In this sense, we should be aware of the limitations and simplifications associated with the type of data used (e.g., averages, imputations), as well as consider whether there is more than one database with the same trait, in which case it would be necessary to evaluate the consistency of the different sources before joining them or choosing one. Another advantage of our approach is that, due to its species-based focus, it is possible to evaluate the variation within the range of the species evaluated to determine sites with higher resource quality (i.e., those more similar to the empirical values) or sites with lower resource quality (i.e., sites with lower values than the empirical values). Due to the simplicity of our method, as well as its applications, it can be very useful in conservation, either to prioritize conservation areas or to determine the risk of extinction of species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15010061/s1. File S1: Complementary description of data manipulation for interaction model generation; File S2: Restricted niche model results; File S3: Predators species traits; File S4: Predator–prey interaction properties. Figure S1: Normalized error (NE) of the mean prey size (MPS) for the nine models evaluated at the predator species-level for each predator species. Figure S2: Normalized error (NE) of the mean prey size (MPS) for the nine models evaluated at the locality-level for each predator species.

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