**Ecography 40: 817–828, 2017**
doi: 10.1111/ecog.02125

Subject Editor: Miguel Araújo. Editor-in-Chief: Miguel Araújo. Accepted 13 June 2016

# Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis

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It is thought that species abundance is correlated with environmental suitability and that environmental variables, scale, and type of model fitting can confound this relationship. We performed a meta-analysis to 1) test whether species abundance is positively correlated with environmental suitability derived from correlative ecological niche models (ENM), 2) test whether studies encompassing large areas within a species range ($>$50%) exhibited higher AS correlations than studies encompassing small areas within a species range ($<$50%), 3) assess which modelling method provided higher AS correlation, and 4) compare strength of the AS relationship between studies using only climatic variables and those that used both climatic and other environmental variables to derive suitability. We used correlation coefficients to measure the relationship between abundance and environmental suitability derived from ENM. Each correlation coefficient was considered an effect size in a random-effects multivariate meta-analysis. In all cases we found a significantly positive relationship between abundance and suitability. This relationship was consistent regardless of scale of study, ENM method, or set of variables used to derive suitability. There was no difference in strength of correlation between studies focusing on large or small areas within a species' range or among ENM methods. Studies using other variables in combination with climate exhibited higher AS correlations than studies using only climatic variables. We conclude that occurrence data can be a reasonable proxy for abundance, especially for vertebrates, and the use of local variables increases the strength of the AS relationship. Use of ENMs can significantly decrease survey costs and allow the study of large-scale abundance patterns using less information. Including only climatic variables in ENM may confound the relationship between abundance and suitability when compared to studies including variables taken locally. However, modelers and conservationists must be aware that high environmental suitability does not always indicate high abundance.

For every species there should be one or a few most favorable sites within its geographic range where its abundance is highest and many other sites of lower quality where it is less abundant but still able to persist (Brown 1984). Such a pattern reflects population response to local conditions (e.g. food resources and climatic conditions) in particular the extent to which local conditions meet species ecological requirements (Hutchinson 1957, Brown 1984).

There is a well documented correlation between distribution and abundance of species (Brown 1995, Gaston 2003). However, He and Gaston (2007) argue that 'how best to estimate abundance from distribution largely remains an unsolved problem'. One way of addressing spatial variation of abundance within a species range is interpolating local abundance data over a geographic domain of interest (Bahn and McGill 2007) relying on the assumption that abundance is spatially autocorrelated (Brown 1995). However, this approach does not allow inference about any ecological process that may mediate the role of environment on species abundance. Habitat selection or resource selection functions (RSF) can also be used to predict abundance (Manly et al. 2002, Boyce et al. 2016). RSFs are proportional to the probability of an area being used by an animal and link populations to their habitats (Boyce and McDonald 1999) and scale animal abundance to the probability of selecting a given habitat (Johnson and Seip 2008).

Correlative ecological niche modelling (ENM) using occurrence data can also provide environmental suitability for a species based on environmental variables where areas with highest suitability could indicate areas that best match a species' ecological niche (Yackulic et al. 2013). The underlying mechanism is based on population demography. Within a species range it is expected that the intrinsic growth rate of populations is positive whereas outside a species range it is expected to be negative (Gaston 2003). However, within a species range the probability of occurrence can be positively or negatively related with the intrinsic growth rate of a population and positively related to the carrying capacity of a population (Thuiller et al. 2014). Therefore areas with high environmental suitability or probability of occurrence tend to harbor larger populations because favorability of local conditions increases birth and survival rates and decrease extinction rate (Morrison et al. 2006). In fact, probability of occurrence is negatively correlated with probability of extinction (Araújo et al. 2002). Extinction events are more common in areas with lower probability of occurrence than in areas with higher probability of occurrence. Spatial autocorrelation in presence data occurs because species exhibit greater aggregations (i.e. high abundance) where the environment is more suitable (Araújo et al. 2002). Therefore, areas of high environmental suitability should also exhibit high abundances. This hypothesis relies on the assumption that population dynamics are in equilibrium with the environment. If populations are changing rapidly, we may not expect to find real and meaningful correlations between abundance and environmental suitability.

Despite environmental determinism being commonly claimed to explain aggregations of individuals of a species, other factors may also play a role on species abundance such as demography (Ehrlén and Morris 2015), philopatry (Stacey and Ligon 1991) or neutral processes (Hubbell 2001). However, even demographic and philopatric processes can be affected by the environment because species only occur at high densities where the environment is suitable (Araújo et al. 2002). To this end, there should be a positive abundance-suitability (AS) relationship and ENM should provide an effective proxy for spatial variation in abundance over geographic space. Furthermore, understanding the AS relationship may elucidate how species respond to environmental conditions, especially under climate change scenarios.

The AS relationship has been tested across a number of different organisms and has also been used for various ecological applications. For example, Mellin et al. (2012) modelled the distribution of two marine mollusks species. They assessed the AS relationship and used it to estimate the potential effects of global change on mollusk populations. If the AS relationship holds true, identifying areas of high environmental suitability will improve our ability to find populations of rare species with narrow habitat requirements (Gogol-Prokurat 2011). In addition, such an approach also enables researchers to forecast areas more prone to biological invasions (Januchowski-Hartley et al. 2011, Kulhanek et al. 2011).

Studies using correlative ENM to relate predicted species abundance with environmental suitability have found varying support for the AS relationship. Some authors have found strong and positive correlations (Ready et al. 2010, Kulhanek et al. 2011, Oppel et al. 2012, Weber and Grelle 2012), while others have found only moderate (Seoane et al. 2005, Elmendorf and Moore 2008, Tellería et al. 2012, Tôrres et al. 2012) or low to non-significant correlations (Pearce and Ferrier 2001, Nielsen et al. 2005, Filz et al. 2013). When AS correlations are low, ENM's are not good predictors of abundance (Jiménez-Valverde et al. 2009). However, a comprehensive analysis encompassing numerous tests addressing the AS relationship is still lacking. Such analysis represents an important step towards formulating generalizations regarding the relationships between suitability derived from ENM's and actual abundance of organisms in nature.

One potential explanation for some weak AS relationships is that spatial scale at which occurrence and abundance are actually measured may affect the strength of the relationship (Nielsen et al. 2005). Indeed, scale can be a key consideration when estimating spatial variation of abundance from occurrence data (He and Gaston 2007). Varying the size of the study area can generate different abundance estimates (Aebischer et al. 1993). Studies carried out over small areas within a species' range may not include enough environmental variation experienced by a species to find a strong AS relationship. In such cases, environmental variables might vary within a relatively small range of values and such incomplete sampling may reduce power of tests (Nielsen et al. 2005, Van Couwenberghe et al. 2012). On the other hand, studies including a large area within a species' geographic range encompass more environmental variation experienced by that species and will likely produce higher correlations than studies considering only small portions of a range (Tôrres et al. 2012, Weber and Grelle 2012). In addition, not covering the entire species range, or at least a large portion of it, decreases the probability of sampling sites with high abundance because few areas harbor many individuals and most areas harbor few individuals (Brown et al. 1995, Martínez-Meyer et al. 2013). So far there has been no analysis examining the AS relationship using different proportions of species ranges (e.g. small vs large areas within ranges).

Other methodological issues may affect the strength of AS correlations. For example, there are three different approaches used to model ecological niches: 1) statistical models, 2) similarity and 3) machine learning methods (Franklin 2010). It is still unclear which approach performs better when trying to correlate abundance with environmental suitability. For example, BIOCLIM (a similarity method) had the best performance in correlating environmental suitability with jaguar abundance among eleven different algorithms, although the correlation was only moderate (Tôrres et al. 2012). On the other hand, machine learning methods and statistical models seem to provide suitability values that correlate better with abundance than similarity methods (Kulhanek et al. 2011, Mellin et al. 2012, Weber and Grelle 2012). Therefore, we are still far from a comprehensive understanding of the effect of using different methods to address the AS relationship.

In addition to issues of proportion of species range and type of modelling method, another cause of varying correlation between environmental suitability and species abundance may be the set of environmental predictors used to derive environmental suitability from occurrence data. For example, the climatic database most used to derive suitability is the Worldclim database (<www.worldclim.org/>), provided by Hijmans et al. (2005). However, it is unlikely that climate is the only influence on species abundance. Moreover, it is widely known that species abundance responds to environmental disturbances (such as distance to cities and amount of pollutants) and conditions other than climate such as tree density, type of soil, or pH (Van Couwenberghe et al. 2012), to namely only a few.

Different algorithms used to derive environmental suitability have been used long enough and as presented above provide conflicting empirical support for the AS relationship.

Hence, it is important to review current knowledge and perform a meta-analysis to quantify the degree to which species abundance is correlated with suitability as well as the influence of methodological issues such as amount of species' range examined, modelling methods or set of variables used to derive environmental suitability. Here our goals are 1) to test whether species abundance is positively correlated with environmental suitability derived from correlative ENMs, 2) to test whether studies encompassing large areas within a species range show higher AS correlations than studies encompassing small areas, 3) to assess which modelling method provides higher AS correlation, and 4) to compare strength of the AS relationship between studies that use only climatic variables with those using both climatic and environmental variables to derive suitability.

## Methods

### Correlation coefficients

We searched for papers that tested the AS relationship using suitability values obtained from correlative ENM in the online database Web of Science (<http://apps.isiknowledge.com>) published up to August 2015. We used the following combination of key-words for searching: ecological niche model* or environmental niche model* or species distribution model* or habitat suitability model* and abundance. For each species we used correlation coefficients provided by the authors to measure the relationship between abundance and environmental suitability derived from occurrence data. The kind of correlation coefficient used varied across studies (e.g. Pearson's r, Spearman's $r_s$, Kendall's tau). Comparing different indices may affect analyses, but we assumed that authors used the most appropriate correlation index for each analysis, providing the best fit for the correlation between abundance and suitability. Furthermore, all correlation coefficients vary between –1 and 1, and therefore provide a standardized measure of the relationship between abundance and suitability that can be compared in a meta-analysis. When more than one modelling algorithm was used to build an ENM, we used the best fit found by the authors, i.e. the highest correlation coefficient regardless of the modelling algorithm used to generate the general pattern of the AS relationship. When the same species was analyzed in more than one study we used the one that used the largest sample size.

When only the coefficient of determination was provided by the authors, we calculated the correlation coefficient by taking the square root of the coefficient of determination (VanDerWal et al. 2009, Tôrres et al. 2012), taking into account if the relationship was positive or negative. When different correlation values were provided using training and test data, we chose only the correlation provided for the training data (Nielsen et al. 2005), because training data are used to develop the model and test data are used to test the model predictions. If correlation values using both presence/absence and presence-only data were provided (Pearce and Ferrier 2001, Nielsen et al. 2005), we selected correlation values considering presence and absence (abundance equal to zero).

### Effect sizes and multivariate meta-analysis model

Meta-analyses focus on combining and contrasting results from different studies to identify emergent patterns among studies. Pattern is normally characterized by a common measure of effect size, of which a weighted average is commonly the output of a meta-analysis (Cooper and Hedges 1994). In this study, each correlation coefficient for each species was considered an effect size, a value that reflects the strength of the relationship between abundance and environmental suitability.

We computed effect size for each species, assessed consistency of effect sizes across species, and computed a summary effect (Borenstein et al. 2009). Correlation coefficients should not be used directly to synthesize effect sizes because the variance depends on correlation strength (Borenstein et al. 2009). Therefore, we converted correlation coefficients to Fisher's z scores and performed analyses using transformed values. In order to present results in a more understandable manner, we converted the summary effect and the confidence intervals back to correlation coefficients.

Studies differed in the set of species analyzed, methods, and the environmental/climatic variables used to derive suitability. In order to account for such differences, we used a random-effects model that includes both variation within and across studies (Borenstein et al. 2009). We assume that selected studies have enough in common to synthesize information.

Some papers dealt with sets of species and therefore provided effect sizes for several related species using the same sampling design, variables, and methods to build ENM's. Several effect sizes from the same study are non-independent (Nakagawa and Santos 2012). In order to account for such non-independence, we used a random-effects multivariate meta-analysis.

In addition to non-independence of correlations from the same study, species relatedness may also affect statistical independence since related species likely have similar ecological characteristics (Harvey and Pagel 1991, Nakagawa and Santos 2012). Each ENM built for every species takes into account variables that are thought to estimate its niche, and for related species such variables tend to be similar (Peterson et al. 1999). However, even with niche similarity across related species, there is no reason to suppose that species abundance in the same geographic region will respond similarly to environmental suitability. Furthermore, in this study we are dealing with very different organisms (e.g. earthworms, mollusks, insects, reptiles, mammals, fishes, and flowering plants) which makes incorporating a comparative method and test for phylogenetic independence of the effect sizes prohibitively difficult [but see how to incorporate phylogenetic effects in a meta-analysis in Adams (2008)]. Therefore, we used the taxonomic family as a surrogate of relatedness among species to account for phylogenetic independence. Thus, we built a random-effects multivariate meta-analysis using both authorship and species family as non-independent factors.

We assume that researchers modelled the potential environmental niche based on the realized niche (observed data), which has already been limited by non-environmental factors (e.g. biotic interactions and demographic constraints). We acknowledge that there may be other species-specific factors influencing local species abundance other than environmental suitability such as time of colonization, interspecific competition and source-sink dynamics. However, here we are only interested in to what extent environmental suitability derived from ENM (not geographic range per se) is related to abundance.

Proportion of the geographic range of each species used to estimate the niche model may influence strength of the AS relationship. In order to account for this effect, we compared the magnitude of correlation from studies carried out over small areas within a species' range ($<50\%$ of a species range) to magnitude of correlation from studies carried out over large areas within a species' range ($>50\%$ of a species range). To determine proportion of species' range that was studied, we compared it visually to maps of species ranges obtained from IUCN (<www.iucnredlist.org/>). For this analysis we considered only mammal and bird species because geographic distributions of invertebrate, reptile, and plant species considered here are poorly known.

To compare influence of the set of variables chosen to derive environmental suitability in the ENMs on the AS relationship, we classified niche models into two groups: 1) climatic niche models and 2) environmental niche models. In climatic niche models, variables included in modelling were exclusively those of climate (e.g. Worldclim variables) and elevation (often used as a proxy for temperature). In environmental niche models, variables included in modelling were both climatic and non-climatic (e.g. salinity, habitat patch size, and soil moisture). Such comparison may identify which kinds of variables provide environmental suitability values that correlate better with species abundance.

## Comparing ENM approaches

To evaluate which ENM approach provides the strongest AS relationship we classified all approaches used to derive suitability into three categories according to Franklin (2010): statistical modelling, similarity and machine learning methods. Statistical modelling is based on presence/absence data and is derived from classical statistical techniques, such as generalized linear models (GLM). These models seek a relationship between species presence/absence and a suite of environmental variables, estimating a probability of occurrence (Yackulic et al. 2013) and they are functionally similar to RSFs (Manly et al. 2002). In statistical modelling certain assumptions are made about the form of the model (which are chosen by the modeler) and all the data are used to estimate the model parameters (Franklin 2010). This approach can provide simple and realistic models, allowing a better understanding of species distribution than more complex methods (Guisan and Zimmermann 2000). Statistical modelling includes GLM (Guisan et al. 2002), generalized additive models (GAM, Yee and Mitchell 1991), mixture discriminant analysis (Manel et al. 1999), and MARS (multivariate adaptive regression splines) (Moisen and Frescino 2002).

Similarity methods are based on presence data only and are simple representations of the ecological niche. They determine for each environmental variable an upper and lower limit for species occurrence (i.e. where the species is likely to occur). This geographic space is called an envelope. Similarity models consider that the ecological optimum for a species is in the centroid of occurrence points in ecological space. The distance between the estimated optimum and observed values for each pixel in the geographic area is inversely related to the environmental suitability for the focal species at that site (Araújo and Peterson 2012). Similarity methods include BIOCLIM (Busby 1991), DOMAIN (Carpenter et al. 1993), Mahalanobis distance (Farber and Kadmon 2003), and AquaMaps (Kaschner et al. 2013).

The machine learning method is a much more complex statistical technique based on presence/absence or presence/pseudo-absence or presence/background data. In contrast to the statistical methods, this approach is a suite of regressions that are used to learn the mapping function directly from the training data to get the best prediction and it does not need prior assumptions as needed in the statistical models (Franklin 2010). In general, this method performs better than statistical and similarity methods in predicting species distributions (Elith et al. 2006). Machine learning methods include Maxent (Phillips and Dudík 2008), GARP (Stockwell and Noble 1992), artificial neural networks (Segurado and Araújo 2004), random forests (Breiman 2001), classification tree analysis (Breiman et al. 1984), and generalized boosting models (Friedman 2001). Although machine learning methods are much more complex algorithms, they are mathematically equivalent to the statistical methods because both relate environmental predictors with presence/absence or presence/background data (Renner and Warton 2013).

Although all three kinds of methods are statistical, we are referring to the first kind as statistical methods for practical reasons. We clustered different modelling approaches using the same general method as described above. We calculated the summary effect size of the AS relationship for each of the three approaches using a multivariate meta-analysis with random-effects. We then compared the summary effect among the three approaches (statistical, similarity and machine learning methods) to assess which better predicts the AS relationship. We made all comparisons mentioned above among model coefficients using the Wald test. We consider statistical significance when $p < 0.05$.

## Publication bias

Studies reporting statistically significant results are more likely to be published than studies reporting non-significant results (Greenwald 1975). If publication bias is a problem, then studies included in a meta-analysis may represent a biased subset of the total number of studies performed (Wang and Bushman 1998). Publication bias can be detected using quantile-quantile plots, which are preferred over funnel plots (Wang and Bushman 1998). In a quantile-quantile plot or normal quantile plot, quantiles of the observed data distribution are plotted against theoretical quantiles of the standard normal distribution (with mean of zero and standard deviation of 1). If observed data have a standard normal distribution, points on the plot will fall close to the line $y = x$ and the slope of the plotted line will be close to 1. Thus we can assume that data are not biased and they come from a single population and the sample size for each study is large enough (Borenstein et al. 2009). To statistically assess publication bias, we added the variance as a moderator into the model and this is similar to the Egger test (Egger et al. 1997) applied to non-hierarchical models. Non significant ($p > 0.05$) moderators in a Wald test indicate no publication bias. All analyses were carried out in the software R ver. 2.14 (R Development Core Team) using the 'metafor' package (Viechtbauer 2010).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.g2fd2> (Weber et al. 2016).

## Results

We obtained 450 correlations between species abundance and environmental suitability derived from ENM from 30 studies on several taxa including fishes, reptiles, birds, mammals, insects, arachnids, earthworms, mollusks, pteridophytes, and flowering plants (Table 1). We did not find any evidence of publication bias in our data both visually (Fig. 1) or statistically (Wald test = 1.101, DF = 1, $p = 0.29$).

Most cases reported a positive relationship between abundance and environmental suitability, although negative correlations were also observed (Fig. 2). The summary effect of correlation between abundance and suitability was moderate when all taxa were analyzed together ($r = 0.55$, 95% confidence interval [CI] = 0.45–0.64, $p < 0.0001$, $k = 450$). A positive relationship between abundance and suitability was consistent across different taxa analyzed: vertebrates ($r = 0.62$, CI = 0.51–0.72, $p < 0.001$, $k = 166$), invertebrates ($r = 0.53$, CI = 0.25–0.72, $p < 0.001$, $k = 133$), and plants ($r = 0.34$, CI = 0.25–0.41, $p < 0.0001$, $k = 151$) (Fig. 3A).

Most cases used machine learning methods ($n = 316$) and statistical models ($n = 118$) to derive suitability and

Table 1. List of the 30 studies included in this meta-analysis showing number of species considered in each study, taxonomic group, method of ecological niche modeling, spatial resolution and number of variables used to model species' ecological niche, and type of abundance data used to correlate with environmental suitability. ANN = artificial neural networks, BRT = boosted regression trees, CEM = climate envelope model, CTA = classification tree analysis, FF = favourability function, GAM = generalized additive models, GARP = genetic algorithm for rule-set production, GBM = generalized boosting models, GLM = generalized linear models, LR = logistic regression, Maxent = maximum entropy, MARS = multivariate adaptive regression splines, MD = Mahalanobis distance, MDA = mixture discriminant analysis, RF = random forests, RSF = resource selection function. Number of species considered here may be different to the original studies because of selection criteria (see Methods section).

| Study | Number of species | Taxonomic group | Method of modelling |
|---|---|---|---|
| Pearce and Ferrier (2001) | 73 | reptiles, birds, mammals, ferns, and flowering plants | Statistical (LR) |
| Nielsen et al. (2005) | 2 | ungulate and fern | Statistical (LR) |
| Seoane et al. (2005) | 53 | birds | Machine learning (BRT) |
| Elmendorf and Moore (2008) | 100 | flowering plants | Machine learning (ANN, BRT) |
| Jedrzejewski et al. (2008) | 1 | carnivore | Statistical (RSF) |
| Jiménez-Valverde et al. (2009) | 46 | arthropods | Machine learning (ANN) |
| Real et al. (2009) | 2 | carnivore and rabbit | Statistical (FF) |
| VanDerWal et al. (2009) | 2 | vertebrates | Machine learning (Maxent) |
| Ready et al. (2010) | 12 | whales and sea fishes | Statistical (GLM, GAM), Machine learning (Maxent, GARP), and Similarity (AquaMaps) |
| Giannoulaki et al. (2011) | 1 | fish | Statistical (GLM) |
| Gogol-Prokurat (2011) | 2 | flowering plants | Machine learning (Maxent) |
| Januchowski-Hartley et al. (2011) | 1 | flowering plant | Machine learning (Maxent) |
| Jones-Farrand et al. (2011) | 5 | birds | Machine learning (CTA) |
| Kulhanek et al. (2011) | 1 | fish | Machine learning (ANN) |
| Estrada and Arroyo (2012) | 2 | seabirds | Statistical (GLM) |
| Guarino et al. (2012) | 9 | fern, conifer, and flowering plants | Statistical (GLM) |
| Mellin et al. (2012) | 2 | mollusks | Statistical (GLM) |
| Oppel et al. (2012) | 1 | seabird | Statistical (GAM, GLM) and Machine learning (RF, BRT) |
| Tellería et al. (2012) | 1 | bird | Machine learning (Maxent) |
| Tôrres et al. (2012) | 1 | carnivore | Statistical (MDA, MARS), Similarity (BIOCLIM, DOMAIN, MD), and Machine learning (Maxent, GARP, CTA, RF, GBM, ANN) |
| Weber and Grelle (2012) | 1 | bat | Machine learning (Maxent) |
| Bucas et al. (2013) | 31 | arthropods, mollusks, polychaetes, algae, and flowering plants | Statistical (GAM, MARS), machine learning (Maxent, RF) |
| Filz et al. (2013) | 61 | butterflies | Machine learning (Maxent) |
| Gutiérrez et al. (2013) | 1 | butterfly | Statistical (GLM) |
| Palm et al. (2012) | 2 | earthworms | Machine learning (BRT) |
| Bean et al. (2014) | 1 | mammal | Machine learning (Maxent) |
| Carrascal et al. (2015) | 19 | birds | Machine learning (BRT, Maxent) |
| Muñoz et al. (2015) | 1 | bird | Statistical (LR, FF) |
| Russel et al. (2015) | 9 | seabirds | Similarity (CEM) |
| Young and Carr (2015) | 7 | reef fishes | Statistical (GAM) |

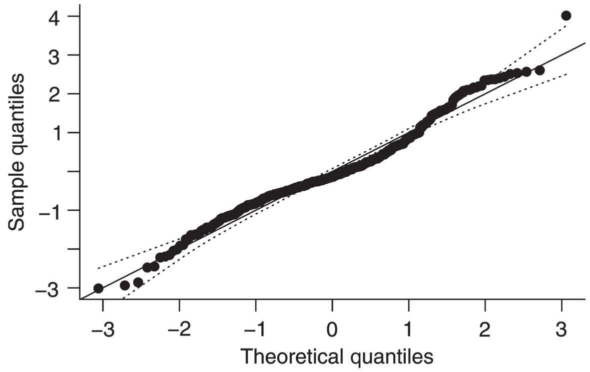

Figure 1. Quantile-quantile plot showing the relationship of the observed sample quantiles (black dots, n = 450) and the theoretical quantiles from the standard normal distribution (mean of zero and standard deviation of 1). Black solid line indicates the mean of the data. Slope of the black solid line is approximately 1, indicating no bias. Dashed lines around the black dots indicate the 95% confidence interval.

correlate it to abundance. Similarity methods were the least used (n = 16). All ENM's generated suitability values that were positively correlated with species abundance. Machine learning methods showed the highest summary effect ($r = 0.59$, CI = 0.44–0.71, $p < 0.0001$, $k = 316$) followed by similarity methods ($r = 0.58$, CI = 0.36–0.73, $p < 0.0001$, $k = 16$) and statistical methods ($r = 0.47$, CI = 0.38–0.54, $p < 0.0001$, $k = 118$). There was no difference in the strength of the AS relationship among ENM methods (Wald test = 0.236, DF = 2, $p = 0.889$; Fig. 3B).

Summary effect of correlation between abundance and suitability was also positive when considering both large and small proportions of species' ranges ($r = 0.51$, CI = 0.26–0.7, $p < 0.0001$, $k = 20$; $r = 0.62$, CI = 0.47–0.73, $p < 0.0001$, $k = 125$; respectively, Fig. 3C). However, there was no difference in the effect sizes between groups (Wald test = 0.09, DF = 1, $p = 0.764$).

Summary effect of the AS correlation was also positive for studies modelling climatic and environmental niches ($r = 0.3$, CI = 0.16–0.43, $p < 0.001$, $k = 120$; $r = 0.58$, CI = 0.48–0.67, $p < 0.0001$, $k = 330$; respectively). However, studies deriving suitability from environmental niches exhibited a higher AS relationship than studies deriving suitability only from climatic niches (Wald test = 7.23, DF = 1, $p = 0.0072$, Fig. 3D).

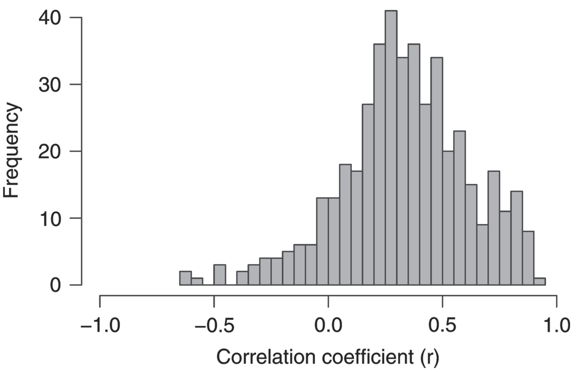

Figure 2. Histogram showing the frequencies of the correlation coefficient (r) testing the relationship between abundance and environmental suitability derived from ENM found for 450 species.

## Discussion

### Abundance-suitability patterns

Environmental suitability values derived from correlative ENM's have recently been used to relate suitability with population density but until now there has been no consensus regarding the ubiquity of this relationship (Jiménez-Valverde et al. 2009, VanDerWal et al. 2009, Weber and Grelle 2012). Our meta-analysis corroborates a general positive correlation between abundance and environmental suitability derived from ENM, although the summary effect of the correlation between abundance and suitability was only moderate and widely variable. This pattern was consistent regardless of taxonomic group, modelling method, proportion of species range utilized, and set of variables included. Most studies used variables such as temperature, precipitation, and measures of disturbance (e.g. crop presence) that are variables related to the Grinnellian niche (Soberón 2007), which are thought to be important in driving species abundance. However, environmental suitability is only one of several factors influencing species abundance over geographic space. That environmental suitability explained approximately 30% ($r = 0.55$) of variation in abundance, on average, is notable, considering that species abundance is a complex ecological trait that is also affected by time of colonization, interspecific competition, demography, and source-sink dynamics (see below). Suitability should be considered a reasonable proxy for species abundance.

Vertebrates and invertebrates showed the highest summary effect sizes among taxonomic groups examined. However, invertebrates also showed the widest confidence interval for the AS correlation. Jiménez-Valverde et al. (2009) suggest that ENM's do not account for arthropod abundance and that suitability should not be used as a surrogate of abundance. Several components of vegetation structure (e.g. plant density and architectural complexity), and microscale variables such as leaf chemical composition and soil moisture may be more important contributors to variation in arthropod abundance than climate and topographic variables (Price et al. 2011), although climate variables may affect arthropod abundance as well. Indeed, studies on invertebrates using both microscale variables (e.g. soil pH, soil moisture, and shrub cover) and climatic variables taken locally over a short time span revealed an average AS correlation higher than studies incorporating only topographic and interpolated climate variables [$r_{mean} = 0.72$, $n = 5$ (Mellin et al. 2012, Palm et al. 2012, Gutiérrez et al. 2013), $r_{mean} = 0.13$, $n = 107$ (Jiménez-Valverde et al. 2009, Filz et al. 2013), respectively]. Therefore, including only climatic variables may weaken the relationship between abundance and suitability for invertebrates, when compared to studies including microscale variables.

In contrast to invertebrates, plants showed the narrowest confidence interval but the lowest summary effect size for the AS correlation. This low correlation may suggest that

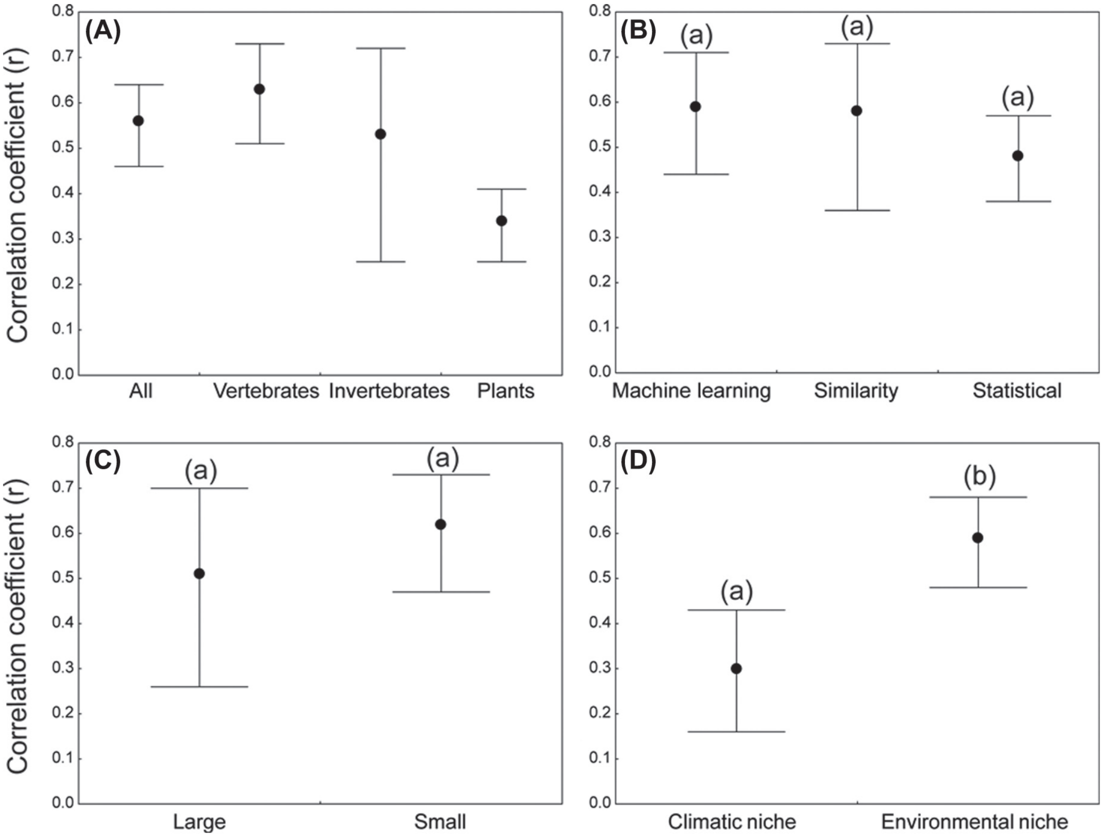

Figure 3. (A) Summary effect of the correlation coefficient (r) calculated for the AS relationship for all species (n = 450), only vertebrates (n = 166), only invertebrates (n = 133), and only plants (n = 151), (B) for the three ENM approaches [machine learning (n = 316), similarity (n = 16) and statistical modeling (n = 118)], (C) for studies carried out in large proportions of species' range (> 50%) (n = 20) and studies carried out in small proportions of species' range (< 50%) (n = 125) for mammals and birds only, and (D) for climatic niche models (n = 120) and environmental niche models (n = 330). All analyses were based on a hierarchical meta-analysis with random-effects model. Mean values (black circles) and 95% confidence intervals (vertical lines) for effect sizes are shown. Different letters in parentheses above confidence intervals indicate significant statistical difference between groups assessed with Wald test ($p < 0.05$).

there are other ecological drivers affecting plant species abundances that are more important than environmental suitability. For instance, competitive exclusion could drive individuals to less favorable areas (Cabral and Kreft 2012). For plants this is especially important because the dominant competitor once established can prevent establishment of subordinate competitor seedlings (Went 1973). Therefore, dominant plant species may generate better ecological niche models than subordinate species because occurrence patterns of dominant species may reflect their niches better than subordinate species (Elmendorf and Moore 2008). On the other hand, neutral processes, such as ecological drift, may influence species abundance rather than niche-based processes (Hubbell 2001). However, it is worth emphasizing that niche and neutral theories are complementary and not conflicting ideas to explain biodiversity patterns (Chave 2004).

## Conceptual and methodological issues underlying the AS relationship

A positive correlation between abundance and suitability can be interpreted as a consequence of the ecological niche. Abundance of a species can be partially explained as a response to local conditions (Hutchinson 1957). When environmental variables meet species requirements species attain high abundances which are generally located at the niche centroid (Maguire 1973, Martínez-Meyer et al. 2013). Furthermore, environmental suitability seems to be related to the carrying capacity of populations (Thuiller et al. 2014). Sites with high suitability tend to harbor larger populations because suitability decreases probability of extinction (Araújo et al. 2002) and increases birth and survival rates (Morrison et al. 2006). Therefore, the link between population demography and local conditions seems to be the driving force of the AS relationship.

However, exactly because of the theoretical reasons described above, we acknowledge that the AS relationship may be more complex than a simple linear relationship. For instance, VanDerWal et al. (2009) showed that suitability predicts only the upper limit of local abundance of 69 vertebrate species and that a linear model explained on average only 12% ($r = 0.35$) of the variation in abundance. Therefore, the AS relationship under some circumstances may be better described by a constraint envelope of triangular shape, which is a common form of relationship between macroecological variables (Brown and Maurer 1987, Brown 1995), whereby the highest abundance corresponds to the highest suitability. However, at higher suitability, abundance can be high or low, whereas at the lowest suitability abundance tends to be low (VanDerWal et al. 2009, Tôrres et al. 2012, Carrascal et al. 2015). Similarly, correlation between abundance and probability of use of habitat (derived from RSF) is also better described by a triangular relationship (Boyce et al. 2016). Unfortunately we were not able to analyze this triangular relationship here because we do not have access to the original data used in the papers sampled. It is not even possible to assess in which cases the AS relationships studied here are better described by a triangular pattern than by a linear correlation coefficient. But it is important to note that if a moderate correlation between abundance and suitability was found using a simple correlation coefficient, if some (or even all) of the relationships analyzed were better described by a triangular envelope, our estimates of the overall magnitude of the relationship between abundance and suitability would be conservative. For instance, if we apply a quantile-regression (Tôrres et al. 2012) to the original data to analyze the AS relationship, we would have higher values of correlations when considering the upper limit of abundance.

Thus, the origins of the triangular relationship between abundance and suitability may be in fact that we are considering only abiotic conditions (Grinnellian niche), but abundance may also be a function of species interactions (Eltonian niche), species dispersal and history (Gaston 2003, Peterson et al. 2011). Therefore, a site can be assigned as highly suitable for a species but a superior competitor or the absence of a fundamental resource may prevent the species of occurring there (leading to species absence in a favorable area) or the species may become rare under these conditions (leading to low abundance in a favorable area) preventing it from attaining high abundance. Demographically, the suitability would be more related to carrying capacity of the region and thus set the upper limit of the triangular relationship, forming a soft boundary (Thuiller et al. 2014). In addition, if in a source-sink dominated metapopulation, good breeding sites in the source are likely to be rare and poor sites in the sink more common. As a result, a large proportion of a population may occur in the sink (Pulliam 1988). Therefore, sink habitats may support higher abundance than source habitats. This situation has serious implications and could easily lead to misleading conclusions about habitat requirements of a species (Van Horne 1983, Pulliam 1988) if one implicitly assumes a positive and linear relationship between abundance and environmental suitability. Also, if samples were taken from portions of the range where the population is most dynamic (high turnover), the probability of detection is lowest (Doherty et al. 2003). Moreover, we know less about how dispersal across regional boundaries may affect population dynamics and, consequently, abundance used to correlate with suitability (Schurr et al. 2012). Furthermore, barriers may prevent a species from colonizing a suitable site, or a species may not colonize climatically suitable areas because it is recent in the phylogeny and has not had enough time to spread to most suitable sites (Weber et al. 2014).

All these hypotheses (species interactions, population dynamics, dispersal and time for colonization) may explain why a species can be rare in a suitable site. As a consequence, the generality of the AS relationship should be accepted with caution because high suitability can indicate low or high abundance. Despite this, such inconsistency may be minimized using more adequate statistical methods, e.g. quantile-regression (Cade and Noon 2003) to describe such patterns. Moreover, this triangular pattern can arise due to several methodological and sampling artifacts as well such as inadequate survey techniques, small number of presences, sampling biases, scale, or unmeasured factors.

Modelling the ecological niche over a small area within a species' range is thought to diminish the strength of the correlation between abundance and suitability (Nielsen et al. 2005) or generate a triangular relationship. However, we demonstrated here that there was no difference in the strength of the AS relationship between studies including large or small areas within species ranges. Thus, the correlation between environmental suitability and abundance holds true regardless of the proportion of a species range that is considered by a study. Nonetheless our conclusion was based on mammals and birds only. Therefore, lack of difference between niche models based on completely sampled and partially sampled geographic ranges should be viewed with caution. We suggest that comparing ENM's developed for the whole species distribution with those including small areas within species range may prove useful to better understand the effect of scale on the AS relationship.

One hindrance to evaluating the AS relationship over the whole range, or even over a large area within a species' range, is that it is expensive and time consuming. One alternative method might be to use published data on relative abundance in well sampled communities across a species' geographic range and use relative abundance to evaluate the AS relationship. This alternative would be much less time and money consuming than gathering data in the field and it seems a promising approach (Weber and Grelle 2012), especially when funding is scarce. However, researchers should be careful when using data obtained from published local communities. These data can be affected by many factors such as disturbance that can increase abundance of generalist species and decrease abundance of sensitive species, seasonal differences because abundance is subject to resources phenology (Stevens and Amarilla-Stevens 2012), and undersampling effects that can make species abundance data less reliable (Yañez-Arenas et al. 2014). After controlling for such sources of variation or including disturbance variables into models, relative abundance data can be used to test AS relationships, but the criteria used by authors should be explicitly provided.

Another effect that should be considered when using relative abundance data is species probability of detection, which influences the density of presence points across sampled sites (Jiménez-Valverde 2011). Researchers cannot be sure if the positive relationship between local abundance and suitability estimated from a well calibrated ENM is a real pattern or is just the consequence of circular reasoning (Jiménez-Valverde 2011). We suggest that if abundance data has enough variation (from sites of low to high abundance) and presence data is widespread across a species' range, this concern may be minimal and the AS relationship can be properly tested. Moreover, the inclusion of absence data and unbiased sampling data has provided better results than studies using only background or pseudo-absence data (Yañez-Arenas et al. 2014, Carrascal et al. 2015).

The three ENM methods generated suitability data that correlate positively with species abundance. Tôrres et al. (2012) suggest that similarity models, such as BIOCLIM, should be preferred over alternative methods to test the AS relationship. Similarly, Ready et al. (2010) also found that similarity methods provide better correlations between abundance and suitability than machine learning and statistical methods. However, the kind of method used to derive environmental suitability seems not to affect the strength of the AS relationship. All methods provided high summary effects for the AS correlation, but they all also exhibited wide confidence intervals. Therefore, we cannot suggest which modelling method is better for correlating suitability with species abundance since all methods showed a similar pattern. Despite a positive AS relationship regardless of the kind of modelling method used, most studies using different algorithms found a wide range of correlations between abundance and environmental suitability, ranging from no correlation to high correlation. Surprisingly no study that used more than one algorithm to derive suitability has tested what the AS relationship would be using an ensemble approach (i.e. the combination of different outputs from different algorithms). Diniz-Filho et al. (2015) analyzed the correlation between mean suitability derived from an ensemble and heterozygosity of an endemic tree species of the Cerrado (Brazil) and found no significant correlation. However, significance varied among algorithms that generated negative, near zero and positive correlations. Similar to the correlation between heterozygosity and suitability, uncertainty found in the AS relationship may also be due the methods chosen for modelling. To avoid such inconsistencies, we suggest using at least one algorithm of each modelling method to assess the AS relationship. The algorithm chosen for modelling is one of the biggest sources of uncertainty in ENMs (Araújo and New 2007, Diniz-Filho et al. 2009), thus ecologists should be aware of that and consider it when correlating species abundance with environmental suitability.

Population growth rates are affected directly by habitat conditions and limiting factors of the environment (Maguire 1973). We observed few authors explicitly justifying why they used particular environmental variables [see examples in Nielsen et al. (2005) and Van Couwenberghe et al. (2012)]. Inclusion of variables in the model should be justified, even briefly, and the selection should include only those variables that authors think affect species abundance. In addition to environmental data, researchers should also have a good understanding of variation in species density across time and space (Johnson and Seip 2008). For instance, if the samples were taken when density is very low due to seasonal variation, small number of localities with inaccurate abundance data may hide or weaken the correlation between abundance and suitability. Sampling design is crucial to properly address the AS relationship. Informed selection is not an easy task and our knowledge of species requirements is often poor (Van Horne 1983). Habitat is the main determinant of distribution and abundance for most organisms (Boyce et al. 2016). Moreover, a habitat that provides cover but no food may still be deemed climatically suitable, even though the species might not be able to persist in that habitat; such a scenario likely would generate a triangular relationship between abundance and suitability. In fact, importance of local conditions was corroborated by the fact that studies using other variables in addition to climate exhibited higher AS correlation than studies using only climate to derive suitability. Climatic niche models can be useful proxies for abundance, but environmental niche models prove to be a better proxy for species abundance than climatic niche models. There are numerous variables that influence spatial variation of abundance and climate is only a subset of these variables. Including local variables into ENM's can improve our ability to generate better proxies for species abundance. However, including large-scale variables other than climate into ENM's at large scales is still a challenge.

## Concluding remarks

For a long time the AS relationship was assumed by ecologists but lack of data on geographic patterns in abundance prevented more general tests. As such data accumulates, the relationship started to be tested for some better known species. The meta-analysis tools used here provide the opportunity to make generalization based on what we know about the AS relationship so far. Moving beyond assumptions creates an opportunity to bring new rigor to macroecology and offers new insights into fundamental ecological process (Sagarin et al. 2006) such as the AS relationship (analyzed here) and the abundant center hypothesis (Sagarin and Gaines 2002). Here we showed that suitability derived from ENM's is positively correlated with species abundance and we discussed that interaction between niche variables and population demography seems to be the mechanism that generates a positive correlation between abundance and suitability. These results suggest that occurrence data can be a reasonable proxy for abundance, especially for vertebrates. Identifying areas where species are most abundant has been an invaluable tool for designing biological reserves (Schoener 1987, Araújo and Williams 2000, Araújo et al. 2004). Therefore, since the AS relationship holds true, ENM can be used as a proxy of species abundance that is a better ecological feature for defining spatial conservation priorities than species occurrence. Applying ENM to systematic conservation planning and selecting those areas that are highly suitable for a species can be effective in protecting source populations. Furthermore, we can predict how species abundance will respond to climate change. Nevertheless, modelers and conservationists must be aware that high environmental suitability does not always indicate high abundance. This relationship can exhibit much variation, as we found in the AS correlations, and be better characterized by a triangular relationship between abundance and suitability which has been commonly found in many studies (VanDerWal et al. 2009, Tôrres et al. 2012, Gutiérrez et al. 2013, Carrascal et al. 2015, Boyce et al. 2016).

Species abundance datasets are rare because collecting such data is money and time consuming (Potts and Elith 2006). Nonetheless, since the AS relationship holds true, researchers can also use presence–absence data as a proxy of species abundance. Use of ENMs can significantly decrease survey costs and allow the study of large-scale abundance patterns using less information. It is worth emphasizing that modelling a species niche does not replace the need for abundance data at large spatial scales, but it improves our understanding of spatial variance of species abundance and reinforces the need to incorporate GIS variables other than climate when correlating environmental suitability with abundance. Although the general relationship between abundance and suitability was moderate, ENM can be used as a useful proxy of abundance, especially for vertebrates.

*Acknowledgements* – We would like to thank Cristina Araujo, Jayme Prevedello, Lorelei E. Patrick, Maria Lucia Lorini, Marinez Siqueira, and Renato Crouzeilles for valorous suggestions that improved the earlier version of this manuscript. We also would like to thank the three referees that carefully read our manuscript. CAPES and CNPq for scholarships to Marcelo M. Weber, and CNPq for Productivity fellowship to Carlos E. V. Grelle. Funding was provided by FAPERJ (Jovem Cientista do Estado) and Rede Clima program/MCT.

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