

# ECOGRAPHY

## Research

### Predicting species abundance by implementing the ecological niche theory

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#### Ecography

44: 1–8, 2021

doi: 10.1111/ecog.05776

Subject Editor and  
Editor-in-Chief: Miguel Araújo  
Accepted 31 August 2021



Species are not uniformly distributed across the landscape. For every species, there should be few favoured sites where abundance is high and many other sites of lower suitability where abundance is low. Consequently, local abundance could be thought of as a natural expression of species response to local conditions. The correlation between abundance and environmental suitability has been well documented, and a recent meta-analysis has suggested that this relationship could be a generality. Despite the importance and potential implication of the abundance–suitability relationship, its predictive power for meaningful extrapolations has been surprisingly poorly explored. In this study, we showed how a highly predictable trend can be extracted from the abundance–suitability relationship, accurately predicting the variation in species abundance at a high spatial resolution. We produced high-quality environmental suitability estimations for 50 endemic species in the Australian Wet Tropics. Environmental suitability derived from species distribution models was related to observed abundance estimated using data from 29 years of uninterrupted monitoring effort. We used the fitted relationship to accurately predict abundance at a fine scale across the species range. Our results showed that the abundance–suitability relationship was strong for endemic species in the Australian Wet Tropics. The predictive power of our models was high, explaining, on average, 55% of the deviance across taxa. Despite inter-specific variation in the strength of the abundance–suitability relationship associated with potential intrinsic estimation biases, our approach provides a powerful tool for predicting abundance across the species range at a fine scale. The potential for robust abundance predictions from occurrence-based species distribution models shown in this study are numerous, and it could have a significant impact in enhancing species conservation and management decisions.

Keywords: abundance prediction, abundance–suitability relationship, niche theory, species distribution models, tropical rainforest



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#### Introduction

A widely held belief in biogeographical ecology is that local abundance reflects how well a particular site meets the needs of a species along many ecological axes

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(Hutchinson 1957, Brown 1984, Holt 2009). This concept is a natural extension of niche theory, formally proposed by G. E. Hutchinson in a seminal essay more than 60 years ago (Hutchinson 1957). The response of a species to local conditions could thus be measured as local abundance, with more favourable sites containing a greater proportion of the species population (Brown 1984).

Unravelling the ecological and environmental conditions that favour species persistence across their range is a central goal in ecology. Indeed, understanding the relationship between species and the environment could provide invaluable insights into forecasting species responses to climate change (VanDerWal et al. 2009) or predicting biological invasions (Kulhanek et al. 2011). However, estimating abundance from species distributions remains an unsolved problem (He and Gaston 2007).

A range of algorithms have been developed to forecast species distributions. These techniques, better known as ecological niche models (Peterson and Soberón 2012), use occurrence data to estimate environmental suitability as a function of ecological and environmental predictors (Hijmans and Graham 2006). The underlying mechanism that determines species occurrence is based on population demography, as presences and absences represent positive and negative population growth rates, respectively (Gaston 2003, Thuiller et al. 2014). In this respect, areas with higher environmental suitability should also have larger populations and vice versa. This hypothesis has been called the abundance–suitability relationship, which states that environmental suitability derived from ecological niche models should explain the spatial variation in abundance over a species’ geographical range (Weber et al. 2017). While evidence suggests that the abundance–suitability relationship could be a generality (Weber et al. 2017), several studies failed to detect an effect (Nielsen et al. 2005, Jiménez-Valverde et al. 2009, Filz et al. 2013, Dallas and Hastings 2018), questioning the ubiquity of this relationship (Dallas and Hastings 2018).

Several factors may explain the weak abundance–suitability relationship in some studies (Estrada and Arroyo 2012). Environmental suitability predictions may be affected by the scale at which occurrence and abundance are measured (Nielsen et al. 2005), and a lack of information about the entire range of a species may increase the probability of biases in sampling species abundance (Martínez-Meyer et al. 2013). Other potential methodological issues could be related to differences in modelling techniques and the appropriate selection of the set of predictors used to model environmental suitability (Weber et al. 2017). Alternatively, intrinsic species factors that may affect the estimation of abundance and/or distribution could also influence the strength of the relationship (Dallas and Hastings 2018). Among these factors, species detectability (Jiménez-Valverde 2011), availability of biological-relevant occurrences (Carrascal et al. 2017) and species interaction (Braz et al. 2020) could play a major role at estimating species habitat suitability.

Previous research in the Australian Wet Tropics (AWT) found a positive correlation between abundance and

environmental suitability (VanDerWal et al. 2009). Yet, the power of prediction reported in the study was low (linear models explained on average only 12% of the variation in abundance), arguing that the relationship could only predict the upper limit of abundance due to the likelihood of important missing niche parameters at any given local site (VanDerWal et al. 2009, Weber et al. 2017). The relationship between environmental suitability and the upper limit of abundance may be valuable when the goal is to make inferences at a broad spatial scale, without the necessity of determining abundance in all places. However, more detailed information at a finer scale is required (e.g. when planning species reintroductions), and an improvement in our models’ predictive power is crucial for meaningful extrapolation of abundance information from modelled environmental suitability (Carrascal et al. 2015).

Here, we show that population abundance can be accurately predicted at a fine scale as a function of environmental suitability derived from ecological niche models. Due to the unavoidable triangularity of the abundance–suitability relationship derived from ecological niche models (Jiménez-Valverde et al. 2021), we do not attempt to infer a precise measure of local abundance but instead produce a precise measure of the spatial variation in population size given the parameters that conform to species’ environmental niches. To achieve this, we produced high-quality environmental suitability predictions using ensemble ecological niche models for 50 endemic species in the AWT. We then examined the degree, sign and significance of the relationship between observed abundance and environmental suitability. We addressed the non-linear nature of the abundance–suitability relationship by fitting general additive models (GAMs) using a Tweedie distribution. Lastly, we explored the potential for the abundance–suitability relationships to be influenced by species traits and sample size.

## Material and methods

### Study system

The AWT is one of the best-studied tropical rainforests worldwide (Williams 2006, VanDerWal et al. 2009). Long-term biodiversity monitoring has been conducted uninterruptedly since 1992, with approximately 11 650 independent surveys conducted across the region. Survey sites were established within large continuous patches of rainforest (Fig. 1). The monitoring of birds, lizards and frogs was conducted at independent points within the study sites, separated by a minimum distance of 0.25 km, while mammal surveys consisted of a one-kilometre-long line transect at each site ( $n = 121$ ). Following VanDerWal et al. (2009), we calculated local abundance using the average relative abundance of each species derived from multiple count surveys at each location. Only independent surveys using identical standardised methodology were considered, and abundance was calculated for locations with a minimum of three independent replicates. A

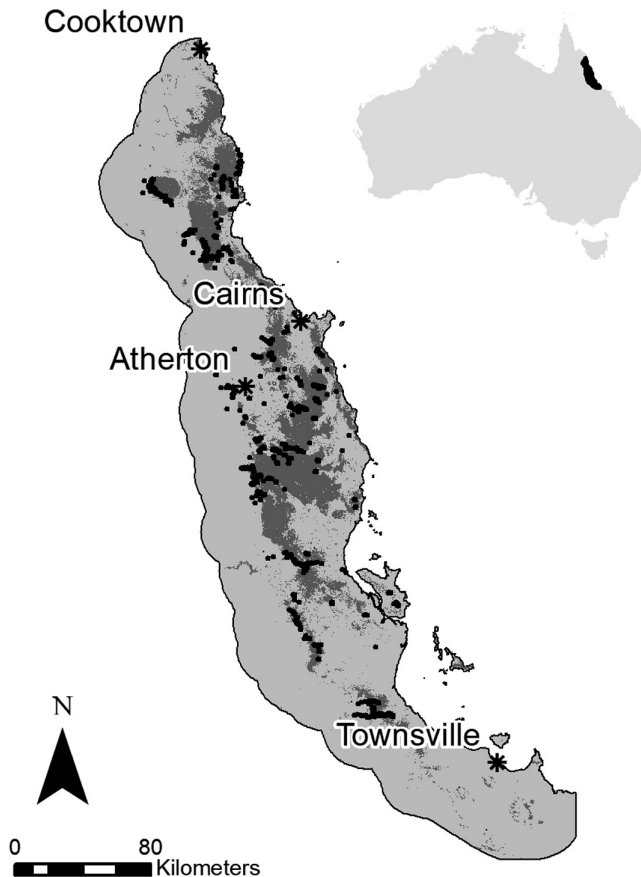


Figure 1. The Australian Wet Tropics bioregion and its location in Australia. Rainforest coverage is shown as dark grey. Survey sites are depicted as black dots and main towns as black asterisks.

detailed protocol for species sampling methodology for abundance calculation can be found in VanDerWal et al. (2009).

Among all vertebrates monitored, 76 species are regionally endemic (Williams et al. 2010). Only regionally endemic species were included in this study to ensure that the environmental suitability predicted by ecological niche models included the species' entire range. Further, we discarded species that were not detected in standardised surveys and whose information was only obtained from opportunistic encounters, as we could not reliably estimate local abundance or determine whether the occurrences were of biological relevance, respectively. Species with sufficient abundance and occurrence information available for analyses included 12 birds, 21 frogs, 4 mammals and 13 reptile species (Supporting information). A detailed description of species traits and distributions can be found in Williams et al. (2010).

Species occurrences were derived from a standardised sampling protocol (Fig. 1). Absence was defined in those locations where a given species was not detected after a minimum of 10 survey replicates. Presences and absences for each species were spatially thinned to reduce potential sampling bias. The spatial thinning was implemented using a minimum nearest neighbour distance algorithm with 1000 iterations, retaining

the dataset with the greatest number of records. We used a thinning distance of 0.25 km, which is the minimum distance between point sampling locations. Spatial thinning was implemented using the 'thin' function within the 'spThin' R package (Aiello-Lammens et al. 2015). Because of the reduced number of true absences in the dataset, we additionally included 7000 background points in the analyses. These background points or pseudo-absences were implemented using the 'disk' strategy, with a minimum distance of 1 km to the closest occurrence, which is the minimum distance between study sites. This approach was selected to avoid the pseudo-absences being too close (avoid pseudo-replication) or too far from the occurrences (localised sampling strategy) (Thuiller et al. 2013).

### Predictor variables

We selected 28 potential variables to predict environmental suitability at 30 arc-second resolution ( $\sim 1 \text{ km}^2$ ). These variables represented climate, topography, soil characteristics, fragmentation, forest structure and ecosystem productivity (Supporting information). Additionally, we provide the methods used to develop precipitation and maximum and minimum temperature seasonality variables in the Supporting information.

Some predictors are likely to show a strong covariation, causing instability in parameter estimation (Dormann et al. 2013). We used the variance inflation factor (VIF) to detect collinearity (Naimi et al. 2014). We found pairs of variables that had the maximum linear correlation (greater than a correlation threshold of 0.7) and excluded the one with the larger VIF. The process was repeated until no pair of variables with a high correlation coefficient remained. This stepwise variable selection was implemented using the 'vifstep' function in the 'usdm' R package (Naimi 2015).

### Ensemble distribution models and environmental suitability estimation

We determined environmental suitability for each species across their entire biogeographical range by training nine different algorithms. Algorithms included surface range envelop, classification tree analysis, random forest, multivariate adaptive regression spline, flexible discriminant analysis, MaxEnt, generalised additive models, generalised boosted regression and artificial neural networks.

We used 'biomod2' R package (Thuiller et al. 2013), as it offers a streamlined framework for building ensemble ecological niche models. Ensemble forecasting or consensus methods have been proved to be an efficient approach to model species ecological niche for a diverse range of species (Marmion et al. 2009), as identifying an appropriate species-specific model selection is usually not straightforward (Elith and Graham 2009). We selected default model tunings within 'biomod2' (Hao et al. 2019) to be consistent with other studies and optimise ensemble modelling performance

(Hao et al. 2020). We used 80% of the data for each species as training data and 20% as model evaluation. This random data split ratio was iterated three times for each algorithm, resulting in a total of 27 models for each species, allowing us to account for intra- and interspecific variation among algorithms (Supporting information). We constructed the ensemble models using the weighted average of individual high-performance models, determined by a quality threshold of true skill statistic (TSS)=0.7 (Allouche et al. 2006). The weights were awarded for each method in proportion to their evaluation scores.

### Abundance–suitability relationship

Empirical population estimates were related to model-predicted environmental suitability using generalised additive models (GAMs). Models were fitted using a Tweedie distribution and a log-link function. A Tweedie distribution was chosen due to the increasing tendency of abundance to be high when environmental suitability reaches high values while presenting a cluster of zeroes when environmental suitability is low (Weber et al. 2017, Jiménez-Valverde et al. 2021). We fitted GAMs using the ‘mgcv’ R package (Wood 2017).

We reported the predictive power of the fit between observed abundance and predicted environmental suitability as the deviance explained by the model. Spearman rank correlation coefficients ( $\rho$ ) were used to quantify the abundance–environmental suitability relationship in terms of degree, sign and significance. We applied a false discovery rate method (Benjamini and Hochberg 1995) to adjust our significance rate for multiple testing.

### The effect of species potential dispersal, sample size, taxa and body mass on the abundance–suitability relationship

The strength of the abundance–suitability relationship may be associated with the accuracy of the estimation of both abundance and distribution. Thus, factors that strongly influence our ability to reliably estimate these parameters, such as species detectability (Jiménez-Valverde 2011, Johnston et al. 2014), could lead to mixed results when different taxa are examined (Dallas and Hastings 2018). To examine the potential influence of intrinsic biases in estimating species abundance and/or distribution, we related the abundance–suitability correlation coefficients ( $\rho$ ) to species body size, sample size, species potential dispersal and taxa (Williams et al. 2010) using multiple linear regression analysis. We expected that species with lower body size, lower potential dispersal and species with a smaller sample size would show a weaker abundance–suitability relationship, as these factors would reduce our ability to detect species, the ability of species to occupy all potentially suitable habitats and the quality of the data used to model the relationship, respectively.

All analyses were performed in R, ver. 4.0 (<www.r-project.org>).

## Results

Overall, trained ensemble ecological niche models performed well (TSS  $\pm$  SD=0.91  $\pm$  0.06; Supporting information). Models accurately captured species presence (sensitivity  $\pm$  SD=97  $\pm$  3%) and absence (specificity  $\pm$  SD=94  $\pm$  4%) as a function of our predictors (Supporting information). The relationship between observed abundance and environmental suitability derived from ecological niche models was strong across endemic species in the AWT ( $\rho \pm$  SD=0.58  $\pm$  0.14; Fig. 2a). Moreover, the spatial variation in observed abundance was largely explained by modelled environmental suitability (deviance explained  $\pm$  SD=0.55  $\pm$  0.23; Fig. 2b), accurately predicting abundance across the species’ geographical range. The significance and sign of the abundance–suitability relationship were consistent across the vertebrate taxa examined (Fig. 2c, Supporting information). Mammals showed the highest consistency, presenting on average the greatest predictive power and strength of the relationship. On the other hand, reptiles and frogs exhibited the largest inter-specific variation, with deviance explained ranging from 10 to >95%. Birds systematically showed a stronger abundance–suitability relationship than frogs and reptiles, but they presented the lowest predictive power on average (Fig. 2c).

Multiple linear regressions allowed us to measure the influence of species traits on the abundance–suitability relationship. The initial model containing the number of occurrences, species potential dispersal, taxa and species mass run into multicollinearity issues, and the variable ‘taxa’ was removed due to its high VIF (VIF=10.73). Stepwise model selection by AIC removed the variable ‘species mass’, considerably improving model performance. The best-performing model fit the inter-specific variation in the abundance–suitability relationship as a function of the number of occurrences and potential dispersal predictors ( $F_{2,47} = 7.392$ ;  $R^2 = 0.21$ ; p-value=0.002; Table 1). Although both predictors showed a positive correlation with the abundance–suitability relationship as expected, only the effect of species potential dispersal showed a statistical significance (Table 1), suggesting that species with a higher dispersal capacity showed a stronger abundance–suitability relationship.

## Discussion

In this study, we have shown that the spatial variation in species abundance can be accurately predicted at high-resolution using niche theory. Our results showed a consistently strong positive correlation between species abundance and environmental suitability derived from correlative ecological niche models. However, the strength of the abundance–suitability relationship may be affected by intrinsic species traits, highlighting potential biases in estimating species abundance and distribution.

Our findings support the hypothesis that local abundance is a reflection of how species respond to local conditions (Brown 1984), which is a direct consequence of species’



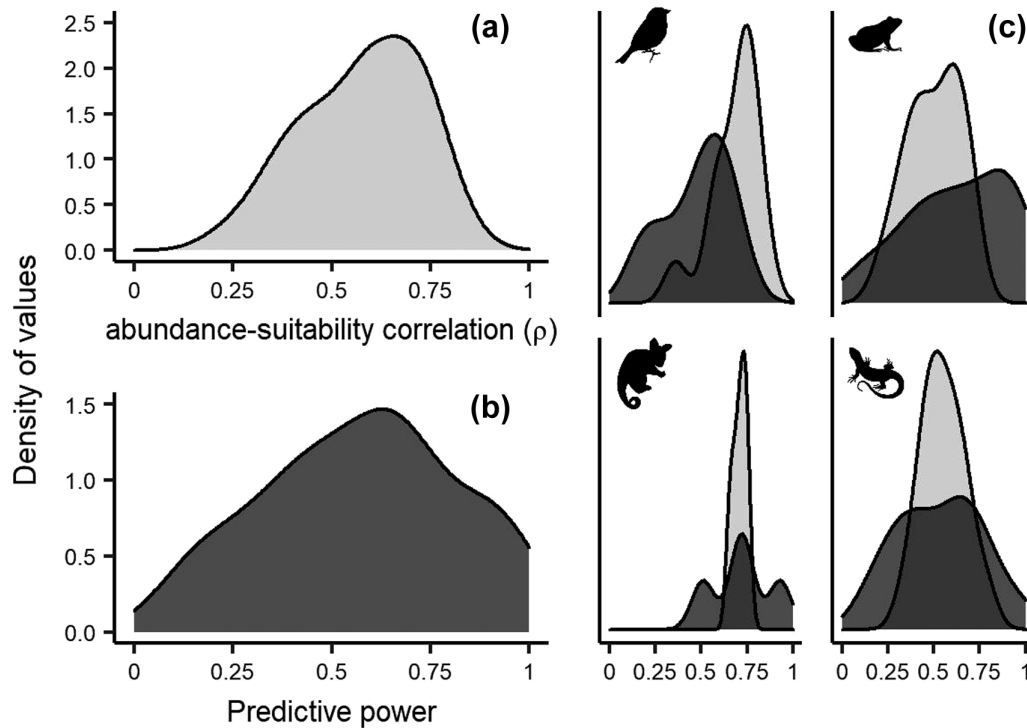


Figure 2. Relationship between species abundance and environmental suitability across 50 endemic vertebrates in the Australian Wet Tropics. Panel (a) shows the degree of correlation between abundance and suitability, estimated using Spearman rank correlation. Panel (b) shows the predictive power of the relationship, measured as the deviance explained by the models. Panel (c) shows an examination of the consistency of the abundance-suitability relationship across taxa.

ecological niche (Hutchinson 1957). Habitats with higher suitability tend to hold a greater proportion of a species population (Weber et al. 2017). The link between demography and local conditions should be a natural result from the decrease in the probability of extinction (Araújo et al. 2002) and an increase in birth and survival rates in high-quality habitats (Bock and Jones 2004, Morrison et al. 2012).

### The effect of covariates in the abundance–suitability relationship

The strength of the abundance–suitability relationship may be influenced by our capacity to accurately determine both species abundance and distribution (Jiménez-Valverde 2011, Weber et al. 2017, Jiménez-Valverde et al. 2021). Likewise, the estimation of these parameters could be inherently affected by species detectability (Seoane et al. 2005, Jiménez-Valverde 2011). The accurate estimation of abundance and suitability could thus present challenges for elusive species (Seoane et al. 2005, Aubry et al. 2017), for which a large sampling effort is often required (Price and Endo 1989).

Our findings showed that, in accordance with our expectations, the abundance–suitability relationship was weaker for species with smaller sample sizes. However, the effect of species’ sample size was not strong enough to show statistical significance (Table 1). Alternatively, physical boundaries and species dispersal limitations could promote higher abundance in climatically unsuitable environments or depress abundance in some otherwise suitable areas (VanDerWal et al. 2009), which could potentially produce near-zero correlations between abundance and suitability (Dallas and Hastings 2018). The effect of dispersal limitation on the abundance–suitability relationship was reflected in our results. We found that species with a more limited dispersal capacity may present a weaker abundance–suitability relationship. These results may reflect the lower data quality for frogs and reptiles species in our study. The higher uncertainty in the abundance–suitability relationship for these taxa could be explained by sampling biases related to the high dependence on weather conditions for the detectability of tropical ectotherms and their inherent dispersal limitations (Williams et al. 2010).

### Prediction of the spatial variation in abundance

Previous research has shown that the abundance–suitability relationship could be described by a wedge or triangular shape. Given the anatomy of this relationship, at higher suitability, abundance can be high or low, whereas at the lowest suitability, abundance is predominantly low (VanDerWal et al. 2009,

Table 1. Multiple linear regression models on covariates related to the abundance–suitability relationship in the Australian Wet Tropics.

Coefficients	Slope $\pm$ SD	t-value	p-value
Intercept	0.346 $\pm$ 0.08	4.258	0.00010
Log(occurrences)	0.032 $\pm$ 0.020	1.586	0.12
Potential dispersal	0.044 $\pm$ 0.021	2.08	0.043

Jiménez-Valverde 2011, Tòrres et al. 2012, Carrascal et al. 2015, Acevedo et al. 2017, Lunghi et al. 2018, Braz et al. 2020, Jiménez-Valverde et al. 2021). The origin of this triangular relationship could be assumed to be related to difficulties in reliably estimating environmental suitability, as abiotic conditions alone are often not enough to accurately discriminate high-quality habitats (Guisan and Thuiller 2005). Biotic components, such as species interactions, could potentially influence species distribution (Giannini et al. 2013, Wisz et al. 2013) and spatial variation in abundance (Gaston 2003, Peterson et al. 2011, Braz et al. 2020). However, biotic information is usually scarce at a large spatial scale and therefore often not explicitly included in ecological niche models.

To what extent can we reliably estimate species abundance as a function of environmental suitability derived from ecological niche models using only abiotic information? Our findings showed that, despite the greater variation in abundance when suitability is high (Supporting information), a highly predictable trend can be extracted from the relationship. Furthermore, we found that using a more suitable set of predictors and a more flexible approach to fitting the non-linear relationship between abundance and suitability can yield a substantially higher predictive power and accuracy than previously reported (Fig. 2, Supporting information) (VanDerWal et al. 2009).

Our study shows the importance of using biologically relevant predictors that potentially shape species populations and distribution. In contrast to VanDerWal et al. (2009), we developed targeted spatial variables based on known limiting factors for endemic vertebrates in the AWT. For example, a measure of length and intensity of thermal seasonality was included (Supporting information), which is sensible given the role of thermal physiological limitation on the distributional range of tropical montane vertebrates (Krockenberger et al. 2012). We also showed the importance of considering different algorithms to model ecological niches for a range of species from different taxa. For example, Maxent, the algorithm used by VanDerWal et al. (2009), showed marked limitations when modelling the niche of some species (Supporting information). These limitations were not observed for ensemble models in our results. In addition to providing a more accurate approximation of species habitat suitability than in previous studies, we modelled the predictive power of the abundance–suitability relationship accounting for the non-linear structure of the correlation, which allowed greater flexibility when predicting abundance for a set of species across taxa. In summary, our approach aimed to reduce the inherent triangularity nature of the abundance–suitability relationship, which resulted in a five-fold increase in prediction power compared to previous studies (VanDerWal et al. 2009).

The potential for robust abundance predictions from occurrence-based ecological niche models shown in this study could have numerous meaningful ecological and conservation applications. Many management plans and threatened species evaluations rely on abundance data to

detect significant population changes in space and time. However, abundance data is scarce, limiting our capacity to understand ecological patterns at a population level. In this regard, the extrapolation of accurate abundance information derived from modelled environmental suitability shown here could provide invaluable insights into how species experience the landscape. For example, when information is limited, accurate predictions of population size in different habitats could be crucial when planning reintroductions (Malone et al. 2018) or identifying priority conservation areas (Wilson et al. 2011). Additionally, understanding how species respond to local conditions could have broad implications for conservation biology, and it could be used to predict the impact of invasive species (Kulhanek et al. 2011) or to estimate the potential impact of climate change on species distribution and abundance (VanDerWal et al. 2009).

*Acknowledgements* – The authors would like to thank James Cook University, Skyrail Foundation, Abiculture, Queensland Department of Environment and Science, Wet Tropics Management Authority, Earthwatch Institute, Rainforest-CRC, Marine and Tropical Research Facility and the National Environmental Research Program for funding support. The authors would also like to thank the many volunteers, students and assistants who have contributed to the fieldwork over the years. Lastly, the authors would like to thank Dr Juan Mula and Tom Bruce for their help in the development of some of the predictor layers used in this study.

*Funding* – James Cook University, Queensland Department of Environment and Science, Wet Tropics Management Authority, Earthwatch Institute, Rainforest-CRC, Marine and Tropical Research Facility and the National Environmental Research Program have funded the long-term vertebrate monitoring project at different stages during the past 29 years.

## Author contributions

**Alejandro de la Fuente:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal); Methodology (lead); Project administration (lead); Resources (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Ben Hirsch:** Conceptualization (supporting); Investigation (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Lucas Cernusak:** Conceptualization (supporting); Investigation (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Stephen Williams:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (equal); Resources (lead); Supervision (lead); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

## Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/ecog.05776>>.

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.0zpc866wv>> (de la Fuente et al. 2021).

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