

 Open access • Journal Article • DOI:10.1086/600087

## **Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance** — [Source link](#)

[Jeremy VanDerWal](#), [Luke P. Shoo](#), [Christopher N. Johnson](#), [Stephen E. Williams](#)

**Institutions:** [James Cook University](#)

**Published on:** 01 Aug 2009 - [The American Naturalist](#) (University of Chicago Press)

**Topics:** [Relative abundance distribution](#), [Occupancy–abundance relationship](#), [Abundance \(ecology\)](#), [Rank abundance curve](#) and [Relative species abundance](#)

Related papers:

- [Maximum entropy modeling of species geographic distributions](#)
- [Novel methods improve prediction of species' distributions from occurrence data](#)
- [Very high resolution interpolated climate surfaces for global land areas.](#)
- [Species Distribution Models: Ecological Explanation and Prediction Across Space and Time](#)
- [Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/abundance-and-the-environmental-niche-environmental-4h9016shax>



CHICAGO JOURNALS



The University of Chicago

---

Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance.

Author(s): Jeremy VanDerWal, Luke P. Shoo, Christopher N. Johnson, and Stephen E. Williams

Source: *The American Naturalist*, Vol. 174, No. 2 (August 2009), pp. 282-291

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/600087>

Accessed: 06/10/2015 22:10

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



*The University of Chicago Press, The American Society of Naturalists, The University of Chicago* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

# Abundance and the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts the Upper Limit of Local Abundance

Jeremy VanDerWal,\* Luke P. Shoo, Christopher N. Johnson, and Stephen E. Williams

Centre for Tropical Biodiversity and Climate Change, School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia

Submitted June 6, 2008; Accepted February 20, 2009; Electronically published June 11, 2009

Online enhancements: appendixes.

**ABSTRACT:** Ecologists seek to understand patterns of distribution and abundance of species. Studies of distribution often use occurrence data to build models of the environmental niche of a species. Environmental suitability (ES) derived from such models may be used to predict the potential distributions of species. The ability of such models to predict spatial patterns in abundance is unknown; we argue that there should be a positive relationship between ES and local abundance. This will be so if ES reflects how well the species' physiological and ecological requirements are met at a site and if those factors also determine local abundance. However, the presence of other factors may indicate that potential abundance is not attained at all sites. Therefore, ES should predict the upper limit of abundance, and the observed relationship with ES should be wedge shaped. We tested the relationship of ES with local abundance for 69 rain forest vertebrates in the Australian wet tropics. Ordinary least squares and quantile regressions revealed a positive relationship between ES and local abundance for most species (>84%). The relationships for these species were wedge shaped. We conclude that ES modeled from presence-only data provides useful information on spatial patterns of abundance, and we discuss implications of this in addressing important problems in ecology.

**Keywords:** abundance, conservation biology, distribution of abundance, ecological niche model, environmental suitability, presence-only model.

## Introduction

Knowledge of patterns of distribution and abundance of species is fundamental to ecology. A large body of work on species-distribution patterns uses predictive habitat models to derive estimates of the environmental suitability for a species across available sites within an area of interest and, thus, to infer likelihood of occurrence. Models can

be as simple as correlations between occurrence data (i.e., locations where a species has been observed) and climatic variables or as complex as mechanistic relationships between the physiology of an organism and its surrounding environment (Elith et al. 2006; Kearney 2006). Either way, estimates of environmental suitability can be used to map potential geographic ranges, and they can be applied to predict many aspects of distribution such as the location of new populations of species in poorly known areas (e.g., guided search effort; Fleishman et al. 2003; Raxworthy et al. 2003; Bourg et al. 2005; Guisan et al. 2006), patterns of occupancy beyond the native range for invasive species (Thuiller et al. 2005; Steiner et al. 2008), and occupancy in different time periods (e.g., distributional shifts under climate change; Araújo et al. 2005; VanDerWal et al. 2009a) or absence from some environments (e.g., ecophysiological constraints; Kearney and Porter 2004).

Distributions of many species may be predicted using basic occurrence data and models of environmental suitability. However, data on spatial variation in abundance within a species' distribution are much more difficult to obtain, and prediction of patterns of spatial abundance remains elusive for most taxa (Sagarin et al. 2006). Abundance is often highly variable among sites within the distribution of a species, typically being high in relatively few sites and low in the majority (Murphy et al. 2006). Sites with high abundance may be clustered in the core of the distribution range, while those with low abundance are more widely distributed around the margins (e.g., Brown 1984), but this pattern does not always hold (e.g., Sagarin and Gaines 2002; Sagarin et al. 2006). For very few species are there data available on local abundance and its correlates from a large enough number of sites to produce models that are able to predict abundance in the way that presence-only models can be used to predict distributions.

It is possible that models of environmental suitability derived from occurrence data could also capture infor-

\* Corresponding author; e-mail: jvanderwal@gmail.com.

mation on spatial variation in abundance. Presence-only ecological niche models make predictions of varying degrees of environmental suitability, from low to high, for any given site, and these are taken to indicate likelihood of occurrence of the species at that site. In general, these models estimate the environmental conditions suitable for species by associating occurrence records with a suite of environmental variables that could reasonably be expected to influence a species' persistence. The approach assumes that such correlative associations provide useful information on the species' environmental requirements. Therefore, the predicted environmental suitability should represent how well the physiological and ecological requirements of a species are met at the site. If these factors also influence abundance (e.g., through physiological and resource constraints on establishment, survivorship, and reproduction), it follows that sites with high environmental suitability will support populations at high abundance.

To our knowledge, the relationship between local abundance and environmental suitability predicted from presence-only data has not been properly investigated. This is despite the fact that some authors have recognized that such a relationship should exist, and they have advocated the use of abundance data as a means to test the accuracy of distribution models (Lobo et al. 2008). Several studies have used presence-absence data and rank correlations of abundance to test for a relationship with environmental suitability (e.g., Pearce and Ferrier 2001; Nielsen et al. 2005). Statistically significant relationships were found for only some species, suggesting low generality and a limited utility of environmental suitability as a predictor of spatial patterns of abundance. However, it is unclear whether outcomes of such analyses would be improved if more comprehensive, continuous abundance data were used.

We hypothesize that relationships between environmental suitability predicted from presence-only ecological niche models and local abundance should be generally positive but that environmental suitability should predict the upper limit of abundance better than mean abundance. This form of relationship is predicted because correlative models of environmental suitability ignore factors such as dispersal capabilities, biotic interactions, microenvironment suitability, and stochastic effects that could result in the species being absent or uncommon at sites that otherwise have high environmental suitability. If this were often the case, the positive relationship between predicted environmental suitability and abundance may in fact be polygonal or wedge shaped. Such limiting relationships have been found between biomass and other environmental suitability indices (e.g., Schroeder and Vangilder 1997), abundance and body-size relationships in macroecology (e.g., Blackburn et al. 1992; Blackburn and Gaston 1998), density and environmental variables (Vaz et al.

2008), competitive interactions between species (Johnson and VanDerWal 2009), and patterns of body size between predators and prey (e.g., Scharf et al. 1998).

Here we provide a direct test of the hypothesis that environmental suitability predicts species abundance patterns, in particular, the upper limits of abundance. We used occurrence records for 69 species of rain forest vertebrates from the Australian wet tropics (AWT) and an ecological niche modeling program, Maxent (Phillips et al. 2006), to generate predictions of environmental suitability. We then regressed predicted environmental suitability against empirical estimates of abundance from many standardized abundance surveys using ordinary least squares (OLS) and quantile regressions to explore the mean and upper limits of the relationship.

### Methods

We utilized a maximum-entropy algorithm (Maxent; Phillips et al. 2006) to model the environmental suitability of the AWT for 69 vertebrate species (table A1 in the online edition of the *American Naturalist*). The AWT is an ~80-km-wide strip of land along the coast of northeast Australia, between  $-16.5^{\circ}\text{N}$  and  $-19.5^{\circ}\text{N}$  (fig. 1; for further description, see Nix 1991; Williams et al. 1996). It is a discrete biogeographical region encompassing a chain of tropical and subtropical rain forests surrounded by drier and warmer environments (Nix 1991; Moritz 2005). A long history of rain forest expansions and contractions has created an assemblage of species with high levels of endemism (Williams and Pearson 1997). The AWT is one of the best-studied tropical rain forests worldwide (Williams 2006). Species for which sufficient abundance and occurrence information were available for this analysis included 59 bird, four frog, and six reptile species (see table A1 for a full list of species used).

Maxent is a novel approach to ecological niche modeling that has been shown to outperform other algorithms or techniques traditionally used in this type of study (Elith et al. 2006; Hernandez et al. 2006) and is relatively insensitive to the number of occurrences used (Hernandez et al. 2006; Wisz et al. 2008). Environmental suitability is estimated as a function of the environmental variables for each cell within a gridded domain. Maxent requires presence records only, incorporates interaction effects of environmental variables, and is a deterministic algorithm, meaning that results always converge to a unique, optimal probability distribution (Phillips et al. 2006).

The ecological niche models were created using species occurrence data and environmental data that included climatic and vegetation information. Occurrence data were collected during intensive field surveys, but they were primarily sourced from extensive incidental observations and

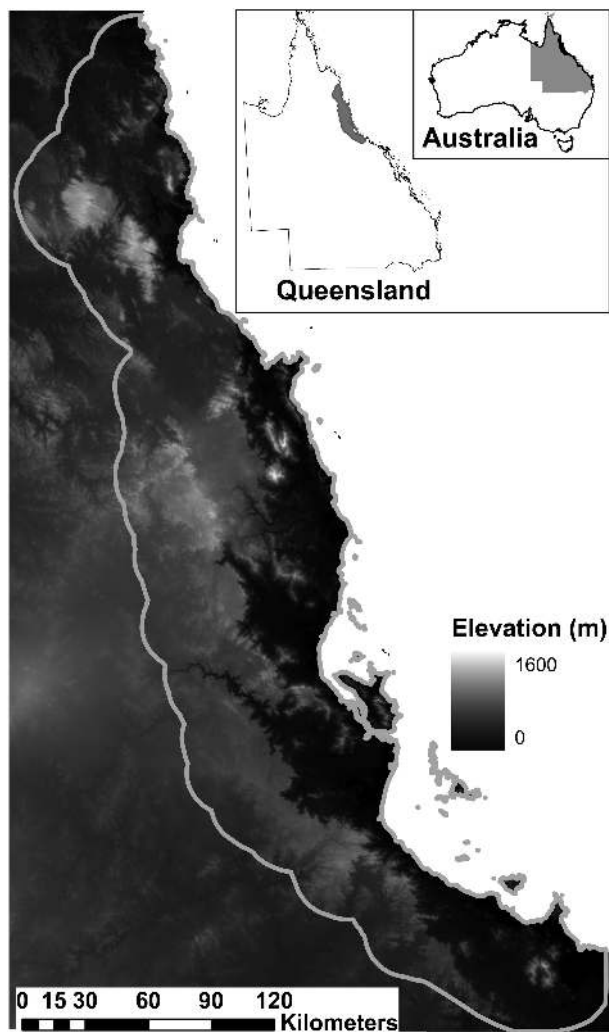


Figure 1: Australian wet tropics region. The analysis region is shown outlined on the digital elevation model and then inset within Queensland and ultimately inset within Australia.

independent data collated from the literature and from institutional databases (as per Williams 2006). We used only geographically unique occurrences (a single occurrence despite the number of records at a location) so that predicted environmental suitability (i.e., likelihood of occurrence) was not unduly biased toward areas of higher abundance in the presence-only models. Climatic data included annual mean temperature, temperature seasonality, maximum temperature of the warmest week, coldest temperature of the coldest week, annual precipitation, precipitation seasonality, precipitation of the driest quarter, and precipitation of the wettest quarter, all of which were derived using the Anuclim 5.1 software (McMahon et al. 1995) and an 80-m-resolution digital elevation model

(DEM; resampled from GEODATA 9-Second DEM, ver. 2; Geoscience Australia, <http://www.ga.gov.au/>). The vegetation data consisted of floristically classified broad vegetation groups (at a resolution of 1 : 2 million; Accad et al. 2006).

Models were trained using geographically unique occurrence data and either ~36,000 background points from a 1-km grid placed over the AWT region or a taxon-specific target group background. This dual approach was adopted because we recognized that sampling effort in our data set was more concentrated in rain forest habitats. This sampling bias has implications for modeling generalist species whose habitats extend beyond the rain forest because of the possibility that environmental suitability will be down-weighted at sites that occur outside the rain forest. To remedy this problem, we employed the target group background method recommended by Phillips and Dudik (2008) to model this subset of generalist species ( $n = 17$ ). For the more specialized species ( $n = 52$ ) that almost entirely used rain forests as their habitats, we used a standard grid consisting of ~36,000 background points to relate available habitat and occurrence data.

Models were then projected at an 80-m resolution onto the spatial layers representing the study area. Maxent produces spatial predictions of environmental suitability from 0 (not suitable) to 1 (most suitable). These values were regressed against estimates of abundance from surveys. To avoid artificially inflating the number of zero-abundance estimates with low predicted environmental suitability, only abundance estimates that fell within the species potential distribution (as defined by a threshold that minimized a combination of training omission rate, cumulative threshold, and the fraction of predicted area) were used. This threshold is automatically reported by Maxent, has been used in other studies (e.g., Prates-Clark et al. 2008; Steiner et al. 2008), and has been found to produce realistic predictions of current distribution as validated by expert opinion (S. E. Williams, Y. M. Williams, L. P. Shoo, and C. Moritz, personal communication).

Species abundance data were derived from many field surveys conducted since 1992 using standardized methods appropriate to different taxa and were compiled in a database maintained by the Centre for Tropical Biodiversity and Climate Change at James Cook University, Townsville, Australia (S. E. Williams, unpublished data). Birds were sampled during dawn surveys that consisted of 30-min, 150-m transects through the forest using both visual observations and calls to identify species ( $n = 59$  species, 1,323 surveys). Amphibians were sampled using either a slow-paced walk (~10-min duration) along a 50-m transect, with counts made of number of individuals calling within 10 m of either side of the transect ( $n = 3$  Microhylidae frog species, 731 surveys), or 200-m visual and



acoustic surveys along rain forest streams ( $n = 1$  stream frog species, 125 surveys). Reptiles were counted during 1 person-hour of active searching of the forest floor and vegetation, as well as shelter sites, such as under logs ( $n = 6$  species, 1,142 surveys). Full details of survey methods are documented in appendix B in the online edition of the *American Naturalist*. For our analysis we used estimates of abundance only from locations that were surveyed two or more times. Multiple counts were reduced to a single value for each location by taking a mean of estimates, in order to reduce the number of extreme-abundance and zero-abundance values that can arise from once-off surveys. Abundance values for each species were rescaled to represent abundance as a proportion of the maximum mean abundance reported for that species, from 0 to 1. The number of occurrences and abundance records and maximum abundance for each species are reported in table A1, with frequencies of abundance and environmental suitability estimates depicted in figures A1, A2 in the online edition of the *American Naturalist*.

The relationship between predicted environmental suitability and abundance was examined using OLS regressions and both linear and nonlinear quantile regressions (for further information on quantile regression, see Cade et al. 1999; Cade and Noon 2003). OLS regressions were used to examine mean abundance as predicted by environmental suitability. Quantile regressions were used to examine the relationship of environmental suitability to the upper limits of abundance (50th, 55th, 60th, 65th, 70th, 75th, 80th, 85th, 90th, 95th, 97.5th, and 99th percentiles for linear quantile regressions and 97.5th percentile for nonlinear quantile regressions).

All analyses were performed using R, version 2.5.1 (<http://www.R-project.org>), and the `quantreg` library, version 4.10 (<http://www.R-project.org>). Nonlinear relationships were fit to an asymptotic curve using the following equation:

$$y = [1 - \exp(-bx)],$$

where the horizontal asymptote was assumed to be 1 (the maximum proportional abundance when abundance for the species was scaled to be between 0 and 1),  $b$  is the rate constant,  $x$  is the independent variable (predicted environmental), and  $y$  is the dependent variable (abundance).

The traditional  $R^2$  measure of fit, based on the decomposition of total sum of squares into explained and residual sums of squares, is not applicable to quantile regressions. Rather, two alternative measures of goodness of fit were estimated: (1) a goodness-of-fit measure proposed by Koenker and Machado (1999) and limited to examining the fit of the linear quantile regressions (this is a local

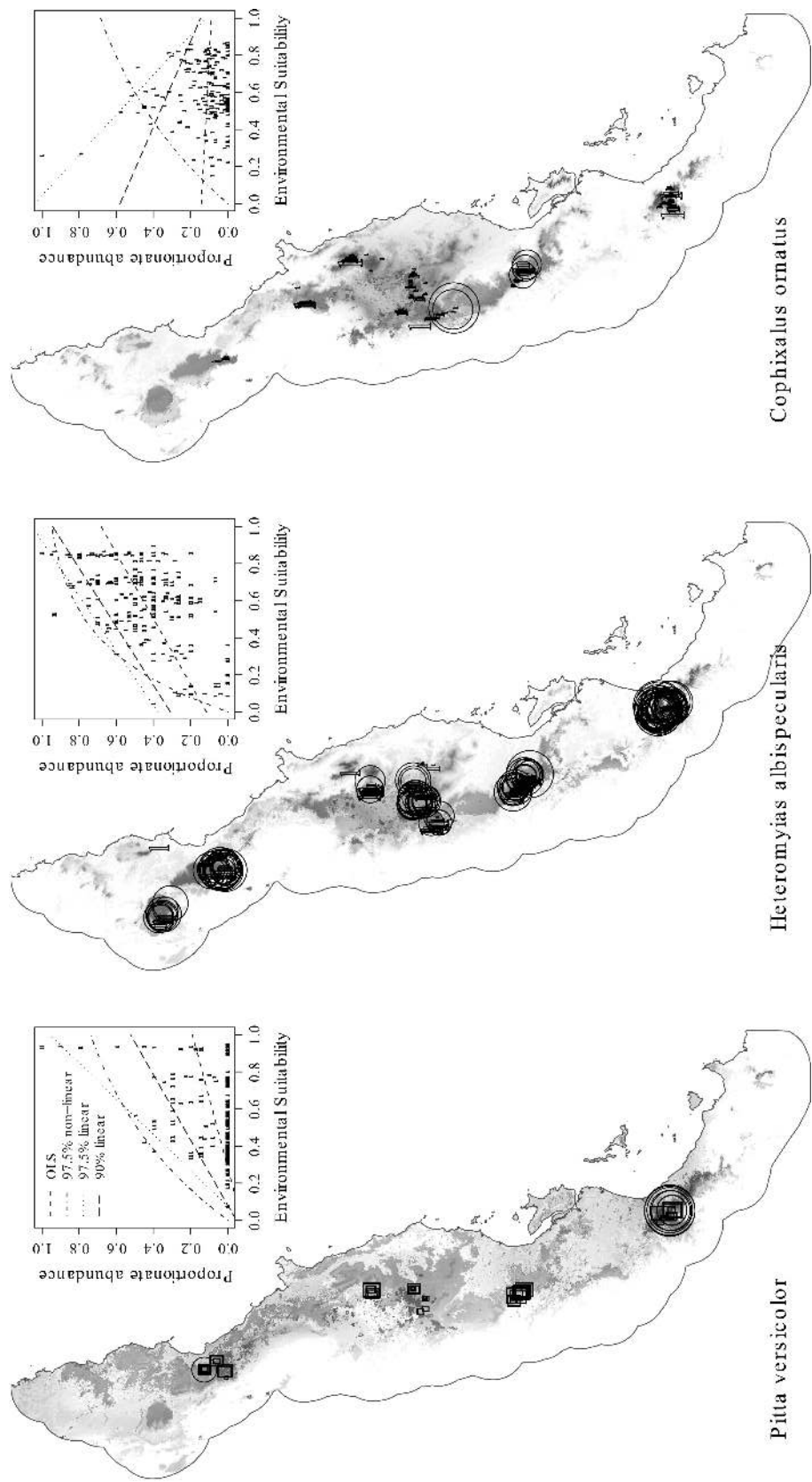
measure of goodness of fit for a specific quantile, not a global measure of goodness of fit over the conditional distribution) and (2) a pseudo  $R^2$  measure that was estimated using equations of Nagelkerke (1991). This measure is not limited to linear quantile regressions, and it has been applied to various regression models (e.g., OLS regression, logistic regression, and regression models incorporating spatial/temporal autocorrelation, as in simultaneous autoregressive models). It permits comparison of all regression models used. Nagelkerke's pseudo  $R^2$  yields the identical value as the traditional  $R^2$  for OLS regression (Lichstein et al. 2002).

## Results

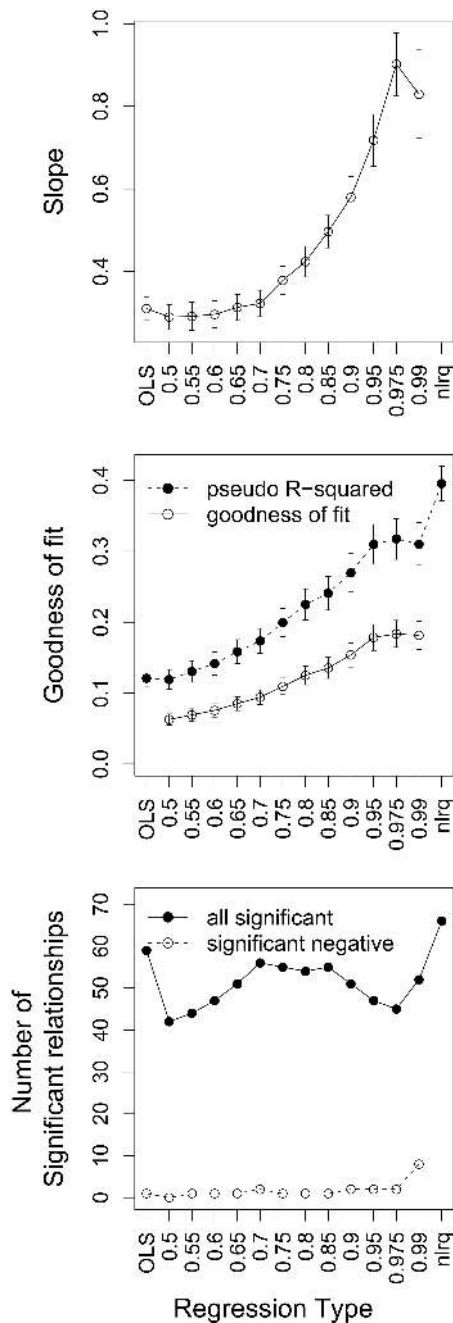
Species were patchily distributed within their geographic distributions (fig. 2). Typically, one or more individuals of a modeled species were recorded at greater than one-half of all survey locations within their predicted distribution (mean = 56.1%, SE = 3.07%, range = 13.2%–96.1%). OLS regression results found that, for 58 of the 69 species, there was a significantly positive relationship between predicted environmental suitability and abundance (table A1). Of the 10 nonsignificant relationships, only two were negative, with a single species having a significantly negative regression. Although most relationships were significantly positive, the amount of variation explained was generally low ( $R^2$  mean  $\pm$  SE =  $0.121 \pm 0.0127$ , range = 0.017–0.486).

Nearly all species showed a polygonal or wedge-shaped spread of points in the space defined by predicted environmental suitability and abundance, with the upper limit of abundance increasing at higher environmental suitability (see table A1; fig. A3 in the online edition of the *American Naturalist*). The linear quantile regressions supported this. In general, the regression slope (a measure of the size of the effect of environmental suitability on the abundance statistic) and the measures of goodness of fit increased with higher percentiles of abundance (fig. 3). Only the 99th percentile had eight significant negative relationships, with all other percentiles having three or less. In most cases, the nonlinear quantile regression provided a best fit (quantitatively and qualitatively) of the relationship between predicted environmental suitability and abundance (figs. 2, 3).

The distributions of points were such that the fitted regressions resembled one of three patterns. In the first pattern, all regression lines emanated from a single (or similar) location on the  $X$ -axis, as in the leftmost panel of figure 2. For these species, the linear regressions appeared to best fit the data. In the second pattern, intercepts of the regressions were highly variable among the fitted relationships, as in the middle panel of figure 2. The non-



**Figure 2:** Distributions and scatterplots of predicted environmental suitability against abundance for each of three representative species. Darker shades represent higher environmental suitability. Circles represent locations for which abundance estimates were used, with increasing size representing increasing local abundance. Regression lines shown represent the relationship fitted using ordinary least squares regression, 90th and 97.5th percentiles of quantile regression, and 97.5th percentile in a nonlinear quantile regression.



**Figure 3:** Summary characteristics of the relationship between predicted environmental suitability and abundance using ordinary least square (OLS) and linear and nonlinear quantile regressions. The X-axis in all panels represents the different regressions/regression quantiles used, starting with OLS regression, followed by the percentiles of the linear quantile regressions, and ending with the 97.5th nonlinear quantile regression (nlrq). *Top*, mean  $\pm$  SE of the slope coefficients that were significantly different from 0. *Middle*, goodness-of-fit measure for quantile regressions (Koenker and Machado 1999) and a pseudo  $R^2$  value (Nagelkerke 1991). *Bottom*, number of significant slopes and significant negative slopes.

linear “saturating” regression provided a better fit of the data in these cases. The first two patterns were by far the most common, while the last pattern was exemplified by the few “exceptions.” The exceptions are exemplified in the right panel of figure 2, where all or some of the linear regressions were found to be negative. In these examples, high abundances were lacking from sites predicted to have high environmental suitability, and low abundances were lacking from sites where environmental suitability was predicted to be low.

## Discussion

We have shown a strong, consistent relationship between predicted environmental suitability from presence-only habitat models and spatial variation in the abundance of species. The majority of species had significant positive relationships between local abundance and environmental suitability. However, little of the variance in abundance could be explained by OLS regression. Previous attempts to relate environmental suitability as predicted from presence-absence logistic regression models and abundance reported relationships that were generally none to weak (Pearce and Ferrier 2001; Nielsen et al. 2005). Examination of the anatomy of the relationship between predicted environmental suitability and abundance reveals that environmental suitability indicates the upper limit of abundance, rather than mean abundance.

At broad spatial scales, it is often possible to identify factors that set a limit on maximum abundance without completely explaining or fully determining abundance in all places (e.g., Thomson et al. 1996; Scharf et al. 1998; Cade et al. 1999; Cade and Noon 2003; Scrivener et al. 2004; Vaz et al. 2008). This is so in our data. When environmental suitability is high, a species may be abundant, but it is not necessarily so. Presumably, other unmeasured abiotic factors (e.g., microclimate) or constraints such as biotic interactions or dispersal limitations depress abundance in some otherwise suitable areas (see Soberón and Peterson 2005 for a similar treatment on geographical expression of the fundamental niche). However, when environmental suitability is low, abundance is consistently low. This produces a polygonal distribution of points over the space defined by predicted environmental suitability and local abundance.

How might these observations affect meaningful extrapolation of abundance information from modeled environmental suitability? Clearly, the answer depends on the application. If the purpose is to estimate relative differences in average abundance between broad areas, then predicted environmental suitability would seem appropriate. In contrast, if we intend to identify locations where a maximum population size might be realized (e.g., in the



reintroduction of an endangered species), then environmental suitability should be used to help narrow the search for priority areas while conceding that other as-yet-unmeasured factors may ultimately determine realized abundance. This has parallels with the findings of Ficetola et al. (2007), who modeled environmental suitability to predict the invasiveness of the American bullfrog in Europe. Environmental suitability was successful in identifying areas susceptible to invasion, but a greater portion of variation in the realized introduction success was achieved when local factors such as hunting pressure were also considered.

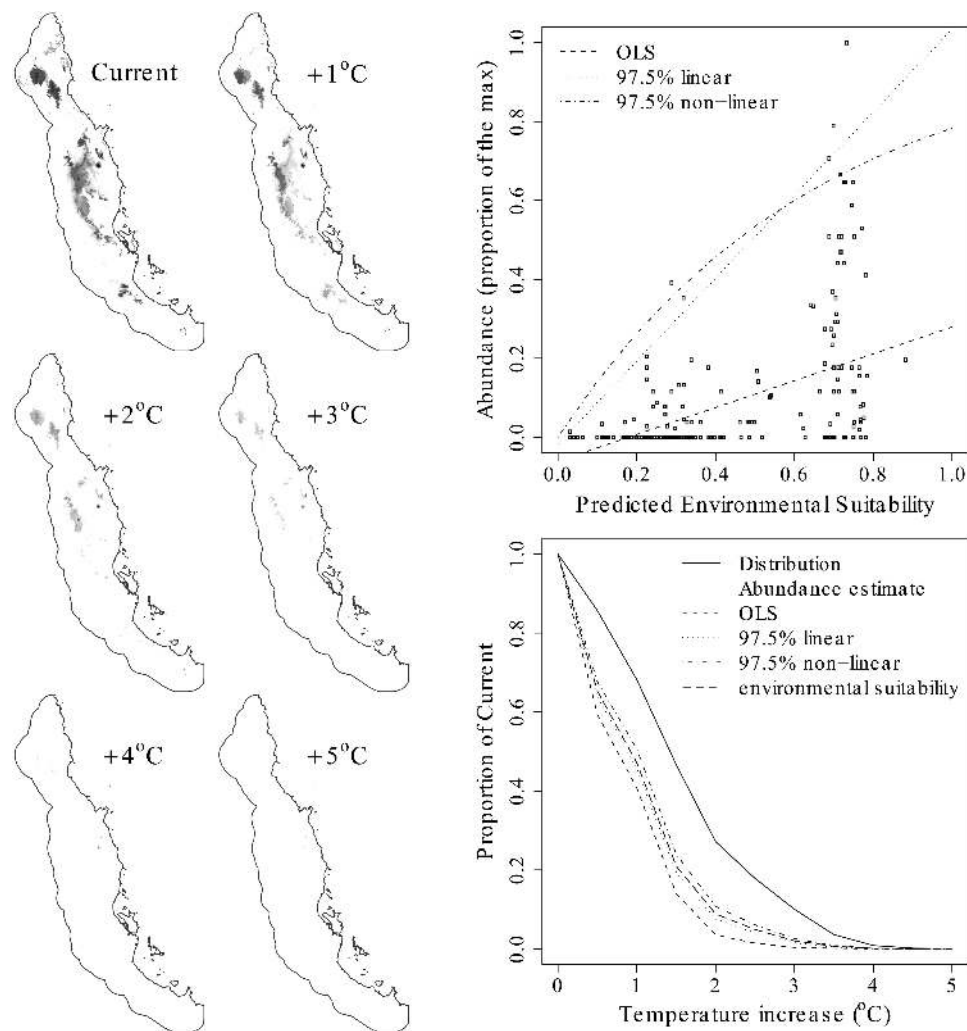
The finding that predicted environmental suitability from presence-only habitat models can provide information on species abundance patterns is likely to be useful in a number of ecological applications. An upper limit derived from predictions of environmental suitability could serve as a useful null model of abundance. Simple deviations from the null predictions at local scales could then set the context for fruitful research targeted at explaining why abundance varies from place to place in otherwise similarly suitable habitats (Colwell et al. 2004). In invasion ecology, ecological niche models identifying environmental similarity between native and target regions are considered to be important in predicting the outcomes of introductions (Thuiller et al. 2006; Richardson and Thuiller 2007). Given the relationship identified here, predicted environmental suitability in the target region could identify regions of greatest potential abundance in the nonnative range (or invasiveness).

The relationship between environmental suitability and local abundance has broad implications for conservation biology in applications where environmental suitability is expected to change over time. Ecological niche models based on climate are widely used to estimate the potential impacts of climate change on species distributions (Beaumont et al. 2007). To date, quantitative estimates of population size during distributional expansion or contraction have proven to be difficult to forecast. This is a major hindrance, as population size and trend are considered to be the best correlates of extinction risk (O'Grady et al. 2004). Such measures are widely used in determining the conservation status of a species (e.g., IUCN 2001), and there are theoretical reasons to expect population size to decline more rapidly with increasing temperature than distribution area would (Shoo et al. 2005). The relationship between predicted environmental suitability and abundance presented here may provide a simple method to predict likely changes in population size associated with distributional changes.

To illustrate this, we used estimates of abundance given environmental suitability to produce a distribution map of the mountain thornbill (*Acanthiza katherina*) weighted

by abundance. We then summed abundance estimates across the distribution to derive an index of current population size. The method was repeated for models projected onto climate surfaces where temperature variables had been manipulated to simulate incremental increases in temperature under future climate warming. We predict that population size will decline with increasing temperature and that it will do so more rapidly than will distribution size (fig. 4). The reason for the discrepancy is simple. Population size is a function of area as well as of locally variable patterns of density. Thus, population size can be highly responsive to a decline in the availability of specific environments that support species at high local densities (as in our case here). These results are consistent across the various measures of abundance derived from OLS regression, 97.5th-percentile linear and nonlinear quantile regressions, and a simple summing of predicted environmental suitability (with the assumed linear relationship representing an intercept of 0 and a slope of 1). Although the absolute estimates of total population size under the current climate differed between regression techniques (i.e., 0.2, 1.1, and 1.2 million individuals for OLS regression and the 97.5th-percentile linear and nonlinear quantile regressions, respectively), the proportional declines under climate simulations were similar and matched those derived from a simple sum of predicted environmental suitability (fig. 4). Thus, even in the absence of abundance information, presence-only ecological niche models are able to provide valuable insights into relative changes in population size.

Exceptions to the main patterns observed in our analyses may also be instructive. That is, three species showed negative OLS relationships (only a single species' slope was significant), and as many as eight species showed significant negative relationships using quantile regressions (at the 99th percentile). A common feature of these species was that they each had one or more surveys reporting high abundance in areas of low predicted environmental suitability. This was often coupled with a lack of high-abundance estimates from highly environmentally suitable areas (as in fig. 2, right). We might interpret such results in two ways: either our abundance data did not adequately describe the true response of these species to environmental suitability or the predictions of environmental suitability themselves were erroneous. The former could occur, for instance, if unexpectedly high estimates of abundance at low suitability are outliers and/or if abundance has been insufficiently sampled from areas of high environmental suitability. Erroneous suitability may have arisen from incorrect model parameterization where, for example, occurrences did not accurately represent the full environmental limits of the species (e.g., Pearson et al. 2007), sampling bias was not appropriately dealt with (e.g., Phil-



**Figure 4:** Proportionate changes in distributional area and total population sized for the mountain thornbill (*Acanthiza katherina*) in the Australian wet tropics. Distributions for each temperature increase are shown. Shaded areas are predicted distributional areas, with darker shading representing higher environmental suitability. Distributional area was estimated by projecting an ecological niche model, created using Maxent, onto climate layers of increasing temperature. Proportional changes in total population size were estimated using regressions created in this study (ordinary least squares [OLS] regression and 97.5th-percentile linear and nonlinear quantile regressions) and a simple summing of the predicted environmental suitability from Maxent.

lips and Dudik 2008), inappropriate pseudoabsences (i.e., background points) were used (e.g., VanDerWal et al. 2009b), or models simply failed to incorporate those factors that are most important in limiting suitability (e.g., biotic interactions, microhabitat features). Unfortunately, with so few “exceptional” species, it is not possible to conduct a rigorous test of these hypotheses. We suspect, though, that responses to unmeasured, microscale variables may be important. For example, the skink lizard *Carlia rubrigularis* reaches high densities along forest edges and in canopy openings where sunlight reaches the forest floor (Wilson 2005). Local availability of sunlight is neither

a factor that is directly modeled in our study nor a factor that is likely to be correlated with broad climate gradients used in our presence-only habitat models.

### Conclusion

To date, it has been unclear whether spatial patterns of abundance in nature could be reconstructed using knowledge of environmental suitability estimated from knowledge of where a species occurs. Our results show that such reconstruction is possible. This result has important implications for many practical applications in ecology, most

notably because direct estimates of abundance for input into spatial models are difficult to acquire and are limited to relatively few species (e.g., Carrascal et al. 2006; Brotons et al. 2007). In contrast, a great deal of species occurrence information is readily available for many species, from many sources (e.g., atlases, museum and herbarium records, incidental observation databases, species lists, and governmental, nongovernmental, and academic organizational databases). The conceptual link between environmental suitability estimated from habitat models and occurrence has been applied prolifically in conservation, planning, and species-management efforts (Pearce and Boyce 2006; Rodriguez et al. 2007). We demonstrate considerable promise that ecological niche models will also be able to provide valuable information on abundance. We strongly encourage other researchers to test the predictive ability of models on other empirical abundance data sets to explore the generality of these findings.

#### Acknowledgments

This research was supported by the James Cook University Research Advancement Program, the Marine and Tropical Sciences Research Facility, the Earthwatch Institute, the Queensland Smart State Program, the Australian Research Council, the Rainforest Cooperative Research Council, and the National Science Foundation. We would like to thank T. Peterson and an anonymous reviewer for valuable comments on earlier drafts of the manuscript.

#### Literature Cited

- Accad, A., V. J. Neldner, B. A. Wilson, and R. E. Niehus. 2006. Remnant vegetation in Queensland: analysis of remnant vegetation 1997–1999–2000–2001–2003, including regional ecosystem information. Queensland Herbarium, Environmental Protection Agency, Brisbane.
- Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species–climate impact models under climate change. *Global Change Biology* 11:1504–1513.
- Beaumont, L. J., A. J. Pitman, M. Poulsen, and L. Hughes. 2007. Where will species go? incorporating new advances in climate modelling into projections of species distributions. *Global Change Biology* 13:1368–1385.
- Blackburn, T. M., and K. J. Gaston. 1998. Some methodological issues in macroecology. *American Naturalist* 151:68–83.
- Blackburn, T. M., J. H. Lawton, and J. N. Perry. 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. *Oikos* 65:107–112.
- Bourg, N. A., W. J. McShea, and D. E. Gill. 2005. Putting a cart before the search: successful habitat prediction for a rare forest herb. *Ecology* 86:2793–2804.
- Brotons, L., S. Herrando, and M. Pla. 2007. Updating bird species distribution at large spatial scales: applications of habitat modelling to data from long-term monitoring programs. *Diversity and Distributions* 13:276–288.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255–279.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–323.
- Carrascal, L. M., J. Seoane, D. Palomino, C. L. Alonso, and J. M. Lobo. 2006. Species-specific features affect the ability of census-derived models to map winter avian distribution. *Ecological Research* 21:681–691.
- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163:E1–E23.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Ficetola, G. F., W. Thuiller, and C. Miaud. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species: the American bullfrog. *Diversity and Distributions* 13:476–485.
- Fleishman, E., R. M. Nally, and J. P. Fay. 2003. Validation tests of predictive models of butterfly occurrence based on environmental variables. *Conservation Biology* 17:806–817.
- Guisan, A., O. Broennimann, R. Engler, M. Vust, N. G. Yoccoz, A. Lehmann, and N. E. Zimmermann. 2006. Using niche-based models to improve the sampling of rare species. *Conservation Biology* 20:501–511.
- Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- International Union for Conservation of Nature (IUCN). 2001. IUCN Red List categories and criteria. Version 3.1. IUCN Species Survival Commission, Cambridge.
- Johnson, C. N., and J. VanDerWal. 2009. Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *Journal of Applied Ecology* 46:641–646.
- Kearney, M. 2006. Habitat, environment and niche: what are we modelling? *Oikos* 115:186–191.
- Kearney, M., and W. P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131.
- Koenker, R., and J. A. F. Machado. 1999. Goodness of fit and related inference processes for quantile regression. *Journal of the American Statistical Association* 94:1296–1310.
- Lichstein, J. W., T. R. Simons, S. A. Shiner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 72:445–463.
- Lobo, J. M., A. Jimenez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17:145–151.
- McMahon, J. P., M. F. Hutchinson, H. A. Nix, and K. D. Ord. 1995. ANUCLIM user's guide. Version 1. Centre for Resource and Environmental Studies, Australian National University, Canberra.
- Moritz, C. 2005. Overview: rain forest history and dynamics in the Australian wet tropics. Pages 313–322 in E. Bermingham, C. W. Dick, and C. Moritz, eds. *Tropical rainforests*. University of Chicago Press, Chicago.

- Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2006. Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography* 15:63–71.
- Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692.
- Nielsen, S. E., C. J. Johnson, D. C. Heard, and M. S. Boyce. 2005. Can models of presence-absence be used to scale abundance? two case studies considering extremes in life history. *Ecography* 28: 197–208.
- Nix, H. 1991. Biogeography: pattern and process. Pages 11–40 in H. A. Nix and M. A. Switzer, eds. *Rainforest animals: atlas of vertebrates endemic to Australia's wet tropics*. Australian National Parks and Wildlife, Canberra.
- O'Grady, J. J., D. H. Reed, B. W. Brook, and R. Frankham. 2004. What are the best correlates of predicted extinction risk? *Biological Conservation* 118:513–520.
- Pearce, J., and S. Ferrier. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation* 98:33–43.
- Pearce, J. L., and M. S. Boyce. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* 43:405–412.
- Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34:102–117.
- Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Prates-Clark, C. D. C., S. S. Saatchi, and D. Agosti. 2008. Predicting geographical distribution models of high-value timber trees in the Amazon Basin using remotely sensed data. *Ecological Modelling* 211:309–323.
- Raxworthy, C. J., E. Martinez-Meyer, N. Horning, R. A. Nussbaum, G. E. Schneider, M. A. Ortega-Huerta, and A. Townsend Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature* 426:837–841.
- Richardson, D. M., and W. Thuiller. 2007. Home away from home: objective mapping of high-risk source areas for plant introductions. *Diversity and Distributions* 13:299–312.
- Rodriguez, J. P., L. Brotons, J. Bustamante, and J. Seoane. 2007. The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions* 13:243–251.
- Sagarin, R. D., and S. D. Gaines. 2002. The “abundant centre” distribution: to what extent is it a biogeographical rule? *Ecology Letters* 5:137–147.
- Sagarin, R. D., S. D. Gaines, and B. Gaylord. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution* 21:524–530.
- Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79:448–460.
- Schroeder, R. L., and L. D. Vangilder. 1997. Tests of wildlife habitat models to evaluate oak-mast production. *Wildlife Society Bulletin* 25:639–646.
- Scrivener, N. J., C. N. Johnson, I. R. Wallis, M. Takasaki, W. J. Foley, and A. K. Krockenberger. 2004. Which trees do wild common brushtail possums (*Trichosurus vulpecula*) prefer? problems and solutions in scaling laboratory findings to diet selection in the field. *Evolutionary Ecology Research* 6:77–87.
- Shoo, L. P., S. E. Williams, and J.-M. Hero. 2005. Potential decoupling of trends in distribution area and population size of species with climate change. *Global Change Biology* 11:1469–1476.
- Soberón, J., and A. T. Peterson. 2005. Interpretation of models of fundamental ecological niches and species' distributions. *Biodiversity Informatics* 2:1–10.
- Steiner, F. M., B. C. Schlick-Steiner, J. VanDerWal, K. D. Reuther, E. Christian, C. Stauffer, A. V. Suarez, S. E. Williams, and R. H. Crozier. 2008. Combined modelling of distribution and niche in invasion biology: a case study of two invasive *Tetramorium* ant species. *Diversity and Distributions* 14:538–545.
- Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. *Ecology* 77:1698–1715.
- Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11:2234–2250.
- Thuiller, W., D. M. Richardson, M. Rouget, S. Proche, and J. R. U. Wilson. 2006. Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology* 87: 1755–1769.
- VanDerWal, J., L. P. Shoo, and S. E. Williams. 2009a. New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *Journal of Biogeography* 36:291–301.
- VanDerWal, J., L. P. Shoo, C. Graham, and S. E. Williams. 2009b. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling* 220:589–594.
- Vaz, S., C. S. Martin, P. D. Eastwood, B. Ernande, A. Carpentier, G. J. Meaden, and F. Coppin. 2008. Modelling species distributions using regression quantiles. *Journal of Applied Ecology* 45:204–217.
- Williams, S. E. 2006. Vertebrates of the wet tropics rainforests of Australia: species distributions and biodiversity. Cooperative Research Centre for Tropical Rainforest Ecology and Management. Rainforest Cooperative Research Centre, Cairns, Queensland.
- Williams, S. E., and R. G. Pearson. 1997. Historical rainforest contractions, localised extinctions and patterns of vertebrate endemism in the rainforests of Australia's wet tropics. *Proceedings of the Royal Society B: Biological Sciences* 264:709–716.
- Williams, S. E., R. G. Pearson, and P. J. Walsh. 1996. Distributions and biodiversity of the terrestrial vertebrates of Australia's wet tropics: a review of current knowledge. *Pacific Conservation Biology* 2:327–362.
- Wilson, S. 2005. A field guide to reptiles of Queensland. Reed New Holland, Sydney.
- Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, and A. Guisan. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763–773.

Associate Editor: Wolf M. Mooij  
 Editor: Donald L. DeAngelis