



Patterns of niche filling and expansion across the invaded ranges of an Australian lizard

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Studies of realized niche shifts in alien species typically ignore the potential effects of intraspecific niche variation and different invaded-range environments on niche lability. We incorporate our detailed knowledge of the native-range source populations and global introduction history of the delicate skink *Lampropholis delicata* to examine intraspecific variation in realized niche expansion and unfilling, and investigate how alternative niche modelling approaches are affected by that variation. We analyzed the realized niche dynamics of *L. delicata* using an ordination method, ecological niche models (ENMs), and occurrence records from 1) Australia (native range), 2) New Zealand, 3) Hawaii, 4) the two distinct native-range clades that were the sources for the New Zealand and Hawaii introductions, and 5) the species' global range (including Lord Howe Island, Australia). We found a gradient of realized niche change across the invaded ranges of *L. delicata*: niche stasis on Lord Howe Island, niche unfilling in New Zealand (16%), and niche unfilling (87%) and expansion (14%) in Hawaii. ENMs fitted to native-range data generally identified suitable climatic conditions at sites where the species has established non-native populations, whereas ENMs based on native-range source clades and non-native populations had lower spatial transferability. Our results suggest that the extent to which realized niches are maintained during invasion does not depend on species-level traits. When realized niche shifts are predominately due to niche unfilling, fully capturing species' responses along climatic gradients by basing ENMs on native distributions may be more important for accurate invasion forecasts than incorporating phylogenetic differentiation, or integrating niche changes in the invaded range.

Identifying locations where alien species are likely to establish and spread is crucial for mitigating their ecological and economic impacts (Liu et al. 2014). The degree of climatic similarity between an invadable location and a species' native geographic range (i.e. 'climate match') is a strong determinant of invasion success (Hayes and Barry 2007, Mahoney et al. 2015), and is routinely used in risk assessment schemes aimed at preventing establishment and spread (Guisan et al. 2013). Ecological niche models (ENMs, also commonly referred to as species distribution models, Peterson and Soberón 2012) correlate the occurrence of species to environmental conditions, and are frequently used to predict the potential distributions of alien species in new regions (Peterson and Vieglais 2001, Thuiller et al. 2005, Jiménez-Valverde et al. 2011). However, correlative ENMs only model the realized Grinnellian niche of a species (i.e. the noninteractive, nonconsumable environmental axes that define a species' distribution in a particular location, Soberón and Nakamura 2009). When using correlative ENMs to project potential distributions of alien species, one therefore assumes that all potentially suitable environments are present in a landscape, that alien species

are in equilibrium with existing environmental conditions (i.e. fill their fundamental niche), and that fundamental niches are conserved across space and time (Broennimann and Guisan 2008, Pearman et al. 2008, Elith et al. 2010, Araújo and Peterson 2012). Violation of these assumptions is difficult to detect without data on a species' physiological tolerances, morphology, and behaviour (Kearney and Porter 2009), but can lead to misspecified environmental relationships, resulting in wasted biosecurity resources or failure to establish management efforts in high risk areas. Nevertheless, the extent to which equilibrium and niche conservatism assumptions influence model interpretation depends critically on the intended use of a model and the conservation decisions that it might support (Araújo and Peterson 2012, Guisan et al. 2013, Guillera-Aroita et al. 2015).

Realized niche shifts are commonly investigated by examining changes in occupied regions of environmental space, or by testing how well ENMs parameterized on a species' native range can predict its invaded range (Guisan et al. 2014). Realized niche shifts can be methodological in origin, resulting from niche mischaracterization within a species' native or invaded ranges. For example, unmeasured

biases in species occurrence records, or calibration of models on a subset of a species' geographic range can lead to an incomplete characterization of a species' realized niche. A related issue is that species often encounter environmental conditions in their invaded ranges that are not available in their native ranges (Broennimann et al. 2012, Early and Sax 2014). Novel environments are problematic for correlative ENMs parameterized on a species' native range, because they require ENMs to extrapolate into unsampled environmental space (Elith et al. 2010). However, realized niche shifts can also reflect ecological and evolutionary processes that lead to niche expansion and niche unfilling (Petitpierre et al. 2012, Guisan et al. 2014, Strubbe et al. 2015). Niche expansion occurs when a species colonizes environmental conditions in its invaded range that are present, but unoccupied in its native range. This situation can arise when a species fails to fill its fundamental niche in its native range due to biotic interactions or dispersal barriers (i.e. non-equilibrium), or when a species undergoes phenotypic changes in the invaded range (i.e. fundamental niche evolution).

Niche unfilling, another cause of realized niche shift, occurs when species fail to colonize climates in the invaded range that are occupied in the native range (Guisan et al. 2014). This situation often reflects the fact that species have not had sufficient time to colonize their potential range (Broennimann and Guisan 2008). Thus, while building ENMs with data from a species' invaded range may incorporate phenotypic changes and more closely approximate the fundamental niche due to the absence of key biotic interactions (Urban et al. 2007), this approach is still limited by the fact that it assumes that species are in environmental equilibrium (Václavík and Meentemeyer 2012). One potential way to lessen the impact of this assumption is to pool data from a species' native and invaded ranges (Escobar et al. 2014). This pooled modelling strategy may allow ENMs to capture: 1) responses to climates in the invaded range that are not present in the native range, 2) phenotypic changes in the invaded range, and 3) climates that are occupied in a species' native range that have not yet been colonized in the invaded range (Broennimann and Guisan 2008, Beaumont et al. 2009).

An additional problem with predicting distributions of alien species in new regions is that source populations might be adapted to only a subset of a species' fundamental niche. If fundamental niches differ between phylogenetic lineages, models parameterized on the entire native range of a species may misspecify a species' potential invaded range (Pearman et al. 2010). For established alien species, matching native-range source clades to introduction locations has been suggested as a potential method for overcoming this limitation (Schulte et al. 2012, Tingley et al. 2015a), but this approach has rarely been tested due to the fact that source populations are difficult to identify.

Most studies of realized niche shifts in alien species have focused on interspecific variation in niche lability. However, biological invasions can be idiosyncratic, as different anthropogenic introductions can involve different native-range lineages and invaded-range environments. Multiple introductions in different environments are therefore needed to adequately determine whether a species is capable of shifting its realized niche when introduced to a new location (Goncalves et al. 2014). Here we incorporate our detailed

knowledge of the introduction history and native-range source populations of the delicate skink *Lampropholis delicata* to explore the extent to which: 1) *L. delicata* has maintained its realized niche in different locations; 2) predictions of invasion risk depend on the geographic origin of occurrence records used to build ENMs (entire native range, native-range source clades, invaded range, or global range); and 3) niche expansion and niche unfilling influence these alternative approaches for predicting invasion risk.

Methods

Study species

Lampropholis delicata is a small lizard species (~35–50 mm adult snout–vent length) that is native to eastern Australia (Chapple et al. 2013a). The species is adept at colonizing regions beyond its native geographic range via human-assisted dispersal (Chapple et al. 2013b), and has established invasive populations in the Hawaiian Islands, New Zealand, and Lord Howe Island (Chapple et al. 2013a). Nine native-range genetic subclades are present in *L. delicata* (Chapple et al. 2011), and the introduction history of the species has been determined (Chapple et al. 2013a). Thus, *L. delicata* provides a model species for assessing the extent to which realized niche shifts and predictions of invasion risk are influenced by the geographic origin of occurrence records.

Species data

Distributional data for *L. delicata* across its native and invaded ranges was obtained from all major Australian Museums (Australian Museum, CSIRO Australian National Wildlife Collection, Museum Victoria, Museum and Art Gallery of the Northern Territory, Queensland Museum, Queen Victoria Museum and Art Gallery, South Australian Museum, Tasmanian Museum and Art Gallery, Western Australian Museum), several USA museums (American Museum of Natural History, Bishop Museum, California Academy of Science, Harvard Museum of Comparative Zoology, UC Berkeley Museum of Vertebrate Zoology, Smithsonian Inst. National Museum of Natural History), the Atlas of Living Australia (<www.ala.org.au/>), the Victorian Biodiversity Atlas (<www.depi.vic.gov.au/environment-and-wildlife/biodiversity/victorian-biodiversity-atlas/>), the New Zealand Herpetofauna database (<www.doc.govt.nz/conservation/native-animals/reptiles-and-frogs/reptiles-and-frogs-distribution-information/electronic-atlas/>), literature records (Baker 1979, Peace 2004), and our own collecting records. Most occurrence records were relatively recent – the median year across all records was 1995, and 81% of records were less than 20 yr old.

In total, we collated 7892, 97, 120, and 42 unique occurrence records from Australia, Hawaii, New Zealand, and Lord Howe Island, respectively. After removing duplicate records within 1 km grid cells (the approximate resolution of our climate data) and thinning native-range records in geographic space, we were left with 1991, 83, 100, and 14 records from each range. Higher human population densities along the

east coast of Australia led to geographic biases in *L. delicata* occurrence records, even after duplicate records within grid cells were removed. While geographic bias does not impact realized niche characterization, environmental bias (i.e. non-random sampling in environmental space) does. Geographic bias can be strongly correlated with environmental bias in Australia (e.g. wetter conditions prevail along the coast). We therefore randomly thinned all occurrence records in geographic space to lessen the potential impact of this bias. This involved calculating the geographic distance between each pair of records, and randomly removing one record in pairs separated by < 5 km. We acknowledge, however, that without information on sampling effort, we cannot separate areas that are highly suitable from those that have been over-sampled (Elith et al. 2010). We did not thin presence records in the species' invaded ranges because fewer presence records were available, and because the spatial distribution of occurrence records was more homogenous in geographic space.

Data on the distribution of each native range clade were taken from Chapple et al. (2011), who sequenced 238 samples from 120 populations across the species' range. Sample sizes in the source clades ranged between 14 and 70. However, these sequenced records represent only a sample of all locations where each clade occurs. Ancillary distribution data from museums, researchers, and atlases did not have information on clade membership. These ancillary records were therefore assigned to a clade based on the minimum Euclidean geographic distance between each record and a record of known clade membership (Schulte et al. 2012, Rosauer and Moritz 2013). More detailed genetic sampling occurred in regions where several clades were present within close geographic proximity, haplotypes were generally not shared between populations, and deep genetic breaks were evident among clades ($> 5\%$ mitochondrial divergence). Thus, the approach used to assign locations to particular clades should be relatively robust.

Climate data

Temperature and precipitation are primary determinants of ectotherm distributions at coarse spatial scales (Araújo et al. 2006). We used eight temperature and precipitation variables from the WorldClim database (Hijmans et al. 2005) representing average and extreme climatic conditions, as well as measures of temporal climatic variability, to characterize the native and invaded realized niches of *L. delicata*: 1) mean annual temperature (bio1), 2) maximum temperature of the warmest month (bio5), 3) minimum temperature of the coldest month (bio6), 4) temperature annual range (bio7), 5) annual precipitation (bio12), 6) precipitation of the wettest month (bio13), 7) precipitation of the driest month (bio14), and 8) precipitation seasonality (bio15). These variables had a spatial resolution of ~ 1 km, and were based on long-term average conditions (1950–2000). We did not use variables that combined temperature and precipitation (e.g. mean temperature of the wettest quarter), as they can be difficult to interpret when projected to different areas (Elith et al. 2013), and because these variables displayed artificial discontinuities between adjacent grid cells in some areas (Escobar et al. 2014). Land cover can be an important

predictor of ectotherm distributions (Tingley and Herman 2009, Gillingham et al. 2012), but we did not include it in our models because of substantial differences in the land cover categories occupied in the native and invaded ranges of *L. delicata*.

Testing for niche shifts

We used the occurrence records and eight bioclimatic variables described above to test whether *L. delicata* has shifted its realized niche in Hawaii, New Zealand, and Lord Howe Island. Climate variables measured at locations across the available backgrounds in Australia, Hawaii, New Zealand, and Lord Howe Island were combined and projected onto the first two axes of a principal components analysis (PCA). These two PCA axes described the global environmental space available to *L. delicata* and explained 83% of the variation in the raw climatic data. This environmental space was then projected onto a grid consisting of 100×100 cells, with minimum and maximum values defined by those present in the available background data. Occurrence records from each geographic range were similarly gridded. Smoothed densities of occurrences and available environments in each grid cell were then calculated using a Gaussian kernel with a standard bandwidth (Silverman 1986), allowing a direct comparison of occurrence densities between the species' native and invaded realized niches that accounts for environmental availability. See Broennimann et al. (2012) for further details.

In Australia, available background environments were defined as grid cells within bioregions where the species presently occurs, in order to constrain the background to ecologically plausible regions of occurrence (using the Interim Biogeographic Regionalisation for Australia: Dept of the Environment 2013, Keith et al. 2014). However, the appropriate background for testing realized niche shifts between native-range source clades and destinations is less clear. One could argue that background environments should only include areas that have been accessible to each clade in its native range (Barve et al. 2011), and that it is inappropriate to change the occurrence points (native clades vs entire native range) without also changing the spatial extent of the background (Kriticos et al. 2014). On the other hand, changing the background extent confounds the influence of using different occurrence records. We therefore used two methods for selecting background environments for the clade-specific analyses. First, we defined clade-specific backgrounds using all grid cells within bioregions where each clade occurs. Second, we used the same background that we used when modelling the entire native range (all bioregions in which the species occurs). For the species' invaded ranges, background environments included all grid cells within 50 km of presence records (Escobar et al. 2014, Stiels et al. 2015). This approach helps control for sampling bias by restricting available environments to geographic areas that are more likely to have been sampled (Fourcade et al. 2014). The choice of 50 km reflects a compromise between including environments that have been accessible to the species (Barve et al. 2011), and covering a broad enough extent to minimize extrapolation and detect climatic differences between presence and

background records (Owens et al. 2013). Bioregions were not used in the species' invaded ranges as *L. delicata* has had insufficient time to colonize all bioregions that are potentially suitable, and because spot-fire introductions in the invaded range have allowed the species to overcome biogeographic barriers (Chapple et al. 2013b).

We quantified niche overlap between the species' native realized niche and each invaded niche separately using Schoener's D, a metric that ranges from 0 (no overlap) to 1 (complete overlap). Estimates of Schoener's D were used to test for niche equivalency and niche similarity (Warren et al. 2008). Niche equivalency was tested by randomly allocating occurrence records to the species' native and invaded niches 1000 times (maintaining the same number of occurrences as observed in each range), and comparing observed and simulated Schoener's D estimates. In contrast, we tested for niche similarity by shifting the centroid of the observed occurrence densities in the invaded range to a random location within the available environmental space 1000 times, each time comparing observed and simulated estimates of Schoener's D (Broennimann et al. 2012). Niche equivalency and niche similarity tests were not conducted using data from Lord Howe Island due to low sample sizes ($n = 14$ grid cells).

We used the environmental and occurrence density grids described above to calculate estimates of realized niche expansion and unfilling (Petitpierre et al. 2012, Guisan et al. 2014). Niche expansion was calculated as the proportion of occupied grid cells (in environmental space) in the invaded niche that did not overlap with the occupied native niche (Petitpierre et al. 2012). Niche unfilling was determined by calculating the proportion of the occupied native niche that did not overlap the occupied invaded niche. Because these metrics are based solely on environments that are common to both ranges, they are not confounded by no-analog environments. Niche change metrics were calculated using the 75th percentile of environments available in each range to remove marginal climates (Petitpierre et al. 2012). The only exception was the comparison between the species' native (Australian) realized niche and its niche on Lord Howe Island. These two areas did not share any environmental space when marginal climates were removed, and thus we used the full suite of environmental conditions (100th percentile) available in both ranges.

Niche modelling

We modelled the realized niche of *L. delicata* using Maxent (ver. 3.3.3k), the same eight bioclimatic variables used in our niche shift analyses, and species occurrence records from: 1) Australia, 2) Hawaii, 3) New Zealand, and 4) the species' global range (including Lord Howe Island). To examine the effect of matching native-range source clades to introduction locations, we also built Maxent models using data from the two distinct clades that were the sources for the New Zealand and Hawaiian introductions (Chapple et al. 2013a). Maxent is an algorithm that attempts to distinguish locations where a species has been detected from background locations using environmental covariates (Phillips et al. 2006). We used the default settings of Maxent, except that we only used smoothed hinge features (regularization multiplier = 2) to

create response curves that are safer for extrapolation (Elith et al. 2010, Tingley et al. 2014).

The number of presence and background records varied considerably between Australia and the species' invaded ranges, and thus pooled models trained on the species' global range were dominated by Australian records. We therefore randomly sampled presence and background records from the species' native and New Zealand ranges to match the number of records in Hawaii (Di Febbraro et al. 2013). To ensure that Australian records were not selected solely from areas with high numbers of records (i.e. over-sampled areas) we weighted the selection of presence records by the inverse of the density of records within a 50 km neighbourhood. This entire process was repeated 10 times to account for uncertainty due to random selection of presence and background records. However, because variation between replicates was minimal, and because ENMs based on different presence and background records cannot be combined reliably, we only show the results of one of the 10 replicates (Guillera-Arroita et al. 2015).

Reciprocal projections of ENMs fitted to data from different geographic regions often involve projecting response curves into unsampled environmental space. We, therefore, examined the climatic similarity between the native and invaded ranges of *L. delicata* using multivariate environmental similarity surfaces (Elith et al. 2010).

Testing the predictive performance of ENMs is problematic when species are not at equilibrium (Elith 2013). Traditional metrics such as Kappa or the area under a receiver operating characteristic curve (AUC) use absence (or background) data, and thus assume that a species has had sufficient time to colonize suitable environments. These metrics are, therefore, inappropriate when modelling species that are still invading or absent from suitable locations for other reasons (Kikillus et al. 2010). Hence, we chose to interrogate ENMs by visually examining predicted distributions, response curves, and maps of multivariate environmental similarity. For example, ENMs that produced ecologically unrealistic predictions or response curves, or frequently required extrapolation into unsampled environmental space were considered less reliable (Elith et al. 2010). As a more formal method of evaluation, we also determined whether ENMs accurately predicted known populations in the invaded range. Ensuring that ENMs encompass known populations is critical, as models that fail to predict the presence of invaded-range populations can lead to under-prediction of a species' eventual geographic distribution. Determining whether models correctly predict invaded-range populations requires selection of a threshold to convert continuous model outputs into presence-absence predictions. Here we used the highest threshold that captured 95% of the native range records to calculate the proportion of invaded range occurrences that were accurately classified by native-range and clade-specific ENMs. However, we acknowledge that there are problems with calculating binary thresholds on presence-only data (Guillera-Arroita et al. 2015), and that this metric does not account for the fact that *L. delicata* may invade additional locations in the future that are poorly predicted by the native-range ENM.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.7vs3d>> (Tingley et al. 2015b).

Results

Niche filling and expansion

Overlap between the native and invaded realized niches of *L. delicata* was low in both New Zealand (Schoener's $D = 0.16$) and Hawaii (Schoener's $D = 0.048$). Niche equivalency was rejected in both cases (simulated median D for both ranges = 0.94, $p = 0.002$). However, the observed overlap between the native and invaded niches of *L. delicata* did not deviate from random expectations (New Zealand: simulated median $D = 0.031$, $p = 0.10$; Hawaii: simulated median $D = 0.11$, $p = 0.65$).

Examining patterns of niche expansion and niche unfilling demonstrated a gradient of realized niche change across

the species' invaded ranges. Comparing the native realized niche of *L. delicata* to its invaded niche on Lord Howe Island revealed complete niche stability (Fig. 1A). In New Zealand (Fig. 1B), there was little evidence of expansion of the species' realized niche into climates that are available in the species' native range (0.1%), and moderate evidence of niche unfilling (16%). Conversely, in Hawaii (Fig. 1C), nearly 14% of the species' invaded niche exists in climates that are not occupied in its native range (i.e. niche expansion), and 87% of the species' native niche remains unfilled. Thus, realized niche shifts between the native and invaded ranges of *L. delicata* were largely due to niche unfilling, although there was moderate evidence for niche expansion in Hawaii. In both New Zealand and Hawaii, *L. delicata* has colonized novel climates that are not available in the species' native range. In both cases, these regions of novel climatic space are wetter than available Australian climates (i.e. have lower values on the PC1 axis; Fig. 1D).

In New Zealand, estimates of realized niche changes were relatively robust to the source of native-range occurrence

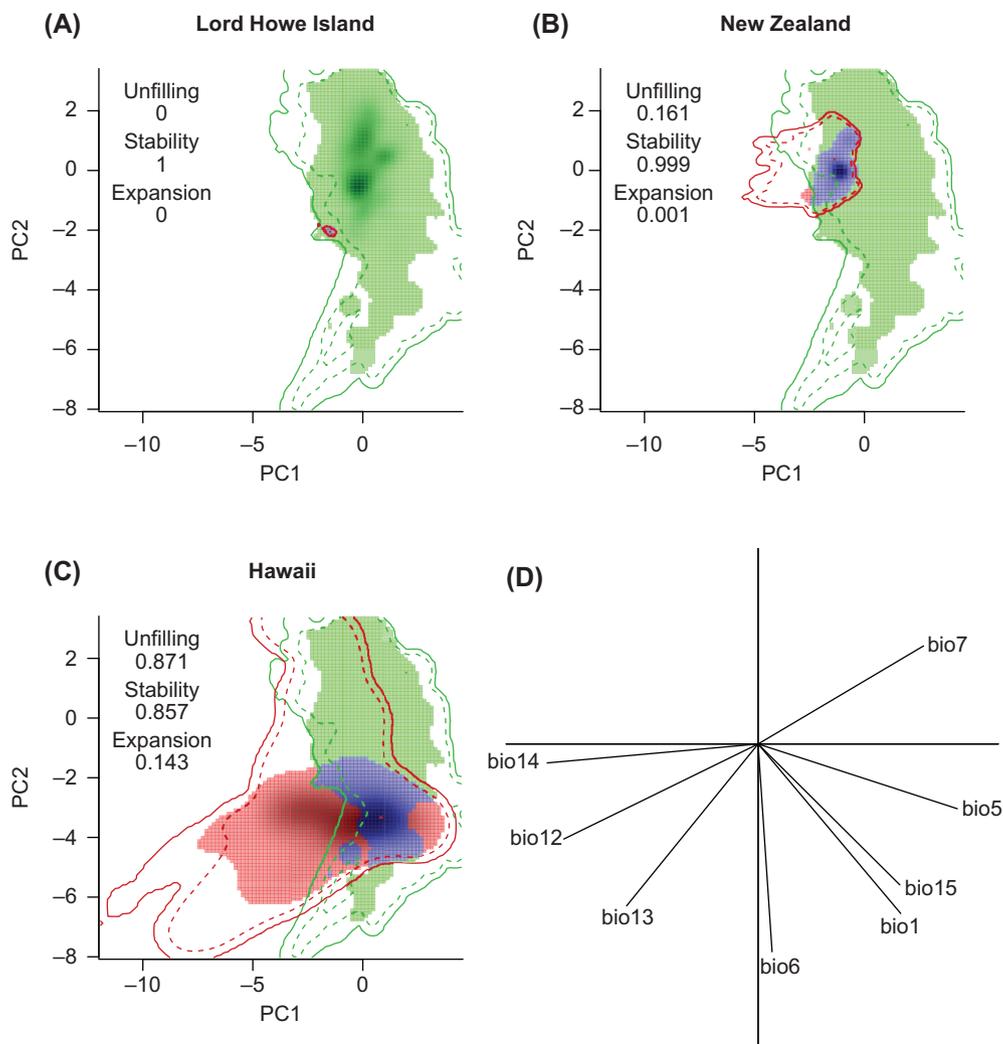


Figure 1. Projection of the Australian (green) and invaded (red) realized niches of *Lampropholis delicata* in climatic space (A–C), represented by the first two axes of a principal components analysis (D). Contours represent 100% (solid line) and 75% (dotted line) of the available climatic space within each range. Densities within these contours (black) correspond to the densities of occurrence records within the occupied climatic space. Blue areas symbolize niche overlap (stability). The correlation circle in panel D shows how the eight climatic predictors are distributed along the first two axes of the principal components analysis. See Methods for variable abbreviations.

records (native-range clade vs entire range) and the definition of available (background) environments (0–2.2% expansion and 14–17% unfilling across all scenarios). However, there was stronger evidence of niche expansion and weaker evidence of niche unfilling in Hawaii when occurrence records from the native-range source clade were used. Estimates of niche expansion and unfilling were higher when background environments included all bioregions that intersected the species' native range (expansion: 83%, unfilling: 44%) than when background environments were restricted to bioregions in which only the native-range clade occurred (expansion: 25%, unfilling: 13%).

Projections of potential distributions

In line with our finding that realized niche shifts were predominately due to niche unfilling, ENMs fitted to occurrence data from the native range of *L. delicata* indicated that there is potential for further range expansion in New Zealand, Hawaii, and Lord Howe Island (Fig. 2). Projecting

the native-range ENM globally revealed that suitable climatic conditions for *L. delicata* also exist in Europe, eastern Madagascar, central Africa, the Neotropics, Australasia and Indo-Malaysia (Fig. 3). The native-range ENM accurately predicted the Australian range of *L. delicata* (Fig. 2), and correctly identified all of the non-native populations in New Zealand (sensitivity = 1) and Lord Howe Island (sensitivity = 1); records from the species' Hawaiian range were predicted with less accuracy (sensitivity = 0.819). Importantly, projecting the native-range ENM onto all three of the species' invaded ranges generally involved only minor extrapolation (Supplementary material Appendix 1, Fig. A1).

ENMs trained on the New Zealand and Hawaiian ranges of *L. delicata* also identified suitable climatic conditions at many of the sites where the species has established invasive populations, but both models grossly over-predicted the species' native range (Fig. 2). Response curves, variable importance values, and maps of multivariate environmental similarity suggest that this over-prediction was due to misspecified environmental relationships and extrapolation in novel environmental space (Supplementary

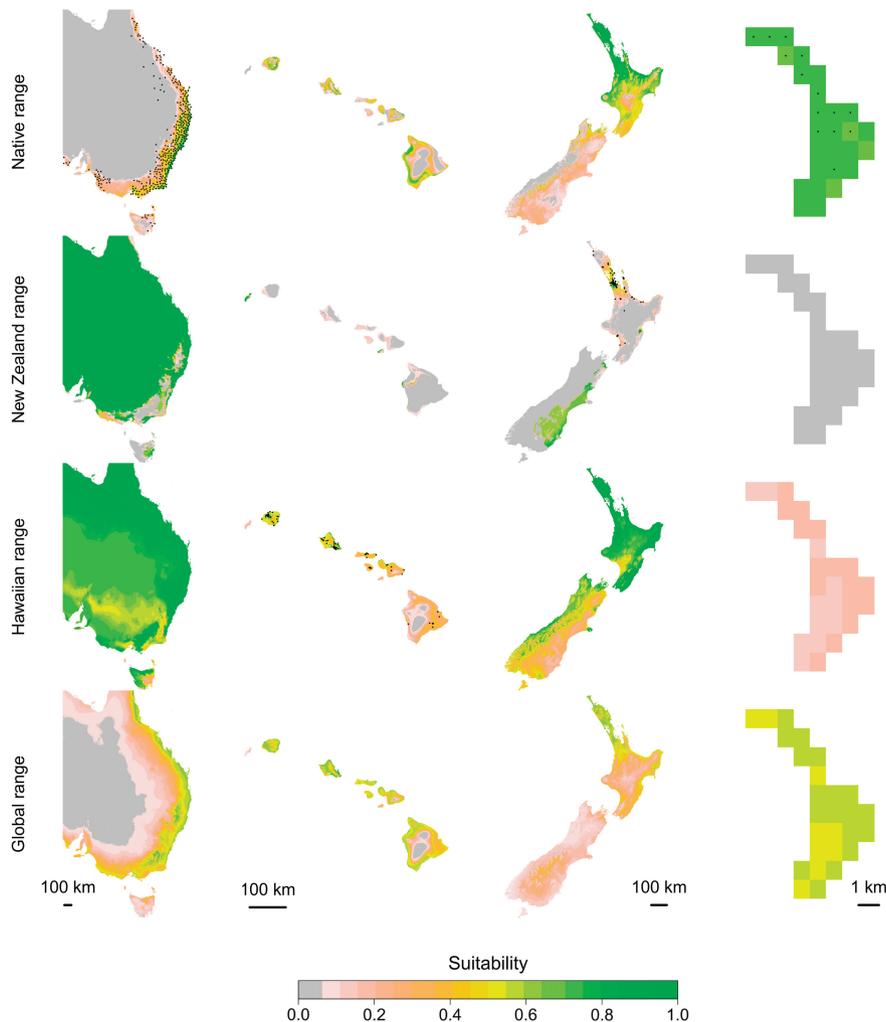


Figure 2. Reciprocal projections of ecological niche models (ENMs) based on data from the native, New Zealand, Hawaiian, and global ranges of *Lampropholis delicata* (rows). ENMs trained on different geographic regions are projected (columns) onto eastern Australia (native range), Hawaii, New Zealand, and Lord Howe Island. Maps show ENM outputs derived from presence-background data, and thus absolute values are not directly comparable across models built with different datasets. Black dots represent occurrence records of *L. delicata*. Native range records have been geographically thinned to improve visibility.

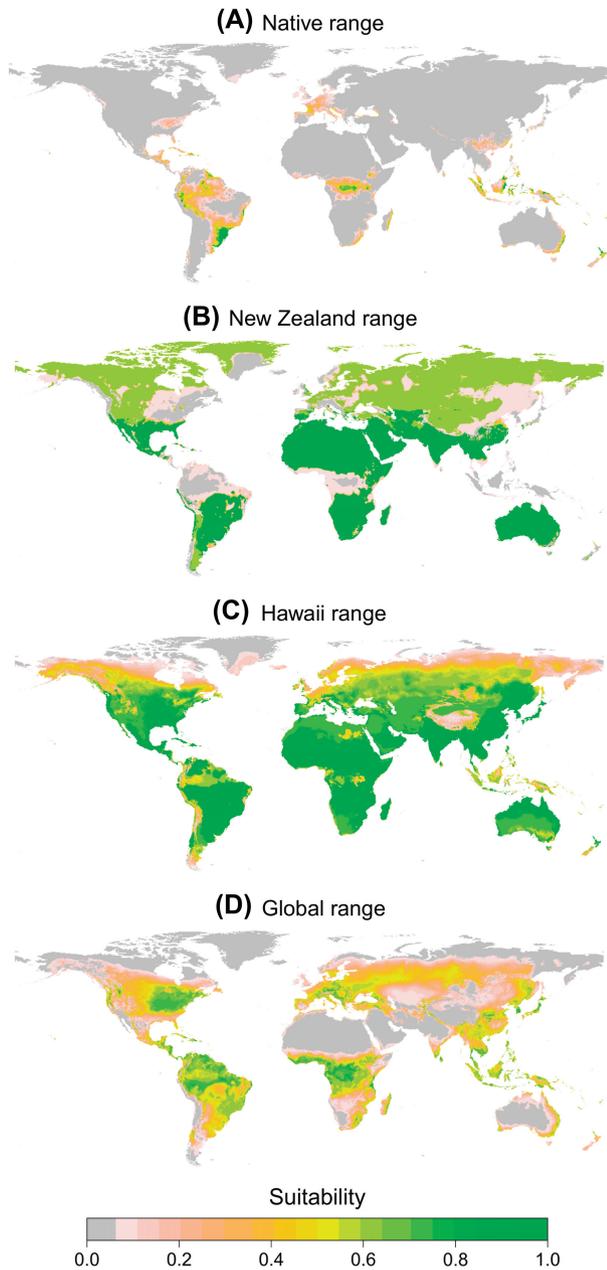


Figure 3. Predicted distribution of *Lampropholis delicata* at the global scale based on ecological niche models (ENMs) parameterized on data from the species' Australian (A), New Zealand (B), Hawaiian (C), and global (D) ranges. ENMs were derived from presence-background data, and thus absolute values are not directly comparable across models built with different datasets.

material Appendix 1, Fig. A2 and A3). The New Zealand ENM had particularly low spatial transferability, assigning low suitability to almost all of the non-native populations in Hawaii and Lord Howe Island (Fig. 2). ENMs based on clade-specific occurrence records and background environments also performed much worse than ENMs based on the species' entire native range when projected onto New Zealand (sensitivity = 0.06) and Hawaii (sensitivity = 0.157; Supplementary material Appendix 1, Fig. A4, A5). Training clade-specific ENMs on background environments from across the species' entire native range increased model sensitivity in Hawaii (0.28) but not in New Zealand (0.06).

In contrast, global ENMs based on occurrence records from all four of the geographic ranges of *L. delicata* were less affected by extrapolation than all other ENMs (Supplementary material Appendix 1, Fig. A1), and correctly predicted both native and invasive populations (Fig. 2). In New Zealand, the inclusion of invaded-range data led to predictions that were more tightly focused around known populations (Fig. 2) compared to the ENM based on the species' native range (Fig. 2). However, the use of native-range data also allowed the global ENM to identify uncolonized locations in New Zealand that were similar to the species' native range. Similarly, the global ENM was able to capture occupied climates in south-eastern Hawaii that were poorly predicted by the native-range ENM.

Discussion

Many risk assessments for alien species rely on correlative comparisons between climate and a species' native distribution, as invaded-range data are either unavailable (pre-border assessment), or limited in the early stages of an invasion (post-border assessment). Thus, risk assessments necessarily assume that species will maintain their native realized niches when introduced to locations beyond their native geographic ranges. Our finding that there is a gradient of realized niche change across the invaded ranges of *L. delicata* shows that the validity of this assumption can vary across locations within a single species. Such intraspecific niche lability suggests that the extent to which realized niches are maintained during invasion does not depend on species-level traits, although studies of intraspecific variation in additional taxa are required. This finding does, however, accord with recent interspecific analyses of realized niche shifts in other vertebrate groups (Strubbe et al. 2013, 2015) where propagule pressure and residence time (a proxy for dispersal limitation) are strong predictors of niche changes. Interestingly, studies of native European trees and invertebrates have shown that potential range filling is correlated with dispersal mode (Hof et al. 2012, Nogués-Bravo et al. 2014), suggesting that dispersal is an important correlate of niche filling in both native and non-native species.

We found that the native and invaded realized niches of *L. delicata* were not statistically equivalent, but niche similarity tests produced equivocal results. However, failure to reject the null hypothesis does not indicate that a shift in the realized niche has occurred. Instead, a lack of statistical significance simply means that we cannot draw conclusions regarding realized niche divergence given the spatial distribution of environmental conditions across the invaded-range backgrounds (Glennon et al. 2014). Previous studies have documented realized niche shifts in a wide variety of taxa, but causes of these shifts remain poorly understood (Guisan et al. 2014). Indeed, few studies have determined to what extent realized niche changes were the result of niche expansion vs niche unfilling, and we are aware of only two studies that have compared these niche change metrics across multiple locations within a single species (Petitpierre et al. 2012, Goncalves et al. 2014). We have shown that shifts in the realized niches of *L. delicata* in New Zealand and Hawaii are largely due to niche unfilling, suggesting that

biotic interactions or dispersal limitations have prevented the species from colonizing the full extent of its native realized niche in its invaded ranges. The limited natural dispersal ability of *L. delicata* coupled with its highly disjunct distribution on individual islands in Hawaii and on the North Island of New Zealand (due to 'spotfire' introductions resulting from human-mediated jump dispersal, Chapple et al. 2013b), suggests that dispersal limitation is the more plausible explanation for this finding. Niche unfilling is also more common than niche expansion in alien plants globally (Petitpierre et al. 2012) and in Holarctic vertebrates (Strubbe et al. 2013, 2015), although niche expansion was relatively common in a sample of the global alien herpetofauna (Li et al. 2014) and in European plants (Early and Sax 2014).

Despite strong evidence for niche unfilling in Hawaii, *L. delicata* has also colonized environments in Hawaii that are available, but unoccupied in its native range (i.e. realized niche expansion). This suggests that *L. delicata* does not fill its native fundamental niche (e.g. due to biotic interactions or dispersal limitations), or that the species' environmental tolerances have changed post-introduction. Determining which of these hypotheses is more likely requires common garden experiments and/or modelling approaches that are capable of capturing the fundamental niche (Tingley et al. 2014). *Lampropholis delicata* has also colonized climates that are not present within the species' native range in Hawaii, and to a lesser extent in New Zealand. These colonization events could also signal fundamental niche evolution, or may simply reflect the fact that available climates in the species' native range only encompass a subset of its fundamental niche (Broennimann et al. 2012, Schulte et al. 2012, Guisan et al. 2014).

Similar to previous studies (Fitzpatrick et al. 2006, Broennimann and Guisan 2008), we have shown that the potential distribution of *L. delicata* differs markedly depending on the geographic origin of occurrence records used to build ENMs. However, determining the 'best' approach (e.g. by comparing the discriminatory ability of ENMs based on different datasets) is problematic when species are not at environmental equilibrium. In such cases, occurrence records will only represent a subset of suitable environments because the species is still spreading (Barve et al. 2011, Elith 2013). Lack of reliable absence data in the invaded range also means that ENMs parameterized on invaded-range occurrences are often fitted with presence-background data, which produce outputs that cannot be reliably compared among different datasets without strict assumptions (Guillera-Aroita et al. 2015). Despite these limitations, reciprocal predictions of ENMs between the native and invaded ranges of *L. delicata* illustrate two important issues regarding the use of correlative ENMs to predict invasion risk.

First, ENMs based on native-range data may provide more reliable predictions of invasion risk when realized niche shifts are predominately due to niche unfilling as opposed to niche expansion (also see Strubbe et al. 2013). The ENM trained on the native range of *L. delicata* correctly identified all of the invasive populations in New Zealand, where the species does not fill its native realized niche. Conversely, in Hawaii, where there was evidence of niche expansion and colonization of extremely novel climates, the native-range ENM under-predicted the current extent of

the species' invaded range. Previous studies have typically found that ENMs based on native-range data under-predict the extent of a species' invaded range (Fitzpatrick et al. 2006, Broennimann et al. 2007, Broennimann and Guisan 2008, Beaumont et al. 2009, Di Febbraro et al. 2013, Hill et al. 2013, Stiels et al. 2015). However, these studies have not tested whether realized niche shifts were due to niche expansion or niche unfilling, and thus the reasons for this under-prediction have often been unclear. Recently, Strubbe et al. (2013) showed that the predictive performance of native-range ENMs increased with increasing niche overlap, and decreased with increasing niche change. Similarly, Tingley et al. (2014) found that a shift in the realized niche of the cane toad *Rhinella marina* was solely due to niche expansion, and accordingly, a native-range ENM under-predicted the extent of the species' Australian invasion.

Second, our results highlight the danger of fitting ENMs to non-equilibrium distributions (Elith et al. 2010), and corroborate earlier studies that have illustrated the importance of fully capturing species' responses along climatic gradients (Thuiller et al. 2004, Barbet-Massin et al. 2010, Owens et al. 2013). Building ENMs with invaded-range data can capture changes in a species' realized niche that occur over the course of its invasion (Urban et al. 2007); however, this approach is constrained by the fact that many species are not in environmental equilibrium in their invaded ranges, which can lead to under-prediction of a species' potential distribution (Václavík and Meentemeyer 2012). For example, in New Zealand, predictions of high invasion risk based on the ENM fitted to New Zealand data were concentrated around the initial introduction point of Auckland, where *L. delicata* has had the longest amount of time to spread (Chapple et al. 2013a). As a result, the New Zealand ENM predicted low suitability at many of the sites where the species has established invasive populations as a result of human-assisted dispersal (Chapple et al. 2013b), and predicted a much smaller potential distribution than the ENM trained on the species' native and Hawaiian ranges. Interestingly, combining native and invaded range data lessened the impact of this non-equilibrium situation, placing emphasis on areas that were climatically similar to those that have already been invaded, but also highlighting areas that were analogous to those within the species' native realized niche (Broennimann and Guisan 2008).

Failure to accurately characterize responses along climatic gradients in the species' invaded ranges also resulted in low spatial transferability of ENM predictions. For example, ENMs parameterized in Hawaii and New Zealand grossly over-predicted the species' native range, and this was largely due to extrapolation in novel environmental space. Examining the native and invaded realized niches of *L. delicata* suggested that niche peripherality in the invaded range, whereby occupied environments are near the limit of the available environmental space, contributed to this extrapolation (Owens et al. 2013). Similarly, ENMs based on the native-range clades that were the sources for the New Zealand and Hawaiian introductions performed poorly when projected onto the species' invaded ranges, plausibly due to the fact that lineages occupy only a subset of their fundamental niche in their native range (i.e. cryptic niche conservatism) (Schulte et al. 2012). Thus, even if phylogenetic

lineages occupy unique realized niches, using data from the entire native range of a species is preferable to building clade-specific ENMs. These results mirror those for the invasive wall lizard *Podarcis muralis*, in which several lineages have established invasive populations outside of their native realized niches (Schulte et al. 2012). Collectively, these findings suggest that ENM predictions based on non-native populations and native-range source clades should be treated with extreme caution when dealing with non-equilibrium situations and novel climates (Elith et al. 2010, Elith 2013, Owens et al. 2013).

Our results also have implications for biosecurity efforts, as our models suggested that *L. delicata* has the potential to substantially expand its range globally. First, projecting the native-range ENM onto geographic space suggests that there is further scope for invasion in New Zealand and Hawaii. *Lampropholis delicata* is listed in New Zealand as an 'unwanted organism' under the Biosecurity Act 1993 (< www.biosecurity.govt.nz/pests/rainbow-skink >), due to its potential impact on the diverse (~100 species), but threatened (Tingley et al. 2013), endemic lizard fauna. A recent analysis of biosecurity interceptions of *L. delicata* in New Zealand (Chapple et al. 2013b) demonstrated that the species is regularly arriving (from the Auckland region or via additional introductions from Australia) in the regions of the country that we have predicted to be suitable. Thus, it may only be a matter of time before *L. delicata* fulfils its potential distribution within New Zealand. Second, our results show that *L. delicata* has the potential to invade several continents and regions beyond its current distribution in the Pacific region (e.g. Europe, north-eastern USA), including noted biodiversity and reptile hotspots such as south-east Asia, South America, central Africa, and Madagascar. The potential for *L. delicata* to outcompete native lizard species in Hawaii (Baker 1979), Lord Howe Island (Chapple et al. 2014), and New Zealand (Peace 2004) has led to biosecurity protocols being developed for the species to limit its spread within these introduced regions (Chapple et al. 2013a, b). Similar protocols should be adopted in the regions identified in the current study as being highly suitable for *L. delicata*, to prevent its continued spread across the globe. Future studies could also refine our coarse climate-driven predictions of invasion risk by incorporating microclimatic conditions (Kearney et al. 2014a, b), land-cover, and anthropogenic factors in a hierarchical framework (Pearson et al. 2004, Tingley and Herman 2009, Gallien et al. 2012).

Conclusion

Studies of realized niche shifts in alien species have made important contributions to the fields of ecology, biogeography, and conservation biology (Guisan et al. 2014), but have traditionally failed to account for the potential effects of intraspecific niche variation and different invaded-range environments on niche lability (cf. Petitpierre et al. 2012, Goncalves et al. 2014). Furthermore, only recently have studies begun to examine the extent to which niche shifts are the result of niche unfilling vs niche expansion (Petitpierre et al. 2012, Strubbe et al. 2013, 2015, Early and Sax 2014, Li et al. 2014, Tingley et al. 2014). Using multiple introductions of distinct genetic lineages to different biogeographic

realms, we have shown that there is considerable variation in the degree of realized niche expansion and unfilling across the invaded ranges of *L. delicata*. Such intraspecific variation in niche lability illustrates the importance of spatial extent in assessing realized niche shifts (Goncalves et al. 2014). Restricting our analyses to Australia and New Zealand, for example, would have led us to falsely conclude that *L. delicata* is not capable of persisting in climates that are beyond the limits of its native realized niche. Intraspecific variation in the potential for realized niche shifts has important implications not only for forecasting invasions, but for modelling any species that is not at environmental equilibrium, including species shifting their ranges as a result of environmental change, and species whose distributions are constrained by biotic interactions or anthropogenic activities (Pearman et al. 2010, Early and Sax 2014).

Our results also provide insight into the ongoing debate regarding the usefulness of ENMs for predicting invasion risk. In the case of *L. delicata*, niche unfilling was more prevalent than niche expansion in both Hawaii and New Zealand, and thus ENMs fitted to the entire native range more accurately predicted the species' Hawaiian and New Zealand distributions than ENMs based on native-range source clades or non-native populations. Further investigations into how niche change metrics influence the transferability of native-range ENMs (as in Strubbe et al. 2013) will help clarify the circumstances in which native-range data are useful for predicting invasion risk.

Acknowledgements – Research was funded by the Australian Research Council (grant to DGC, Project Number DP0771913), the National Geographic Society (grant to DGC and MBT, CRE 8085-06), the Allan Wilson Centre for Molecular Ecology and Evolution (to DGC), and a Monash Univ. School of Biological Sciences Small Grant (to DGC). RT was funded by the Australian Research Council Centre of Excellence for Environmental Decisions.

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Supplementary material (Appendix ECOG-01576 at <www.ecography.org/appendix/ecog-01576>). Appendix 1.