BIODIVERSITY RESEARCH

Invasion success of a global avian invader is explained by within-taxon niche structure and association with humans in the native range

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ABSTRACT

Aim To mitigate the threat invasive species pose to ecosystem functioning, reliable risk assessment is paramount. Spatially explicit predictions of invasion risk obtained through bioclimatic envelope models calibrated with native species distribution data can play a critical role in invasive species management. Forecasts of invasion risk to novel environments, however, remain controversial. Here, we assess how species' association with human-modified habitats in the native range and within-taxon niche structure shape the distribution of invasive populations at biogeographical scales and influence the reliability of predictions of invasion risk.

Location Africa, Asia and Europe.

Methods We use ~1200 native and invasive ring-necked parakeet (*Psittacula krameri*) occurrences and associated data on establishment success in combination with mtDNA-based phylogeographic structure to assess niche dynamics during biological invasion and to generate predictions of invasion risk. Niche dynamics were quantified in a gridded environmental space while bioclimatic models were created using the biomod2 ensemble modelling framework.

Results Ring-necked parakeets show considerable niche expansion into climates colder than their native range. Only when incorporating a measure of human modification of habitats within the native range do bioclimatic envelope models yield credible predictions of invasion risk for parakeets across Europe. Invasion risk derived from models that account for differing niche requirements of phylogeographic lineages and those that do not achieve similar statistical accuracy, but there are pronounced differences in areas predicted to be susceptible for invasion.

Main conclusions Information on within-taxon niche structure and especially association with humans in the native range can substantially improve predictive models of invasion risk. To provide policymakers with robust predictions of invasion risk, including these factors into bioclimatic envelope models is recommended.

Keywords
Bioclimatic envelope models, human influence, invasive species, niche shift, *Psittacula krameri*, risk assessment.

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Diversity and Distributions

INTRODUCTION

Biological invasions are a major global environmental and economic problem (Sala *et al.*, 2000). As eradication is frequently costly and sometimes impossible, attempting to limit the further introduction and spread of invasive species is the most effective and cost-efficient management strategy (Leung *et al.*, 2002). To identify potentially invasive species, risk assessment protocols based on species traits associated with invasiveness have been developed (Keller *et al.*, 2011). Spatially explicit predictions of invasion risk derived from bioclimatic envelope models [also referred to as species distribution models (SDM) or ecological niche models (ENM)] calibrated with native species distributions are increasingly incorporated into such invasive species risk assessments (Beaumont *et al.*, 2014). To assess potential invasion risk, bioclimatic envelope models estimate the geographical distribution of climates suitable for invasive species (Araújo & Peterson, 2012). Applications of these models to invasive species, however, fail to consider how association with human-modified habitats in the native range, a species trait strongly associated with invasion success (Keller *et al.*, 2011), might modify the distributional limits sets by climate. Also, models typically do not appreciate how the existence of phylogeographic lineages with differing niche requirements can influence forecasts of invasion risk (Pearman *et al.*, 2010). Ignoring these factors may result in mismatches between predicted potential and realized invasive distributions, fuelling doubts about the suitability of bioclimatic envelope models for anticipating biological invasions (Guisan *et al.*, 2014).

Therefore, we assess three key assumptions underlying bioclimatic envelope models: (1) that species' distributions are largely governed by climate (Araújo & Peterson, 2012), (2) that a species' current native distribution corresponds with the total set of climate conditions under which it can persist (Peterson, 2003) and (3) that the climatic niche remains conserved across time and space (Broennimann *et al.*, 2007). Climate is generally recognized as a chief driver of species' distributions at large spatial scales (Araújo & Peterson, 2012), although the broad distributional limits governed by climate may be modified by factors such as habitat availability, biotic interactions and dispersal limitations (Soberon, 2007). Erroneous predictions of the potential distribution of invasive species are often attributed to species adaptations in response to selection pressures imposed by the novel environment (Whitney & Gabler, 2008). However, within the native range, species may also evolve pre-adaptations to invasiveness; strong selection imposed by human modification of habitats within the native range is likely to lead to adaptation prior to introduction elsewhere (Hufbauer *et al.*, 2012). As human activities tend to promote similar ecological conditions across biogeographical areas (Savard *et al.*, 2000), species or populations associated with human-modified habitats in the native range can be expected to successfully invade similar areas elsewhere. It is therefore surprising that predictions of invasion risk obtained from bioclimatic envelope models have not yet explicitly considered how human modification of habitats might modify distributional limits set by climate.

Bioclimatic envelope models assume that a species' invasive distribution can be predicted from its native niche characteristics (Peterson, 2003). Niche theory indeed predicts that for relatively recent events such as biological invasions, conservatism of the fundamental native niche is expected (Peterson, 2011), although species may, in the invaded range, occupy different portions of their fundamental niche compared to the native range (Guisan *et al.*, 2014). Empirical studies on the prevalence of (realized) niche conservatism have yielded mixed results. Two large scale studies on European plants introduced to North America found niche conservatism was the dominant pattern for weedy, widespread plant species (Petitpierre *et al.*, 2012), while niche expansion into climates not occupied in the native range was common for plants with smaller native ranges (Early & Sax, 2014). Niche conservatism was the norm for non-native vertebrates introduced to Europe and North America (Strubbe *et al.*, 2013, 2014), whereas a global study on amphibians and reptiles found widespread evidence for niche expansion (Li *et al.*, 2014). To better understand the mechanisms underlying patterns of niche conservatism, here, we question the inherent assumption that pooling occurrence data from across the entire native range of a species adequately describes the full range of climatic conditions in which invasive populations can establish and survive. This assumption may be violated when phylogeographic lineages with differing niche requirements are present. Species may not represent a single evolutionary entity (Pearman *et al.*, 2010), and as species-level models smooth across environmental response curves of specific lineages, ignoring within-taxon niche structure risks erroneous predictions of a species' potential distribution (D'Amen *et al.*, 2013). Despite their potential to improve predictions of invasion risk, within-taxon niche structures have only received scant attention in invasive species management (Beaumont *et al.*, 2014).

Here, using a unique dataset on the distribution of a global avian invader, the ring-necked parakeet (*Psittacula krameri*), we test whether accounting for within-taxon niche structure and association with humans in the native range leads to more accurate predictions of invasion risk. Ring-necked parakeets are native to large parts of Africa and Asia. Across their native range, they have benefited from the conversion of natural habitats to agro-ecosystems (Bruggers & Beck, 1979; Khan, 2002) and reach their highest breeding densities near human settlements and cultivated crops (Khan *et al.*, 2004). These parakeets are a globally widespread invasive species, and they compete with native birds and bats and cause damage to crops (Strubbe & Matthysen, 2009a; Hernández-Brito *et al.*, 2014; Peck *et al.*, 2014). In this study, we present the most complete information on the distribution of ring-necked parakeets to date, comprising a set of about 1200 (686 native and 513 invasive) occurrences

collected at a finer resolution than has previously been reported, 123 failed and successful introduction events across Europe, plus a high-resolution mtDNA molecular phylogeny derived from 98 museum specimens geospatially selected to cover the parakeet's native range and from feather samples collected at 13 invaded sites across Europe. We expect that incorporating within-taxon niche structure into bioclimatic envelope models will result in important differences in the geographical distribution of climate predicted as suitable for parakeets across Europe and that accounting for association with human-modified habitats in the native range will allow for more accurate predictions of the potential European distribution of this ubiquitous avian invader.

METHODS

DNA isolation, amplification and sequencing

DNA was extracted from toe-pad samples (n = 98) collected from specimens at the Natural History Museum (Tring, UK) and from contemporary feather samples collected in Europe (n = 13 locations), using a Bioline Isolate Genomic DNA extraction kit (Bioline, UK). Finely chopped samples were suspended in 400 μl lysis buffer and 25 μl proteinase K and incubated at 55 °C overnight (or until the material had completed digested). Processing of samples from museum specimens was carried out in a dedicated museum DNA laboratory, under a UV-irradiated fume hood to destroy any contaminants. Negative controls were included to ensure no contamination during the DNA extraction and PCR procedures. Amplification of mtDNA control region and cytochrome b was conducted using a specifically designed suite of short fragment primers (see Appendix S1 in Supporting Information). Cycle parameters comprised an initial hot start of 95 °C for 1 min followed by 35 cycles of 95 °C/15 s, 52 °C/15 s and 72 °C/10 s, followed by a final 10 min 72 °C incubation-period. All amplicons were examined by agarose gel electrophoresis, and PCR product was purified and amplified using a 3730xl analyser (Applied Biosystems; Macrogen Inc., Seoul, South Korea). The concatenated DNA sequence dataset was condensed into haplotypes using the software programme 'TCS' (Clement et al., 2000).

Phylogenetic analysis

To identify native phylogroups, Bayesian phylogenetic inference was implemented in MrBayes v3.2 (Ronquist & Huelsenbeck, 2003) using the CIPRES Science Gateway (Miller et al., 2010) with 10 million generations over four parallel Monte Carlo Markov chains (MCMC), under an HKY evolutionary model (Felsenstein, 1981). Tracer v1.6 (Rambaut & Drummond, 2007) was used to assess convergence. After discarding the first 25% as burn-in, tree topologies were summarized in a 50% consensus tree. To identify native haplotypes in the invasive range, the combined native and invasive dataset was condensed into haplotypes using TCS

(Clement et al., 2000). All node values with a posterior probability of > 50 were used to identify phylogroups.

Occurrence data and environmental variables

Ring-necked parakeet occurrence data (i.e. longitude–latitude) were extracted from a range of databases [Global Biodiversity Information Facility (GBIF, www.gbif.org), ORNIS (www.ornisnet.org) and natural history museums], scientific papers and grey literature (e.g. government or NGO reports, bird trip reports and parakeet observations posted on the image hosting website Flickr.com). Occurrence data were retained only when their spatial resolution was ≤ 5′ (i.e. 0.083° or ~10 × 10 km, assessment of spatial accuracy based on information present in the source data, or through pers. comm. with observers). In the invaded range, to minimize the risk of including parakeet occurrences that do not correspond to an established population, we did not include observations from areas where evidence suggests introduced populations went extinct (see Strubbe & Matthysen, 2009b). Also, parakeet occurrences were checked against national and regional breeding bird atlases, and when in doubt about the status of a certain population, we sought advice from regional experts (through the COST Action network 'ParrotNet'). In total, we gathered 8667 ring-necked parakeet occurrences (Europe: 6634, Africa: 515, Asia: 1518), but as we used only one occurrence per grid cell, the final database comprised 1199 observations (Europe: 513, Africa: 211 and Asia: 475; Appendix S2). Data on parakeet introduction success were taken from Strubbe & Matthysen (2009b) (n = 123 introduction events). Minimum convex and Thiessen polygons circumscribing the geographical distribution of each mtDNA clade were then applied to assign parakeet occurrences to phylogroups (Appendix S2).

Environmental variables considered are a set of eight climatic variables assumed to impose direct and indirect constraints on avian distributions (Araújo et al., 2009): annual mean temperature (bio_1), mean temperature of the warmest month (t_max), mean temperature of the coldest month (t_min), temperature seasonality (bio_4), annual precipitation (bio_12), precipitation of the wettest month (bio_13), precipitation of the driest month (bio_14) and precipitation seasonality (bio_15). These variables were derived from the WorldClim database (Hijmans et al., 2005) and represent mean values over the 1961–1990 period at a 0.083° resolution. The 'human footprint' a quantitative measure of human alteration of terrestrial environments based on human population size, land use and infrastructure was derived from Sanderson et al. (2002) at a resolution of 30″ and resampled to the 0.083° resolution of the climate and parakeet occurrence data.

Niche analyses

To assess niche differences between phylogroups and between native and invasive parakeet populations, we used the

Broennimann *et al.* (2012) framework. This framework applies kernel smoothers to densities of species occurrence in a gridded environmental space to calculate metrics of niche overlap (quantified by Schoener's D, 0: no overlap, 1: complete overlap). Using a randomization test whereby the measured niche overlap is compared against a null distribution of 100 simulated overlap values, we test whether parakeet niches are more similar to each other than expected by chance (i.e. niche similarity, Broennimann *et al.*, 2012). We first assessed whether ring-necked parakeet climatic niches differed significantly between phylogroups (i.e. Africa versus Asian, and phylogroups within each continent), using all biomes occupied by parakeets across their native range as background area (Guisan *et al.*, 2014). Second, native and invasive ring-necked parakeet occurrences were used to assess whether native niche characteristics are conserved during the invasion process (using a niche similarity test), and to determine whether parakeets have colonized in the invaded range climates not occupied in the native range (i.e. niche expansion, Petitpierre *et al.*, 2012). Niche metrics are calculated on the climate space shared by native and invasive ranges (sensu Petitpierre *et al.*, 2012). Background areas should reflect the set of areas a species could potentially have encountered since its presence in the region (Barve *et al.*, 2011). Therefore, in Europe, we buffered each locality where parakeets have been introduced with a distance equal to the minimum invasion speed recorded for birds (i.e. 4.59 km year^{-1}, derived from Blackburn *et al.*, 2009) multiplied by the number of years since introduction (see Strubbe *et al.*, 2013 for details). In doing so, we obtained an ecologically realistic European background (models were also run using the whole of Europe as background, but this did not affect our main results, Appendix S3).

Bioclimatic envelope models

Bioclimatic envelope models were run in R (R Core Team, 2014) using the ensemble modelling framework biomod2 (Thuiller *et al.*, 2013). We applied five different modelling algorithms: generalized linear models (GLM), generalized boosted models (GBM), multivariate adaptive regression splines (MARS), random forest (RF) and maximum entropy (Maxent) to identify areas at risk of invasion. Models were fitted with default settings unless stated otherwise. Models were run with a single set of 10,000 pseudo-absences drawn from the same native-range background area as used for the niche analyses described above. Pseudo-absences were generated randomly from all grid cells in background area that were not presences (Wisz & Guisan 2009). For each modelling algorithm, presences and pseudo-absences used to calibrate the model were weighted such as to ensure neutral (0.5) prevalence (Petitpierre *et al.*, 2012). Each model was subjected to 10-fold cross-validation with a 80–20% random split of the presence data for training-testing each replicate, respectively. Models were evaluated using the true skill statistic (TSS), and to exclude inaccurate models, only those with

TSS > 0.7 were kept for generating ensemble projections (Thuiller *et al.*, 2013) of parakeet invasion risk in Europe, using unweighted averaging across models. Relative variable importance (0–1) was obtained through the randomization procedure described by Thuiller *et al.* (2013).

Following the procedures described above, we first fitted a 'clade' model, using as presences all native-range grid cells occupied by parakeets (i.e. occurrences pooled across all phylogroups). Then, we built separate models for each phylogroup, using as presences all occupied grid cells located within phylogroup range boundaries. A composite 'subclade' model was developed from the phylogroup predictions to summarize predictions of parakeet occurrence across all phylogroups. Because phylogroup models may differ in prevalence, to construct the subclade model, we first made the phylogroup models comparable by standardizing the average probabilities of occurrence for each phylogroup along the environmental gradients considered. Then, we calculated the mean probability of occurrence of at least one of the related phylogroups for grid cells using the multiplicative probability method described in Pearman *et al.* (2010). Clade and subclade models were fitted with and without human footprint, resulting in four different ensemble predictions of parakeet invasion risk in Europe. To exclude the possibility that differences in model performance are merely due to the adding of one predictor variable (human footprint) to the models, we also fitted models with a randomized version of the human footprint variable. To further assess the importance of human footprint, models described above were also run with the human footprint as sole predictor variable. Model transferability was assessed using European parakeet occurrence data ($n = 513$), applying the full range of evaluation statistics available in biomod2, plus two statistics specifically designed for presence-only models (the 10-fold and the continuous Boyce index, Hirzel *et al.*, 2006). To convert the continuous clade and subclade ensemble predictions of invasion risk into discrete predictions of parakeet presence and absence across Europe, an optimal TSS threshold was calculated based on the European parakeet occurrences. Lastly, a climatic multivariate environmental similarity surface (MESS) map was calculated for Europe. This map indicates areas where climatic variables occur outside the range of values contained in model training regions, and predictions of invasion risk in these areas should be treated cautiously (Elith *et al.*, 2010).

RESULTS

Phylogenetic analysis

Mitochondrial DNA sequences comprising 868 bp (cytochrome b: 346 bp, control region: 522 bp) were sampled from 98 parakeet specimens (Africa: 38, Asia: 60). In total, 44 unique haplotypes were identified (Africa: 16, Asia: 26). A Bayesian phylogenetic tree provides support for 17 haplotype clades (Africa: 6, Asia: 11; posterior probabilities > 50, i.e.

the 'phylogroups', Appendix S1). The six African phylogroups correspond to six largely parapatric groupings arranged longitudinally along the Sahel region, whereby only the most eastern phylogroups show some range overlap. The 11 Asian phylogroups, in contrast, show a much more complex spatial pattern with varying levels of range overlap between phylogroups. Phylogroup sample sizes varied from 2 to 17 specimens (mean: 6) for African phylogroups, and from 1 to 17 (mean: 6) for Asia. Note that for the niche analyses and the bioclimatic envelope models, parakeet occurrences that fell within overlapping polygons were randomly assigned to one of the polygons. That way, each lineage was represented in the overlapping area, without sampling the same data point multiple times (Kalkvik et al., 2012). Sample sizes used for modelling varied from 14 to 59 occurrences (mean: 35) for African phylogroups and from 6 to 126 (mean: 48) for Asia (Appendix S2).

Niche analyses

Assessing climatic niche positions of the different phylogroups reveals that significant within-taxon niche structure is present within both Africa and Asia (Appendix S3). Phylogroups occupy partially overlapping but distinct portions of the climate space available in the native range, and climatic niches are not more similar to each other than expected by chance (multiple niche similarity test $P > 0.05$; within Africa: niche overlap D between phylogroups equals 0.30 ± 0.19 (mean and standard deviation), range: 0.07–0.69; within Asia: $0.11 \pm 0.0.17$, range: 0.00–0.72, Appendix S3). Niche overlap between African and Asian phylogroups is low (D: 0.059), and while the African niche is more similar to the Asian niche than expected by chance (niche similarity P: 0.0099), the reverse is not true (niche similarity P: 0.14).

African ring-necked parakeet populations have only 1% of their niche outside the niche of the Asian populations, and the African niche is thus a subset of the Asian niche (Appendix S3). Niche overlap between native (i.e. Africa and Asia) and invasive (i.e. Europe) parakeet populations is low (D: 0.003). Native and invasive niches are more similar to each other than expected by chance (niche similarity P: 0.0099), yet parakeets in Europe show significant niche expansion as they have 87% of their invasive distribution outside their native climatic niche (Fig. 1). Niche differences between the native and invasive range are largely attributable to a shift along the first PCA axis of the climate space, indicating that in Europe, ring-necked parakeets have colonized areas far colder than their native range (Fig. 1). Of the 44 native-range mtDNA haplotypes, 14 (11 Asian, 3 African) were also detected in Europe. The small European sample size (i.e. feathers collected at 13 roost sites only) precluded meaningful tests of niche conservatism per haplotype (i.e. sensu Broennimann et al., 2012). Yet, given the shift towards colder climates in Europe, we hypothesized that parakeet haplotypes with a lower native cold tolerance limit should have a higher probability of persisting in Europe. We therefore, for each haplotype, in the native-range climate space, derived its cold native niche limit (i.e. minimum value along the temperature-dominated x-axis of the climate space, Fig. 1) and found that haplotypes present in Europe have significantly lower native cold niche limits than haplotypes not retrieved in Europe (t-test: $t = -4.14$, d.f. $= 15.8$, $P = 0.00079$, Appendix S4).

Bioclimatic envelope models

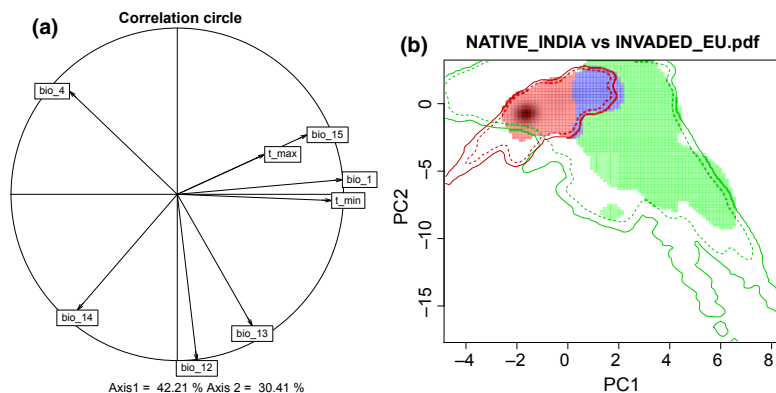When considering climatic variables only, bioclimatic envelope models that take the contribution of within-taxon niche

Figure 1 Climate niche dynamics between native and invaded ring-necked parakeet ranges. (a) Shows the contribution of the climatic variables on the two axes of the PCA and the percentage of inertia explained by the two axes. (b) Depicts ring-necked parakeet native and invasive niches. The solid and dashed contour lines illustrate, respectively, 100% and 50% of the available environment in the native range (green lines: Africa + Asia, background defined as all biomes occupied across the native range) and in the invasive range (red lines: Europe, using the ecologically realistic definition of the background, see text). Green areas represent climates only occupied in the native range and blue indicates climates occupied in both the native and non-native range, while red areas indicate niche expansion in the invaded range. Shading indicates the density of occurrences of the species by cell in the invaded range. The first PCA axis (x-axis, 42.4% of the variation) is mainly determined by temperature gradients, and the second axis (y-axis, 30.4%) chiefly represents precipitation patterns (Appendix S3).

structure (i.e. the 17 phylogroups) into account (the 'subclade' model) and those that do not (the 'clade' model) both fail to accurately predict the current invaded distribution (Fig. 2a, b), although they accurately predict parakeet occurrence across the native range (Europe: continuous Boyce index: −0.87 for the clade model vs. −0.60 for the subclade model; native range: Boyce index: 0.96 and 1.00, respectively; results are similar across a range of evaluation statistics, Appendix S5). The clade model was not successful in discriminating between failed and successful parakeet introductions to Europe (logistic regression between climatic suitability and outcome of introduction, P = 0.914), whereas the subclade model explains a modest part of the variation in introduction outcomes (*P*: 0.018, Nagelkerke R^2: 0.09, Appendix S6), mainly because it correctly predicts a higher introduction success in the Mediterranean. The MESS map (Fig. 2f) shows that parakeets have not invaded those European climates that lie outside the climatic conditions available to parakeets in their native range. This indicates that the failure of native-range climate-only models cannot be attributed to model extrapolation into unsampled environmental space.

When we included human footprint as a variable into the bioclimatic envelope models, transferability of both the clade and subclade models increased dramatically (Fig. 2c, d). Clade and subclade models that include human modification of habitats in the native range perform equally well at forecasting parakeet occurrence in Europe (Boyce index: 0.93 and 0.94, respectively). This increase in model performance is not merely due to the adding of an extra environmental variable, as models fitted with a randomized human footprint do not perform any better in predicting parakeet occurrence across Europe than climate-only models do: Boyce index −0.86 and −0.72, respectively (Appendix S5). Models built with human footprint as sole predictor variable could not adequately model ring-necked parakeet distribution across the native range (i.e. TSS of all models < 0.7 criterion, see above), precluding ensemble forecasts of invasion risk for Europe based on human footprint only. Although clade and subclade models combining human footprint and climate produced similar evaluation statistics, there are marked differences in the actual areas predicted to be suitable for parakeets (Figs 2 & 3). Whereas both models predict that parakeets will occur mainly in parts of the Mediterranean

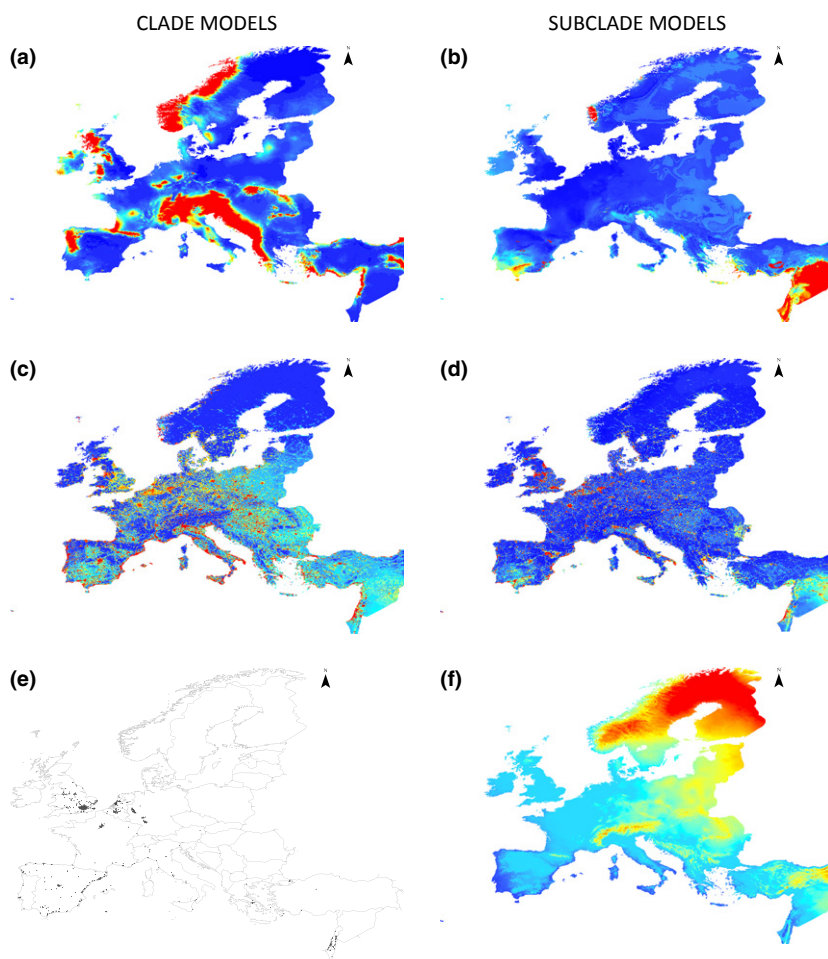CLADE MODELS   SUBCLADE MODELS

Figure 2 Predictions of invasion risk for ring-necked parakeets derived from native-range-based bioclimatic envelope models. Left versus right panes show models ignoring (a, c) and accounting for differing niche requirements of phylogeographic lineages (b, d), while upper versus lower panels depict models without (a, b) and with (c, d) human footprint. Warmer colours indicate a higher predicted risk of parakeet invasion. The black dots in (e) depict locations with established parakeet populations, used to validate native-range-based forecast of invasion risk. (f) Present the multivariate environmental similarity surface (MESS) map, whereby areas in red have one or more climatic variables outside the range present in the training data, so predictions in those areas should be treated with strong caution.
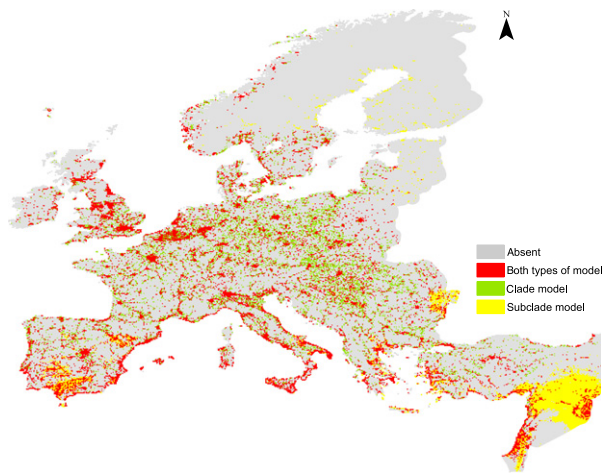
Figure 3 Predictions of invasion risk for ring-necked parakeet in Europe derived from bioclimatic envelope models including association with human-modified habitats in the native range. Continuous model outputs (Fig. 2) were converted to binary predictions of invasion risk. Areas at risk according to both models without (see Fig. 2c) and with (see Fig. 2d) phylogeographic structure are indicated in red. Green indicates predicted parakeet presence only by a model without phylogeographic structure. Yellow delineates areas only marked as suitable by a model with phylogeographic structure.

and in major human population centres in north-west Europe (designating 11% of Europe as suitable, Fig. 3), the clade model considers larger parts of central and eastern Europe as suitable for parakeets (19% of Europe, Fig. 3). The subclade model, in contrast, indicates that more extensive areas in southern Spain, Greece, Romania and parts of Turkey and the Middle East are at risk of parakeet invasion (16%, Fig. 3). After including human footprint into the models, both clade and subclade models can accurately discriminate between failed and successful parakeet introductions, although the subclade model performs better at discriminating failed introductions (clade model AIC: 126, Nagelkerke R^2: 0.37, $P < 0.0001$, false-negative rate: 0.37 vs. subclade model AIC: 121, Nagelkerke R^2: 0.41, $P < 0.0001$, false-negative rate: 0.05, Appendix S6).

Across the native range, adding human footprint did not further improve the already high accuracy of predictions of parakeet occurrence (clade model Boyce index: 1.00; subclade: 0.91), but resulted in more pronounced, fine-grained predictions, largely within the distributional limits identified by the climate-only models (Appendix S7). Analysis of variable importance reveals that human footprint is highly important in the clade model for the native range (footprint: 0.64 ± 0.12, temperature variables: 0.17 ± 0.18, range 0.10–0.30, precipitation variables: 0.12 ± 0.11, range 0.02–0.26), while the subclade model attributes more weight to temperature and precipitation gradients as well (temperature: 0.32 ± 0.16, range 0.01–0.65, precipitation: 0.21 ± 0.16, range 0.02–0.85, footprint: 0.47 ± 0.18, range 0.23–0.86, Appendix S8).

DISCUSSION

Our results support the hypothesis that association with humans in the native range may allow invasive species persistence in areas outside of their native climatic niche and that accounting for within-taxon niche structure can result in significant changes to predictions of invasion risk. Violating the key model assumptions that climate governs the broad outlines of species distributions and that within-taxon niche structure is insignificant can thus introduce substantial error into predictions of invasion risk derived from bioclimatic envelope models.

Given its strong effect on the accuracy of predictions of invasion risk, incorporating information on association with human-modified habitats in the native range should be integrated into bioclimatic envelope models, if they are to effectively guide invasive species management. Association with human-modified habitats in the native range may enable ring-necked parakeets to exploit equivalent human-modified landscapes in Europe, allowing them to colonize areas far colder than their native range. Ring-necked parakeets have almost 90% of their invasive distribution outside their native climatic niche (Fig. 1), and this is among the highest values of niche expansion known for vertebrates (Strubbe et al., 2013; Li et al., 2014). Previous studies suggest niche expansion into climates not occupied in the native range is more likely for species with small native ranges (plants, Early & Sax, 2014; amphibians and reptiles, Li et al., 2014), for species introduced longer ago or that have invaded areas located at lower latitudes than the native range (amphibians and reptiles, Early & Sax, 2014). Ring-necked parakeets, however, have a very large native range and have been introduced relatively recent (most European introductions stem from after 1970, Strubbe & Matthysen, 2009b) to much higher latitudes than their native range. Our results thus identify, for the first time, association with humans in the native range as a factor influencing climatic niche expansion during biological invasion. Climate influences species distributions directly through species' physiological tolerances or indirectly through its effect on available habitats, food resources and biotic interactions such as the presence of competitors (Araújo & Peterson, 2012, Wisz et al. 2013). The fact that ring-necked parakeets thrive in Europe suggests they may be physiologically capable of colonizing colder parts of the climate space in their native range as well. Possibly, a lack of resources and/or competition with congeneric species such as slaty-headed (P. himalayana) and Lord Derby's Parakeet (P. derbiana) restricts the ring-necked parakeets' native northernmost distribution limits. Indeed, endotherms such as birds are often able to tolerate a wide range of environmental conditions, but this comes at a potentially high energetic cost (Porter & Kearney, 2009). In Europe, radio-tracking (Clergeau & Vergnes, 2011; Strubbe & Matthysen, 2011) and habitat selection studies (Strubbe & Matthysen, 2007; Newson et al., 2010) indicate that parakeets prefer to forage in city parks and gardens, where bird feeders and ornamental vegetation present parakeets with abundant food. Urban areas also offer an

abundance of suitable nesting sites, as large, old trees are often retained for their aesthetic value. In the colder parts of Europe, parakeets increasingly breed in holes and crevices within the thermal insulation layers of buildings; in Germany, for example, such a more favourable microclimate enables them to achieve a higher breeding success compared to natural cavities (Braun, 2007). Moreover, in urban gardens, parakeets have been shown to be behaviourally dominant over native birds during foraging (Peck *et al.*, 2014). Abundant resources and a lack of competitors may underlie the invasion success of ring-necked parakeets in environments far removed from their native (realized) niche. Yet, to elucidate the extent to which thermal and energetic constraints influence ring-necked parakeet distributional limits in their native versus non-native ranges, mechanistic niche models (which use species' functional traits and physiological tolerances for model fitting, Kearney *et al.*, 2010) are required. Furthermore, although little is known about interactions between *Psittacula* species in their native range, the hypothesis of competitive release as an underlying driver of ring-necked parakeet invasion success in Europe may be tested by assessing whether predicted geographical distribution patterns across the native range (derived from bioclimatic models) match expectations under competitive exclusion (sensu Gutiérrez *et al.*, 2014).

The fact that lineages associated with cold climates in the native range are more prevalent across Europe suggests that these lineages may be better adapted to European climates. Such an invasion scenario has been found before; for example, Rey *et al.* (2012) showed that the invasion of Mediterranean Israel by the tropical ant *Wasmannia auropunctata* could be explained by adaptation to cold at the southern limit of the native range before introduction to Israel. Yet, although large numbers of parakeets from both Africa and Asia have been imported to Europe (Morgan, 1993), more detailed knowledge on propagule pressure is required to rule out alternative explanations such as the possibility that more birds originating from colder parts of the native rang have escaped or been released across Europe. Also, it should be noted that our phylogeny is based on a set of neutral genetic markers and that consequently, patterns of within-taxon niche variation may be due to regional differences in available climates, to adaptation to local environments or to other drivers such as biotic interactions. However, populations are often adapted to local environments and genotype-by-environment interactions are common in widespread species (Pearman *et al.*, 2010). This study is the first fine-scale assessment of ring-necked parakeet genetic structure, but differences among lineages in morphology and life history traits such as timing of reproduction have been reported within and between Africa and Asia (Forshaw, 1978). Such traits may be genetically based and therefore likely to respond to selection (Bradshaw & Holzapfel, 2006) in the parakeet's invasive range. Indeed, variance in laying dates between European and native (Asian) parakeet populations suggests that in Europe, parakeets are delaying their breeding in response to colder temperatures (Shwartz *et al.*, 2009). These differences

in morphology, life history and occupied climates suggest parakeet mtDNA-derived lineages may indeed diverge in features supplementary to the neutral genetic markers used to identify phylogeographic structure. Our results thus suggest the clade model captures lineage-specific responses to environmental gradients that are undetectable using the clade model (Appendix S8). Incorporating such within-taxon niche structure into bioclimatic envelope models only slightly increased model predictive accuracy, but nonetheless leads to important differences in spatial predictions of invasion risk for Europe (Figs 2 & 3). The climate-only clade model is strongly influenced by precipitation gradients (Appendix S8), resulting in erroneous predictions of parakeet occurrence for Europe's wetter areas (i.e. parts of the Atlantic and Adriatic coast, and along mountain chains, Fig. 2a). The climate-only subclade model indicates certain phylogeographic lineages indeed respond strongly to precipitation gradients (Appendix S8), although in general, the subclade model is more strongly driven by temperature gradients. The climate-only subclade model accordingly correctly predicts some of the Mediterranean parakeet populations, and except for a high precipitation zone along the coast of Norway, it assigns a low invasion risk to coastal areas and mountain chains (Fig. 2b). Both climate-only models, however, fail to accurately forecast ring-necked parakeet occurrence across north-west Europe. When including the human footprint, the major difference between the clade and subclade model is that the latter places more weight on temperature and precipitation gradients (Appendix S8), whereas the clade model exhibits a higher dependency on human footprint. Consequently, the clade model predicts a higher invasion risk across human-dominated habitats in colder parts of continental Europe (Fig. 2c, d) as well. This becomes especially apparent when converting the predictions of invasion risk into discrete predictions of parakeet presence and absence (Fig. 3), showing that particularly in east and central Europe, the clade model predicts as suitable areas that are geographically peripheral to areas predicted as suitable by the subclade model. In contrast, in southern Europe, the subclade model predicts more extensive areas to be at risk of parakeet invasion, reflecting the different weightings given by the clade and subclade model to climate and human modification of habitats.

Taken together, our results agree with other findings (Strubbe *et al.*, 2013, 2014; Early & Sax, 2014; Guisan *et al.*, 2014; Li *et al.*, 2014), suggesting that while rapid post-introduction evolution (i.e. a change in the fundamental Grinnellian niche, Soberon, 2007) cannot be ruled out, climatic niche differences between native and invasive ranges are probably related to ecological factors governing the occupancy of the fundamental niche in native versus invaded ranges. This has important ramifications for the use of bioclimatic envelope models as risk assessment tools, as well as, more fundamentally, for understanding how climate and local factors interact to determine species' distributions. Pearson & Dawson (2003) suggested a hierarchical approach to modelling environment–biota relationships whereby bioclimatic envelope models should form

the first step, identifying the broad outlines of species' distributions. Within the area designated as climatically suitable for a species, models including factors such as land cover and habitat preferences can then be applied to elucidate the fine-grained structure of distributions. We suggest that, at least for invasive species, this framework may not be universally applicable, as association with human-modified habitats in the native range may allow species to overcome their (realized) native-range climatic limitations in human-modified landscapes elsewhere. Trait-based species risk assessments consider association with human-modified habitats in the native range to be a reliable predictor of invasion success (Keller *et al.*, 2011), especially for mammals and birds (Jeschke & Strayer 2006). Our results show that applying a simple and universal variable such as the human footprint can considerably increase the accuracy of predictions of invasion risk, and this finding opens up real perspectives for devising and implementing more robust management strategies for a large number of invasive species. Information about the presence and geographical distribution of phylogeographic lineages may be not be readily available for all invasive species, but subspecies range maps can often be derived from the literature, at least for terrestrial vertebrates. Subspecies are generally based on discontinuities in the geographical distribution of phenotypic traits instead of molecular phylogenies, but can generally be considered useful proxies of patterns of divergence among populations (Phillimore & Owens, 2006). We therefore argue that, in order to provide to policymakers models that can accurately predict invasion risk, explicit evaluation of within-taxon niche structure and especially of association with humans in the native range is recommended.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Phylogenetic analyses on ring-necked parakeet museum specimens (native range) and contemporary feathers (invasive range).

Appendix S2 Native-range data on the distribution of ring-necked parakeets across their native range (haplotypes + occurrence data).

Appendix S3 Analysis of ring-necked parakeet niche dynamics within the native range and between the native and invasive range.

Appendix S4 Invasive range data on the distribution of ring-necked parakeet haplotypes in Europe.

Appendix S5 Predictions of ring-necked parakeet distribution across the native and invasive range: model evaluation statistics.

Appendix S6 Data on ring-necked parakeet introduction success in Europe.

Appendix S7 Predictions of ring-necked parakeet distribution across the native and invasive range: distribution maps.

Appendix S8 Variable importance derived from bioclimatic envelope models.

BIOSKETCH

Diederik Strubbe is a post-doc working on biological invasions. His research interests include how ecological niche models, evolution and phylogenetic information can be integrated to unravel mechanisms underlying invasion success of non-native species.

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