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

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4 Short running title: Towards better predictions of invasion risk

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26 Abstract

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

35 **Location** Africa, Asia and Europe

36 **Methods:** We use ~1,200 native and invasive ring-necked parakeet (*Psittacula krameri*)
37 occurrences and their associated data on establishment success in combination with mtDNA-
38 based phylogeographic structure to assess niche dynamics during biological invasion and to
39 generate predictions of invasion risk. Niche dynamics were quantified in a gridded
40 environmental space while bioclimatic models were created using the biomod2 ensemble
41 modelling framework.

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

49 **Main conclusions** Information on within-taxon niche structure and especially association
50 with humans in the native range can substantially improve predictive models of invasion risk.

51 In order to provide policy-makers with robust predictions of invasion risk, including these
52 factors into bioclimatic envelope models is recommended.

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

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76 (A) Introduction

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78 Biological invasions are a major global environmental and economic problem (Sala *et al.*,
79 2000). As eradication is frequently costly and sometimes impossible, attempting to limit the
80 further introduction and spread of invasive species is the most effective and cost-efficient
81 management strategy (Leung *et al.*, 2002). To identify potentially invasive species, risk
82 assessment protocols based on species traits associated with invasiveness have been
83 developed (Keller *et al.*, 2011). Spatially explicit predictions of invasion risk derived from
84 bioclimatic envelope models (also referred to as Species Distribution Models (SDM) or
85 Ecological Niche Models (ENM)) calibrated with native species distributions are increasingly
86 incorporated into such invasive species risk assessments (Beaumont *et al.*, 2014). To assess
87 potential invasion risk, bioclimatic envelope models estimate the geographical distribution of
88 climates suitable for invasive species (Araújo & Peterson, 2012). Applications of these
89 models to invasive species however fail to consider how association with human-modified
90 habitats in the native range, a species trait strongly associated with invasion success (Keller *et*
91 *al.*, 2011), might modify the distributional limits sets by climate. Also, models typically do
92 not appreciate how the existence of phylogeographic lineages with differing niche
93 requirements can influence forecasts of invasion risk (Pearman *et al.*, 2010). Ignoring these
94 factors may result in mismatches between predicted potential and realized invasive
95 distributions, fuelling doubts about the suitability of bioclimatic envelope models for
96 anticipating biological invasions (Guisan *et al.*, 2014).

97 Therefore, we assess three key assumptions underlying bioclimatic envelope models: (i) that
98 species' distributions are largely governed by climate (Araújo & Peterson, 2012), (ii) that a
99 species' current native distribution corresponds with the total set of climate conditions under
100 which it can persist (Peterson, 2003), and (iii) that the climatic niche remains conserved

101 across time and space (Broennimann *et al.*, 2007). Climate is generally recognized as a chief
102 driver of species' distributions at large spatial scales (Araújo & Peterson, 2012), although the
103 broad distributional limits governed by climate may be modified by factors such as habitat
104 availability, biotic interactions and dispersal limitations (Soberon, 2007). Erroneous
105 predictions of the potential distribution of invasive species are often attributed to species
106 adaptations in response to selection pressures imposed by the novel environment (Whitney &
107 Gabler, 2008). However, within the native range, species may also evolve pre-adaptations to
108 invasiveness; strong selection imposed by human modification of habitats within the native
109 range is likely to lead to adaptation prior to introduction elsewhere (Hufbauer *et al.*, 2012).
110 As human activities tend to promote similar ecological conditions across biogeographical
111 areas (Savard *et al.*, 2000), species or populations associated with human-modified habitats in
112 the native range can be expected to successfully invade similar areas elsewhere. It is therefore
113 surprising that predictions of invasion risk obtained from bioclimatic envelope models have
114 not yet explicitly considered how human modification of habitats might modify distributional
115 limits set by climate.

116 Bioclimatic envelope models assume that a species' invasive distribution can be predicted
117 from its native niche characteristics (Peterson, 2003). Niche theory indeed predicts that for
118 relatively recent events such as biological invasions, conservatism of the fundamental native
119 niche is expected (Peterson, 2011), although species may, in the invaded range, occupy
120 different portions of their fundamental niche compared to the native range (Guisan *et al.*,
121 2014). Empirical studies on the prevalence of (realized) niche conservatism have yielded
122 mixed results. Two large scale studies on European plants introduced to North America found
123 niche conservatism was the dominant pattern for weedy, widespread plant species (Petitpierre
124 *et al.*, 2012) while niche expansion into climates not occupied in the native range was
125 common for plants with smaller native ranges (Early & Sax, 2014). Niche conservatism was

126 the norm for non-native vertebrates introduced to Europe and North America (Strubbe *et al.*,
127 2013; Strubbe *et al.*, 2014), whereas a global study on amphibians and reptiles found
128 widespread evidence for niche expansion (Li *et al.*, 2014). To better understand the
129 mechanisms underlying patterns of niche conservatism, here, we question the inherent
130 assumption that pooling occurrence data from across the entire native range of a species
131 adequately describes the full range of climatic conditions in which invasive populations can
132 establish and survive. This assumption may be violated when phylogeographic lineages with
133 differing niche requirements are present. Species may not represent a single evolutionary
134 entity (Pearman *et al.*, 2010), and as species-level models smooth across environmental
135 response curves of specific lineages, ignoring within-taxon niche structure risks erroneous
136 predictions of a species' potential distribution (D'Amen *et al.*, 2013). Despite their potential
137 to improve predictions of invasion risk, within-taxon niche structures have only received
138 scant attention in invasive species management (Beaumont *et al.* 2014).

139 Here, using a unique dataset on the distribution of a global avian invader, the ring-necked
140 parakeet (*Psittacula krameri*), we test whether accounting for within-taxon niche structure
141 and association with humans in the native range leads to more accurate predictions of
142 invasion risk. Ring-necked parakeets are native to large parts of Africa and Asia. Across their
143 native range, they have benefited from the conversion of natural habitats to agro-ecosystems
144 (Bruggers & Beck, 1979; Khan, 2002), and reach their highest breeding densities near human
145 settlements and cultivated crops (Khan *et al.*, 2004). These parakeets are a globally
146 widespread invasive species, they compete with native birds and bats and cause damage to
147 crops (Strubbe & Matthysen, 2009a; Hernández-Brito *et al.*, 2014; Peck *et al.*, 2014). In this
148 study, we present the most complete information on the distribution of ring-necked parakeets
149 to date, comprising a set of about 1,200 (686 native and 513 invasive) occurrences collected
150 at a finer resolution than has previously been reported, 123 failed and successful introduction

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

159

160 (A) Methods

161 (B) DNA isolation, amplification and sequencing

162 DNA was extracted from toe-pad samples (n=98) collected from specimens at the Natural
163 History Museum (Tring, UK) and from contemporary feather samples collected in Europe
164 (n=13 locations), using a Bioline Isolate Genomic DNA extraction kit (Bioline, UK). Finely-
165 chopped samples were suspended in 400ul lysis buffer and 25ul proteinase K and incubated
166 at 55°C overnight (or until the material had completed digested). Processing of samples from
167 museum specimens was carried out in a dedicated museum DNA laboratory, under a UV-
168 irradiated fume hood to destroy any contaminants. Negative controls were included to ensure
169 no contamination during the DNA extraction and PCR procedures. Amplification of mtDNA
170 control region and cytochrome b was conducted using a specifically designed suite of short
171 fragment primers (see Appendix S1 in Supporting Information). Cycle parameters comprised
172 an initial hot start of 95°C for 1 minute followed by 35 cycles of 95°C/15secs, 52°C/15secs
173 and 72°C/10secs, followed by a final 10 minutes 72°C incubation period. All amplicons were
174 examined by agarose gel electrophoresis and PCR product was purified and amplified using a
175 3730xl analyser (Applied Biosystems; Macrogen Inc.). The concatenated DNA sequence

176 dataset was condensed into haplotypes using the software programme ‘TCS’ (Clement *et al.*,
177 2000).

178

179 (B) Phylogenetic analysis

180 To identify native phylogroups, Bayesian phylogenetic inference was implemented in
181 MrBayes v3.2 (Ronquist & Huelsenbeck, 2003) using the CIPRES Science Gateway (Miller
182 *et al.*, 2010) with 10 million generations over four parallel Monte Carlo Markov Chains
183 (MCMC), under an HKY evolutionary model (Felsenstein, 1981). Tracer v1.6 (Rambaut &
184 Drummond, 2007) was used to assess convergence. After discarding the first 25% as burn-in,
185 tree topologies were summarized in a 50% consensus tree. To identify native haplotypes in
186 the invasive range, the combined native and invasive dataset was condensed into haplotypes
187 using TCS (Clement *et al.*, 2000). All node values with a posterior probability of >50 were
188 used to identify phylogroups.

189

190 (B) Occurrence data and environmental variables

191 Ring-necked parakeet occurrence data (i.e. longitude-latitude) were extracted from a range of
192 databases (Global Biodiversity Information Facility (GBIF, www.gbif.org), ORNIS
193 (www.ornisnet.org) and natural history museums), scientific papers and grey literature (e.g.
194 government or NGO reports, bird trip reports and parakeet observations posted on the image
195 hosting website Flickr.com). Occurrence data were retained only when their spatial resolution
196 was $\leq 5'$ (i.e. 0.083° or $\sim 10 \times 10$ km, assessment of spatial accuracy based on information
197 present in the source data, or through pers. comm. with observers). In the invaded range, to
198 minimize the risk of including parakeet occurrences that do not correspond to an established
199 population, we did not include observations from areas where evidence suggests introduced
200 populations went extinct (see Strubbe & Matthysen, 2009b). Also, parakeet occurrences were

201 checked against national and regional breeding bird atlases, and when in doubt about the
202 status of a certain population, we sought advice from regional experts (through the COST
203 Action network ‘ParrotNet’). In total, we gathered 8,667 ring-necked parakeet occurrences
204 (Europe: 6,634, Africa: 515, Asia: 1,518), but as we used only one occurrence per grid cell,
205 the final database comprised 1,199 observations (Europe: 513, Africa: 211 and Asia: 475;
206 Appendix S2). Data on parakeet introduction success were taken from Strubbe & Matthysen
207 (2009b) (n=123 introduction events). Minimum convex and Thiessen polygons
208 circumscribing the geographic distribution of each mtDNA clade were then applied to assign
209 parakeet occurrences to phylogroups (Appendix S2).

210 Environmental variables considered are a set of eight climatic variables assumed to impose
211 direct and indirect constraints on avian distributions (Araújo *et al.*, 2009): annual mean
212 temperature (bio_1), mean temperature of the warmest month (t_max), mean temperature of
213 the coldest month (t_min), temperature seasonality (bio_4), annual precipitation (bio_12),
214 precipitation of the wettest month (bio_13), precipitation of the driest month (bio_14) and
215 precipitation seasonality (bio_15). These variables were derived from the WorldClim
216 database (Hijmans *et al.*, 2005) and represent mean values over the 1961-1990 period at a
217 0.083° resolution. The ‘human footprint’, a quantitative measure of human alteration of
218 terrestrial environments based on human population size, land use and infrastructure was
219 derived from Sanderson *et al.* (2002) at a resolution of 30’’ and resampled to the 0.083°
220 resolution of the climate and parakeet occurrence data.

221

222 (B) Niche analyses

223 To assess niche differences between phylogroups and between native and invasive parakeet
224 populations, we used the Broennimann *et al.* (2012) framework. This framework applies
225 kernel smoothers to densities of species occurrence in a gridded environmental space to

226 calculate metrics of niche overlap (quantified by Schoener's D, 0: no overlap, 1: complete
227 overlap). Using a randomization test whereby the measured niche overlap is compared
228 against a null distribution of 100 simulated overlap values, we test whether parakeet niches
229 are more similar to each other than expected by chance (i.e. niche similarity, Broennimann *et*
230 *al.*, 2012). We first assessed whether ring-necked parakeet climatic niches differed
231 significantly between phylogroups (i.e. Africa vs. Asian, and phylogroups within each
232 continent), using all biomes occupied by parakeets across their native range as background
233 area (Guisan *et al.*, 2014). Second, native and invasive ring-necked parakeet occurrences
234 were used to assess whether native niche characteristics are conserved during the invasion
235 process (using a niche similarity test), and to determine whether parakeets have colonized in
236 the invaded range climates not occupied in the native range (i.e. niche expansion, Petitpierre
237 *et al.*, 2012). Niche metrics are calculated on the climate space shared by native and invasive
238 ranges (*sensu* Petitpierre *et al.* 2012). Background areas should reflect the set of areas a
239 species could potentially have encountered since its presence in the region (Barve *et al.*,
240 2011). Therefore, in Europe, we buffered each locality where parakeets have been introduced
241 with a distance equal to the minimum invasion speed recorded for birds (i.e. 4.59 km/year,
242 derived from Blackburn *et al.*, 2009) multiplied by the number of years since introduction
243 (see Strubbe *et al.*, 2013 for details). In doing so, we obtained an ecologically realistic
244 European background (models were also run using the whole of Europe as background, but
245 this did not affect our main results, Appendix S3).

246

247 (B) Bioclimatic envelope models

248 Bioclimatic envelope models were run in R (R Core Team, 2014) using the ensemble
249 modelling framework biomod2 (Thuiller *et al.*, 2013). We applied five different modelling
250 algorithms: generalized linear models (GLM), generalized boosted models (GBM),

251 multivariate adaptive regression splines (MARS), random forest (RF) and maximum entropy
252 (MaxEnt) to identify areas at risk of invasion. Models were fitted with default settings unless
253 stated otherwise. Models were run with a single set of 10,000 pseudo-absences drawn from
254 the same native-range background area as used for the niche analyses described above.
255 Pseudo-absences were generated randomly from all grid cells in background area that were
256 not presences (Wisz & Guisan 2009). For each modelling algorithm, presences and pseudo-
257 absences used to calibrate the model were weighted such as to ensure neutral (0.5) prevalence
258 (Petitpierre et al. 2012). Each model was subjected to 10-fold cross validation with a 80-20%
259 random split of the presence data for training-testing each replicate, respectively. Models
260 were evaluated using the True Skill Statistic (TSS), and to exclude inaccurate models, only
261 those with $TSS > 0.7$ were kept for generating ensemble projections (Thuiller *et al.*, 2013) of
262 parakeet invasion risk in Europe, using unweighted averaging across models. Relative
263 variable importance (0 to 1) was obtained through the randomization procedure described by
264 Thuiller *et al.* (2013).

265 Following the procedures described above, we first fitted a ‘clade’ model, using as presences
266 all native-range grid cells occupied by parakeets (i.e. occurrences pooled across all
267 phylogroups). Then, we built separate models for each phylogroup, using as presences all
268 occupied grid cells located within phylogroup range boundaries. A composite ‘subclade’
269 model was developed from the phylogroup predictions to summarize predictions of parakeet
270 occurrence across all phylogroups. Because phylogroup models may differ in prevalence, to
271 construct the subclade model, we first made the phylogroup models comparable by
272 standardizing the average probabilities of occurrence for each phylogroup along the
273 environmental gradients considered. Then, we calculated the mean probability of occurrence
274 of at least one of the related phylogroups for grid cells using the multiplicative probability
275 method described in Pearman *et al.* (2010). Clade and subclade models were fitted with and

276 without human footprint, resulting in four different ensemble predictions of parakeet invasion
277 risk in Europe. To exclude the possibility that differences in model performance are merely
278 due to the adding of one predictor variable (human footprint) to the models, we also fitted
279 models with a randomized version of the human footprint variable. To further assess the
280 importance of human footprint, models described above were also run with the human
281 footprint as sole predictor variable. Model transferability was assessed using European
282 parakeet occurrence data (n=513), applying the full range of evaluation statistics available in
283 biomod2, plus two statistics specifically designed for presence-only models (the 10-fold and
284 the continuous Boyce index, Hirzel *et al.*, 2006). To convert the continuous clade and
285 subclade ensemble predictions of invasion risk into discrete predictions of parakeet presence
286 and absence across Europe, an optimal TSS threshold was calculated based on the European
287 parakeet occurrences. Lastly, a climatic multivariate environmental similarity surface
288 (MESS) map was calculated for Europe. This map indicates areas where climatic variables
289 occur outside the range of values contained in model training regions, and predictions of
290 invasion risk in these areas should be treated cautiously (Elith *et al.*, 2010).

291

292 (A) Results

293 (B) Phylogenetic analysis

294 Mitochondrial DNA sequences comprising 868bp (cytochrome b: 346bp, control region:
295 522bp) were sampled from 98 parakeet specimens (Africa: 38, Asia: 60). In total, 44 unique
296 haplotypes were identified (Africa: 16, Asia: 26). A Bayesian phylogenetic tree provides
297 support for 17 haplotype clades (Africa: 6, Asia: 11; posterior probabilities > 50, i.e. the
298 ‘phylogroups’, Appendix S1). The 6 African phylogroups correspond to 6 largely parapatric
299 groupings arranged longitudinally along the Sahel region, whereby only the most eastern
300 phylogroups show some range overlap. The 11 Asian phylogroups, in contrast, show a much

301 more complex spatial pattern with varying levels of range overlap between phylogroups.
302 Phylogroup sample sizes varied from 2 to 17 specimens (mean: 6) for African phylogroups,
303 and from 1 to 17 (mean: 6) for Asia. Note that for the niche analyses and the bioclimatic
304 envelope models, parakeet occurrences that fell within overlapping polygons were randomly
305 assigned to one of the polygons. That way, each lineage was represented in the overlapping
306 area, without sampling the same data point multiple times (Kalkvik *et al.*, 2012). Sample
307 sizes used for modelling varied from 14 to 59 occurrences (mean: 35) for African
308 phylogroups, and from 6 to 126 (mean: 48) for Asia (Appendix S2).

309

310 (B) Niche analyses

311 Assessing climatic niche positions of the different phylogroups reveals that significant
312 within-taxon niche structure is present within both Africa and Asia (Appendix S3).
313 Phylogroups occupy partially overlapping but distinct portions of the climate space available
314 in the native range, and climatic niches are not more similar to each other than expected by
315 chance (multiple niche similarity test P-values > 0.05; within Africa: niche overlap D
316 between phylogroups equals 0.30 ± 0.19 (mean and standard deviation), range: 0.07-0.69;
317 within Asia: $0.11 \pm 0.0.17$, range: 0.00-0.72, Appendix S3). Niche overlap between African
318 and Asian phylogroups is low (D: 0.059), and while the African niche is more similar to the
319 Asian niche than expected by chance (niche similarity P-value: 0.0099), the reverse is not
320 true (niche similarity P-value: 0.14). African ring-necked parakeet populations have only 1%
321 of their niche outside the niche of the Asian populations, and the African niche is thus a
322 subset of the Asian niche (Appendix S3). Niche overlap between native (i.e. Africa and Asia)
323 and invasive (i.e. Europe) parakeet populations is low (D: 0.003). Native and invasive niches
324 are more similar to each other than expected by chance (niche similarity P-value: 0.0099), yet
325 parakeets in Europe show significant niche expansion as they have 87% of their invasive

326 distribution outside their native climatic niche (Fig. 1). Niche differences between the native
327 and invasive range are largely attributable to a shift along the first PCA-axis of the climate
328 space, indicating that in Europe, ring-necked parakeets have colonized areas far colder than
329 their native range (Fig. 1). Of the 44 native-range mtDNA haplotypes, 14 (11 Asian, 3
330 African) were also detected in Europe. The small European sample size (i.e. feathers
331 collected at 13 roost sites only) precluded meaningful tests of niche conservatism per
332 haplotype (i.e. sensu Broennimann *et al.*, 2012). Yet, given the shift towards colder climates
333 in Europe, we hypothesized that parakeet haplotypes with a lower native cold tolerance limit
334 should have a higher probability of persisting in Europe. We therefore, for each haplotype, in
335 the native-range climate space, derived its cold native niche limit (i.e. minimum value along
336 the temperature-dominated x-axis of the climate space, Fig. 1) and found that haplotypes
337 present in Europe have significantly lower native cold niche limits than haplotypes not
338 retrieved in Europe (t-test: $t = -4.14$, d.f. = 15.8, P-value = 0.00079, Appendix S4).

339

340 (B) Bioclimatic envelope models

341 When considering climatic variables only, bioclimatic envelope models that take the
342 contribution of within-taxon niche structure (i.e. the 17 phylogroups) into account (the
343 ‘subclade’ model) and those that do not (the ‘clade’ model) both fail to accurately predict the
344 current invaded distribution (Fig. 2a,b), although they accurately predict parakeet occurrence
345 across the native range (Europe: continuous Boyce-index: -0.87 for the clade model vs. -0.60
346 for the subclade model; native range: Boyce-index: 0.96 and 1.00, respectively; results are
347 similar across a range of evaluation statistics, Appendix S5). The clade model was not
348 successful in discriminating between failed and successful parakeet introductions to Europe
349 (logistic regression between climatic suitability and outcome of introduction, $P = 0.914$)
350 whereas the subclade model explains a modest part of the variation in introduction outcomes

351 (P: 0.018, Nagelkerke R^2 : 0.09, Appendix S6), mainly because it correctly predicts a higher
352 introduction success in the Mediterranean. The MESS map (Fig. 2f) shows that parakeets
353 have not invaded those European climates that lie outside the climatic conditions available to
354 parakeets in their native range. This indicates that the failure of native-range climate-only
355 models cannot be attributed to model extrapolation into unsampled environmental space.

356 When we included human footprint as a variable into the bioclimatic envelope models,
357 transferability of both the clade and subclade models increased dramatically (Fig. 2c, d).
358 Clade and subclade models that include human modification of habitats in the native range
359 perform equally well at forecasting parakeet occurrence in Europe (Boyce index: 0.93 and
360 0.94, respectively). This increase in model performance is not merely due to the adding of an
361 extra environmental variable, as models fitted with a randomized human footprint do not
362 perform any better in predicting parakeet occurrence across Europe than climate-only models
363 do: Boyce index -0.86 and -0.72, respectively (Appendix S5). Models built with human
364 footprint as sole predictor variable could not adequately model ring-necked parakeet
365 distribution across the native range (i.e. TSS of all models < 0.7 criterion, see above),
366 precluding ensemble forecasts of invasion risk for Europe based on human footprint only.

367 Although clade and subclade models combining human footprint and climate produced
368 similar evaluation statistics, there are marked differences in the actual areas predicted to be
369 suitable for parakeets (Fig. 2, Fig. 3). Whereas both models predict that parakeets will occur
370 mainly in parts of the Mediterranean and in major human population centres in north-west
371 Europe (designating 11% of Europe as suitable, Fig. 3), the clade model considers larger
372 parts of central and eastern Europe as suitable for parakeets (19% of Europe, Fig. 3). The
373 subclade model, in contrast, indicates that more extensive areas in southern Spain, Greece,
374 Romania and parts of Turkey and the Middle East are at risk of parakeet invasion (16%, Fig.
375 3). After including human footprint into the models, both clade and subclade models can

376 accurately discriminate between failed and successful parakeet introductions, although the
377 subclade model performs better at discriminating failed introductions (clade model AIC: 126,
378 Nagelkerke R^2 : 0.37, $P < 0.0001$, false negative rate: 0.37 vs. subclade model AIC: 121,
379 Nagelkerke R^2 : 0.41, $P < 0.0001$, false negative rate: 0.05, Appendix S6).

380 Across the native range, adding human footprint did not further improve the already high
381 accuracy of predictions of parakeet occurrence (clade model Boyce-index: 1.00; subclade:
382 0.91), but resulted in more pronounced, fine-grained predictions, largely within the
383 distributional limits identified by the climate-only models (Appendix S7). Analysis of
384 variable importance reveals that human footprint is highly important in the clade model for
385 the native range (footprint: 0.64 ± 0.12 , temperature variables: 0.17 ± 0.18 , range 0.10 - 0.30,
386 precipitation variables: 0.12 ± 0.11 , range 0.02-0.26) while the subclade model attributes
387 more weight to temperature and precipitation gradients as well (temperature: 0.32 ± 0.16 ,
388 range 0.01 - 0.65, precipitation: 0.21 ± 0.16 , range 0.02 - 0.85, footprint: 0.47 ± 0.18 , range
389 0.23 - 0.86, Appendix S8).

390

391 (A) Discussion

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

398

399 Given its strong effect on the accuracy of predictions of invasion risk, incorporating
400 information on association with human-modified habitats in the native range should be

401 integrated into bioclimatic envelope models, if they are to effectively guide invasive species
402 management. Association with human-modified habitats in the native range may enable ring-
403 necked parakeets to exploit equivalent human-modified landscapes in Europe, allowing them
404 to colonize areas far colder than their native range. Ring-necked parakeets have almost 90%
405 of their invasive distribution outside their native climatic niche (Fig. 1), and this is among the
406 highest values of niche expansion known for vertebrates (Strubbe *et al.*, 2013; Li *et al.*,
407 2014). Previous studies suggest niche expansion into climates not occupied in the native
408 range is more likely for species with small native ranges (plants, Early & Sax, 2014;
409 amphibians and reptiles, Li *et al.*, 2014), for species introduced longer ago or that have
410 invaded areas located at lower latitudes than the native range (amphibians and reptiles, Early
411 & Sax, 2014). Ring-necked parakeets, however, have a very large native range and have been
412 introduced relatively recent (most European introductions stem from after 1970, Strubbe &
413 Matthysen, 2009b) to much higher latitudes than their native range. Our results thus identify,
414 for the first time, association with humans in the native range as a factor influencing climatic
415 niche expansion during biological invasion. Climate influences species distributions directly
416 through species' physiological tolerances or indirectly through its effect on available habitats,
417 food resources and biotic interactions such as the presence of competitors (Araújo &
418 Peterson, 2012). The fact that ring-necked parakeets thrive in Europe suggests they may be
419 physiologically capable of colonizing colder parts of the climate space in their native range as
420 well. Possibly, a lack of resources and/or competition with congeneric species such as slaty-
421 headed (*P. himalayana*) and Lord Derby's Parakeet (*P. derbiana*) restricts the ring-necked
422 parakeets' native northernmost distribution limits. Indeed, endotherms such as birds are often
423 able to tolerate a wide range of environmental conditions but this comes at a potentially high
424 energetic cost (Porter & Kearney, 2009). In Europe, radio-tracking (Clergeau & Vergnes,
425 2011; Strubbe & Matthysen, 2011) and habitat selection studies (Strubbe & Matthysen, 2007,

426 Newson *et al.*, 2010) indicate that parakeets prefer to forage in city parks and gardens, where
427 bird feeders and ornamental vegetation present parakeets with abundant food. Urban areas
428 also offer an abundance of suitable nesting sites, as large, old trees are often retained for their
429 aesthetic value. In the colder parts of Europe, parakeets increasingly breed in holes and
430 crevices within the thermal insulation layers of buildings; in Germany, for example, such a
431 more favourable microclimate enables them to achieve a higher breeding success compared
432 to natural cavities (Braun, 2007). Moreover, in urban gardens, parakeets have been shown to
433 be behaviourally dominant over native birds during foraging (Peck *et al.*, 2014). Abundant
434 resources and a lack of competitors may underlie the invasion success of ring-necked
435 parakeets in environments far removed from their native (realized) niche. Yet, to elucidate
436 the extent to which thermal and energetic constraints influence ring-necked parakeet
437 distributional limits in their native versus non-native ranges, mechanistic niche models
438 (which use species' functional traits and physiological tolerances for model fitting, Kearney *et*
439 *al.*, 2010) are required. Furthermore, although little is known about interactions between
440 *Psittacula* species in their native range, the hypothesis of competitive release as an
441 underlying driver of ring-necked parakeet invasion success in Europe may be tested by
442 assessing whether predicted geographic distribution patterns across the native range (derived
443 from bioclimatic models) match expectations under competitive exclusion (*sensu* Gutiérrez *et*
444 *al.*, 2014).

445

446 The fact that lineages associated with cold climates in the native range are more prevalent
447 across Europe suggests that these lineages may be better adapted to European climates. Such
448 an invasion scenario has been found before, e.g. Rey *et al.* (2012) showed that the invasion of
449 Mediterranean Israel by the tropical ant *Wasmannia auropunctata* could be explained by
450 adaptation to cold at the southern limit of the native range before introduction to Israel. Yet,

451 although large numbers of parakeets from both Africa and Asia have been imported to
452 Europe (Morgan, 1993), more detailed knowledge on propagule pressure is required to rule
453 out alternative explanations such as the possibility that more birds originating from colder
454 parts of the native range have escaped or been released across Europe. Also, it should be noted
455 that our phylogeny is based on a set of neutral genetic markers, and that consequently,
456 patterns of within-taxon niche variation may be due to regional differences in available
457 climates, to adaptation to local environments or to other drivers such as biotic interactions.
458 However, populations are often adapted to local environments and genotype-by-environment
459 interactions are common in widespread species (Pearman *et al.*, 2010). This study is the first
460 fine-scale assessment of ring-necked parakeet genetic structure, but differences among
461 lineages in morphology and life-history traits such as timing of reproduction have been
462 reported within and between Africa and Asia (Forshaw, 1978). Such traits may be genetically
463 based and therefore likely to respond to selection (Bradshaw & Holzapfel, 2006) in the
464 parakeet's invasive range. Indeed, variance in laying dates between European and native
465 (Asian) parakeet populations suggests that in Europe, parakeets are delaying their breeding in
466 response to colder temperatures (Shwartz *et al.* 2009). These differences in morphology, life-
467 history and occupied climates suggest parakeet mtDNA-derived lineages may indeed diverge
468 in features supplementary to the neutral genetic markers used to identify phylogeographic
469 structure. Our results thus suggest the clade-model captures lineage-specific responses to
470 environmental gradients that are undetectable using the clade model (Appendix S8).
471 Incorporating such within-taxon niche structure into bioclimatic envelope models only
472 slightly increased model predictive accuracy, but nonetheless leads to important differences
473 in spatial predictions of invasion risk for Europe (Fig. 2, Fig. 3). The climate-only clade
474 model is strongly influenced by precipitation gradients (Appendix S8), resulting in erroneous
475 predictions of parakeet occurrence for Europe's wetter areas (i.e. parts of the Atlantic and

476 Adriatic coast, and along mountain chains, Fig. 2a). The climate-only subclade model
477 indicates certain phylogeographic lineages indeed respond strongly to precipitation gradients
478 (Appendix S8), although in general, the subclade model is more strongly driven by
479 temperature gradients. The climate-only subclade model accordingly correctly predicts some
480 of the Mediterranean parakeet populations, and except for a high precipitation zone along the
481 coast of Norway, it assigns a low invasion risk to coastal areas and mountain chains (Fig. 2b).
482 Both climate-only models however fail to accurately forecast ring-necked parakeet
483 occurrence across north-west Europe. When including the human footprint, the major
484 difference between the clade and subclade model is that the latter places more weight on
485 temperature and precipitation gradients (Appendix S8) whereas the clade model exhibits a
486 higher dependency on human footprint. Consequently, the clade model predicts a higher
487 invasion risk across human-dominated habitats in colder parts of continental Europe (Fig. 2c,
488 2d) as well. This becomes especially apparent when converting the predictions of invasion
489 risk into discrete predictions of parakeet presence and absence (Fig. 3), showing that
490 particularly in east and central Europe, the clade model predicts as suitable areas that are
491 geographically peripheral to areas predicted as suitable by the subclade model. In contrast, in
492 southern Europe, the subclade model predicts more extensive areas to be at risk of parakeet
493 invasion, reflecting the different weightings given by the clade and subclade model to climate
494 and human modification of habitats.

495

496 Taken together, our results agree with other findings (Strubbe *et al.*, 2013; Early & Sax,
497 2014; Guisan *et al.*, 2014; Li *et al.*, 2014; Strubbe *et al.*, 2014), suggesting that while rapid
498 post-introduction evolution (i.e. a change in the fundamental Grinnellian niche, Soberon
499 2007) cannot be ruled out, climatic niche differences between native and invasive ranges are
500 probably related to ecological factors governing the occupancy of the fundamental niche in

501 native versus invaded ranges. This has important ramifications for the use of bioclimatic
502 envelope models as risk assessment tools, as well as, more fundamentally, for understanding
503 how climate and local factors interact to determine species' distributions. Pearson and
504 Dawson (2003) suggested a hierarchical approach to modelling environment-biota
505 relationships whereby bioclimatic envelope models should form the first step, identifying the
506 broad outlines of species' distributions. Within the area designated as climatically suitable for
507 a species, models including factors such as land-cover and habitat preferences can then be
508 applied to elucidate the fine-grained structure of distributions. We suggest that, at least for
509 invasive species, this framework may not be universally applicable, as association with
510 human-modified habitats in the native range may allow species to overcome their (realized)
511 native-range climatic limitations in human-modified landscapes elsewhere. Trait-based
512 species risk assessments consider association with human-modified habitats in the native
513 range to be a reliable predictor of invasion success (Keller *et al.*, 2011), especially for
514 mammals and birds (Jeschke & Strayer 2006). Our results show that applying a simple and
515 universal variable such as the human footprint can considerably increase the accuracy of
516 predictions of invasion risk, and this finding opens up real perspectives for devising and
517 implementing more robust management strategies for a large number of invasive species.
518 Information about the presence and geographical distribution of phylogeographic lineages
519 may be not be readily available for all invasive species, but subspecies range maps can often
520 be derived from the literature, at least for terrestrial vertebrates. Subspecies are generally
521 based on discontinuities in the geographical distribution of phenotypic traits instead of
522 molecular phylogenies, but can generally be considered useful proxies of patterns of
523 divergence among populations (Phillimore & Owens, 2006). We therefore argue that, in order
524 to provide to policy-makers models that can accurately predict invasion risk, explicit

525 evaluation of within-taxon niche structure and especially of association with humans in the
526 native range is recommended.

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719 Biosketches

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721 **Diederik Strubbe** is a post-doc working on biological invasions. His research interests
722 include how ecological niche models, evolution and phylogenetic information can be
723 integrated to unravel mechanisms underlying invasion success of non-native species. **Hazel**
724 **Jackson** is a PhD candidate focussing on phylogeny, biogeography and population genetics
725 of avian invaders. **Jim Groombridge** is Reader in Conservation Biology, primarily interested
726 in population restoration, population ecology, conservation genetics and evolutionary studies
727 involving phylogeny reconstruction. **Erik Matthysen** is a professor studying population
728 dynamics, genetics and behavioural ecology of animals, including birds, mammals and
729 insects. D.S. conceived the project, ran all niche analyses and bioclimatic envelope models
730 and led the writing. H.J. carried out all genetic analyses. All authors contributed substantially
731 to the writing.

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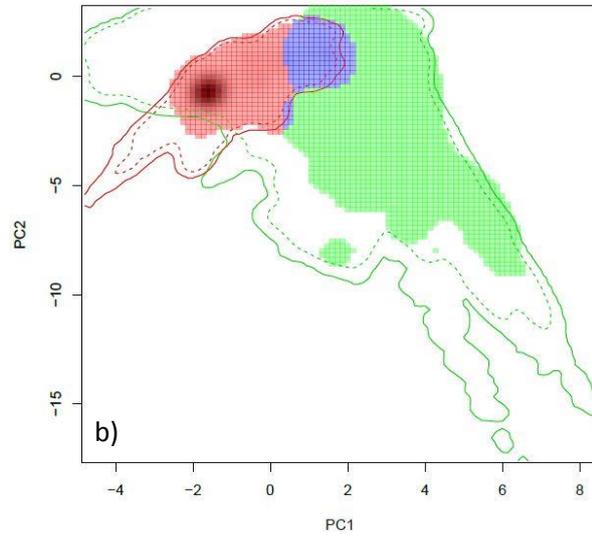
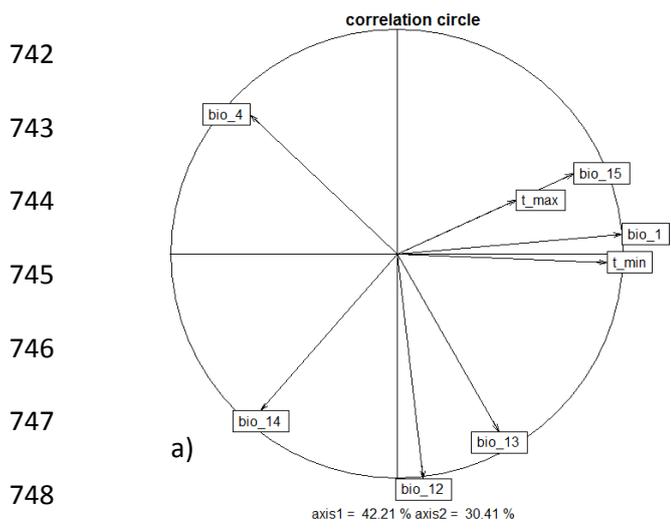
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741 Figure 1



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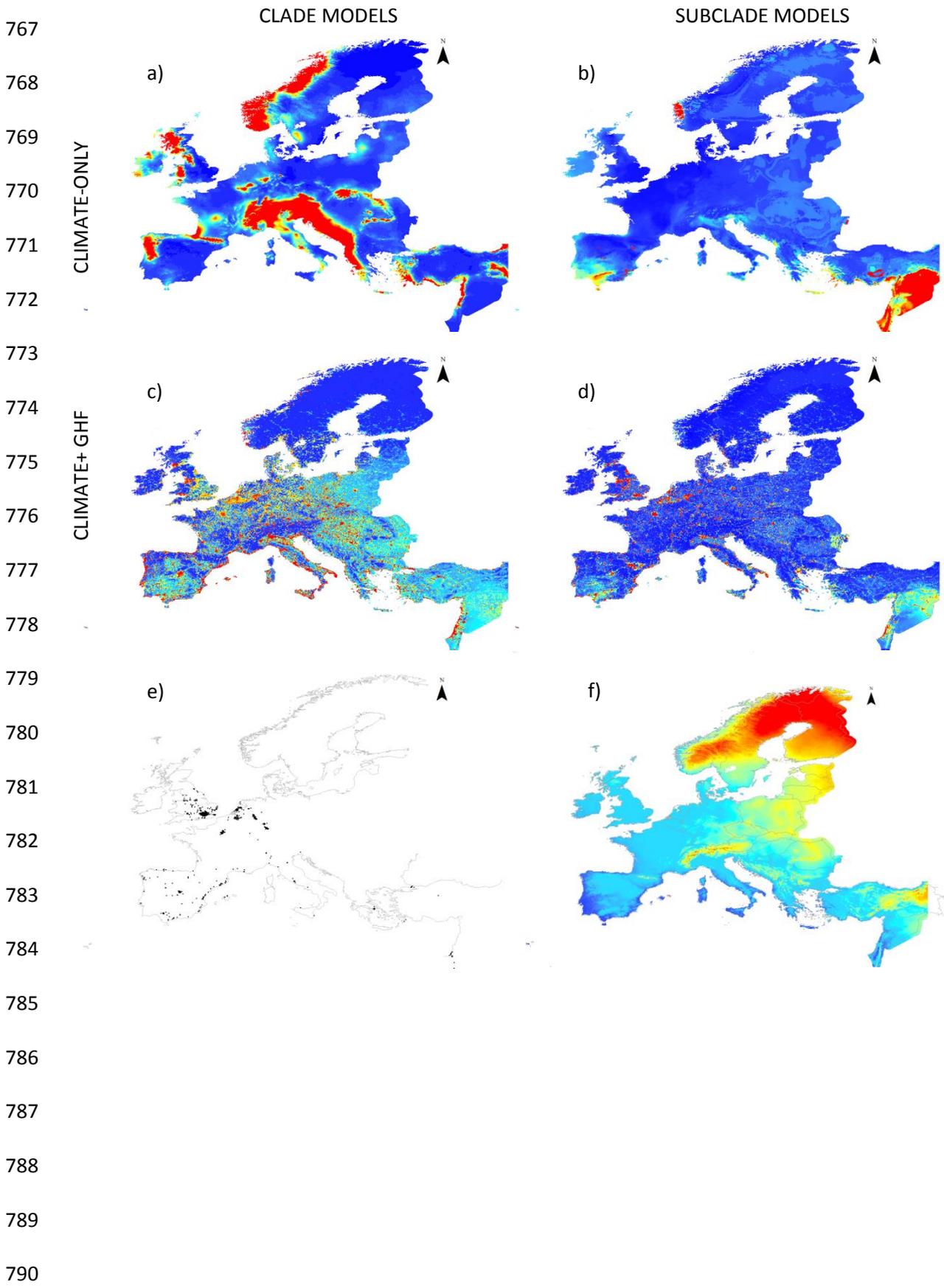
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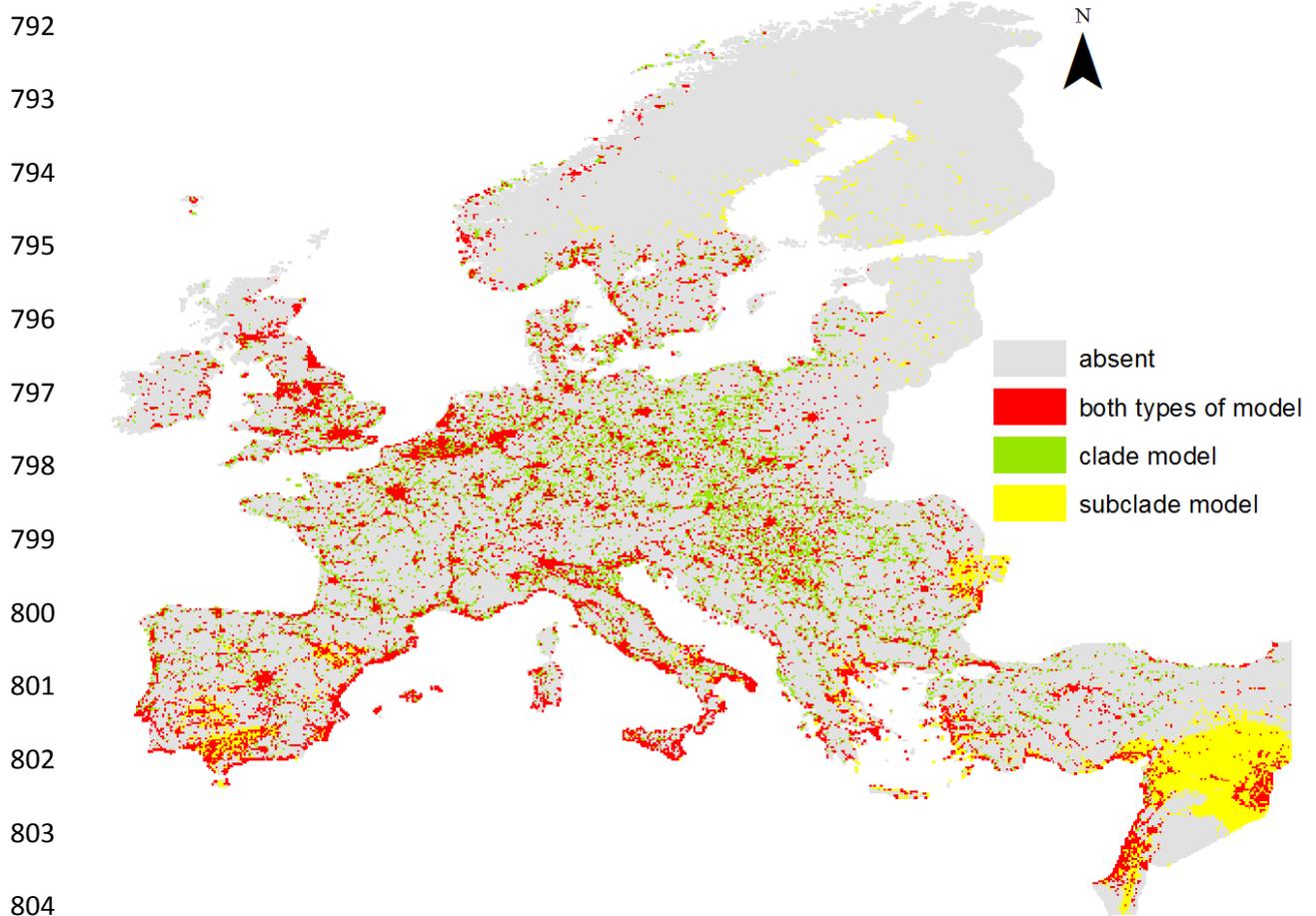
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766 Fig. 2



791 Figure 3



816 Figure legends

817 Figure 1

818 Climate niche dynamics between native and invaded ring-necked parakeet ranges. Fig. 1a
819 shows the contribution of the climatic variables on the two axes of the PCA and the
820 percentage of inertia explained by the two axes. Fig. 1b depicts ring-necked parakeet native
821 and invasive niches. The solid and dashed contour lines illustrate, respectively, 100% and
822 50% of the available environment in the native range (green lines: Africa + Asia, background
823 defined as all biomes occupied across the native range) and in the invasive range (red lines:
824 Europe, using the ecologically realistic definition of the background, see text). Green areas
825 represent climates only occupied in the native range, blue indicates climates occupied in both
826 the native and non-native range while red areas indicate niche expansion in the invaded
827 range. Shading indicates the density of occurrences of the species by cell in the invaded
828 range. The first PCA-axis (x-axis, 42.4% of the variation) is mainly determined by
829 temperature gradients, the second axis (y-axis, 30.4%) chiefly represent precipitation patterns
830 (Appendix S3).

831

832 Figure 2

833 Predictions of invasion risk for ring-necked parakeets derived from native-range based
834 bioclimatic envelope models. Left vs. right panes show models ignoring (Fig. 2a, 2c) and
835 accounting for differing niche requirements of phylogeographic lineages (Fig. 2b, 2d) while
836 upper vs lower panels depict models without (Fig. 2a, 2b) and with (Fig. 2c, 2d) human
837 footprint. Warmer colours indicate a higher predicted risk of parakeet invasion. The black
838 dots in Fig. 2e depict locations with established parakeet populations, used to validate native-

839 range based forecast of invasion risk. Fig. 2f present the MESS map, whereby areas in red
840 have one or more climatic variables outside the range present in the training data, so
841 predictions in those areas should be treated with strong caution.

842

843 Figure 3

844 Predictions of invasion risk for ring-necked parakeet in Europe derived from bioclimatic
845 envelope models including association with human-modified habitats in the native range.
846 Continuous model outputs (Fig 2) were converted to binary predictions of invasion risk.
847 Areas at risk according to both models without (see Fig. 2c) and with (see Fig. 2d)
848 phylogeographic structure are indicated in red. Green indicates predicted parakeet presence
849 only by a model without phylogeographic structure. Yellow delineates areas only marked as
850 suitable by a model with phylogeographic structure.

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860 SUPPORTING INFORMATION

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

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

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

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

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

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

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

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

875 **Appendix S8.** Variable importance derived from bioclimatic envelope models.

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