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3 An overlooked invader? Ecological niche, invasion success and range dynamics of the Alexandrine
4 parakeet in the invaded range

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28 **Abstract**

29

30 Parrots and parakeets (Aves, Psittaciformes) are prominent among avian invaders, as more than 16% of
31 living species are currently breeding with at least one population outside their native range. Most
32 studies have been carried out on ring-necked and monk parakeets, as they are the most successful
33 invasive parrots globally. Recently, however, reports of invasive Alexandrine parakeet *Psittacula*
34 *eupatria* have increased. Here, we summarize the current knowledge on the current occurrence of
35 Alexandrine parakeets outside the natural range and assess the degree of niche conservatism during the
36 invasion process. Our results show that Alexandrine parakeets have established invasive populations
37 predominantly in Europe, parts of the Middle east and Far Eastern countries such as Japan and
38 Singapore. During the ongoing invasion of Europe, the Alexandrine parakeet considerably expanded its
39 niche into colder climates with respect to those occupied in the native range. Our results offer some
40 support to the hypothesis that interspecific facilitation with previously established ring-necked
41 parakeets *Psittacula krameri* may contribute to niche expansion and invasion success of congeneric
42 Alexandrine parakeets. Species Distribution Models including both native and invaded range
43 occurrence data predict a high invasion risk across multiple parts of the globe where the species is
44 currently not yet present, thus indicating a high potential for the species for further invasion success
45 and range expansion.

46

47 **Keywords:** Interspecific facilitation, niche conservatism, Psittaciformes, *Psittacula eupatria*, range
48 expansion

49

50 **Introduction**

51

52 The most cost-effective strategy to mitigate the threat invasive species pose to biodiversity, economy
53 and human wellbeing is to prevent the introduction of species highly likely to become invasive
54 (Genovesi and Shine 2004). Therefore, several risk assessment methods have been devised. Such
55 assessments typically rely on species traits linked to invasiveness, the identification of invasion
56 pathways and increasingly include predictions of invasion risk derived from correlative Species
57 Distribution Models (Peterson et al. 2008; Peterson and Soberón 2012; Beaumont et al. 2014). SDMs

58 are statistical techniques that relate species occurrences to aspects of the environment to characterize
59 species' environmental niches (Peterson et al. 2008). SDMs estimate the geographical distribution of
60 climates suitable for invasive species to assess potential invasion risk (Araujo & Peterson, 2012). Thus,
61 a basic assumption of these models is that species' realized native environmental niches remain
62 conserved during the invasion process (Araujo & Peterson, 2012). Recent studies have documented
63 contrasting results on the prevalence of niche conservatism during invasions, potentially resulting in
64 erroneous predictions of invasion risk. For instance, niche expansion into climates not occupied in the
65 native range was found to be rare for invasive plants globally (Petitpierre et al. 2012), as well as for
66 birds introduced to Europe and Holarctic vertebrates (Strubbe et al. 2013; Strubbe et al. 2015), but it
67 was relatively common among a sample of the global invasive herpetofauna (Akmentins and Cardozo
68 2010; Nori et al. 2011; Li et al. 2014; Tingley et al. 2015) and for European plants with small native
69 ranges (Early and Sax 2014). Thus, elucidating the factors influencing the degree of niche
70 conservatism, as well as the associated reliability of SDM-derived spatially explicit forecast of invasion
71 risk, is paramount for effective invasive species management policies.

72 Birds offer an excellent opportunity to study underlying drivers of niche expansion into climates not
73 occupied in the native range. Although invasive birds generally only are relatively minor threat to
74 economy and the environment when compared to other taxa (e.g. mammals: Genovesi et al. 2009),
75 impacts may be substantial in some cases (reviewed by Kumschick and Nentwig 2010). More
76 importantly, birds are remarkably recurrent among introduced animals, with at least 973 introduced
77 species worldwide, 420 of which have currently established viable populations (Blackburn *et al.*,
78 2015). Among birds, parakeets and parrots are particularly successful as invaders (Strubbe and
79 Matthysen 2009; Mori et al. 2013). Due to their popularity as pets, about two-thirds of all parrot
80 species are commonly traded outside their natural range (Cassey et al. 2004; Menchetti and Mori
81 2014), to sustain the global pet market (Drews 2001). More than 16% of the 352 extant parrot species
82 have established exotic breeding populations worldwide (Menchetti and Mori 2014). This invasive
83 success may be attributed mainly to the high propagule pressure of species trade for the pet industry
84 (Drews 2001; Cassey et al. 2004; Blackburn et al. 2009; Mori et al. 2014), and to the behavioural
85 flexibility associated with the comparatively relative large brain size of Psittaciformes (cf. Ratcliffe et
86 al. 2006; Mason et al. 2013). Several parakeet species have built up sizeable invasive populations

87 throughout the world, and their impacts on native biodiversity, ecosystem functioning, human activities
88 and health are increasingly reported (Menchetti and Mori 2014).

89 The literature on invasive parakeets is dominated by studies on ring-necked (*Psittacula krameri*) and
90 monk parakeet (*Myiopsitta monachus*) in Europe and North America, both of which established
91 invasive populations mainly in the 1970s and 1980s (Strubbe and Matthysen 2009; Mori et al., 2013).
92 More recently, reports of populations of another parakeet invader, the Alexandrine parakeet *Psittacula*
93 *eupatria*, increased. Alexandrine parakeets are medium-sized parrots, naturally distributed from
94 Afghanistan to Vietnam, through India and Indochina, and northwards to Nepal and Bhutan (Juniper
95 and Parr 1998). Alexandrine parakeets remain rather common in parts of their native range, but a recent
96 assessment found evidence for a general rapid decline across the species' range. Subsequently, the
97 species was uplisted to "Near Threatened" by the IUCN (BirdLife International 2015), as habitat loss
98 and poaching for pet trade are likely to negatively affect populations in the near future. Alexandrine
99 parakeets in their native range mainly inhabit moist and dry forests and woodlands, but may also be
100 present in cultivated areas, mangroves and plantations (Juniper and Parr 1998). Some populations are
101 reported to persist in urban areas as well (Khera et al. 2009). Alexandrine parakeets are relatively
102 popular cage birds, and CITES trade data (see Table 1 in Appendix) indicate that between 1981 (the
103 earliest Alexandrine parakeet trade record available) and 2014, at least 57.772 Alexandrine parakeets
104 have been imported into countries outside their natural distribution range. Most Alexandrine parakeets
105 have been imported in Asia by Japan and United Arab Emirates (totalling 47.9% of all imported birds),
106 followed by European Union countries (37.2 %, with imports by Germany, Belgium and Great Britain
107 accounting for 47.7% of all European imports) and United States (3.8%). In Europe, indications of
108 rapid population growth derived from monitoring programmes and concerns about damage to
109 agriculture and competition with native cavity-nesting species have prompted invasive species risk
110 assessments for the species in Belgium and the Netherlands (Weiserbs 2009; van Kleunen et al. 2010).
111 In addition, a recent EU-wide horizon scanning exercise identified the Alexandrine parakeets as one of
112 the 95 species considered to represent a high risk of establishment, spread and threat to biodiversity
113 and associated ecosystem services across the EU within the next ten years (Roy et al. 2014).

114 Studying niche dynamics and possible underlying drivers in an early stage of the invasion process can
115 contribute to a better understanding of the factors facilitating successful invasions. Therefore, here, first
116 we summarized the current knowledge on the extant occurrence of *P. eupatria* outside its natural range,

117 reporting all information on trends and sizes of such alien populations. Furthermore, we assessed the
118 degree of niche conservatism during Alexandrine parakeet invasions and we tested two hypotheses to
119 explain observed niche changes. Strubbe et al. (2015) showed that the invasion of Europe by ring-
120 necked parakeets can be explained by ring-necked parakeet association with humans in the native
121 range, and we test whether this holds for the closely-related Alexandrine parakeet as well. Invasion
122 facilitation, i.e. positive interaction between species in the same trophic guild (Gross 2008), was
123 recently recognized as an important potential mechanism in the invasion process by alien species
124 (McIntire and Fajardo 2014). Although controversial, the invasional meltdown hypothesis (Simberloff
125 and Von Holle 1999; Simberloff 2006) postulates that positive interactions among invaders may trigger
126 positive feedback, which in turn increases impacts and promotes secondary invasions. Ring-necked and
127 Alexandrine parakeets are often found in sympatry in the invaded range, and we test whether niche
128 dynamics and invasion success of *P. eupatria* is influenced by prior presence of the congeneric *P.*
129 *krameri*. Lastly, we tested whether alternative SDM modeling strategies (i.e. models fitted with native-
130 range data only versus models based on pooled data from all the range) allow for the formulation of
131 reliable predictions of Alexandrine parakeet invasion risk throughout the globe.

132

133 **Materials and methods**

134

135 *Data sources*

136 Occurrence records of *P. eupatria* in both native and invaded range were collected through a range of
137 sources: (i) scientific papers on alien species distributions; (ii) books, ornithological reports and grey
138 literature (including observations posted on the image hosting website flickr.com); (iii) online
139 databases (i.e. iNaturalist, Global Biodiversity Information Facility (GBIF)); (iv) observations carried
140 out by experts and local birdwatchers. We accepted downloaded occurrences if they came from areas
141 known to have invasive populations of *P. eupatria* (based on the literature sources mentioned above); if
142 occurrences came from ‘unknown’ areas we assessed data reliability by contacting authors, searching
143 for literature confirming species presence or corroborated by pictures. Occurrences were only retained
144 if their spatial resolution was $\leq 5'$ (i.e. 0.083° or $\sim 10 \times 10$ km). Overall, we collected reports of free-
145 ranging *P. eupatria* for a total of 1,502 occurrences from 10 native (N = 653 records; see Table 1) and
146 22 invaded (N = 848 records) countries. Records range from single individuals, potentially being

147 occasional escapees, to well-established and increasing populations of up to a several hundreds of
148 birds. Invasive range occurrences were retained only when additional evidence (as described above)
149 indicated the presence of self-sustaining invasive populations. Before any analysis, we applied spatial
150 thinning to remove records closer than a minimum nearest neighbour distance to reduce the effect of
151 possible spatial sampling bias, using the spThin R package (Aiello-Lammens et al. 2015). This distance
152 was obtained through a SpThin automated randomization approach that varies distances in order to
153 determine the best balance between bias removal and signal weakening (e.g. the distance that
154 maximizes performance in spatially independent evaluations). The final dataset used for niche and
155 distribution modelling consisted of 210 Alexandrine parakeet occurrences (native range: 163; invasive
156 range: 47; Appendix 1).

157

158 *Environmental variables*

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

170

171 *Niche analysis*

172 We used the Broennimann et al. (2012) and Petitpierre et al. (2012) frameworks to assess whether the
173 Alexandrine parakeet’s climatic niche remains conserved during the invasion process, and to quantify
174 the extent to which any niche differences between native and invasive ranges are due to niche unfilling
175 versus niche expansion (see below). These frameworks apply kernel smoothers to densities of species
176 occurrence in a gridded environmental space to calculate metrics of niche overlap (quantified by

177 Schoener's D, 0: no overlap, 1: complete overlap). While multiple approaches have been proposed to
178 study niche dynamics based on occurrence and spatial environmental data, we opted for the
179 Broennimann et al. (2012) and Petitpierre et al. (2012) method as it has been shown to be robust
180 against variable sampling efforts and because it takes into account biases related to the dependence of
181 species occurrences on the frequency of environmental conditions that occur across geographical areas
182 (reviewed in Guisan et al. 2014). We first tested whether Alexandrine parakeet niches are more similar
183 to each other than expected by chance (i.e. test of niche similarity, Broennimann *et al.*, 2012) by using a
184 randomization test whereby the measured overlap is compared against a null distribution of 100
185 simulated overlap values. We then assessed whether Alexandrine parakeets have colonized in the
186 invaded range climates not occupied in the native range (i.e. niche expansion, defined as the proportion
187 of occurrence densities in the invasive distribution located in different climatic conditions than the
188 native distribution, Petitpierre *et al.*, 2012). Lastly, we calculated the amount of native niche unfilling
189 in the invaded range (i.e. the proportion of the densities in the native distribution located in different
190 conditions than the invasive distribution, Petitpierre et al. 2012). Niche metrics are calculated on the
191 climate space shared by native and invasive ranges (*sensu* Petitpierre et al. 2012). Background areas for
192 comparing native versus non-native niches should reflect the set of areas a species could potentially
193 have encountered since its presence in the region (Barve et al., 2011). The choice of the background
194 area can influence model outcomes (Van Der Wal et al. 2009), but appropriate backgrounds are in
195 practise difficult to delineate (Barve et al. 2011). Therefore, following Guisan et al. (2004), in the
196 native range, we extracted as background all biomes in which the species occurs, using the biome
197 classification of Olson et al. (2001). The following biomes were used to form the native range
198 background: tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf
199 forests, tropical and subtropical coniferous forests, temperate broadleaf and mixed forests, tropical and
200 subtropical grasslands, savannas, and shrublands, deserts and xeric shrublands, and finally mangroves.
201 In the invasive range, we estimated the extent of the geographical area that could have been colonized
202 by Alexandrine parakeet populations since their establishment by buffering each locality where
203 Alexandrine parakeets have been introduced with a distance equal to the minimum invasion speed
204 recorded for birds (i.e. 4.59 km/year, derived from Blackburn *et al.*, 2009) multiplied by the number of
205 years since introduction (see Strubbe *et al.*, 2013 for details). In doing so, we obtained an ecologically
206 realistic invasive-range background. For comparison, models were also run using all invaded biomes as

207 background. Thus, to robustly quantify niche dynamics during the Alexandrine parakeet invasion
208 process, we assess niche dynamics using a background area strongly defined by assumed dispersal
209 limitations during range expansion (the ecologically realistic background) versus a ‘no dispersal
210 constraints’ background (the all invaded biomes background).

211

212 *Species distribution models*

213 Species distribution models were run in R using the ensemble modelling framework biomod2 (Thuiller
214 *et al.*, 2013). We applied five different modelling algorithms: generalized linear models (GLM),
215 generalized boosted models (GBM), multivariate adaptive regression splines (MARS), random forest
216 (RF) and maximum entropy (MaxEnt) to identify areas with climates suitable for Alexandrine
217 parakeets. We ran three different modelling scenarios: (1) an SDM based on native-range occurrence
218 data and climate variables, (2) a native-range SDM with climate variables and the human footprint, (3)
219 an SDM with climate variables and pooled native and invasive range occurrence data. Models were
220 fitted with default settings unless stated otherwise. Pseudo-absences were selected using a ‘target-
221 group’ approach to limit spatial sampling biases (Philips *et al.* 2009). Therefore, for the areas covered
222 by the biome-based background used for the niche analyses described above, from the GBIF, we
223 downloaded all avian observation records. A single set of 10,000 pseudo-absences was then randomly
224 drawn from biome-based background grid cells that contained at least one bird observation and that
225 were not Alexandrine parakeet presences (following Wisz and Guisan 2009). Each model was
226 subjected to 10-fold cross validation with a 80-20% random split of the presence data for training-
227 testing each replicate, respectively.

228 We used the True Skill Statistic (TSS) for model evaluation, and only those with $TSS > 0.7$ were kept
229 for generating ensemble projections of global Alexandrine parakeet invasion risk to exclude inaccurate
230 models, using unweighted averaging across models (Thuiller *et al.*, 2013). Model transferability of the
231 two native-range occurrences only based SDMs was assessed based on the invasive-range Alexandrine
232 parakeet occurrence data ($n=47$), using the (continuous) Boyce-index (Hirzel *et al.*, 2006). The Boyce-
233 index measures how much model predictions differ from a random distribution of observed presences
234 across prediction gradients (Boyce *et al.* 2002). It is the most appropriate metric for presence-only
235 models and varies between -1 and +1. Higher values indicate better models; values close to zero
236 represent models that do not differ from random predictions model while negative values indicate

237 counter predictions. Relative variable importance (0 to 1) was obtained through the randomization
238 procedure described by Thuiller et al. (2013). Lastly, a global climatic multivariate environmental
239 similarity surface (MESS) map was calculated. This map indicates areas where climatic variables occur
240 outside the range of values contained in model training regions (here defined as the biomes in which
241 the species naturally occurs, see above), and predictions of invasion risk in these areas should be
242 treated cautiously (Elith et al. 2010).

243

244 *Interspecific facilitation*

245 We related presence or absence of *P. krameri* to *P. eupatria* invasion success using a χ^2 -test to test
246 whether the presence of previously established populations of *P. krameri* may facilitate the invasion
247 success of *P. eupatria*. To perform this test, it is necessary to define what a successful versus failed
248 Alexandrine parakeet introduction event entails. For example, the introduction of a single individual
249 cannot lead to the establishment of a self-sustaining invasive population. As detailed information on
250 Alexandrine parakeet introductions is only seldom available, we applied two contrasting scenarios
251 here. First, using a ‘liberal’ approach, we accepted as introduction event all first *P. eupatria*
252 occurrences reported in a given area, i.e. we included all “first occurrence” records, considering as a
253 “success” even isolated breeding records or limited numbers of individuals. Second, we applied a
254 “conservative” approach where we only considered as “success” those populations designated as
255 established (i.e. self-sustaining) according to local experts and published data.

256

257 **Results**

258

259 *Presence of invasive Alexandrine parakeet populations*

260 Recorded alien populations of *P. eupatria* varied in their status and size. Largest populations in Europe
261 are found in Belgium (Brussels: Weiserbs and Jacob 2007), Germany (Köln: Bauer and Woog 2008)
262 and the Netherlands (Amsterdam: Van Kleunen et al. 2010), each comprising 100-300 individuals and
263 showing an increasing trend. Reproductive events are also reported from Greece (Crete: Panagiotys
264 Kouvropalos, personal communication 2012) and Italy (Rome: Angelici and Fiorillo 2015). Several
265 self-sustaining colonies are also present in the Middle East: Turkey (Istanbul: Yassin Darvish, personal
266 communication 2015), United Arab Emirates (Jennings 2010) and Iran (Tehran: Khaleghizadeh et al.

267 2004), with smaller nuclei being reported in Algeria (Fahroud Kassal, personal communication 2015),
268 Saudi Arabia (Jennings 2004; Lever 2005) and Qatar (Jennings 2010). Breeding populations are also
269 present in Hong Kong (Holt 2006) and Tokyo (Kawakami and Kanouchi 2012), but no data are
270 available on population trends and size. Single records of isolated individuals also come from
271 Australia, Poland, Morocco, Israel, Spain, Canary Islands, China and USA. First records of
272 Alexandrine parakeet breeding outside the native range of the species are all relatively recent (see
273 Appendix), some dating back to early 80's (Germany, Bahrain), but most populations have been
274 reported since the mid 90's (e.g. UK, Belgium, Netherlands, Iran) or later (e.g. Japan). While most
275 populations detected are reportedly increasing in numbers and expanding their ranges, there is also
276 evidence of local extinctions in the invaded range: the flock in Merseyside (UK) was reportedly shot
277 (Butler 2002) and no recent record is available after that, as well as at other sites in UK where the
278 species was detected; the status of populations in Yemen and Bahrein is also uncertain as they both
279 may be extinct, after assessments in 2003 and 2015, respectively. For a detailed country-by-country
280 assessment and history of invasion, see Appendix.

281

282 *Niche conservatism and predictions of invasion risk*

283 When considering climatic variables only, native-range based SDMs cannot accurately predict the
284 invasive distribution of Alexandrine parakeets (Boyce-index: -0.70 when measured against the biome
285 background, -0.59 against the ecologically realistic background) while they do accurately model the
286 species' native distribution (Boyce-index: 0.93, Fig 1a). Adding human footprint to the model does not
287 improve model transferability (Boyce-index: -0.70 and -0.86; 0.97 for the native-range, Fig. 1b).
288 Variable importance (Table 1) shows that both models with and without human footprint are mainly
289 influenced by temperature gradients, which are > 50% more important than precipitation variables.
290 Human footprint contributes little to model performance (i.e. variable importance of only 0.07 ± 0.06).
291 When pooling native and invasive occurrence data, SDMs accurately capture both the native and
292 invasive Alexandrine parakeet occurrences (Boyce-index 0.93 and 0.90, Fig. 1c). When pooling
293 occurrence data, precipitation variables become more important than temperature gradients. The MESS
294 map (Fig. 1d) shows that Alexandrine parakeets have not invaded climates that lie outside the climatic
295 conditions available to parakeets in their native range. This indicates that the failure of native-range
296 climate-only models cannot be attributed to model extrapolation into unsampled environmental space.

297 Niche analyses were conducted in a gridded environmental space formed by the first two axes of a
298 Principal Component Analysis on the eight climatic variables applied here. These axes explained 78.6
299 to 81.4% of the inertia (biome background axis 1: 49.0%, axis 2 = 29.6 %, ecologically realistic
300 background: axis 1: 50.4%, axis 2: 31.0 %). In both cases, the first PCA axis is dominated by
301 temperature gradients while the second axis predominantly represents precipitation gradients (Table 2).
302 Niche overlap between native and invasive Alexandrine parakeet populations is low (D: 0.14 for the
303 biome background, 0.13 for the ecologically realistic background), yet tests of niche similarity show
304 that, independent of the background area used, Alexandrine parakeet invasive niches are more similar
305 to the native niche than expected by chance (P-value < 0.05). Despite this evidence for niche
306 conservatism, invasive Alexandrine parakeets show significant niche expansion as they have 65 to 67%
307 of their invasive distribution outside their native climatic niche (Fig. 2). Niche differences between the
308 native and invasive range are largely attributable to a shift along the first PCA-axis of the climate
309 space, indicating that during the invasion process, Alexandrine parakeets have colonized areas far
310 colder than their native range. Niche unfilling varies from 53% (biome background, Fig. 2a) to 8%
311 (ecologically realistic background, Fig. 2b).

312

313 *Interspecific facilitation*

314 We collected a total of 37 “first occurrence” records. The presence of *P. krameri* in the area of *P.*
315 *eupatria* “first occurrence” records positively affected the success of *P. eupatria* under the “liberal”
316 scenario ($\chi^2= 4.75$, $p=0.043$), with *P. eupatria* reproduction being more frequently observed (n=23) in
317 areas where *P. krameri* colonies already occurred. However, under the conservative scenario, the
318 positive influence of *P. krameri* on *P. eupatria* invasion success fails to reach statistical significance,
319 possibly because of the lower sample size of this test (n=19, $\chi^2= 2.65$, $p=0.1$).

320 Noticeably, hybrids and mixed-species breeding pairs were also reported in some of the areas (n=6)
321 where the parental species co-occur.

322

323

324 **Discussion**

325

326 Increasing numbers of *P. eupatria* populations are establishing outside the species' native range,
327 particularly in Europe and in the Middle East. While the invaded areas in the Middle East have
328 climates largely similar to parts of the Alexandrine parakeet's native range, during the ongoing
329 invasion of Europe, this parakeet has considerably expanded its niche into climates much colder than
330 those occupied in the native range. Strubbe et al. (2015) suggested that parakeet invasions into colder
331 climates may be explained by "prior-adaptation" to human-modified habitats in the native range (cf.
332 Hufbauer et al. 2012). For example, including the human footprint variable into native-range SDMs
333 considerably increased the accuracy of predictions of invasion risk for ring-necked parakeets,
334 suggesting that association with humans in the native range facilitates their persistence in areas outside
335 of their native climatic niche. This seems not to be true for Alexandrine parakeets, as models with and
336 without the human footprint have a similarly low predictive accuracy. This may be due to ecological
337 differences between these two *Psittacula* species; ring-necked parakeets have benefited from the
338 conversion of natural habitats to agro-ecosystems and now reach their highest breeding densities in
339 urban areas (Khan 2002; Khan et al. 2004). Although occasionally reported also in urban areas in the
340 native range, Alexandrine parakeets are considered to be more sensitive to human-induced habitat
341 alterations, as is also suggested by its IUCN status (BirdLife International 2015). Recent studies
342 suggest niche expansion is rare for species with large native ranges and broad environmental niches
343 (Capiñha et al. 2014; Early and Sax 2014; Li et al. 2014), while contrasting results have been found for
344 residence time in the native range. Li et al. (2014) found that niche expansion was more likely for
345 amphibians and reptiles introduced earlier into a new range, whereas Early and Sax (2014) found that
346 time since introduction decreased niche expansion for European plants introduced to North America.
347 These results do not help explaining the niche expansion into colder climates shown by Alexandrine
348 parakeets, whose native range is rather wide (Juniper and Parr 1998), and whose first introductions
349 mostly date back to the early 1990s (this manuscript). Our results offer statistically weak but clear
350 support to the hypothesis that interspecific facilitation with *P. krameri* may contribute to niche
351 expansion and invasion success of *P. eupatria*. These two parakeet species, which are closely related
352 and rather similar in appearance, may form mixed-species flocks and/or join communal roost sites.
353 Single individuals or small nuclei of *P. eupatria* may potentially benefit of this association by predator

354 avoidance (*sensu* Weatherhead 1983) and/or information transfer (e.g. on foraging, nesting and
355 roosting locations; *sensu* Ward and Zahavi 1973) from an established population of *P. krameri*. Such
356 associations, together with parrot longevity (Costantini et al. 2008), may also increase individual
357 survival, potentially giving single *P. eupatria* more chances to encounter potential partners, e.g. after
358 new releases. Empirical observations on sympatric invasive Alexandrine and ring-necked parakeets are
359 scarce. Weiserbs and Jacob (2007) mention that in Brussels, following introduction, Alexandrine
360 parakeets joined ring-necked parakeet flocks. At least during the breeding season, both parakeet
361 species were most often observed in monospecific rather than mixed species flocks (authors, personal
362 observations), even though Claes and Matthysen (2005) reported that Alexandrine parakeets were
363 dominant over ring-necked parakeets at bird feeders. Also in Brussels, Alexandrine parakeets
364 commonly breed in tree cavities previously occupied by ring-necked parakeets (Diederik Strubbe,
365 personal observations), and such cavity-takeovers have also been reported from Wiesbaden, Germany
366 (Detlev Franz, personal communication). We can however not rule out alternative explanations. Urban
367 bird feeding has recently been shown to particularly benefit introduced bird species (Galbraith et al.
368 2015), and more empirical studies are necessary to determine which ecological and/or behavioural
369 mechanisms underlie Alexandrine parakeet invasion success in colder climates, and the extent to which
370 interactions with previously established ring-necked parakeets matter. It should also be noted that while
371 hybridization between ring-necked and Alexandrine parakeets seems to be uncommon in the native
372 range, it frequently occurs in captivity and has been reported several times in the invaded range.
373 Hybrids of the first generation are fertile (Krause 2004) and present intermediate morphological
374 features between *P. krameri* and *P. eupatria* (Krause 2004), i.e. intermediate size between the parental
375 species and orange to light-brown wing patch (absent in *P. krameri* and deep red in *P. eupatria*).

376 When SDMs trained on only the native range fail to predict the full extent of a species invasion, an
377 alternative modelling strategy is to fit models using data from both native and invaded ranges. This
378 ensures reliable predictions of invasion risk in areas of the invaded range that are not yet invaded but
379 where suitable conditions similar to the native range occur (Broennimann and Guisan 2008).
380 Alexandrine parakeet models including both native and invaded range occurrence data predict high
381 habitat suitability, i.e. higher invasion risk, in extended areas where the species is currently not (yet)
382 present, e.g. large parts of the Mediterranean basin, Central America and Australia. The widespread
383 availability of currently unoccupied but suitable habitats indicates a high potential for the species for

384 further range expansion in the invaded range. *P. eupatria* is a popular pet throughout the globe and is
385 thus commonly being highly available in pet shops. Although being generally more expensive than
386 other parakeets (e.g. ring-necked and monk parakeets), it is also large sized (wing length up to 26 cm)
387 and produces loud, noisy calls, all factors that may lead owners to abandon their pet and facilitate
388 escapes. Such a potentially high propagule pressure (Duncan et al. 2003), paired with possible
389 facilitation by *P. krameri* colonies, suggests that *P. eupatria* may be able to colonize the ample suitable
390 habitats available to it in the invaded range in the near future. Once introduced and established with
391 viable populations, invasive alien species are generally difficult to eradicate and their management
392 generally is highly expensive (Kolar and Lodge 2001). Currently, the Alexandrine parakeet is
393 considered an invasive species in Belgium and the Netherlands, largely because of its relatively rapid
394 population growth and geographical spread. Such rapid growth has also been reported from Germany,
395 e.g. the population of an urban park in Köln increased from 8 original pairs to about 200 individuals in
396 less than 20 years (Detlev Franz personal communication). The increasing numbers of breeding records
397 in new countries presented here and the fact that most known breeding populations were only recently
398 reported, predominantly between the last 10-15 years, suggests that an invasion process is already on-
399 going at a large scale. During a recent EU-level workshop aimed at prioritising invasive alien species
400 prevention efforts through horizon scanning, experts unanimously agreed that Alexandrine parakeets
401 should be considered as a high priority species for risk assessment. The experts listed competition for
402 nesting cavities with native species, disease transmission, damage to agriculture and interactions with
403 other invasive species as major mechanisms through which Alexandrine parakeets are likely to threaten
404 biodiversity and ecosystem services (Roy et al. 2014). Impacts such as crop and tree damage as well
405 as competition with cavity-dwelling wildlife (e.g. birds and bats) have already been extensively
406 reported for the congeneric ring-necked parakeet (e.g. Strubbe and Matthysen 2009; Williams et al.
407 2010; Hernandez-Brito et al. 2014; Menchetti et al. 2014), and this study suggests that interactions
408 between Alexandrine parakeets and other invasive species (such as ring-necked parakeets) are indeed
409 likely.

410 This study thus contributes to inform conservation planning for invasive alien parrots, highlighting the
411 importance to focus on species at an early stage of the invasion process, when management actions
412 may still be affordable and potentially successful. The Alexandrine parakeet is currently not considered
413 a major threat, and consequently environmental agencies may overlook its presence and associated

414 risks. Our study corroborates the EU horizon scanning findings on the potential for invasiveness of this
415 parakeet species. Given the ample climatically suitable habitat available to the species revealed by
416 distribution models calibrated on combined native and invasive range occurrence data, future increases
417 in numbers and geographical spread across favourable areas throughout its invaded range are likely.
418 Management options aimed at limiting further population growth or even population removal should
419 thus be evaluated.

420

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422

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430

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599

600 **Tables**

601

602 Table 1 – SDM Variable Importance

| | Native climate | range: Native range: human footprint | climate + Native and invasive range pooled: climate |
|---------------------------------------|-------------------|--|---|
| annual mean temperature | 0.47 ± 0.31 | 0.49 ± 0.30 | 0.22 ± 0.23 |
| temperature seasonality | 0.41 ± 0.36 | 0.41 ± 0.36 | 0.35 ± 0.32 |
| mean temperature of the warmest month | 0.31 ± 0.25 | 0.28 ± 0.23 | 0.38 ± 0.26 |
| mean temperature of the coldest month | 0.27 ± 0.26 | 0.27 ± 0.25 | 0.23 ± 0.21 |
| annual precipitation | 0.18 ± 0.14 | 0.19 ± 0.14 | 0.45 ± 0.17 |
| precipitation of the wettest month | 0.22 ± 0.18 | 0.21 ± 0.20 | 0.53 ± 0.32 |
| precipitation of the driest month | 0.14 ± 0.13 | 0.12 ± 0.10 | 0.22 ± 0.21 |
| precipitation seasonality | 0.35 ± 0.19 | 0.34 ± 0.21 | 0.38 ± 0.18 |
| human footprint | | 0.07 ± 0.06 | |

603

604

605 Table 2 – Principle Component Analyses Variable Contributions

606

| | Biome background | | Ecologically realistic background | |
|---------------------------------------|------------------|--------|-----------------------------------|--------|
| | axis 1 | axis 2 | axis 1 | axis 2 |
| annual mean temperature | 0.48 | 0.13 | 0.48 | -0.11 |
| temperature seasonality | -0.42 | 0.20 | -0.28 | 0.41 |
| mean temperature of the warmest month | 0.36 | 0.35 | 0.45 | 0.11 |
| mean temperature of the coldest month | 0.48 | 0.01 | 0.44 | -0.24 |
| annual precipitation | 0.19 | -0.58 | -0.13 | -0.58 |
| precipitation of the wettest month | 0.25 | -0.48 | -0.01 | -0.54 |
| precipitation of the driest month | -0.12 | -0.47 | -0.32 | -0.34 |
| precipitation seasonality | 0.34 | 0.18 | 0.41 | 0.09 |

607 **Figure captions**

608

609 **Figure 1.** Predictions of invasion risk for Alexandrine parakeets obtained from ensemble SDMs. Fig.
610 1a represents a native-range based model employing climate variables only, Fig. 1b is native-range
611 model combining climate variables and the human footprint. Fig. 1c pictures invasion risk derived from
612 a climate-only model built by pooling both native and invasive range occurrence data. Warmer colours
613 indicate higher predicted habitat suitability. Fig. 1d presents the MESS map, whereby areas in red have
614 one or more climatic variables outside the range present in the training data, so predictions in those
615 areas should be treated with strong caution. Fig. 1e shows the occurrence data used in the analyses
616 (after spatial thinning), green: native range occurrences (n=163), red: invasive range occurrences
617 (n=47).

618

619 **Figure 2.** Climate niche dynamics between native and invaded Alexandrine parakeet ranges. Fig. 1a
620 represent the climate space of the biome background, Fig. 2b the ecologically realistic background (see
621 text). The solid and dashed contour lines illustrate, respectively, 100% and 50% of the available
622 environment in the native range (green lines) and in the invasive range (red lines). Green areas
623 represent climates only occupied in the native range, blue indicates climates occupied in both the native
624 and non-native range while red areas indicate niche expansion in the invaded range. Shading indicates
625 the density of occurrences of the species by cell in the invaded range. The first PCA-axes are mainly
626 determined by temperature gradients, the second axes chiefly represent precipitation patterns (Table 2).