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

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

Keywords Interspecific facilitation · Niche conservatism · Psittaciformes · *Psittacula eupatria* · Range expansion

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Introduction

The most cost-effective strategy to mitigate the threat invasive species pose to biodiversity, economy and human wellbeing is to prevent the introduction of species highly likely to become invasive (Genovesi and Shine 2004). Therefore, several risk assessment methods have been devised. Such assessments typically rely on species traits linked to invasiveness, the identification of invasion pathways and increasingly include predictions of invasion risk derived from correlative Species Distribution Models (Peterson et al. 2008; Peterson and Soberón 2012; Beaumont et al. 2014). SDMs are statistical techniques that relate species occurrences to aspects of the environment to characterize species' environmental niches (Peterson et al. 2008). SDMs estimate the geographical distribution of climates suitable for invasive species to assess potential invasion risk (Araujo and Peterson 2012). Thus, a basic assumption of these models is that species' realized native environmental niches remain conserved during the invasion process (Araujo and Peterson 2012). Recent studies have documented contrasting results on the prevalence of niche conservatism during invasions, potentially resulting in erroneous predictions of invasion risk. For instance, niche expansion into climates not occupied in the native range was found to be rare for invasive plants globally (Petitpierre et al. 2012), as well as for birds introduced to Europe and Holarctic vertebrates (Strubbe and Matthysen 2013; Strubbe et al. 2015), but it was relatively common among a sample of the global invasive herpetofauna (Akmentins and Cardozo 2010; Nori et al. 2011; Li et al. 2014) and for European plants with small native ranges (Early and Sax 2014). Thus, elucidating the factors influencing the degree of niche conservatism, as well as the associated reliability of SDM-derived spatially explicit forecast of invasion risk, is paramount for effective invasive species management policies.

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

The literature on invasive parakeets is dominated by studies on ring-necked (*Psittacula krameri*) and monk parakeet (*Myiopsitta monachus*) in Europe and North America, both of which established invasive populations mainly in the 1970s and 1980s (Strubbe and Matthysen 2009; Mori et al. 2013). More recently, reports of populations of another parakeet invader, the Alexandrine parakeet *Psittacula eupatria*, increased. Alexandrine parakeets are medium-sized parrots, naturally distributed from Afghanistan to Vietnam, through India and Indochina, and northwards to Nepal and Bhutan (Juniper and Parr 1998). Alexandrine parakeets remain rather common in parts of their native range, but a recent assessment found evidence for a general rapid decline across the species' range. Subsequently, the species was uplisted to "Near Threatened" by the IUCN (BirdLife International 2015), as habitat loss and poaching for pet trade are likely to negatively affect populations in the near future. Alexandrine parakeets in their native range mainly inhabit moist and dry forests and woodlands, but may also be present in cultivated areas, mangroves and plantations (Juniper and Parr 1998). Some populations are reported to persist in urban areas as well (Khera et al. 2009). Alexandrine parakeets are relatively popular cage birds, and CITES trade data

(see Table 1 in Appendix of supplementary material) indicate that between 1981 (the earliest Alexandrine parakeet trade record available) and 2014, at least 57,772 Alexandrine parakeets have been imported into countries outside their natural distribution range. Most Alexandrine parakeets have been imported in Asia by Japan and United Arab Emirates (totalling 47.9 % of all imported birds), followed by European Union countries (37.2 %, with imports by Germany, Belgium and Great Britain accounting for 47.7 % of all European imports) and United States (3.8 %). In Europe, indications of rapid population growth derived from monitoring programmes and concerns about damage to agriculture and competition with native cavity-nesting species have prompted invasive species risk assessments for the species in Belgium and the Netherlands (Weiserbs 2009; van Kleunen et al. 2010). In addition, a recent EU-wide horizon scanning exercise identified the Alexandrine parakeets as one of the 95 species considered to represent a high risk of establishment, spread and threat to biodiversity and associated ecosystem services across the EU within the next 10 years (Roy et al. 2015).

Studying niche dynamics and possible underlying drivers in an early stage of the invasion process can contribute to a better understanding of the factors facilitating successful invasions. Therefore, here, first we summarized the current knowledge on the extant occurrence of *P. eupatria* outside its natural range, reporting all information on trends and sizes of such alien populations. Furthermore, we assessed the degree of niche conservatism during Alexandrine parakeet invasions and we tested two hypotheses to explain observed niche changes. Strubbe et al. (2015) showed that the invasion of Europe by ring-necked parakeets can be explained by ring-necked parakeet association with humans in the native range, and we test whether this holds for the closely-related Alexandrine parakeet as well. Invasion facilitation, i.e. positive interaction between species in the same trophic guild (Gross 2008), was recently recognized as an important potential mechanism in the invasion process by alien species (McIntire and Fajardo 2014). Although controversial, the invasional meltdown hypothesis (Simberloff and Von Holle 1999; Simberloff 2006) postulates that positive interactions among invaders may trigger positive feedback, which in turn increases impacts and promotes secondary invasions. Ring-necked and Alexandrine parakeets are often found in sympatry in the invaded range, and we test whether niche dynamics and invasion success of *P. eupatria* is influenced by prior presence of the congeneric *P. krameri*. Lastly, we tested whether alternative SDM modeling strategies (i.e. models fitted with native-range data only vs. models based on pooled data from all the range) allow for the formulation of reliable predictions of Alexandrine parakeet invasion risk throughout the globe.

Materials and methods

Data sources

Occurrence records of *P. eupatria* in both native and invaded range were collected through a range of sources: (1) scientific papers on alien species distributions; (2) books, ornithological reports and grey literature (including observations posted on the image hosting website flickr.com); (3) online databases [i.e. iNaturalist, Global Biodiversity Information Facility (GBIF)]; (4) observations carried out by experts and local birdwatchers. We accepted downloaded occurrences if they came from areas known to have invasive populations of *P. eupatria* (based on the literature sources mentioned above); if occurrences came from 'unknown' areas we assessed data reliability by contacting authors, searching for literature confirming species presence or corroborated by pictures. Occurrences were only retained if their spatial resolution was $\leq 5'$ (i.e. 0.083° or $\sim 10 \times 10$ km). Overall, we collected reports of free-ranging *P. eupatria* for a total of 1502 occurrences from 10 native (N = 653 records; see Table 1) and 22 invaded (N = 848 records) countries. Records range from single individuals, potentially being occasional escapees, to well-established and increasing populations of up to a several hundreds of birds. Invasive range occurrences were retained only when additional evidence (as described above) indicated the presence of self-sustaining invasive populations. Before any analysis, we applied spatial thinning to remove records closer than a minimum nearest neighbour distance to reduce the effect of possible spatial sampling bias, using the spThin R package (Aiello-Lammens et al. 2015). This distance was obtained through a SpThin automated randomization approach that varies distances in order to determine the best balance between bias removal

Table 1 SDM variable importance

	Native range: climate	Native range: climate + human footprint	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	

and signal weakening (e.g. the distance that maximizes performance in spatially independent evaluations). The final dataset used for niche and distribution modelling consisted of 210 Alexandrine parakeet occurrences (native range 163; invasive range 47: Appendix of supplementary material).

Environmental variables

Environmental variables here 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 (i.e. identical to the resolution of the parakeet occurrence data). 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 analysis

We used the Broennimann et al. (2012) and Petitpierre et al. (2012) frameworks to assess whether the Alexandrine parakeet's climatic niche remains conserved during the invasion process, and to quantify the extent to which any niche differences between native and invasive ranges are due to niche unfilling versus niche expansion (see below). These frameworks apply 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). While multiple approaches have been proposed to study niche dynamics based on occurrence and spatial environmental data, we opted for the Broennimann et al. (2012) and Petitpierre et al. (2012) method as it has been shown to be robust against variable sampling efforts and because it takes into account biases related to the dependence of species occurrences on the frequency of environmental conditions that occur across geographical areas (reviewed in Guisan et al. 2014). We first tested whether Alexandrine parakeet niches are more similar to each other than expected by chance (i.e. test of niche similarity, Broennimann et al. 2012) by using a randomization test whereby the measured overlap is compared against a null distribution of 100 simulated overlap values. We then assessed whether Alexandrine parakeets have colonized in the invaded range climates not occupied in the native range (i.e. niche expansion, defined as the proportion of occurrence densities in the invasive distribution located in different climatic conditions than the native distribution, Petitpierre et al. 2012). Lastly, we calculated the amount of native niche unfilling in the invaded range (i.e. the proportion of the densities in the native distribution located in different conditions than the invasive distribution, 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 for comparing native versus non-native niches should reflect the set of areas a species could potentially have encountered since its presence in the region (Barve et al. 2011). The choice of the background area can influence model outcomes (Van Der Wal et al. 2009), but appropriate backgrounds are in practise difficult to delineate (Barve et al. 2011). Therefore, following Guisan et al. (2014), in the native range, we extracted as background all biomes in which the species occurs, using the biome classification of Olson et al. (2001). The following biomes were used to form the native range background: tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests, tropical and subtropical coniferous forests, temperate broadleaf and mixed forests, tropical and subtropical grasslands, savannas, and shrublands, deserts and xeric shrublands, and finally mangroves. In the invasive range, we estimated the extent of the geographical area that could have been colonized by Alexandrine parakeet populations since their establishment by buffering each locality where Alexandrine parakeets have been introduced with a distance equal to the minimum invasion speed recorded for birds (i.e. 4.59 km/year, derived from Blackburn et al. 2009) multiplied by the number of years since introduction (see Strubbe and Matthysen 2013 for details). In doing so, we obtained an ecologically realistic invasive-range background. For comparison, models were also run using all invaded biomes as background. Thus, to robustly quantify niche dynamics during the Alexandrine parakeet invasion process, we assess niche dynamics using a background area strongly defined by assumed dispersal limitations during range expansion (the ecologically realistic background) versus a 'no dispersal constraints' background (the all invaded biomes background).

Species distribution models

Species distribution models were run in R 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 with climates suitable for Alexandrine parakeets. We ran three different modelling scenarios: (1) an SDM based on native-range occurrence data and climate variables, (2) a native-range SDM with climate variables and the human footprint, (3) an SDM with climate variables and pooled native and invasive range occurrence data. Models were fitted with default settings unless stated otherwise. Pseudo-absences were selected using a 'target-group' approach to limit spatial sampling biases (Phillips et al. 2009). Therefore, for the areas covered by the biome-based background used for the niche analyses described above, from the GBIF, we downloaded all avian observation records. A single set of 10,000 pseudo-absences was then randomly drawn from biome-based background grid cells that contained at least one bird observation and that were not Alexandrine parakeet presences (following Wisz and Guisan 2009). Each model was subjected to tenfold cross validation with a 80–20 % random split of the presence data for training–testing each replicate, respectively.

We used the True Skill Statistic (TSS) for model evaluation, and only those with TSS > 0.7 were kept for generating ensemble projections of global Alexandrine parakeet invasion risk to exclude inaccurate models, using unweighted averaging across models (Thuiller et al. 2013). Model transferability of the two native-range occurrences only based SDMs was assessed based on the invasive-range Alexandrine parakeet occurrence data ($n = 47$), using the (continuous) Boyce-index (Hirzel et al. 2006). The Boyce-index measures how much model predictions differ from a random distribution of observed presences across prediction gradients (Boyce et al. 2002). It is the most appropriate metric for presence-only models and varies between -1 and $+1$. Higher values indicate better models; values close to zero represent models that do not differ from random predictions model wile negative values indicate counter predictions. Relative variable importance (0–1) was obtained through the randomization procedure described by Thuiller et al. (2013). Lastly, a global climatic multivariate environmental similarity surface (MESS) map was calculated. This map indicates areas where climatic variables occur outside the range of values contained in model training regions (here defined as the biomes in which the species naturally occurs, see above), and predictions of invasion risk in these areas should be treated cautiously (Elith et al. 2010).

Interspecific facilitation

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

Results

Presence of invasive Alexandrine parakeet populations

Recorded alien populations of *P. eupatria* varied in their status and size. Largest populations in Europe are found in Belgium (Brussels: Weiserbs and Jacob 2007), Germany (Köln: Bauer and Woog 2008) and the Netherlands (Amsterdam: Van Kleunen et al. 2010), each comprising 100–300 individuals and showing an increasing trend. Reproductive events are also reported from Greece (Crete: Panagiotys Kouvropalos, personal communication 2012) and Italy (Rome: Angelici and Fiorillo 2015). Several self-sustaining colonies are also present in the Middle East: Turkey (Istanbul: Yassin Darvish, personal communication 2015), United Arab Emirates (Jennings 2010) and Iran (Tehran: Khalegizadeh 2004), with smaller nuclei being reported in Algeria (Fahroud Kassal, personal communication 2015), Saudi Arabia (Jennings 2004; Lever 2005) and Qatar (Jennings 2010). Breeding populations are also present in Hong Kong (Holt 2006) and Tokyo (Kawakami and Kanouchi 2012), but no data are available on population trends and size. Single records of isolated individuals also come from Australia, Poland, Morocco, Israel, Spain, Canary Islands, China and USA. First records of Alexandrine parakeet breeding outside the native range of the species are all relatively recent (see Appendix of supplementary material), some dating back to early 80s (Germany, Bahrain), but most populations have been reported since the mid 90s (e.g. UK, Belgium, Netherlands, Iran) or later (e.g. Japan). While most populations detected are reportedly increasing in numbers and expanding their ranges, there is also evidence of local extinctions in the invaded range: the flock in Merseyside (UK) was reportedly shot (Butler 2002) and no recent record is available after that, as well as at other sites in UK where the species was detected; the status of populations in Yemen and Bahrein is also uncertain as they both may be extinct, after assessments in 2003 and 2015, respectively. For a detailed country-by-country assessment and history of invasion, see Appendix of supplementary material.

Niche conservatism and predictions of invasion risk

When considering climatic variables only, native-range based SDMs cannot accurately predict the invasive distribution of Alexandrine parakeets (Boyce-index −0.70 when measured against the biome background, −0.59 against the ecologically realistic background) while they do accurately model the species' native distribution (Boyce-index 0.93, Fig. 1a). Adding human footprint to the model does not improve model transferability (Boyce-index −0.70 and −0.86; 0.97 for the native-range, Fig. 1b). Variable importance (Table 1) shows that both models with and without human footprint are mainly influenced by temperature gradients, which are >50 % more important than precipitation variables. Human footprint contributes little to model performance (i.e. variable importance of only 0.07 ± 0.06). When pooling native and invasive occurrence data, SDMs accurately capture both the native and invasive Alexandrine parakeet occurrences (Boyce-index 0.93 and 0.90, Fig. 1c). When pooling occurrence data, precipitation variables become more important than temperature gradients. The MESS map (Fig. 1d) shows that Alexandrine parakeets have not invaded

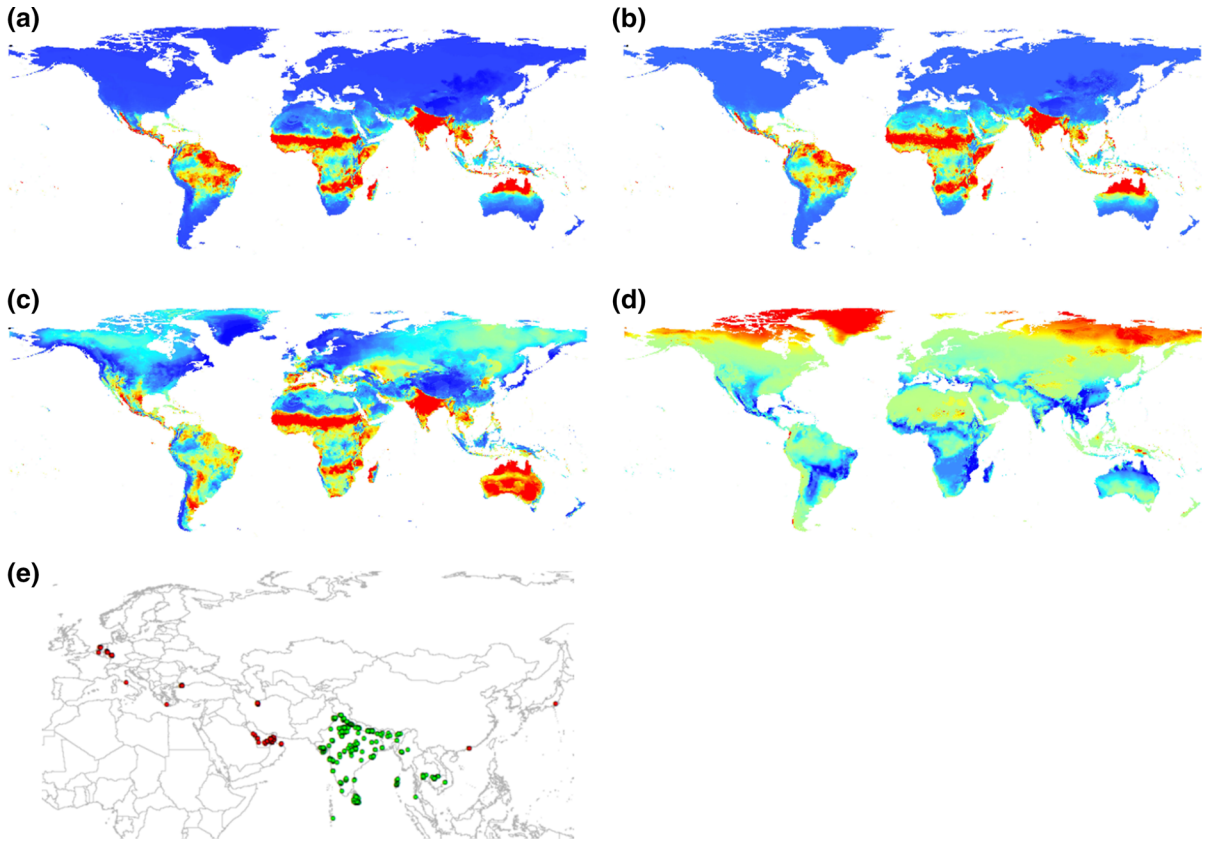

Fig. 1 Predictions of invasion risk for Alexandrine parakeets obtained from ensemble SDMs. **a** A native-range based model employing climate variables only, **b** native-range model combining climate variables and the human footprint. **c** Pictures invasion risk derived from a climate-only model built by pooling both native and invasive range occurrence data. *Warmer colours* indicate higher predicted habitat suitability. **d** The 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. **e** The occurrence data used in the analyses (after spatial thinning), *green* native range occurrences (n = 163), *red* invasive range occurrences (n = 47)

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.

Niche analyses were conducted in a gridded environmental space formed by the first two axes of a Principal Component Analysis on the eight climatic variables applied here. These axes explained 78.6–81.4 % of the inertia (biome background axis 1: 49.0 %, axis 2 = 29.6 %, ecologically realistic background: axis 1: 50.4 %, axis 2: 31.0 %). In both cases, the first PCA axis is dominated by temperature gradients while the second axis predominantly represents precipitation gradients (Table 2). Niche overlap between native and invasive Alexandrine parakeet populations is low (D: 0.14 for the biome background, 0.13 for the ecologically realistic background), yet tests of niche similarity show that, independent of the background area used, Alexandrine parakeet invasive niches are more similar to the native niche than expected by chance (p value <0.05). Despite this evidence for niche conservatism, invasive Alexandrine parakeets show significant niche expansion as they have 65–67 % of their invasive distribution outside their native climatic niche (Fig. 2). 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 during the invasion process, Alexandrine parakeets have

Table 2 Principle component analyses variable contributions

	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

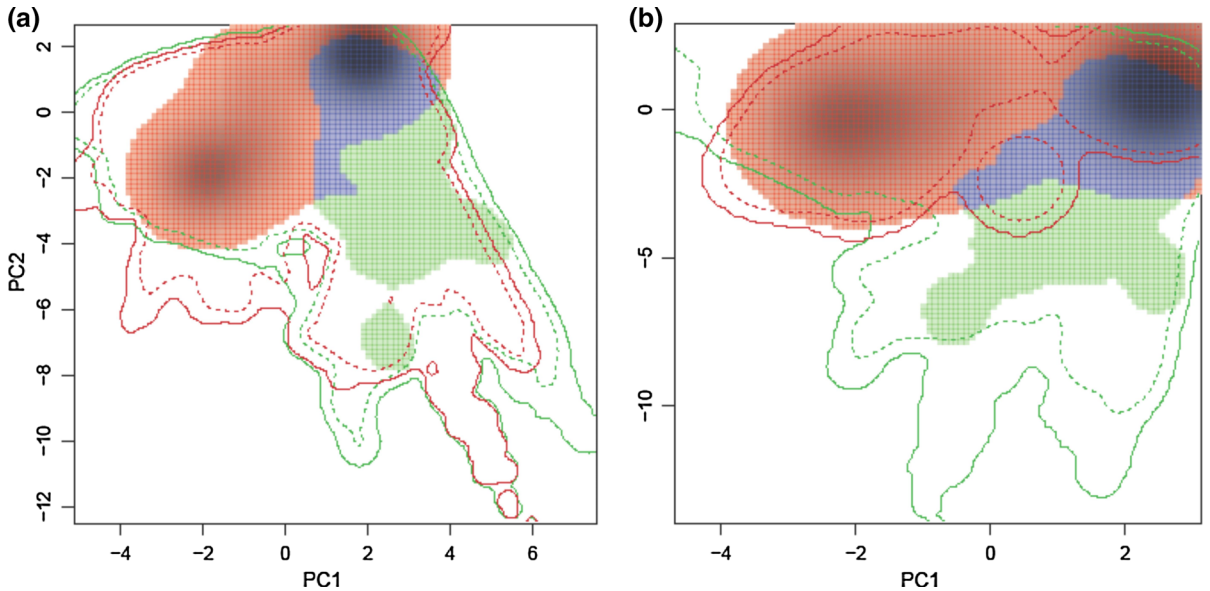

Fig. 2 Climate niche dynamics between native and invaded Alexandrine parakeet ranges. **a** The climate space of the biome background, **b** the ecologically realistic background (see text). The *solid* and *dashed contour lines* illustrate, respectively, 100 and 50 % of the available environment in the native range (*green lines*) and in the invasive range (*red lines*). *Green areas* represent climates only occupied in the native range, *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-axes are mainly determined by temperature gradients, the second axes chiefly represent precipitation patterns (Table 2)

colonized areas far colder than their native range. Niche unfilling varies from 53 % (biome background, Fig. 2a) to 8 % (ecologically realistic background, Fig. 2b).

Interspecific facilitation

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

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

Discussion

Increasing numbers of *P. eupatria* populations are establishing outside the species' native range, particularly in Europe and in the Middle East. While the invaded areas in the Middle East have climates largely similar to parts of the Alexandrine parakeet's native range, during the ongoing invasion of Europe, this parakeet has considerably expanded its niche into climates much colder than those occupied in the native range. Strubbe et al. (2015) suggested that parakeet invasions into colder climates may be explained by "prior-adaptation" to human-modified habitats in the native range (cf. Hufbauer et al. 2012). For example, including the human footprint variable into native-range SDMs considerably increased the accuracy of predictions of invasion risk for ring-necked parakeets, suggesting that association with humans in the native range facilitates their persistence in areas outside of their native climatic niche. This seems not to be true for Alexandrine parakeets, as models with and without the human footprint have a similarly low predictive accuracy. This may be due to ecological differences between these two *Psittacula* species; ring-necked parakeets have benefited from the conversion of natural habitats to agro-ecosystems and now reach their highest breeding densities in urban areas (Khan 2002; Khan et al. 2004). Although occasionally reported also in urban areas in the native range, Alexandrine parakeets are considered to be more sensitive to human-induced habitat alterations, as is also suggested by its IUCN status (BirdLife International 2015). Recent studies suggest niche expansion is rare for species with large native ranges and broad environmental niches (Capiñha et al. 2014; Early and Sax 2014; Li et al. 2014), while contrasting results have been found for residence time in the native range. Li et al. (2014) found that niche expansion was more likely for amphibians and reptiles introduced earlier into a new range, whereas Early and Sax (2014) found that time since introduction decreased niche expansion for European plants introduced to North America. These results do not help explaining the niche expansion into colder climates shown by Alexandrine parakeets, whose native range is rather wide (Juniper and Parr 1998), and whose first introductions mostly date back to the early 1990s (this manuscript). Our results offer statistically weak but clear support to the hypothesis that interspecific facilitation with *P. krameri* may contribute to niche expansion and invasion success of *P. eupatria.* These two parakeet species, which are closely related and rather similar in appearance, may form mixed-species flocks and/or join communal roost sites. Single individuals or small nuclei of *P. eupatria* may potentially benefit of this association by predator avoidance (sensu Weatherhead 1983) and/or information transfer (e.g. on foraging, nesting and roosting locations; sensu Ward and Zahavi 1973) from an established population of *P. krameri*. Such associations, together with parrot longevity (Costantini et al. 2008), may also increase individual survival, potentially giving single *P. eupatria* more chances to encounter potential partners, e.g. after new releases. Empirical observations on sympatric invasive Alexandrine and ring-necked parakeets are scarce. Weiserbs and Jacob (2007) mention that in Brussels, following introduction, Alexandrine parakeets joined ring-necked parakeet flocks. At least during the breeding season, both parakeet species were most often observed in monospecific rather than mixed species flocks (authors, personal observations), even though Claes and Matthysen (2005) reported that Alexandrine parakeets were dominant over ring-necked parakeets at bird feeders. Also in Brussels, Alexandrine parakeets commonly breed in tree cavities previously occupied by ring-necked parakeets (Diederik Strubbe, personal observations), and such cavity-takeovers have also been reported from Wiesbaden, Germany (Detlev Franz, personal communication). We can however not rule out alternative explanations. Urban bird feeding has recently been shown to particularly benefit introduced bird species (Galbraith et al. 2015), and more empirical studies are necessary to determine which ecological and/or behavioural mechanisms underlie Alexandrine parakeet invasion success in colder climates, and the extent to which interactions with previously established ring-necked parakeets matter. It should also be noted that while hybridization between ring-necked and Alexandrine parakeets seems to be uncommon in the native range, it frequently occurs in captivity and has been reported several times in the invaded range. Hybrids of the first generation are fertile (Krause 2004) and

present intermediate morphological features between *P. krameri* and *P. eupatria* (Krause 2004), i.e. intermediate size between the parental species and orange to light-brown wing patch (absent in *P. krameri* and deep red in *P. eupatria*).

When SDMs trained on only the native range fail to predict the full extent of a species invasion, an alternative modelling strategy is to fit models using data from both native and invaded ranges. This ensures reliable predictions of invasion risk in areas of the invaded range that are not yet invaded but where suitable conditions similar to the native range occur (Broennimann and Guisan 2008). Alexandrine parakeet models including both native and invaded range occurrence data predict high habitat suitability, i.e. higher invasion risk, in extended areas where the species is currently not (yet) present, e.g. large parts of the Mediterranean basin, Central America and Australia. The widespread availability of currently unoccupied but suitable habitats indicates a high potential for the species for further range expansion in the invaded range. *P. eupatria* is a popular pet throughout the globe and is thus commonly being highly available in pet shops. Although being generally more expensive than other parakeets (e.g. ring-necked and monk parakeets), it is also large sized (wing length up to 26 cm) and produces loud, noisy calls, all factors that may lead owners to abandon their pet and facilitate escapes. Such a potentially high propagule pressure (Duncan et al. 2003), paired with possible facilitation by *P. krameri* colonies, suggests that *P. eupatria* may be able to colonize the ample suitable habitats available to it in the invaded range in the near future. Once introduced and established with viable populations, invasive alien species are generally difficult to eradicate and their management generally is highly expensive (Kolar and Lodge 2001). Currently, the Alexandrine parakeet is considered an invasive species in Belgium and the Netherlands, largely because of its relatively rapid population growth and geographical spread. Such rapid growth has also been reported from Germany, e.g. the population of an urban park in Köln increased from 8 original pairs to about 200 individuals in $<$20 years (Detlev Franz, personal communication). The increasing numbers of breeding records in new countries presented here and the fact that most known breeding populations were only recently reported, predominantly between the last 10–15 years, suggests that an invasion process is already on-going at a large scale. During a recent EU-level workshop aimed at prioritising invasive alien species prevention efforts through horizon scanning, experts unanimously agreed that Alexandrine parakeets should be considered as a high priority species for risk assessment. The experts listed competition for nesting cavities with native species, disease transmission, damage to agriculture and interactions with other invasive species as major mechanisms through which Alexandrine parakeets are likely to threaten biodiversity and ecosystem services (Roy et al. 2015). Impacts such as crop and tree damage as well as competition with cavity-dwelling wildlife (e.g. birds and bats) have already been extensively reported for the congeneric ring-necked parakeet (e.g. Strubbe and Matthysen 2009; Williams et al. 2010; Hernández-Brito et al. 2014; Menchetti et al. 2014), and this study suggests that interactions between Alexandrine parakeets and other invasive species (such as ring-necked parakeets) are indeed likely.

This study thus contributes to inform conservation planning for invasive alien parrots, highlighting the importance to focus on species at an early stage of the invasion process, when management actions may still be affordable and potentially successful. The Alexandrine parakeet is currently not considered a major threat, and consequently environmental agencies may overlook its presence and associated risks. Our study corroborates the EU horizon scanning findings on the potential for invasiveness of this parakeet species. Given the ample climatically suitable habitat available to the species revealed by distribution models calibrated on combined native and invasive range occurrence data, future increases in numbers and geographical spread across favourable areas throughout its invaded range are likely. Management options aimed at limiting further population growth or even population removal should thus be evaluated.

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