



Lovebirds in the air: trade patterns, establishment success and niche shifts of *Agapornis* parrots within their non-native range

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Abstract Understanding the factors influencing the establishment of non-native species is pivotal with regards to the development of effective biosecurity policies. In this paper, we aim to assess the role of climate matching, trade patterns and breeding origin as drivers of establishment success of introduced lovebirds (*Agapornis* species). A comprehensive database on the worldwide distribution of eight species of non-native lovebirds (including establishment success and population size from 21 countries

spanning 27 years) was compiled. We combined climate-based species distribution models with environmental niche analyses to evaluate environmental suitability and potential niche shifts in the introduced range of lovebirds. Then, we tested whether combining habitat suitability with information on trade, introduction effort and breeding origin (captive-bred or wild-caught) of imported birds can improve model predictions at the country level. Although climate-based models fit well with the current distribution of non-native lovebirds at 5-arcminute resolution and significant niche similarity was found for 3 species, we also observed successful establishments in areas climatically distinct from those occupied in native ranges. At the country level, only a significant relationship between the number of established populations and both the number of introduction sites and

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the year of first importation was observed. A significant effect of breeding origin was not found, but most traded birds had a captive-bred origin. Our work contributes to the growing evidence of the complexity of the invasion process and the difficulty of pre-introduction invasion assessments based solely on the characteristics of the recipient environments for the *Agapornis* species. Surveillance protocols should be applied to both wild-caught and captive-bred lovebirds, as additional data becomes available to better tease apart the role of origin in those species.

Keywords *Agapornis* · Non-native species · Bird trade · Niche shift · Propagule pressure

Introduction

In recent years, the international pet trade has emerged as the main introduction pathway of non-native bird species worldwide (Hulme 2015; Abellán et al. 2017), with no evidence that current trade rates will decrease in the near future (Cassey et al. 2015; Reino et al. 2017). Awareness about the relationship of trade with both number and richness of established non-native species in a country, as well as on its relevant impacts, has highlighted the need to develop effective mitigation strategies (Westphal et al. 2008; Menchetti and Mori 2014). Indeed, once established, the eradication of invasive non-native species is an expensive and challenging operation, which may be strongly opposed by members of the general public and animal-rights movements, particularly when concerning charismatic

species (Bertolino and Genovesi 2003; Estévez et al. 2015; Hulme 2015; Crowley et al. 2019).

Understanding which traded species are most likely to be released and successfully establish into the wild is essential to prevent invasions (Genovesi and Shine 2004). Event-level factors, e.g. the number of released individuals in a location to which they are not native (propagule pressure)—which incorporates estimates of the absolute number of individuals involved in any one release event (propagule size) and the number of discrete release events (propagule number: Lockwood et al. 2005)—or the year since first introduction, together with species-specific life-history traits have been described as key drivers of invasion success (Duncan et al. 2003; Blackburn et al. 2015; Abellán et al. 2017). Additionally, habitat suitability of introduction sites and, particularly, climatic similarity with native ranges have been reported as pivotal to predict invasion success (Cassey et al. 2004; Mori et al. 2014; Cardador et al. 2016). Many invasive species conserve their original environmental niche in invaded areas (Strubbe and Matthysen 2009). Thus, species distribution models (hereafter, SDMs) trained with occurrence data in native ranges have been proposed as valuable first screening tools to identify the most readily invaded regions (Thuiller et al. 2005; Cardador et al. 2017). However, some species might thrive in areas climatically different from the native range (Ancillotto et al. 2015; Strubbe et al. 2015) or occupy only a small part of suitable available habitats (Strubbe et al. 2013; Sales et al. 2017). Consequently, conservation biologists need to be aware of potential niche shifts (i.e., expansion or unfilling) in introduced ranges

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in order to improve predictions and management (Early and Sax 2014).

Parrots include the most traded bird taxa because of their universal popularity as pets (Tella and Hiraldo 2014; Mori et al. 2017), most notably the budgerigar *Melopsittacus undulatus* and lovebirds *Agapornis* spp. (Gismondi 1991). Parrots species are included among the most widespread introduced and invasive birds in the world (Cassey et al. 2004; Strubbe and Matthysen 2009). Self-sustaining non-native populations have been reported for over 60 parrot species worldwide (Menchetti and Mori 2014), locally affecting viability and reproductive success of native fauna, as well as having socioeconomic impact (Menchetti and Mori 2014; White et al. 2019). The principal driving causes of their success are related to high propagule pressure and their behavioural adaptability to new environments (Cassey et al. 2004; Ancillotto et al. 2015), as well as the fact that most traded individuals have a wild-caught origin (and thus have higher invasive potential than birds bred in captivity, Abellán et al. 2017; Cabezas et al. 2013; Carrete and Tella 2015). Among parrots, lovebirds represent growing invaders worldwide (Menchetti and Mori 2014). These species may become agricultural pests (e.g. *A. personatus* in Kenya: Lever 2005; Menchetti and Mori 2014) and have important detrimental impacts on native fauna and human infrastructures (Menchetti and Mori 2014). Despite this, systematic attempts to quantify the distribution and frequency of introduction of these parrot species in non-native areas, as well as efforts to understand potential factors driving their invasion success, are missing (Holt et al. 2005; Uehling et al. 2019). So far, most literature on non-native parrots relates to two species, the ring-necked parakeet *Psittacula krameri* and the monk parakeet *Myiopsitta monachus*, which have the most widely distributed populations among non-native parrots (Strubbe et al. 2015; Pârâu et al. 2016; Postigo et al. 2019). However, main drivers of lovebird success may differ from those of other species. This knowledge gap may limit opportunities for prevention and management.

In this paper, we assess the relevant role of climate matching, trade patterns and breeding origin of individuals (wild-caught or captive-bred) as drivers of establishment success of lovebirds. For this, we compiled a comprehensive database on worldwide distribution, establishment success and population size of non-native lovebird populations. This database

includes 371 records from 21 countries spanning 27 years. We combined SDMs based on climatic variables with environmental niche analyses, to evaluate the environmental suitability in introduced ranges of lovebirds. We then assessed the potential niche shift between native and introduced distributions. To conclude, we tested whether combining habitat suitability predictions with information on trade (i.e. year of first importation, number of birds imported), propagule number (i.e., number of introduction sites) and breeding origin of imported birds (wild-caught origin or captive-bred) can explain variation in establishment rate of lovebird populations across countries.

Materials and methods

Study species

Lovebirds include nine species of small (body size = 13–17 cm: Forshaw 2010), stocky-bodied parrots. Collectively, they are naturally distributed in sub-Saharan Africa (Forshaw 2010), and the grey-headed lovebird, *A. canus*, is naturally present in Madagascar (Forshaw 2010). One species (*A. nigrigenis*) is classified as “Vulnerable”, two other (*A. fischeri* and *A. lilianae*) as “Near Threatened”, with the remaining designated “Least Concern” (Forshaw 2010). All lovebird species are widely traded, except for the rare *A. swinderianus*, which therefore has been excluded of analyses (Forshaw 2010). As a consequence, non-native populations of the eight traded species have been reported in at least one country outside of their native range, mainly deriving from unintentional releases (Lever 1987, 2005; Menchetti and Mori 2014).

Lovebirds feed mostly on cultivated plants (Forshaw 2010) and can be agricultural pests in their native range, with this potentially extending to introduced areas if they reach high population densities (e.g. *A. personatus* in Kenya: Lever 2005; Menchetti and Mori 2014). Apart from this, the limited information available on non-native lovebirds highlights that additional potential impacts on native fauna may occur, including the displacement of native birds from breeding sites, as well as damage to electric wires (Menchetti and Mori 2014).

Established populations outside lovebird native ranges

A detailed literature search was conducted on ISI Web of Science, Scopus, Google Scholar and the Zoological Record, to collect occurrences of breeding lovebird populations in the wild, outside their native ranges. We used combinations of the following keywords, in ten languages (English, Italian, French, Spanish, Portuguese, German, Bulgarian, Russian, Romanian and Mandarin): *Agapornis**, lovebird*, breeding, non-native*, alien*, introduc*, invas*, allochthonous, naturalized. Further articles and books detected within the resulting reference list were also included, as well as unpublished observations by authors. We cannot rule out that other papers reporting non-native lovebird populations may occur in different languages (e.g. Arabic, Afrikaans), although we checked all of the main languages used in the scientific literature (cf. Ammon 2001). Occurrences of lovebirds in aviaries or in small enclosures ($N = 22$ occurrences) were not included in our analyses. Additional occurrences were obtained by checking once a week, for 6 months, bird observation websites (i.e. iNaturalist, eBird and Christmas Bird Count: Mori et al. 2017), as well as main Social Networks (Facebook and Twitter), image-hosting websites (Flickr) and YouTube. In these searches, we used the same keywords as in our literature search. When a photo, video or record (i.e. report by local ornithologists and birdwatchers) was detected, we contacted local birdwatchers/ornithologists, photographers and video-makers to confirm and obtain coordinates of the record and to provide us with any further relevant information (i.e., number of individuals, nesting probability, first and final date lovebirds were observed). Only data collected between 2000 and 2018 were considered, to maximize efforts to contact and obtain reliable information from authors.

An introduction was considered successful when at least two pairs of lovebirds bred for $\geq$ three breeding seasons (Andreotti et al. 2001) and there were no indications of a population crash or extinction after this period. Preliminary analyses showed that considering the small number of crashed or currently extinct populations (i.e. excluding single escapes or non-breeding populations) as successful do not modify modelling results. To conclude, since for recent records it may be too early to determine whether

introductions were successful or not, analyses both considering and omitting the most recent records (i.e., those with first recorded date > 2010) were conducted.

Trade patterns

As lovebird species are listed under CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), their international trade requires permits detailing the countries of origin and destination of the individuals involved. Furthermore, declaration of international trade of captive-bred individuals is mandatory for CITES species. We compiled information on the total number of live lovebirds reported by CITES that have been legally traded to a given country from 1981 (the first year for which CITES compiled records for these species) to 2013: www.trade.cites.org. (Accessed on 29th January 2018). For each trade event, information on the number of individuals involved came from the importer country (24%), the exporter country (54%) or both (22%). This is not likely to affect our results since, when available, information provided by the importer and the exporter countries were highly correlated (Pearson correlation coefficient: $r = 0.88$). In such cases, the maximum number of individuals reported was used for analyses. Information on breeding origin (wild-caught vs. captive-bred birds) of traded individuals was also compiled when available. Although, for *A. roseicollis* declarations were voluntary after the application of the EU Regulation 1332/2005, we prefer not to omit trade data after 2005. We obtained highly correlated estimates of trade per country and species when considering data after 2005 or not (Pearson correlation coefficient, total trade: $r = 0.96$, trade of wild-caught individuals: $r = 0.99$, trade of captive-bred individuals, $r = 0.95$).

Environmental suitability and niche analyses

In order to evaluate the environmental suitability of *Agapornis* introduced ranges and to assess the potential realized niche shift between native and invaded distributions, we used SDMs and niche analyses. Environmental suitability was characterized using an ensemble model of four correlative SDM techniques: generalized linear models (GLM: McCullagh and Nelder 1989), MAXENT (Phillips et al. 2006),

gradient boosting machine (GBM: Friedman 2001) and random forest (RF: Breiman 2001). All SDMs were run using *BIOMOD2*, an ensemble-modelling R package developed by Thuiller et al. (2009), in R 3.4.0 (R Core Team 2017).

We trained our models using occurrence data in native ranges, since we were interested in assessing how similarity with native realized niches affects the establishment in the introduced range. Occurrence data for *Agapornis* species in native ranges were compiled from the Global Biodiversity Information Facility (GBIF). Locations were integrated into a Geographic Information System (GIS) at 5-arcminute resolution, which corresponds approximately to 10×10 km. Locations with lower resolutions were not retained. Duplicate samples within the same grid cell were handled as single observations. Final sample size ranged between 1 and 182 occurrences per species, with 664 occurrences in total. Only species with over 15 locations were retained for successive analyses, to ensure at least 10 locations were available for model training (Stockwell and Peterson 2002) during subsampling (see methods below).

Climatic variables for analyses were extracted from WorldClim (www.worldclim.org, Accessed on 4th October 2017) (Hijmans et al. 2005), a high-resolution global climate database widely used to construct SDMs. We extracted data on eight climatic variables which are known to affect bird distributions (Cardador et al. 2016, 2017): annual mean temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the driest month, precipitation of the wettest month and precipitation seasonality. All layers were compiled at 5-arcminute resolution to match occurrence data resolution.

Models were run with a single set of 10,000 pseudo-absences randomly drawn from all biomes occupied by each species across its native ranges (Guisan et al. 2014), using the biome classification by Olson et al. (2001). Presences and pseudo-absences were weighted (0.5) as such to ensure neutral prevalence (Phillips et al. 2006). To reduce uncertainty caused by sampling artefacts we used subsampling and conducted 10 replicates for each model by dividing the occurrence data into random training (70%) and test (30%) data sets. However, full models considering total sample size provided highly concordant performance

(Table S1 in Appendix 1 in Supporting Information) and predictions (Pearson correlation coefficient, mean $\pm$ SD = 0.85 ± 0.16 , range: 0.54–1). For each species, consensus models were generated as averaged means of all models. Averaged models were cross-evaluated using the area under the receiver operating characteristic curve (AUC) (Phillips et al. 2006) and the true skill statistic (TSS) values (Allouche et al. 2006) in the training region. To reduce problems related to model extrapolation, model projections (Fig. S1, Appendix 1 in Supporting Information) were adjusted using multivariate environmental similarity surfaces (MESS) (Elith et al. 2010). Environmental suitability in highly dissimilar areas (MESS < -20) (Mateo et al. 2014) was considered to be 0 (Figs. S2 and S3, Appendix 1 in Supporting Information). To conclude, we assessed the agreement between model predictions and distribution of real occurrences (i.e. locations with successfully established populations at 5-arcminute resolution) in introduced ranges. For this, we used the Boyce-index, which ranges from -1 to 1 , with the highest value indicating the highest match (Hirzel et al. 2006). As background for such analyses, we estimated the extent of the geographical area that could have been colonized by non-native lovebirds, in two ways: (1) all countries where species have been imported and (2) areas around introduction sites (Strubbe et al. 2013). For the latter, we buffered each locality where lovebirds were introduced with a distance equal to the minimum invasion speed recorded for birds (i.e. 4.59 km/year: Blackburn et al. 2009) multiplied by the number of years since first occurrence in each locality, using ArcMap 10.5 (Strubbe et al. 2013). This software was used for all GIS-related analyses.

We also calculated niche similarity between native and introduced ranges using niche analyses following the framework proposed by Broennimann et al. (2012). This involved the application of kernel smoothers to species occurrences in gridded environmental space to calculate metrics of niche overlap. The gridded environmental space for analyses was that formed by the first two axes of a Principal Component Analysis (hereafter, PCA) based on the eight climatic variables considered (see above). Climate data for PCA analyses was that at 0.5-arcmin pixels included in the potential native and alien ranges of all lovebird species. The potential native range for each species comprised of all biomes in which the species occurs in

native areas (Strubbe et al. 2015). For potential alien range, we considered the geographical area that could have been colonized by each species (i.e., all countries where species have been imported or areas around introduction sites, see above). We conducted a single PCA with data on potential native and alien ranges of all species to obtain comparable results among species; however, results obtained when conducting niche analyses in gridded environmental spaces defined by the first two components of PCAs conducted separately for each species were highly consistent (Table S2 in Appendix 1 in Supporting Information). PCAs were performed on the correlation matrix using the “stats” package in R v.3.4.0 (R Core Team 2017). For each species, measurement of niche overlap across occurrence densities obtained by kernel smoothers in the gridded environmental space used the Schoener’s D metric (Schoener 1970), which ranges from 0 (no overlap) to 1 (full overlap). We then conducted niche similarity tests, whereby a measured niche overlap was compared against a null distribution of 100 simulated overlap values (obtained when comparing the observed niche overlap with niche overlap values obtained by drawing occurrences in the potential alien range of that species at random: Warren et al. 2008; Broennimann et al. 2012). Note that since potential alien ranges were defined using two different approaches (see above), we repeated similarity tests twice. Following Petitpierre et al. (2012), we also calculated niche expansion (i.e., the proportion of alien occurrence densities in conditions different to those covered by native occurrence densities) and niche unfilling (i.e., the proportion of suitable conditions in the native range not occupied in the alien range) for each species. Analyses were conducted using the “ecospat” package (Di Cola et al. 2017) in R v.3.4.0.

Combining trade data with SDMs

We assessed whether combining habitat suitability predictions with information on introduction history (i.e. year of first importation, number of birds imported and breeding origin) can contribute to explain establishment rate of lovebirds in their non-native range. Since information on introduction history was not available at 0.5-arcmin resolution, we conducted our analyses at a coarser scale, that is at a country level. We used generalized linear mixed models (GLMMs)

with mean environmental suitability in each country (i.e., the mean of probability values derived from SDM predictions at 0.5-arcmin pixels included in that country), year of first importation, total number of birds imported, breeding origin (proportion of wild-caught vs. captive-breed birds) and the interaction between number of imported birds and breeding origin as predictors. Additionally, the total number of 0.5 arcmin locations per country with the presence of *Agapornis* species according to the compiled database (‘introduction sites’ hereafter) was also included in the model as a direct estimate of propagule number as well as of potential sampling bias. Species was included as a random intercept factor, and number of populations established per country was the response variable (Poisson error distribution and log-link function). To be consistent with trade data, only records for which first recorded date was later than 1980 were used for analyses. We only considered countries where lovebirds have been imported according to CITES data; the total sample size was 507 (range: 31–117 per species).

Results

Trade patterns

Since 1981, more than 44 million bird specimens were reported to be traded, comprising nine lovebird species and their hybrids, across 230 different countries and from both captive and wild-caught origins. The international commerce of lovebirds varied throughout the last 35 years, although two major peaks may be identified: one in the second-half of the 1980s and another starting in the mid-1990s and lasting until 2006 (Fig. 1; Figs. S4, S5 and S6, Appendix 2 in Supporting Information). However, trade of *A. roseicollis* is no longer required to be reported to CITES since 2005. The lovebird trade was confirmed to be dominated by birds bred in captivity, representing about 77% of the total traded individuals (approximately 35 million birds), whereas wild-caught birds represented only about 2% of the trade composition. The remaining trade involved other sources, including unreported sources, which represented a considerable volume of birds (17% and over 770, 000 birds traded since 1981).

Trade volumes varied considerably across species and associated reported trade sources. *A. fischeri* was

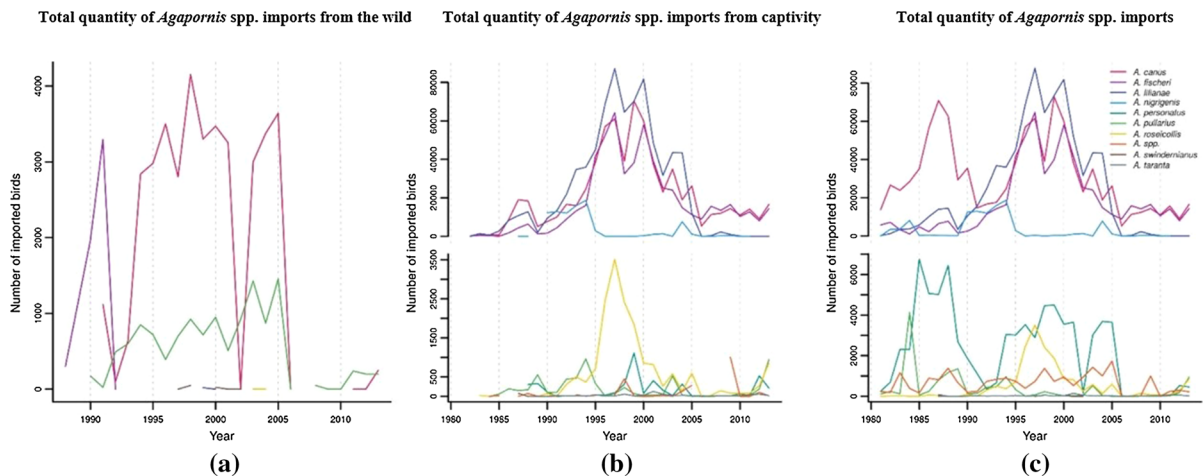


Fig. 1 Total number of imported lovebird individuals: captured from the wild (a), captive-bred (b) and pooled data (c)

reported to be taken from the wild (11%), but birds with unreported breeding origin represented about 31% (> 575,000 individuals) of the trade volume for this species. A similar situation was reported for *A. lilianae*, with unreported sources of trade representing about 42% (> 10,000 birds) of the trade volume for this species.

Presence of non-native lovebird breeding populations

A total of 371 records of non-native lovebird presence (from 260 different 0-5 arcmin locations) were detected, 36.8% from published studies and 63.2% from online platforms, social network and websites. Sixteen papers reporting the presence of introduced breeding populations of lovebirds were retrieved (Appendix 3 in Supporting Information): 50% were in English, 25% in French, 12.5% in Italian and 12.5% in Spanish.

Occurrences of non-native lovebirds throughout the world belonged to at least eight species (*A. canus*, *A. fischeri*, *A. lilianae*, *A. nigrigenis*, *A. personatus*, *A. pullarius*, *A. roseicollis* and *A. taranta*) and their hybrids (Fig. 2) and were distributed in Europe, Africa, North America and Oceania (Australia). About 20% of observed occurrences belonged to breeding, self-sustaining populations of five species. These included the four most traded species, i.e. *A. fischeri* (25 records, six established populations), *A. roseicollis* (20 records, nine populations), *A. personatus* (16 records, seven populations) and *A. canus* (eight

records, six populations). The fifth species, *A. lilianae*, was present with two established populations in South Africa, near the native range (Fig. 2). All records of established populations were in urban or suburban environments, except for three populations breeding in barns surrounded by meadows.

Most records belonged to single individuals escaped from cages (65.0%), small groups (5.8%, on average 27 individuals per group), breeding pairs that did not breed for more than 3 years (3.9%) and locally extinct populations (5.9%).

Predictions of invasion risk and realized niche shifts

Models trained with data from the species' native ranges showed high model performance in the training regions according to both AUC (mean $\pm$ SD: 0.98 ± 0.02) and TSS values (0.86 ± 0.09) (Table S1, Appendix 1 in Supporting Information). In the non-native range, native range based SDMs (Fig. S3, Appendix 1 in Supporting Information) consistently predicted the distribution of established non-native populations of lovebirds for three species, *A. roseicollis*, *A. fischeri* and *A. personatus*. Boyce indices ranged from 0.47 to 0.92 for these species either when omitting or not the most recent data (Table 1). Niche similarity tests also showed evidence of niche conservatism (similarity test significant) with respect to random expectations for the same three species, with some variations according to analyses assumptions (Table 1). However, overall overlap

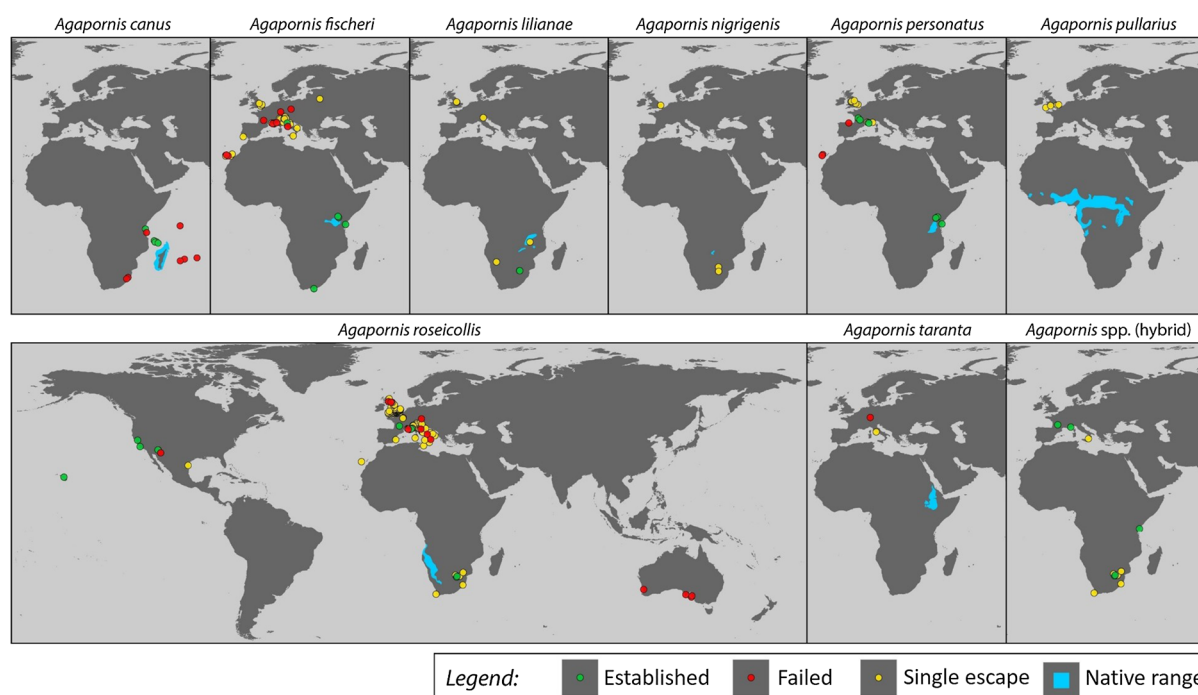


Fig. 2 Distribution of collected occurrences of lovebirds in the introduced range. Native ranges were taken from IUCN Red List website (www.iucnredlist.org. Accessed on 21st May 2018).

between niches occupied in native areas and introduced ranges were low for all species (D : 0.03–0.24 when considering all data; D : 0.03–0.22 when omitting recent records; Table 1).

Niche analyses were conducted in a gridded environmental space formed by the first two axes of a PCA on the eight climatic variables considered. These axes explained 82% of the inertia. The first PCA axis (54%) predominantly represented temperature gradients (warmer climates with low seasonality) while the second axis (28%) represented precipitation gradients (wetter climates with low precipitation seasonality, Table 2). Established locations of *Agapornis* species in the introduction range showed 58–78% of their niche outside climatic conditions used in their native areas (34–74% when omitting recent records). Niche differences between the native range and established non-native populations appeared to be related to both a shift along the first and second PCA-axis of the climate space, indicating that during the invasion process, lovebirds have colonized colder and wetter areas in respect to their native range (Fig. 3). Niche unfilling varies from 0.3 to 98% among species (Table 1).

The category “Failed” include small groups and breeding pairs that did not breed or did it for less than three years, as well as all the other currently extinct populations

Establishment success

When jointly analysed, only the effect of the year of first importation and the number of introduction sites were significant in models (Table 3). Thus, the number of locations with established populations increased the earlier the importation date in each country and the larger the number of introduction sites. Effects of climate suitability and breeding origin were not statistically supported. The total percentage of deviance explained by the model was 27.2% (24.7% when omitting more recent records).

Discussion

Species invasion processes may be the result of multiple drivers, which are often difficult to separate from each other. Our results show that at the country level non-native lovebird establishment rate is largely dominated by event-level effects: the number of established populations is mostly linked to the year of first introduction and the number of introduction sites. The role of introduction effort and year of first

Table 1 Niche comparisons and model transferability between native and invaded distributions of *Agapornis* species

Niche overlap according to the D metric, significance of niche similarity tests (P) and estimates of niche stability, expansion and unfilling are provided. Boyce index describing how well native-range-based SDMs project onto the invaded range is also provided

Results based on the complete data or omitting recent records (first reported year > 2010) are shown. Dispersal-limitations from introductions sites or importing countries were used as background

* $P < 0.10$; ** $P < 0.05$

Species	D	P	Stability	Expansion	Unfilling	Boyce index
Dispersal-limited						
Complete data						
<i>A. canus</i>	0.05	0.55	0.26	0.74	0.98	– 0.11
<i>A. fischeri</i>	0.16	0.07*	0.22	0.78	0.93	0.89
<i>A. personatus</i>	0.05	0.13	0.26	0.74	0.13	0.47
<i>A. roseicollis</i>	0.20	0.01**	0.30	0.70	0.27	0.57
Omitting recent records						
<i>A. canus</i>	0.05	0.41	0.26	0.74	0.98	– 0.05
<i>A. fischeri</i>	0.22	0.03**	0.39	0.61	0.67	0.88
<i>A. personatus</i>	0.16	0.01**	0.38	0.62	0.02	0.47
<i>A. roseicollis</i>	0.19	0.01**	0.47	0.53	0.50	0.50
Importing countries						
Complete data						
<i>A. canus</i>	0.03	0.06*	0.37	0.63	0.98	0.07
<i>A. fischeri</i>	0.06	0.03**	0.31	0.69	0.87	0.92
<i>A. personatus</i>	0.24	0.02**	0.42	0.58	0.02	0.86
<i>A. roseicollis</i>	0.12	0.03**	0.35	0.65	0.02	0.85
Omitting recent records						
<i>A. canus</i>	0.03	0.07*	0.37	0.63	0.98	0.07
<i>A. fischeri</i>	0.10	0.03**	0.43	0.57	0.55	0.92
<i>A. personatus</i>	0.31	0.01**	0.66	0.34	0.003	0.86
<i>A. roseicollis</i>	0.17	0.01**	0.47	0.53	0.40	0.80

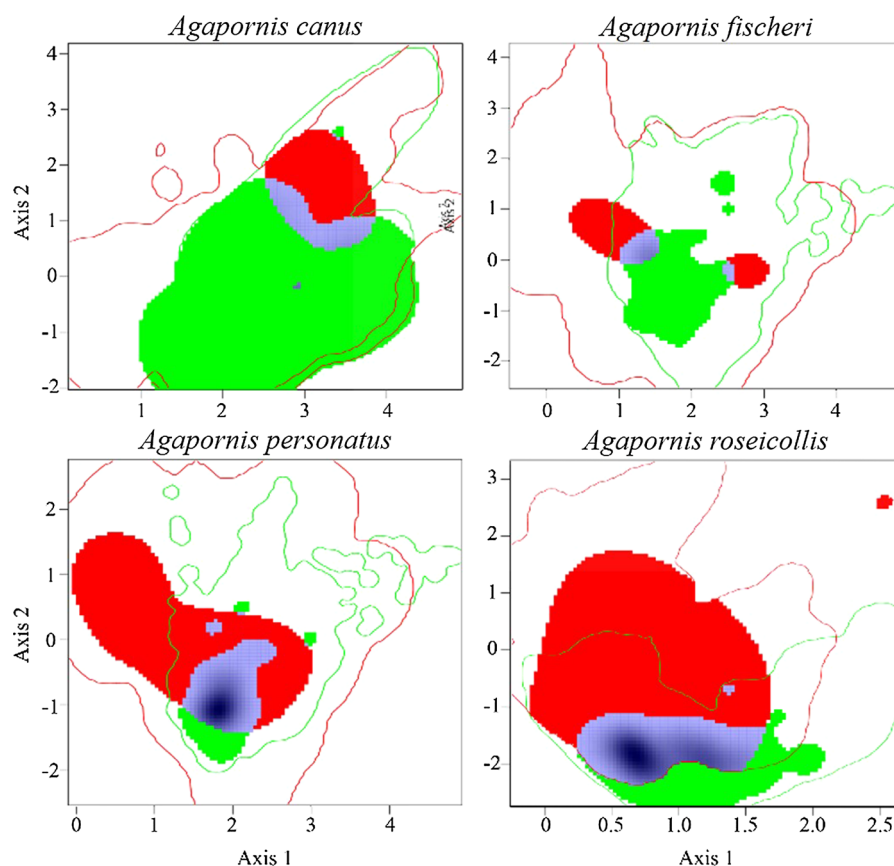
Table 2 Results of a principal component analyses on eight bioclimatic variables for native and invasive ranges of *Agapornis* species

Variable	Axis 1	Axis 2
Annual mean temperature	0.45	– 0.20
Temperature seasonality	– 0.44	0.11
Maximum temperature of warmest month	0.35	– 0.34
Minimum temperature of coldest month	0.46	– 0.21
Annual precipitation	0.32	0.46
Precipitation of wettest month	0.35	0.27
Precipitation of driest month	0.13	0.58
Precipitation seasonality	0.15	– 0.47

importation as key drivers of invasion success has been widely recognized (Blackburn et al. 2015; Abellán et al. 2017; Mori et al. 2018a). Increased introduction effort would increase invasion chances for different reasons (Allendorf and Luikart 2009; Simberloff 2009), such as reducing the relative impact

of environmental and demographic stochasticity (e.g. Allee effect, avoidance of inbreeding, e.g. for the globally invasive crabs *Carcinus* spp. and the common chamaeleon in western Europe: Darling et al. 2008; Basso et al. 2019) and by introducing adaptive genetic variation to new areas on which selection can act (e.g. for the garlic mustard in North America and the Siberian chipmunk in Italy: Durka et al. 2005; Mori et al. 2018b). In particular, increased propagule number (introduction sites) seems to enhance establishment probability primarily by diminishing impacts of environmental stochasticity, whereas propagule size primarily lessens effects of demographic stochasticity (Simberloff 2009). Additionally, the year since first introduction could also influence the establishment of lovebirds in each country because of its relationship with propagule pressure and introduction effort (a longer time since introduction is likely to result in higher cumulative numbers of individuals released and the number of introduction sites). The positive effect of year since first introduction on establishment rate can also be related to additional population and evolutionary processes (e.g.,

Fig. 3 Climate niche comparisons between native and invaded ranges of *Agapornis* species. The solid contour lines illustrate the 100% 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. The first PCA-axes are mainly determined by temperature gradients and the second axes by precipitation (Table 2)



adaptations to the new habitat) that could generate lag phases at the start of the growth of non-native bird populations (Aagaard and Lockwood 2014; Simberloff 2009).

At a finer resolution, climatic niche models fit overall well the current distribution of non-native lovebirds at 5-arcminute resolution and niche similarity was higher than expected by chance for three out of four species with available data. Even so, niche expansions into novel climatic conditions were observed for all species considered. Thus, although establishments tend to be non-randomly distributed across available climatic conditions, *Agapornis* species may still have notable success in areas climatically distinct from those occupied in their native ranges, as has been reported for other parrot species (Ancillotto et al. 2015; Strubbe et al. 2015). This pattern could be related to different processes. On the one hand, studies using species occurrences and spatial climatic data to characterize species' niches model the realized (i.e., the occupied), not the

fundamental niche (Guisan et al. 2014). Also, niche shifts may be contingent upon the environmental variables used (Guisan et al. 2014). On the other hand, most populations of introduced lovebirds occur within human settlements, i.e. urban and suburban habitats. Anthropogenic landscapes may help to overcome physiological and resource limitations locally imposed by climate through food provisioning (Clergeau and Vergnes 2011; Le Louarn et al. 2018), low predator/competitor densities (Gering and Blair 1999; Sorace 2002) and higher temperatures with respect to natural areas (Taha 1997; Niemelä et al. 2011). For example, lovebirds are reported to use cavities in (heated) buildings to breed and to roost during the winter (central Italy: Laurenti and Paci 2015; South Africa: C. Symes and D. Hernández-Brito, pers. comm.), where environmental temperature is higher than in natural areas. Additionally, the halt of supplementary feeding has been the cause of the *Agapornis* population extinction in the Canary Islands (D. Hernández-Brito, pers. comm.), showing that food

Table 3 Results for GLMMs relating establishment success (i.e., number of established populations) of *Agapornis* species in introduction ranges with year of first importation, climate

suitability, number of birds imported, number of introduction sites and breeding origin (percentage of wild-caught versus captive-bred birds)

Variables	Estimate $\pm$ SE	Deviance (%)
Complete data		
First importation year	– 4.09 $\pm$ 1.29	27.21
Climate suitability	– 0.09 $\pm$ 0.33	
Birds imported	0.07 $\pm$ 0.24	
Breeding origin	– 0.80 $\pm$ 0.82	
Introduction sites	0.14 $\pm$ 0.05	
Birds imported $\times$ breeding origin	– 0.03 $\pm$ 0.66	
Omitting recent records		
First importation year	– 4.28 $\pm$ 1.72	24.66
Climate suitability	– 0.05 $\pm$ 0.47	
Birds imported	0.09 $\pm$ 0.28	
Breeding origin	– 0.77 $\pm$ 0.97	
Introduction sites	0.11 $\pm$ 0.09	
Birds imported $\times$ breeding origin	0.12 $\pm$ 0.77	

Species was included in all models as a random term. All continuous predictors were standardized before modelling. Deviance explained by the models is shown

Models results for the period 1980–2015 (complete data) and 1980–2010 (omitting recent records) area shown

Coefficients with significant *P* values (*P* < 0.05) are shown in bold. N = 507

provisioning was a driver of establishment. Finally, we cannot discard that other relevant factors such as propagule pressure, that could not be accounted for at this spatial resolution, could have a more relevant role than climate matching also at this spatial scale. Particularly, taking into account that we are mostly dealing with contemporary invasion processes, current distributions may partly reflect the characteristics of the new introduction localities (Colautti et al. 2006) rather than optimum environmental conditions, which might be more likely to be moved into during spread (Abellán et al. 2017).

Apart from event-level factors and climate matching, breeding origin may also be affecting establishment success. Previous studies have shown that captive-bred individuals have low probabilities to establish non-native breeding populations (Carrete and Tella 2008; Cabezas et al. 2013). Thus, the predominant trade of captive-bred lovebirds could be the main cause of the relatively low numbers of non-native lovebird populations established worldwide. This pattern is striking when compared to other parrot species which have been traded in similar numbers but

mainly involving wild-caught individuals (Edelaar et al. 2015; Pârâu et al. 2016). Conversely, our models on establishment do not support an effect of captive breeding: the proportion of captive-bred versus wild-caught birds failed to explain establishment. One possibility is that we lacked statistical power to detect an effect of breeding origin on top of event-level effects (e.g. Pigot et al. 2018): wild-caught lovebirds recorded in the legal trade mainly belong to uncommon pets or uncommon species in the native range, i.e. *A. pullarius* and *A. nigrigenis*, for which no established populations are known outside the native range (Lever 1987, 2005; Menchetti and Mori 2014). Additionally, for a considerable fraction of trade records, information on bird breeding origin was unavailable. Another option is that the importance of breeding origin depends on the habitat that is utilised by the invaders. It has been suggested that the main reason of the higher invasiveness of wild-caught exotic species with respect to captive-bred ones is the loss of antipredatory behaviour in captivity (Carrete and Tella 2008, 2015). Most populations of introduced lovebirds occur within or in the surroundings of

human settlements, and urban habitats are considered to be “safe environments” in terms of predator density (see above). This specific ecological context may have helped introduced lovebirds to cope with their behavioural limitations related to captive-breeding.

From an applied point of view, our work contributes to the growing evidence of the complexity of the invasion process and the difficulty of pre-introduction invasion risk assessments (Cardador et al. 2016; Abellán et al. 2017), which often assume that it is possible to predict invasion outcomes based on the characteristics of the recipient environments. *Agapornis* species are able to occupy climate niches in the non-native range that differ substantially from those of the native range, and event-level factors appeared to be more relevant factors of establishment at a coarser resolution. In this respect, because establishment success is largely influenced by event-level factors, limiting the transport and release of non-native species would be the most effective strategy (Leung et al. 2002). This is likely to have occurred after the application of the wild-bird trade ban in the European Union in 2005, which affected some of the countries with higher introductions of these parrots (Fig. 2).

Indeed, lovebird trade after the ban nearly collapsed according to CITES data, which should have directly reduced introduction numbers (Cardador et al. 2017; Reino et al. 2017). Despite this, over 50% of new sites with the presence of *Agapornis* species were reported during the period 2006–2017, and a further breeding site of *A. roseicollis* has been detected for the first time in 2019 (N = 6, Porto Corsini, Ravenna, Italy). This could be explained by the accumulated number of birds already traded before the ban, as well as by an increase in domestic trade of captive-bred species (Cassey et al. 2015; Cardador et al. 2019) not reported by CITES data, since the European trade ban only affected wild-caught individuals (Cassey et al. 2015; Cardador et al. 2019). Additionally, we cannot discount that other factors may have contributed to the observed pattern. *A. roseicollis* was no longer CITES-listed after 2005, when declarations of their trade become voluntary. The removal of *A. roseicollis* from the CITES database may have promoted illegal trade, with animal traffickers and smugglers declaring their wild-caught lovebirds as non-CITES listed species to avoid filing paperwork (e.g., Nijman et al. 2012). This may have resulted in the decline we observed for the international trade of a CITES-listed

species, *A. fischeri*, immediately after the removal of *A. roseicollis*. Accordingly, the US-only trade trend including both CITES and non-CITES data did not show any notable lovebird decline after 2005 (D. Simberloff pers. comm. 2019). Captive-bred individuals of CITES-listed species also require a mandatory declaration by owners, and may still be quite widespread. However, while captive-bred birds are much less likely to establish in the wild with respect to wild-caught birds (Carrete and Tella 2008, 2015), surveillance protocols should also be applied to them, as additional data becomes available to better tease apart the role of origin in *Agapornis* species.

Despite their wide distribution as pets (Gismondi 1991; Menchetti and Mori 2014), our paper represents the first work summarising and analysing the distribution and the potential spread of introduced lovebirds, thus improving the knowledge on their invasive status (cf. Menchetti and Mori 2014; White et al. 2019). Disentangling the contributions of climate and introduction effort is a current and popular issue in biological invasions (Di Febbraro et al. 2019; Mori et al. 2019). We revealed both niche shifts and conservatism in the non-native range of lovebird species, particularly by using introduction effort as a predictor of invasion, as well as showing the lack of applicability of climate variables at coarser scales. Given the potential wide adaptability of non-native lovebirds, further research is required to quantify impacts by these parrots on native ecosystems and wildlife and their perception by the public (Crowley et al. 2019; Luna et al. 2019), which is largely still lacking (White et al. 2019), to address potential management actions (Menchetti and Mori 2014).

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conducted most of the analyses. LM organized the first dataset on data collected by DHB, RLW, LR, PE, BN, LGP and MLL, LR analysed and wrote the part focusing on trade. All authors participated in writing the final manuscript. Two anonymous reviewers and the Editor-in-Chief, Prof. Daniel Simberloff, kindly provided us with constructive comments on our first draft.

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