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

Running title: Non-native lovebirds: trade patterns and establishment success

Authors: Emiliano Mori[1,*,§], Laura Cardador[2,*], Luís Reino[3,4], Rachel L. White[5], Dailos Hernández-Brito[6], Marine Le Louarn[7], Lorenzo Mentil[8], Pim Edelaar[9], Liviu G. Pârâu[10], Boris P. Nikolov[11], Mattia Menchetti[12,13]

1. Dipartimento di Scienze della Vita, Università degli Studi di Siena, Via P.A. Mattioli 4, 53100, Siena, Italy. ORCID ID: 0000-0001-8108-7950.
2. Centre for Biodiversity and Environment Research, Department of Genetics, Evolution, and Environment, University College London, London WC1E 6BT, United Kingdom.
3. CIBIO/InBIO-Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, n°9, 4485-661 Vairão, Portugal.
4. CEABN/InBIO, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal.
5. School of Pharmacy and Biomolecular Sciences, University of Brighton, Brighton, UK. ORCID ID: 0000-0003-0694-7847.
6. Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Avda. Américo Vespucio, 41092, Sevilla, Spain. ORCID ID: 0000-0002-5203-3512.
7. Laboratoire Population Environnement Développement, Aix Marseille Univ, IRD, LPED, Marseille, France. ORCID ID: 0000-0002-0816-5761.
8. Dipartimento di Biologia Ambientale, Università degli Studi Roma Tre, Viale G. Marconi 446, 00146 Roma, Italy.
9. Department of Molecular Biology and Biochemical Engineering, University Pablo de Olavide, Seville, Spain.
10. Institute of Pharmacy and Molecular Biotechnology, Department Biology, Heidelberg University, Im Neuenheimer Feld 364, 69120 Heidelberg, Germany. ORCID ID 0000-0002-8307-6136

33 11.   Bulgarian Ornithological Centre, Institute of Biodiversity and Ecosystem

34   Research, Bulgarian Academy of Sciences, 1 Tsar Osvoboditel Blvd., 1000 Sofia,

35   Bulgaria. ORCID ID: 0000-0001-8818-8607.

36 12. Institut de Biologia Evolutiva (CSIC-Universitat Pompeu Fabra), Barcelona, Spain.

37   ORCID ID: 0000-0002-0707-7495.

38 13. Dipartimento di Biologia, Università degli Studi di Firenze, Via Madonna del Piano

39   6, 50019 Sesto Fiorentino (Florence), Italy.

40

41 *, These authors contributed equally to the paper.

42 §, Corresponding author. Email: moriemiliano@tiscali.it

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Abstract

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46 Understanding the factors influencing the establishment of non-native species is pivotal

47 with regards to the development of effective biosecurity policies. In this paper, we aim to

48 assess the role of climate matching, trade patterns and breeding origin as drivers of

49 establishment success of introduced lovebirds (*Agapornis* species). A comprehensive

50 database on the worldwide distribution of eight species of non-native lovebirds (including

51 establishment success and population size from 21 countries spanning 27 years) was

52 compiled. We combined climate-based species distribution models with environmental

53 niche analyses to evaluate environmental suitability and potential niche shifts in the

54 introduced range of lovebirds. Then, we tested whether combining habitat suitability with

55 information on trade, introduction effort and breeding origin (captive-bred or wild-

56 caught) of imported birds can improve model predictions at the country level. Although

57 climate-based models fit well with the current distribution of non-native lovebirds at 5-

58 arcminute resolution and significant niche similarity was found for 3 species, we also

59 observed successful establishments in areas climatically distinct from those occupied in

60 native ranges. At the country level, only a significant relationship between the number of

61 established populations and both the number of introduction sites and the year of first

62 importation was observed. A significant effect of breeding origin was not found, but most

63 traded birds had a captive-bred origin. Our work contributes to the growing evidence of

64 the complexity of the invasion process and the difficulty of pre-introduction invasion

65 assessments based solely on the characteristics of the recipient environments for the

66 *Agapornis* species. Surveillance protocols should be applied to both wild-caught and

67 captive-bred lovebirds, as additional data becomes available to better tease apart the role

68 of origin in those species.

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70 **Keywords**: *Agapornis;* non-native species; bird trade; niche shift; propagule pressure.

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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, Lockwood and Cassey 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. 2009; 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 in order to improve predictions and management (Early and Sax, 2014).

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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.

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145 year of first importation, number of birds imported), propagule number (i.e., number of

146 introduction sites) and breeding origin of imported birds (wild-caught origin or captive-

147 bred) can explain variation in establishment rate of lovebird populations across countries.

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149 **MATERIALS AND METHODS**

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151 *Study species*

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153 Lovebirds include nine species of small (body size = 13-17 cm: Forshaw, 2010), stocky-

154 bodied parrots. Collectively, they are naturally distributed in sub-Saharan Africa

155 (Forshaw 2010), and the grey-headed lovebird, *A. canus*, is naturally present in

156 Madagascar (Forshaw 2010). One species (*A. nigrigenis*) is classified as "Vulnerable",

157 two other (*A. fischeri* and *A. lilianae*) as "Near Threatened", with the remaining

158 designated "Least Concern" (Forshaw 2010). All lovebird species are widely traded,

159 except for the rare *A. swinderianus*, which therefore has been excluded of analyses

160 (Forshaw 2010). As a consequence, non-native populations of the eight traded species

161 have been reported in at least one country outside of their native range, mainly deriving

162 from unintentional releases (Lever 1987; Lever 2005; Menchetti and Mori 2014).

163 Lovebirds feed mostly on cultivated plants (Forshaw 2010) and can be agricultural

164 pests in their native range, with this potentially extending to introduced areas if they reach

165 high population densities (e.g. *A. personatus* in Kenya: Lever 2005; Menchetti and Mori

166 2014). Apart from this, the limited information available on non-native lovebirds

167 highlights that additional potential impacts on native fauna may occur, including the

168 displacement of native birds from breeding sites, as well as damage to electric wires

169 (Menchetti and Mori 2014).

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171 *Established populations outside lovebird native ranges*

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173 A detailed literature search was conducted on ISI Web of Science, Scopus, Google

174 Scholar and the Zoological Record, to collect occurrences of breeding lovebird

175 populations in the wild, outside their native ranges. We used combinations of the

176 following keywords, in ten languages (English, Italian, French, Spanish, Portuguese,

177 German, Bulgarian, Russian, Romanian and Mandarin): *Agapornis**, lovebird*, breeding,

178 non-native*, alien*, introduc*, invas*, allochthonous, naturalized. Further articles and

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179 books detected within the resulting reference list were also included, as well as

180 unpublished observations by authors. We cannot rule out that other papers reporting non-

181 native lovebird populations may occur in different languages (e.g. Arabic, Afrikaans),

182 although we checked all of the main languages used in the scientific literature (cf. Ammon

183 2001). Occurrences of lovebirds in aviaries or in small enclosures (N = 22 occurrences)

184 were not included in our analyses. Additional occurrences were obtained by checking

185 once a week, for 6 months, bird observation websites (i.e. iNaturalist, eBird and

186 Christmas Bird Count: Mori et al. 2017), as well as main Social Networks (Facebook and

187 Twitter), image-hosting websites (Flickr) and YouTube. In these searches, we used the

188 same keywords as in our literature search. When a photo, video or record (i.e. report by

189 local ornithologists and birdwatchers) was detected, we contacted local

190 birdwatchers/ornithologists, photographers and video-makers to confirm and obtain

191 coordinates of the record and to provide us with any further relevant information (i.e.,

192 number of individuals, nesting probability, first and final date lovebirds were observed).

193 Only data collected between 2000 and 2018 were considered, to maximize efforts to

194 contact and obtain reliable information from authors.

195   An introduction was considered successful when at least two pairs of lovebirds

196 bred for ≥ three breeding seasons (Andreotti et al. 2001) and there were no indications of

197 a population crash or extinction after this period. Preliminary analyses showed that

198 considering the small number of crashed or currently extinct populations (i.e. excluding

199 single escapes or non-breeding populations) as successful do not modify modelling

200 results. To conclude, since for recent records it may be too early to determine whether

201 introductions were successful or not, analyses both considering and omitting the most

202 recent records (i.e., those with first recorded date > 2010) were conducted.

203

204 *Trade patterns*

205

206   As lovebird species are listed under CITES (Convention on International Trade in

207 Endangered Species of Wild Fauna and Flora), their international trade requires permits

208 detailing the countries of origin and destination of the individuals involved. Furthermore,

209 declaration of international trade of captive-bred individuals is mandatory for CITES

210 species. We compiled information on the total number of live lovebirds reported by

211 CITES that have been legally traded to a given country from 1981 (the first year for which

212 CITES compiled records for these species) to 2013: www.trade.cites.org. (Accessed on

213   29th January 2018). For each trade event, information on the number of individuals

214   involved came from the importer country (24%), the exporter country (54%) or both

215   (22%). This is not likely to affect our results since, when available, information provided

216   by the importer and the exporter countries were highly correlated (Pearson correlation

217   coefficient: r = 0.88). In such cases, the maximum number of individuals reported was

218   used for analyses. Information on breeding origin (wild-caught *vs*. captive-bred birds) of

219   traded individuals was also compiled when available. Although, for *A. roseicollis*

220   declarations were voluntary after the application of the EU Regulation 1332/2005, we

221   prefer not to omit trade data after 2005. So, we obtained highly correlated estimates of

222   trade per country and species (Pearson correlation coefficient, total trade: r = 0.96, trade

223   of wild-caught individuals: r = 0.99, trade of captive-bred individuals, r = 0.95).

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225   *Environmental suitability and niche analyses*

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227   In order to evaluate the environmental suitability of *Agapornis* introduced ranges

228   and to assess the potential niche shift between native and invaded distributions, we used

229   SDMs and niche analyses. Environmental suitability was characterized using an ensemble

230   model of four correlative SDM techniques: generalized linear models (GLM: McCullagh

231   and Nelder 1989), MAXENT (Phillips et al. 2006), gradient boosting machine (GBM:

232   Friedman 2001) and random forest (RF: Breiman 2001). All SDMs were run using

233   *BIOMOD2*, an ensemble-modelling R package developed by Thuiller, Lafourcade,

234   Engler, and Araújo (2009), in R 3.1.3 (R Development Core Team 2016).

235   We trained our models using occurrence data in native ranges, since we were

236   interested in assessing how similarity with native niches affects the establishment in the

237   introduced range. Occurrence data for *Agapornis* species in native ranges were compiled

238   from the Global Biodiversity Information Facility (GBIF). Locations were integrated into

239   a Geographic Information System (GIS) at 5-arcminute resolution, which corresponds

240   approximately to 10 × 10 km. Locations with lower resolutions were not retained.

241   Duplicate samples within the same grid cell were handled as single observations. Final

242   sample size ranged between 1 and 182 occurrences per species, with 664 occurrences in

243   total. Only species with over 15 locations were retained for successive analyses, to ensure

244   at least 10 locations were available for model training (Stockwell and Peterson 2002)

245   during subsampling (see methods below).

246   Climatic   variables   for   analyses   were   extracted   from   WorldClim

247   (www.worldclim.org. Accessed on 04th October 2017) (Hijmans et al. 2005), a high-

248   resolution global climate database widely used to construct SDMs. We extracted data on

249   eight climatic variables which are known to affect bird distributions (Cardador et al. 2016;

250   Cardador et al. 2017): annual mean temperature, temperature seasonality, maximum

251   temperature of the warmest month, minimum temperature of the coldest month, annual

252   precipitation, precipitation of the driest month, precipitation of the wettest month and

253   precipitation seasonality. All layers were compiled at 5-arcminute resolution to match

254   occurrence data resolution.

255   Models were run with a single set of 10,000 pseudo-absences randomly drawn from

256   all biomes occupied by each species across its native ranges (Guisan et al. 2014), using

257   the biome classification by Olson et al. (2001). Presences and pseudo-absences were

258   weighted (0.5) as such to ensure neutral prevalence (Phillips, Anderson, and Schapire,

259   2006). To reduce uncertainty caused by sampling artefacts we used subsampling and

260   conducted 10 replicates for each model by dividing the occurrence data into random

261   training (70%) and test (30%) data sets. However, full models considering total sample

262   size provided highly concordant performance (Table S1 in Appendix 1) and predictions

263   (Pearson correlation coefficient, mean ± SD = 0.85 ± 0.16, range: 0.54 - 1). For each

264   species, consensus models were generated as averaged means of all models. Averaged

265   models were cross-evaluated using the area under the receiver operating characteristic

266   curve (AUC) (Phillips, Anderson, and Schapire, 2006) and the true skill statistic (TSS)

267   values (Allouche, Tsoar, and Kadmon, 2006) in the training region. To reduce problems

268   related to model extrapolation, model projections were adjusted using multivariate

269   environmental similarity surfaces (MESS) (Elith, Kearney and Phillips, 2010).

270   Environmental suitability in highly dissimilar areas (MESS < -20) (Mateo et al. 2014)

271   was considered to be 0 (Figg. S1, S2 and S3, Appendix 1 in Supporting Information). To

272   conclude, we assessed the agreement between model predictions and distribution of real

273   occurrences (i.e. locations with successfully established populations) in introduced

274   ranges. For this, we used the Boyce-index, which ranges from -1 to 1, with the highest

275   value indicating the highest match (Hirzel et al. 2006). As background for such analyses,

276   we estimated the extent of the geographical area that could have been colonized by non-

277   native lovebirds, in two ways: 1) all countries where species have been imported and 2)

278   areas around introduction sites (Strubbe et al. 2013). For the latter, we buffered each

279   locality where lovebirds were introduced with a distance equal to the minimum invasion

280 speed recorded for birds (i.e. 4.59 km/year: Blackburn et al. 2009) multiplied by the

281 number of years since first occurrence in each locality, using ArcMap 10.5 (Strubbe et al.

282 2013). This software was used for all GIS-related analyses.

283   We also calculated niche similarity between native and introduced ranges using

284 niche analyses following the framework proposed by Broennimann et al. (2012). This

285 involved the application of kernel smoothers to species occurrences in gridded

286 environmental space to calculate metrics of niche overlap. The gridded environmental

287 space for analyses was that formed by the first two axes of a Principal Component

288 Analysis (hereafter, PCA) based on the eight climatic variables considered (see above).

289 Climate data for PCA analyses was that at 0.5-arcmin pixels included in the potential

290 native and alien ranges of all lovebird species. The potential native range for each species

291 comprised of all biomes in which the species occurs in native areas (Strubbe et al. 2015).

292 For potential alien range, we considered the geographical area that could have been

293 colonized by each species (i.e., all countries where species have been imported or areas

294 around introduction sites, see above). We conducted a single PCA with data on potential

295 native and alien ranges of all species to obtain comparable results among species;

296 however, results obtained when conducting niche analyses in gridded environmental

297 spaces defined by the first two components of PCAs conducted separately for each species

298 were highly consistent (Table S2 in Appendix 1 in Supporting Information). PCAs were

299 performed on the correlation matrix using the "*stats*" package (R Core Team 2012) in R

300 v.3.1.1 (R Foundation for Statistical Computing, Wien, Austria: cran.r-project.org). For

301 each species, measurement of niche overlap across occurrence densities obtained by

302 kernel smoothers in the gridded environmental space used the Schoener's D metric

303 (Schoener 1970), which ranges from 0 (no overlap) to 1 (full overlap). We then conducted

304 niche similarity tests, whereby a measured niche overlap was compared against a null

305 distribution of 100 simulated overlap values (obtained when comparing the observed

306 niche overlap with niche overlap values obtained by drawing occurrences in the potential

307 alien range of that species at random: Warren et al. 2008; Broennimann et al. 2012). Note

308 that since potential alien ranges were defined using two different approaches (see above),

309 we repeated similarity tests twice. Following Petitpierre *et al.*, (2012), we also calculated

310 niche expansion (i.e., the proportion of alien occurrence densities in conditions different

311 to those covered by native occurrence densities) and niche unfilling (i.e., the proportion

312 of suitable conditions in the native range not occupied in the alien range) for each species.

313 Analyses were conducted using the *"ecospat"* package (Broennimann et al. 2014) in R

314 v.3.1.1.

315

316 *Combining trade data with SDMs*

317

318   We assessed whether combining habitat suitability predictions with information

319 on introduction history (i.e. year of first importation, number of birds imported and

320 breeding origin) can contribute to explain establishment rate of lovebirds in their non-

321 native range. Since information on introduction history was not available at 0.5-arcmin

322 resolution, we conducted our analyses at a coarser scale, that is at a country level. We

323 used generalized linear mixed models (GLMMs) with mean environmental suitability in

324 each country (i.e., the mean of probability values derived from SDM predictions at 0.5-

325 arcmin pixels included in that country), year of first importation, total number of birds

326 imported, breeding origin (proportion of wild-caught vs. captive-breed birds) and the

327 interaction between number of imported birds and breeding origin as predictors.

328 Additionally, the total number of 0.5 arcmin locations per country with the presence of

329 *Agapornis* species according to the compiled database ('introduction sites' hereafter) was

330 also included in the model as a direct estimate of propagule number as well as of potential

331 sampling bias. Species was included as a random intercept factor, and number of

332 populations established per country was the response variable (Poisson error distribution

333 and log-link function). To be consistent with trade data, only records for which first

334 recorded date was later than 1980 were used for analyses. We only considered countries

335 where lovebirds have been imported; the total sample size was 507 countries (range: 31-

336 117 countries per species).

337

338 **RESULTS**

339

340 *Trade patterns*

341

342   Since 1981, more than 44 million bird specimens were reported to be traded,

343 comprising nine lovebird species and their hybrids, across 230 different countries and

344 from both captive and wild-caught origins. The international commerce of lovebirds

345 varied throughout the last 35 years, although two major peaks may be identified: one in

346 the second-half of the 1980s and another starting in the mid-1990s and lasting until 2006

347 (Fig. 2; Figs. S4, S5 and S6, Appendix 2 in Supporting Information). However, trade of
348 *A. roseicollis* is no longer required to be reported to CITES since 2005. The lovebird trade
349 was confirmed to be dominated by birds bred in captivity, representing about 77% of the
350 total traded individuals (approximately 35 million birds), whereas wild-caught birds
351 represent only about 2% of the trade composition. The remaining trade involves other
352 sources, including unreported sources, which represent a considerable volume of birds
353 (17% and over 770, 000 birds traded since 1981).

354   Trade volumes vary considerably across species and associated reported trade
355 sources. *A. fischeri* is reported to be taken from the wild (11%), but birds with unreported
356 breeding origin represented about 31% (> 575,000 individuals) of the trade volume for
357 this species. A similar situation is reported for *A. lilianae*, with unreported sources of
358 trade representing about 42% (>10,000 birds) of the trade volume for this species.

359

360 *Presence of non-native lovebird breeding populations*

361

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

368   Occurrences of non-native lovebirds throughout the world belong to at least eight
369 species (*A. canus*, *A. fischeri, A. lilianae, A. nigrigenis, A. personatus, A. pullarius, A.*
370 *roseicollis* and *A. taranta*) and their hybrids (Fig. 1) and were distributed in Europe,
371 Africa, North America and Oceania (Australia). About 20% of observed occurrences
372 belong to breeding, self-sustaining populations of five species. These include the four
373 most traded species, i.e. *A. fischeri* (25 records, six established populations)*, A. roseicollis*
374 (20 records, nine populations), *A. personatus* (16 records, seven populations) and *A.*
375 *canus* (eight records, six populations). The fifth species, *A. lilianae*, is present with two
376 established populations in South Africa, near the native range (Fig. 1). All records of
377 established populations were in urban or suburban environments, except for three
378 populations breeding in barns surrounded by meadows.

379   Most records belonged to single individuals escaped from cages (65.0%), small

380 groups (5.8%, on average 27 individuals per group), breeding pairs that did not breed for

381 more than 3 years (3.9%) and locally extinct populations (5.9%).

382

383 *Predictions of invasion risk and niche shifts*

384

385   Models trained with data from the species' native ranges showed high model

386 performance in the training regions according to both AUC (mean ± SD: 0.98 ± 0.02) and

387 TSS values (0.86 ± 0.09) (Table S1, Appendix 1 in Supporting Information). In the non-

388 native range, native range based SDMs (Figs. S2 and S3, Appendix 1 in Supporting

389 Information) accurately predicted the distribution of established non-native populations

390 of lovebirds for three species, *A. roseicollis*, *A. fischeri* and *A. personats.* Boyce indices

391 ranged from 0.47 to 0.92 for these species either when omitting or not the most recent

392 data (Table 1). Niche similarity tests also showed evidence of niche conservatism

393 (similarity test significant) with respect to random expectations for the same three species,

394 with some variations according to analyses assumptions (Table 1). However, overall

395 overlap between niches occupied in native areas and introduced ranges were low for all

396 species (D: 0.03 to 0.24 when considering all data; D: 0.03 to 0.22 when omitting recent

397 records; Table 1).

398   Niche analyses were conducted in a gridded environmental space formed by the

399 first two axes of a PCA on the eight climatic variables considered. These axes explained

400 82% of the inertia. The first PCA axis (54%) predominantly represented temperature

401 gradients (warmer climates with low seasonality) while the second axis (28%)

402 represented precipitation gradients (drier climates with low precipitation seasonality,

403 Table 3). Established locations of *Agapornis* species in the introduction range showed 58-

404 78% of their niche outside climatic conditions used in their native areas (34-74% when

405 omitting recent records). Niche differences between the native range and established non-

406 native populations appeared to be related to both a shift along the first and second PCA-

407 axis of the climate space, indicating that during the invasion process, lovebirds have

408 colonized colder and drier areas in respect to their native range (Fig. 3). Niche unfilling

409 varies from 0.3 % to 98% among species (Table 1).

410

411 *Establishment success*

412

413   When jointly analysed, only the effect of the year of first importation and the

414   number of introduction sites were significant in models (Table 2). Thus, the number of

415   locations with established populations increased the earlier the importation date in each

416   country and the larger the number of introduction sites. Effects of climate suitability and

417   breeding origin were not statistically supported. The total percentage of deviance

418   explained by the model was 27.2% (24.7% when omitting more recent records).

419

420   **DISCUSSION**

421

422   Species invasion processes may be the result of multiple drivers, which are often

423   difficult to separate from each other. Our results show that at the country level non-native

424   lovebird establishment rate is largely dominated by event-level effects: the number of

425   established populations is mostly linked to the year of first introduction and the number

426   of introduction sites. The role of introduction effort and year of first importation as key

427   drivers of invasion success has been widely recognized (Blackburn et al. 2015, Abellán

428   et al. 2017; Mori et al. 2018a). Increased introduction effort would increase invasion

429   chances for different reasons (Allendorf and Luikart 2009, Simberloff 2009), such as

430   reducing the relative impact of environmental and demographic stochasticity (e.g. Allee

431   effect, avoidance of inbreeding, e.g. for the globally invasive crabs *Carcinus* spp. and the

432   common chamaeleon in western Europe: Darling et al. 2008; Basso et al. 2019) and by

433   introducing adaptive genetic variation to new areas on which selection can act (e.g. for

434   the garlic mustard in North America and the Siberian chipmunk in Italy: Durka et al.

435   2005; Mori et al. 2018b). In particular, increased propagule number (introduction sites)

436   seems to enhance establishment probability primarily by diminishing impacts of

437   environmental stochasticity, whereas propagule size primarily lessens effects of

438   demographic stochasticity (Simberloff 2009). Additionally, the year since first

439   introduction could also influence the establishment of lovebirds in each country because

440   of its relationship with propagule pressure and introduction effort (a longer time since

441   introduction is likely to result in higher cumulative numbers of individuals released and

442   the number of introduction sites). The positive effect of year since first introduction on

443   establishment rate can also be related to additional population and evolutionary processes

444   (e.g., adaptations to the new habitat) that could generate lag phases at the start of the

445   growth of non-native bird populations (Aagaard and Lockwood 2014, Simberloff 2009).

446   At a finer resolution, climatic niche models fit well the current distribution of non-
447 native lovebirds at 5-arcminute resolution and niche similarity was higher than expected
448 by chance for three out of four species with available data. Even so, niche expansions into
449 novel climatic conditions were observed for all species considered. Thus, although
450 establishments tend to be non-randomly distributed across available climatic conditions,
451 *Agapornis* species may still have notable success in areas climatically distinct from those
452 occupied in their native ranges, as has been reported for other parrot species (Ancillotto
453 et al. 2015; Strubbe et al. 2015). This pattern could be related to different processes. On
454 the one hand, studies using species occurrences and spatial climatic data to characterize
455 species' niches model the realized (i.e., the occupied), not the fundamental niche (Guisan
456 et al. 2014). Also, niche shifts may be contingent upon the environmental variables used
457 (Guisan et al. 2014). On the other hand, most populations of introduced lovebirds occur
458 within human settlements, i.e. urban and suburban habitats. Anthropogenic landscapes
459 may help to overcome physiological and resource limitations locally imposed by climate
460 through food provisioning (Clergeau and Vergnes 2011; Le Louarn et al. 2018), low
461 predator/competitor densities (Gering and Blair 1999; Sorace 2002) and higher
462 temperatures with respect to natural areas (Taha 1997; Niemelä et al. 2011). For example,
463 lovebirds are reported to use cavities in (heated) buildings to breed and to roost during
464 the winter (central Italy: Laurenti and Paci 2015; South Africa: C. Symes and D.
465 Hernández-Brito, pers. comm.), where environmental temperature is higher than in
466 natural areas. Additionally, the halt of supplementary feeding has been the cause of the
467 *Agapornis* population extinction in the Canary Islands (D. Hernández-Brito, pers.
468 comm.), showing that food provisioning was a driver of establishment. Finally, we cannot
469 discard that other relevant factors such as propagule pressure, that could not be accounted
470 for at this spatial resolution, could have a more relevant role than climate matching also
471 at this spatial scale. Particularly, taking into account that that we are mostly dealing with
472 contemporary invasion processes, current distributions may partly reflect the
473 characteristics of the new introduction localities (Colautti 2006) rather than optimum
474 environmental conditions, which might be more likely to be moved into during spread
475 (Abellán *et al.*, 2017).

476   Apart from event-level factors and climate matching, breeding origin may also be
477 affecting establishment success. Previous studies have shown that captive-bred
478 individuals have low probabilities to establish non-native breeding populations (Carrete
479 and Tella 2008; Cabezas et al. 2013). Thus, the predominant trade of captive-bred

15

480   lovebirds could be the main cause of the relatively low numbers of non-native lovebird

481   populations established worldwide. This pattern is striking when compared to other parrot

482   species which have been traded in similar numbers but mainly involving wild-caught

483   individuals (Edelaar et al. 2015; Pârâu et al. 2016). Conversely, our models on

484   establishment do not support an effect of captive breeding: the proportion of captive-bred

485   vs. wild-caught birds failed to explain establishment. One possibility is that we lacked

486   statistical power to detect an effect of breeding origin on top of event-level effects (e.g.

487   Pigot et al. 2018): wild-caught lovebirds recorded in the legal trade mainly belong to

488   uncommon pets or uncommon species in the native range, i.e. *A. pullarius* and *A.*

489   *nigrigenis*, for which no established populations are known outside the native range

490   (Lever 1987; Lever 2005; Menchetti and Mori 2014). Additionally, for a considerable

491   fraction of trade records, information on bird breeding origin was unavailable. Another

492   option is that the importance of breeding origin depends on the habitat that is utilised by

493   the invaders. It has been suggested that the main reason of the higher invasiveness of

494   wild-caught exotic species with respect to captive-bred ones is the loss of antipredatory

495   behaviour in captivity (Carrete and Tella 2008; 2015). Most populations of introduced

496   lovebirds occur within or in the surroundings of human settlements, and urban habitats

497   are considered to be "safe environments" in terms of predator density (see above). This

498   specific ecological context may have helped introduced lovebirds to cope with their

499   behavioural limitations related to captive-breeding.

500   From an applied point of view, our work contributes to the growing evidence of the

501   complexity of the invasion process and the difficulty of pre-introduction invasion risk

502   assessments (Cardador et al. 2016; Abellán et al. 2017), which often assume that it is

503   possible to predict invasion outcomes based on the characteristics of the recipient

504   environments. *Agapornis* species are able to occupy climate niches in the non-native

505   range that differ substantially from those of the native range, and event-level factors

506   appeared to be more relevant factors of establishment at a coarser resolution. In this

507   respect, because establishment success is largely influenced by event-level factors,

508   limiting the transport and release of non-native species would be the most effective

509   strategy (Leung et al. 2002). This is likely to have occurred after the application of the

510   wild-bird trade ban in the European Union in 2005, which affected some of the countries

511   with higher introductions of these parrots (Figure 1).

512   Indeed, lovebird trade after the ban nearly collapsed according to CITES data,

513   which should have directly reduced introduction numbers (Cardador et al. 2017, Reino et

514 al. 2017). Despite this, over 50% of new sites with the presence of *Agapornis* species

515 were reported during the period 2006–2017, and a further breeding site of *A. roseicollis*

516 has been detected for the first time in 2019 (N = 6, Porto Corsini, Ravenna, Italy). This

517 could be explained by the accumulated number of birds already traded before the ban, as

518 well as by an increase in domestic trade of captive-bred species (Cassey et al. 2015;

519 Cardador et al. 2019) not reported by CITES data, since the European trade ban only

520 affected wild-caught individuals (Cassey et al. 2015; Cardador et al. 2019). Additionally,

521 we cannot discount that other factors may have contributed to the observed pattern. *A.*

522 *roseicollis* was no longer CITES-listed after 2005, when declarations of their trade

523 become voluntary. The removal of *A. roseicollis* from the CITES database may have

524 promoted illegal trade, with animal traffickers and smugglers declaring their wild-caught

525 lovebirds as non-CITES listed species to avoid filing paperwork (e.g., Nijman et al. 2012).

526 This may have resulted in the decline we observed for the trade of a CITES-listed species,

527 *A. fischeri*, immediately after the removal of *A. roseicollis*. Accordingly, the US-only

528 trade trend including both CITES and non-CITES data did not show any notable lovebird

529 decline after 2005 (D. Simberloff pers. comm. 2019). Captive-bred individuals of CITES-

530 listed species also require a mandatory declaration by owners, and may still be quite

531 widespread. However, while captive-bred birds are much less likely to establish in the

532 wild with respect to wild-caught birds (Carrete and Tella 2008; 2015), surveillance

533 protocols should also be applied to them, as additional data becomes available to better

534 tease apart the role of origin in *Agapornis* species.

535   Despite their wide distribution as pets (Gismondi 1991; Menchetti and Mori 2014),

536 our paper represents the first work summarising and analysing the distribution and the

537 potential spread of introduced lovebirds, thus improving the knowledge on their invasive

538 status (cf. Menchetti and Mori 2014; White et al. 2019). Disentangling the contributions

539 of climate and introduction effort is a current and popular issue in biological invasions

540 (Di Febbraro et al. 2019; Mori et al. 2019). We revealed both niche shifts and

541 conservatism in the non-native range of lovebird species, particularly by using

542 introduction effort as a predictor of invasion, as well as showing the lack of applicability

543 of climate variables at coarser scales. Given the potential wide adaptability of non-native

544 lovebirds, further research is required to quantify impacts by these parrots on native

545 ecosystems and wildlife and their perception by the public (Crowley et al. 2019, Luna et

546 al. 2019), which is largely still lacking (White et al. 2019), to address potential

547 management actions (Menchetti & Mori 2014).

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

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Table 2. 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). 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. Note that results for some models that did not converge are not shown. Coefficients with significant P values (P < 0.05) are shown in bold. N = 507.

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

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Table 3. 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

801

802   **Figure captions**

803

804   **Figure 1.** Distribution of collected occurrences of lovebirds in the introduced range.

805   Native ranges were taken from IUCN Red List website (www.iucnredlist.org. Accessed

806   on 21st May 2018). The category "Failed" include small groups and breeding pairs that

807   did not breed or did it for less than three years, as well as all the other currently extinct

808   populations.

809

810   **Figure 2.** Total number of imported lovebird individuals: captured from the wild (a),

811   captive-bred (b) and pooled data (c).

812

813   **Figure 3.** Climate niche comparisons between native and invaded ranges of *Agapornis*

814   species. The solid contour lines illustrate the 100% of the available environment in the

815   native range (green lines) and in the invasive range (red lines). Green areas represent

816   climates only occupied in the native range, grey indicates climates occupied in both the

817   native and non-native range while red areas indicate niche expansion in the invaded range.

818   Shading indicates the density of occurrences of the species by cell. The first PCA-axes

819   are mainly determined by temperature gradients and the second axes by precipitation

820   (Table 2).

Agapornis canus · Agapornis fischeri · Agapornis lilianae · Agapornis nigrigenis · Agapornis personatus · Agapornis pullarius

Agapornis roseicollis · Agapornis taranta · Agapornis spp. (hybrid)

Legend: Established | Failed | Single escape | Native range

(a)   (b)   (c)