

1 **Original Article**

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3 **Combining trade data and niche modelling improves predictions of the origin and**  
4 **distribution of non-native European populations of a globally invasive species**

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26 **ABSTRACT**

27 **Aim** Although propagule pressure and environmental constraints are among the most  
28 important factors determining invasion success, studies considering both factors  
29 simultaneously are scarce. Moreover, while recent evidence suggests that the  
30 environmental requirements of individuals from different geographic ranges may be  
31 different, the role of propagule origin in invasions has been largely overlooked. Our  
32 aim was to disentangle the relative role of niche requirements, propagule origin and  
33 propagule pressure on the distribution of an invasive bird species.

34 **Location** Europe, Asia and Africa

35 **Methods** We used species distribution models, niche and deviance partitioning analyses  
36 to investigate the relative roles of propagule pressure (international trade), origin of  
37 individuals (Asian or African), and environmental constraints in determining the  
38 distribution of invasive ring-necked parakeets across 25 European countries.

39 **Results** Differences between niches of native Asian and African parakeets were found,  
40 with the Asian niche matching the European niche more closely. In the invasive  
41 European range, distribution of parakeets was mainly explained by the pure effect of  
42 year of first importation (as a proxy of time since first introduction), the pure effect of  
43 geographic origin of propagules and the joint effect of environmental suitability and  
44 year of first importation, but not by overall propagule pressure. Only when taking into  
45 account the fraction of individuals whose native niche fitted better the European  
46 conditions – Asian parakeets – was the role of propagule pressure highlighted by  
47 models.

48 **Main conclusions** While environmental-based predictions calibrated on native ranges  
49 can constitute a useful first-screening tool, incorporating information about propagule  
50 pressure and especially about the variability in its geographic origin may result in a

51 much more thorough assessment of invasion risk. Trade data reveal as a valuable proxy  
52 of propagule origin and pressure that can be combined with niche modelling for  
53 predicting the fate of trade-mediated invasions in a variety of organisms.

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55 **Keywords:** geographic origin, habitat suitability, international trade, invasive risks,  
56 propagule pressure, *Psittacula krameri*, ring-necked parakeet.

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## 77 INTRODUCTION

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79 Invasive species can result in important ecological and economic costs when they  
80 become well-established and widespread, and consequently more difficult to eradicate  
81 (Genovesi, 2005; Hulme, 2006). Thus, a better understanding of the factors and  
82 mechanisms leading to the successful transition between these last stages of the invasion  
83 process is a major conservation challenge (Thuiller *et al.*, 2005; Levine & Antonio,  
84 2014) and fundamental to the effective implementation of accurate risk predictions and  
85 informed decision-making.

86         Several studies have suggested that propagule pressure (understood as a  
87 composite measure of the number of individuals released into a region in which they are  
88 not native) is one of the most important factors explaining invasion success (Colautti *et*  
89 *al.*, 2006; Blackburn *et al.*, 2009, 2015). While some species-specific life history traits  
90 are also relevant (e.g., Sol *et al.*, 2012), increased propagule pressure favours invasions  
91 by overcoming environmental and demographic stochasticity, avoiding genetic  
92 bottlenecks and by introducing adaptive genetic variation to new areas on which  
93 selection can act (Facon *et al.*, 2006; Simberloff, 2009).

94         Nevertheless, the effect of propagule pressure may be constrained by  
95 environmental characteristics of the areas where the non-native species are introduced  
96 (Gallardo & Aldridge, 2013). Indeed, recent evidence shows that most invasive species  
97 conserve their native environmental niche in invaded areas (Stiels *et al.* 2011;  
98 Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013), suggesting that environmental suitability  
99 (i.e., similarity with native ranges) is a major constraint for invasion establishment and  
100 spread, with no or little effect of propagule pressure expected if no suitable habitat is  
101 available. Climate has often been proposed as the main range-limiting factor among

102 environmental variables, especially at large spatial scales (Huntley *et al.*, 2007), with an  
103 incremental increase in the importance of other factors such as topography or land uses  
104 at finer scales (Mackey *et al.*, 2001).

105 Propagule pressure and environmental suitability may also interact at different  
106 temporal or spatial scales (Warren *et al.*, 2012), which may make it more difficult to  
107 separate their effects. Despite the potential implications of combined effects, studies  
108 considering both factors simultaneously are scarce (Colautti *et al.*, 2006) and usually  
109 rely on commerce-related surrogates of propagule pressure, such as human population  
110 density or human influence indexes that indirectly measure the extent to which humans  
111 might knowingly or unknowingly facilitate the long-distance transport of organisms  
112 (Gallardo & Aldridge, 2013; Gallardo *et al.*, 2015). More importantly, although recent  
113 evidence suggests that environmental requirements of individuals from different  
114 geographic ranges may be different (Broennimann & Guisan, 2008; Beaumont *et al.*,  
115 2009), studies conducted thus far have overlooked the role of propagule origin in  
116 invasions, assuming that species-environment relationships are constant across the  
117 whole native range of the species. This holds important ecological interest but also  
118 applied relevance. Many non-native species currently arrive at new areas because of  
119 their importation as trade commodities (Hulme *et al.*, 2008). If individuals coming from  
120 different geographic origins have different ecological niches, their invasion success is  
121 also likely to differ across different recipient environments. Thus, a better understanding  
122 of the importance of not only propagule pressure but also its origin as predictors of  
123 invasion success is needed for robust management planning.

124 In this study, we apply a multivariate approach to disentangle the relative roles of  
125 propagule pressure, origin of individuals and environmental constraints in limiting the  
126 non-native distribution of an invasive species. We focus on the ring-necked parakeet

127 *Psittacula krameri* (Scopoli, 1769), one of the most widespread invasive bird species of  
128 the world (Lever, 2005; CABI, 2014), also considered amongst the 100 worst alien  
129 species in Europe (<http://www.europe-aliens.org/speciesTheWorst.do>) with impacts on  
130 native fauna (Strubbe & Matthysen, 2009; Strubbe *et al.*, 2010; Hernández-Brito *et al.*,  
131 2014; Peck *et al.*, 2014). This species stands up as a good study model for our approach,  
132 since it is native to two large, geographically disjoint regions (sub-Saharan Africa and  
133 South-Asia, mostly the Indian subcontinent), and has been largely traded to Europe as a  
134 wild-caught cage bird species thus resulting in a number of invasive populations due to  
135 accidental escape or release of individuals (Carrete & Tella, 2008; Strubbe &  
136 Matthysen, 2009). This process of invasion provides a unique opportunity to identify  
137 some of the ecological factors limiting the invasion of species with widespread native  
138 distributions while considering potential niche differences associated with propagule  
139 pressure and origin. Moreover, our study builds upon recent research on distribution  
140 modelling and invasion genetics of ring-necked parakeets. First, Strubbe *et al.* (2015)  
141 demonstrated that niche requirements varied between the African and Asian  
142 phylogenetic lineages of the species, making Asian individuals more suitable to invade  
143 the new European environments. However, Strubbe *et al.* (2015) did not consider the  
144 role of propagule pressure, which may confound the actual role of niche similarity in  
145 shaping current invasion ranges (Colautti *et al.*, 2006). Second, Jackson *et al.* (2015)  
146 found that Asian haplotypes were more prevalent in invasive populations in Europe,  
147 being consistent with niche distribution modelling results (Strubbe *et al.*, 2015) but also  
148 with a higher proportion (75%) of Asian individuals imported in the seven European  
149 countries studied (Jackson *et al.*, 2015). However, by comparing the proportion of  
150 Asian/African haplotypes with the proportion of Asian/African birds imported in each  
151 country, Jackson *et al.* (2015) found that the proportion of Asian genes was higher than

152 expected in four countries, lower than expected in two countries, and nearly identical in  
153 one country. As authors recognised, these apparent contradictions might arise from the  
154 fact that trade data is available at the country level while only particular populations  
155 were genetically screened within each country. Local environmental suitability for  
156 Asian or African parakeets may differ from that of the whole country.

157 We add here a novel, complementary study based on deviance partitioning analysis  
158 to identify the pure and joint contributions of environmental suitability (obtained from  
159 species distribution models and niche analyses), propagule pressure (number of  
160 individuals imported) and origin (African versus Asian individuals) on the current  
161 species distribution across 25 European countries. To our knowledge, this is the first  
162 study that employs deviance partitioning analyses to assess drivers of spatial invasion.  
163 Environmental suitability, trade of this species and its invasiveness greatly vary among  
164 countries, thus allowing a broader examination than the subset of successfully invaded  
165 countries considered by Jackson *et al.* (2015). Our study demonstrates a framework to  
166 disentangle the contribution of environmental suitability, propagule origin and pressure,  
167 valid for many other globally traded and invasive organisms.

168

## 169 **MATERIALS AND METHODS**

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### 171 **Species distribution and environmental data**

172

173 Occurrence data of ring-necked parakeets was compiled from the eBird database  
174 (<http://ebird.org/>, Sullivan *et al.*, 2009) and complemented with data from GBIF (Global  
175 Biodiversity Information Facility, <http://data.gbif.org>). The quality of the data was  
176 checked against broad spatial data provided by CABI-Invasive Species Compendium

177 (<http://www.cabi.org/isc/>), the European project DAISIE (Delivering Alien Invasive  
178 Species Inventories for Europe, <http://www.europe-aliens.org/>) and the IUCN/ISSG  
179 (Invasive Species Specialist Group, <http://www.issg.org/database>). Overall, broad  
180 spatial patterns were highly concordant among sources and thus considered robust for  
181 analyses (see Fig. S1 in Appendix S1 for graphical comparisons). Locations were  
182 integrated into a Geographic Information System (GIS) at 5-arcminute resolution, which  
183 corresponds approximately to 10 x 10 km. Duplicate samples within the same grid cell  
184 were handled as single observations. Final sample size was 1 745 grids with the  
185 presence of the species: 1 070 belonging to the native Asian range, 140 to the native  
186 African range and 535 to the invaded European range (according to BirdLife  
187 International, 2014; del Hoyo *et al.*, 1997). Although four subspecies have been  
188 described for the species (two in each native range), we worked at the species level  
189 because recent genetic evidence demonstrated partial overlapping patterns in the  
190 geographic distribution and ecological niches for most phylogenetic groups within  
191 Asian and African ranges (Strubbe *et al.*, 2015).

192 We compiled data on altitude as well as seven bioclimatic variables (obtained  
193 from WORLDCLIM, <http://www.worldclim.org/>) (Hijmans *et al.*, 2005) commonly  
194 used in avian distribution modelling to represent bioclimatic controls: annual mean  
195 temperature, temperature seasonality, maximum temperature of the warmest month,  
196 minimum temperature of the coldest month, annual precipitation, precipitation of the  
197 driest month, and precipitation seasonality. We also compiled data on land-use  
198 composition and population density, since habitat and human influence are likely to  
199 affect species distributions at small spatial scales (Mackey *et al.*, 2001). Land-use  
200 composition was obtained from the Global Land Cover Facility (<http://glcf.umd.edu/>) as  
201 a variable with five categories: woodlands (including forests and savannahs), open lands



202 (including shrubland and grassland), croplands, urban and others (including wetlands,  
203 ice and barren areas, as habitats not suitable for the species). Population density was  
204 obtained from the Oak Ridge National Laboratory (<http://www.ornl.gov/sci/landscan>)  
205 corresponding to year 2010. All layers were derived at 5-arcminute resolution to match  
206 occurrence data resolution.

207

## 208 **Niche comparisons**

209

210 We assessed potential niche differences between African and Asian native populations  
211 of ring-necked parakeets, and whether this translates into differences in environmental  
212 suitability in Europe using species distribution models (SDMs) and niche overlap  
213 analyses. SDMs were calibrated using occurrence data in each native range (Asia and  
214 Africa) and the set of bioclimatic and human-related variables as predictors. It should be  
215 noted that the niche of ring-necked parakeets considered here relates to the Grinnellian  
216 niche concept, i.e. the response of species to a given set of non-consumable variables  
217 that influence their large-scale geographical distribution (Soberón, 2007).

218 While it is generally accepted that the potential range distribution of invasive  
219 species is best addressed using its global coverage (Broennimann & Guisan, 2008), we  
220 only used native information for model calibration because the focus of this study was  
221 not to produce the best-fit model in the invasive range, but to determine the  
222 environmental similarity between the two native and the invasive ranges. SDMs were  
223 implemented in MAXENT 3.3.3k software, one of the best-performing and most  
224 frequently used methods for developing SDMs (Elith *et al.*, 2006), but similar results  
225 were obtained using other modelling techniques (Fig. S2 from Appendix S1). We  
226 selected 500 iterations for model convergence and employed the regularization

227 procedure to prevent overfitting (Phillips & Dudík, 2008). Although Multivariate  
228 Environmental Similarity Surface (MESS) analysis suggested that extrapolation outside  
229 the calibration range is not a problem in our case (see Appendix S2 for more detailed  
230 information), we applied clamping when modelling (Phillips *et al.*, 2006). Exploratory  
231 analyses showed that using real presence-absence data did not improve the accuracy of  
232 models (Appendix S2). Additionally, their inclusion in models could constrain the  
233 obtained range nearer to the realized distribution, thereby underestimating potential  
234 suitable areas (Chefaoui & Lobo, 2008; Appendix S2). For this reason, random samples  
235 of background pixels (10 000) were used as pseudo-absences to construct models. To  
236 ensure that selected pseudo-absences provided the most accurate results and biologically  
237 meaningful fit between species occurrence and predictor variables, we tested different  
238 minimum and maximum distances to occurrence points covering biomes occupied by  
239 the species in native ranges (Table S1 in Appendix S1), and selected 100-500 km as the  
240 optimum distance (VanDerWal *et al.*, 2009). We also confirmed that differences in  
241 sample sizes between African and Asian native ranges are not likely to affect our results  
242 (Appendix S2).

243       To minimize potential biases associated with differences in geographic  
244 distribution of birding effort, we produced bias grids using information on total  
245 surveyed grids (i.e., those for which complete bird lists had been provided at least once)  
246 retrieved from eBird (Sullivan *et al.*, 2009). We derived a kernel density map of birding  
247 effort at a 5-arcminute resolution using ArcMap 9.3 and rescaled it from 1 to 20 to  
248 reduce numeric disparities (Elith *et al.*, 2010). The birding effort map was implemented  
249 in the bias-file option of Maxent; that is, an inverse weight to its birding effort was  
250 applied to each occurrence in the database, thereby reducing the importance of  
251 oversampled areas.

252 Model accuracy was assessed by dividing the species occurrence data into  
253 random training (70%) and test (30%) datasets, a splitting procedure repeated 10 times.  
254 Models were evaluated on the test data using the area under the receiver operating  
255 characteristics curve (AUC), a threshold-independent assessment measure (Phillips *et*  
256 *al.*, 2006). AUC values range from 0 to 1, where 1 indicates perfect model performance  
257 and 0.5 indicates predictive discrimination no better than random (but see criticisms in  
258 Lobo *et al.*, 2008). We also calculated the true skill statistic (TSS). TSS ranges from -1  
259 to +1, where +1 indicates perfect agreement and values of zero or less indicate a  
260 performance no better than random (Allouche *et al.*, 2006). We transformed model  
261 predictions into binary maps using the 10% fixed cumulative logistic threshold from  
262 Maxent (omission rate ~10%) to be conservative while also accounting for potential  
263 errors in occurrence data.

264 For niche overlap analyses we followed the framework proposed by Broennimann  
265 *et al.* (2012) that allows calculating niche overlap while correcting for differences in the  
266 availability of environments between study areas. This involves (1) the application of  
267 multivariate analyses to summarize environmental variables in a one- or two-  
268 dimensional environmental space; (2) calculation of the density of occurrences across  
269 the environmental space; (3) measurement of niche overlap across the environmental  
270 space; and (4) statistical tests using randomization approaches.

271 In our case, the environmental space was defined by the gradient of predicted  
272 probabilities obtained with the above-described Maxent models. This method has been  
273 shown to produce unbiased results, and is likely to be more useful than other  
274 multivariate analyses when environmental differences are important between the  
275 compared ranges (Broennimann *et al.*, 2012). We then applied kernel smoothers to  
276 calculate occurrence density across the environmental gradients (see Fig. 1 for a

277 graphical representation). Overlap was measured using the metric  $D$  (Warren *et al.*,  
278 2008), which ranges from 0 (no overlap) to 1 (full overlap). We then conducted niche  
279 similarity tests, whereby a measured niche overlap was compared against a null  
280 distribution of 100 simulated overlap values (obtained when comparing the observed  
281 niche in one range with niches obtained by drawing occurrences at random in the other  
282 and *vice versa*) (Warren *et al.*, 2008; Broennimann *et al.*, 2012). Note that the niche  
283 similarity test is, thus, bidirectional. If the observed overlap is greater than 95% of 100  
284 simulated values (one-tailed test), occupied environments in both ranges are more  
285 similar to each other than expected by chance taking into account environmental  
286 availability. Analyses were conducted using the ‘ecospat’ library (Broennimann *et al.*,  
287 2014) in R v.3.1.1 (R Development Core Team, 2014).

#### 288 **Propagule pressure and geographic origin**

289  
290 Contrarily to deliberate bird introductions conducted in the past, where the actual  
291 number of introduced individuals was often well known (Blackburn *et al.*, 2009),  
292 determining propagule pressure for recent avian introductions is a harder task since  
293 most of them arose from the accidental escape of internationally traded birds (e.g.,  
294 Carrete & Tella, 2008). We thus relied on the number of imported individuals as a  
295 reasonable surrogate of propagule pressure (Blackburn *et al.*, 2015), since it should  
296 positively correlate with the number of accidentally escaped or released (i.e.,  
297 introduced) individuals. Since the ring-necked parakeet is listed by the Convention on  
298 International Trade in Endangered Species of Wild Flora and Fauna (CITES,  
299 <http://www.cites.org>), its international trade requires permits detailing the countries of  
300 origin and destination of the individuals involved. Therefore, propagule pressure was  
301 estimated as the total number of live parakeets reported by CITES that have been legally

302 traded to Europe from 1981 (the first year for which CITES compiled records for this  
303 species) to 2014 (although the species was not traded after 2011, Appendix S3). While  
304 the current European distribution of ring-necked parakeets is the result of a process  
305 starting earlier than CITES records in some countries (Lever, 2005; CABI, 2014), the  
306 establishment (of new populations) and population spread –even for the earliest  
307 populations- lay within the temporal period considered in our analyses.

308         Using the above information, we first assessed spatial patterns in parakeet  
309 importations into Europe related to their origin, by comparing the numbers of Asian and  
310 African birds imported by each of the 25 countries included in this study. Since year of  
311 first importations could also influence the establishment and spread of parakeets in each  
312 country, due to lag phases in the growth of exotic bird populations (Aagaard &  
313 Lockwood, 2014), we also obtained the year of first importation for each country and  
314 parakeets' origin (Asian versus African). These spatio-temporal patterns were explored  
315 through Wilcoxon Signed Rank Tests and Chi-square test in R software.

316

### 317 **Partitioning environmental suitability, propagule pressure and geographic origin**

318

319 We assessed the relative contribution of environmental suitability, propagule pressure,  
320 geographical origin of individuals and the interaction of propagule pressure ×  
321 geographic origin on the distribution patterns of ring-necked parakeets across Europe  
322 using deviance partitioning. We only considered European countries where the species  
323 had been imported (n = 25), thus excluding from analyses seven countries where the  
324 species was not recorded. Deviance partitioning is a quantitative statistical method  
325 which separates the amount of deviance explained by the pure effects of each  
326 explanatory variable in a model from the amount explained by joint effects that cannot

327 unambiguously be attributed to one variable or another due to collinearity (Heikkinen *et*  
328 *al.*, 2005; Carrete *et al.*, 2007). It entails the calculation of incremental improvements in  
329 model fit due to the inclusion of each variable in every possible model. For these  
330 calculations we conducted (partial) generalized linear models (GLM) containing  
331 different combinations of the predictor variables and the proportion of surveyed grids  
332 occupied in each country as the response variable (numerator: number of occupied  
333 grids; denominator: number of surveyed grids according to eBird data; binomial error  
334 distribution and logit-link function). Surface of suitable habitat was calculated as the  
335 percentage of suitable habitat for Asian and African parakeets in each country according  
336 to binary predictions of Maxent models. However, since surface of suitable habitat for  
337 African parakeets showed little variation among countries and was close to zero (mean  
338  $\pm$  sd:  $0.1 \pm 0.5$  %), only the percentage of suitable habitat according to Asian models  
339 was retained to avoid overparametrization. Nevertheless, if observed differences in  
340 occupied environmental niches between African and Asian parakeets, and thus in model  
341 predictions in Europe, simply result from differences in the realized – and not the  
342 fundamental – niche (Broennimann & Guisan, 2008; Beaumont *et al.*, 2009); suitable  
343 habitat in the invasive range according to Asian models (which include most of the  
344 African niche, see results) is expected to be representative of environmental suitability  
345 for both African and Asian parakeets. Propagule pressure corresponded to the total  
346 number of individuals traded into each European country, and geographical origin to the  
347 proportion of individuals originating from Asia. Since the proportion of occupied grids  
348 per country is likely to vary according to its surface (for example, the probability of  
349 occupying the 100% of grid cells is not likely to be the same for a country of 10 km<sup>2</sup> or  
350 1 000 km<sup>2</sup> if all other conditions –like propagule pressure and year of first importation -  
351 are identical), we included the natural logarithm of country surface as an offset in all

352 models. Additionally, to reduce potential effects of variation in importation periods  
353 among countries, we repeated our analyses including year of first importation (which  
354 was not-significantly different between Asian and African parakeets but showed high  
355 variation among countries - see results) in our models.

356

## 357 **RESULTS**

358

### 359 **Niche comparison between native and invasive ranges**

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361 Models calibrated with data from the species' two native ranges predicted occurrences  
362 in the training region with high AUC (AUC = 0.88 for Africa and AUC = 0.92 for Asia)  
363 and TSS values (TSS = 0.57 for Africa and TSS = 0.66 for Asia), which indicates high  
364 model performance.

365 African and Asian niches are more similar to each other than expected by chance  
366 (D based on environmental gradient calibrated in Africa [ $D_{\text{Afr}}$ ] = 0.32,  $P < 0.01$ ; D  
367 based on environmental gradient calibrated in Asia [ $D_{\text{Asia}}$ ] = 0.26;  $P < 0.02$ ). However,  
368 while the Asian ring-necked parakeet has most of its niche (68%) outside the African  
369 native niche (Fig. 1a), the reverse is not true (95% of the African niche was within the  
370 Asian niche; Fig. 1b and Table S2 in Appendix S1). This observation indicates that the  
371 African niche is a small subset of the Asian one, which leads to differences in  
372 environmental suitability for both populations in Europe.

373 Maxent models calibrated in native ranges suggested that most of the European  
374 surface area is suitable for the Asian population, while almost no habitat is suitable for  
375 the African population (Fig. 2, see also Fig. S2 from Appendix S1 for results using  
376 other modelling techniques). Accordingly, we found a high and significant overlap

377 between Asian and European occupied niches ( $D_{\text{Asia}} = 0.77$ , P-range = 0.01 – 0.02). In  
378 contrast, the overlap between the African and the European occupied niches was very  
379 low ( $D_{\text{Afr}} = 0.0003$ ) and non-significantly higher than expected by chance based on the  
380 habitat available in Africa.

381

## 382 **Trade data**

383

384 In total, 408 174 ring-necked parakeets were imported by European countries in the  
385 period 1981-2011 (Table S3 in Appendix S3), coming in similar numbers from Africa  
386 (44%) and Asia (56%), without differences in their origin as a whole (Wilcoxon paired  
387 rank test,  $W = 205.5$ ,  $P = 0.25$ ,  $n = 25$ ). Significant differences between Asian and  
388 African parakeets were neither found for year of first importation ( $W = 82.5$ ,  $P = 0.47$ ).  
389 However, the proportion of Asian imports largely varied among countries (Chi-square =  
390 115893.8,  $P < 0.001$ , Fig. 3), as well as year of first importation (Table S3 in Appendix  
391 S3).

392

## 393 **Relative importance of environmental suitability, propagule pressure and** 394 **geographic origin**

395

396 Univariate models showed positive and significant relationships between all explanatory  
397 variables (i.e., environmental suitability, propagule pressure and geographic origin) and  
398 occupancy rate across the 25 European countries. However, when jointly analysed in a  
399 multivariate model, only the effect of environmental suitability and geographic origin  
400 remained significant (Table 1). Thus, the occupancy rate of invaded countries mostly  
401 increased with the availability of suitable habitats and the proportion of individuals



402 traded from Asia (Fig. 4). Similar results were obtained when first year of importation  
403 was included as a control in models; as expected, occupancy rate increased the earlier  
404 the importation date in each country (Table 1). The total percentage of deviance  
405 explained by environmental suitability, propagule pressure and geographic origin was  
406 31.8%. This value increased to 54.9 % when year of first importation was also included  
407 in models. Deviance partitioning analysis showed that the pure effect of environmental  
408 suitability followed by geographic origin contributed the most to explaining variation of  
409 occupancy patterns, while the pure effect of propagule pressure was close to 0 (Fig. 5).  
410 Pure contribution of environmental suitability decreased, however, when year of first  
411 importation was also included in models, since the 93.7% of deviance explained by this  
412 variable was shared by the deviance explained by year of first importation (Fig. S3 in  
413 Appendix S1). When taking into account only the Asian fraction of traded individuals in  
414 a *post hoc* model, propagule pressure contributed significantly to occupancy rate when  
415 jointly analysed with environmental suitability and year of first importation (Table 2).  
416 The pure effect of environmental suitability also become non-significant when jointly  
417 analysed with year of first importation, due to their mentioned shared effect.

418

## 419 **DISCUSSION**

420

### 421 **Joint assessment of multiple drivers of spatial distribution**

422

423 The spatial distribution of invasive species can reflect the cumulative effects of  
424 numerous factors that are often difficult to disentangle. Our results show that the  
425 distribution of ring-necked parakeets across Europe is mainly explained by the pure  
426 effects of geographic origin of propagules and year of first importation (reflecting time

427 since first introduction) and the joint effect of environmental suitability and year of first  
428 importation, but not by propagule pressure as a whole. Our multivariate model fits well  
429 with the current distribution of ring-necked parakeets in Europe (ca. 32% of the  
430 deviance explained or 55% when controlling for dates of first importation in models),  
431 particularly taking into account that we are dealing with a contemporary invasion  
432 process (i.e., the species is currently spreading across Europe; Strubbe & Matthysen,  
433 2009) and thus a large portion of suitable habitats may still not be occupied (Cardador *et*  
434 *al.*, 2014; Strubbe *et al.*, 2013). At this stage, the occupation of suitable habitat -  
435 particularly if large areas are available due to tolerance to a broad range of climatic and  
436 habitat conditions as seems to be the case- is highly constrained by dispersal and  
437 colonization processes (Václavík & Meentemeyer, 2012). This may explain the major  
438 role of year of first importation in present-day occurrences of ring-necked parakeets in  
439 Europe. Indeed, higher percentages of suitable habitat at the country level are not likely  
440 to result into higher occupancy rates unless there has been enough time for accidentally  
441 escaping birds, building up populations and spreading. It is also worth mentioning that  
442 our results arose from the application of models to relatively broad habitat units  
443 (European countries), and information at a finer resolution –unfortunately not available  
444 for propagule pressure in our study model- would likely improve model accuracy  
445 (Rahbek & Graves, 2001). At this scale, populations with higher occupancy rates in  
446 Europe were those that had not only more suitable habitat to spread but also more time  
447 (joint effect), which does not allow separating the pure effect of environmental  
448 suitability from year of first introduction. However, the pure effect of environmental  
449 suitability is likely to be more apparent with time, as the distribution of the species is  
450 closer to the equilibrium (Václavík & Meentemeyer, 2012).

451

452 **The role of the geographic origin of propagules**

453

454 According to niche comparisons, only the niche of Asian parakeets appeared to fit  
455 the European conditions. This supports and reinforces the conclusion of Strubbe *et al.*  
456 (2015), since it holds after we simultaneously considered the effects of variability in  
457 propagule size and dates of importation among countries. These results are in line with  
458 current literature reflecting the importance of niche similarity between native and  
459 invaded ranges to explain the success of invasive species distribution (Petitpierre *et al.*,  
460 2012; Strubbe *et al.*, 2013), while highlighting the importance of considering the largely  
461 overlooked variability in geographic origin of propagules. Our results are also  
462 concordant with recent genetic evidence showing that, although Asian and African ring-  
463 necked parakeets were introduced into Europe in similar numbers (this study), genetic  
464 markers of established invaders mostly match those of Asian populations (Jackson *et*  
465 *al.*, 2015). Moreover, a genetic screening of European and North American introduced  
466 populations of the also highly invasive monk parakeet (*Myiopsitta monachus*) indicates  
467 the same pattern, suggesting that propagules came from a restricted native range despite  
468 the fact that the species has been imported from several South American countries  
469 (Edelaar *et al.*, 2015).

470 Differences in environmental niches of Asian and African ring-necked parakeets  
471 can result from local adaptation, genetic drift or phenotypic plasticity across geographic  
472 ranges, thus leading to differences in environmental tolerances (Broennimann & Guisan,  
473 2008; Beaumont *et al.*, 2009). However, we cannot rule out that differences in occupied  
474 environmental niches are simply reflecting differences in the realized niche of the  
475 species (Broennimann & Guisan, 2008; Beaumont *et al.*, 2009). Even in this case,  
476 gained experience or skills in using environments similar to those available in Europe

477 could have conferred invasive advantages to the Asian population. Sample size  
478 differences could also affect results if they lead to differences in environment variability  
479 captured by occurrences in different ranges. However, we do not think this is our case,  
480 since our lower sample size (140 occurrences for Africa) lies within the minimum  
481 sample size needed for accurate modelling (Stockwell & Peterson, 2002) and is well  
482 distributed across all the African range. Finally, potential differences in their ability to  
483 reach different stages of the invasion process associated with the wild-bird trade  
484 (Carrete *et al.*, 2012) may also have promoted this pattern. CITES data show that both  
485 Asian and African parakeets reached the transport stage in similar numbers. However,  
486 more research is needed to know whether their likelihood of adapting to captive  
487 conditions and later escaping and establishing in the wild is the same.

488

### 489 **The role of propagule pressure**

490

491 Propagule pressure has been shown as one of the main determinants of  
492 establishment success of many non-native species (Lockwood *et al.*, 2005; Simberloff,  
493 2009; Blackburn *et al.*, 2015). The strongest evidence comes from past deliberate  
494 introductions of birds, for which numbers of introduced propagules were accurately  
495 reported (Blackburn *et al.*, 2009; Blackburn *et al.*, 2013). However, current avian  
496 introductions mostly originate from the international transport and accidental escape of  
497 birds (Carrete & Tella, 2008; Blackburn *et al.*, 2010), where actual propagule sizes are  
498 much more difficult –or impossible- to estimate. This applies not only to a large number  
499 of cage bird species (Carrete & Tella, 2008) but also to a variety of non-native flora and  
500 fauna unintentionally introduced through their international trade (Hulme *et al.*, 2008).  
501 Here, we used the number of imported individuals as a reliable proxy of propagule

502 pressure for trade-mediated introductions, which can be considered a more direct  
503 surrogate of trade intensity than other recently applied measures such as human  
504 population density or human influence indexes (Gallardo & Aldridge, 2013; Gallardo *et*  
505 *al.*, 2015).

506 A striking result from our study, with broad implications for others, is that the role  
507 of propagule pressure can be completely masked if the origin of propagules matters and  
508 it is not considered in analyses of invasiveness. The current European distribution of  
509 ring-necked parakeets is mainly related to the additive effects of propagule origin,  
510 environmental suitability and year of first importation but not to the effect of the total  
511 number of imported individuals (propagule pressure). However, the role of propagule  
512 pressure was highlighted when only taking into account the fraction of individuals  
513 whose niche fitted European conditions, which are probably more able to survive.

514 Our study also helps to clarify the actual relationship between propagule origin and  
515 propagule pressure in our study model. Jackson *et al.* (2015) found some inconsistencies  
516 between the ratio of Asian/African haplotypes and the ratio of Asian/African imports in  
517 seven European countries, probably because trade data was obtained at the country level  
518 while only a few local populations could be screened for genetic composition within  
519 each country. This may be the case of Spain -as highlighted by the authors- where the  
520 proportion of African genes was larger than expected attending to trade data. The fact  
521 that the two sampled Spanish populations were sited in Seville and Madrid, two of the  
522 very few and small areas where habitat is suitable for African parakeets (see Figure S2  
523 in Appendix S2), may explain the discrepancy. Our study, however, where both  
524 environmental suitability and trade were measured at the same spatial scale (countries),  
525 supports a positive effect of the proportion (and propagule pressure) of Asian parakeets  
526 on the species distribution across 25 European countries.

527

528 **Improving risk assessments**

529

530 From an applied point of view, our work contributes to the growing evidence that  
531 environmental-based predictions calibrated with occurrence data in native ranges can  
532 serve as a first-screening tool to predict the fate of introduced species in new areas  
533 (Peterson, 2003; Thuiller *et al.*, 2005). However, incorporating data about propagule  
534 pressure and, especially, about variability in the geographic origin of propagules may  
535 result in a more thorough assessment of invasion risk (Strubbe *et al.*, 2015). In our case  
536 study, a straightforward management action is suggested: the banning of the importation  
537 of Asian ring-necked parakeets—while maintaining or even increasing the importation of  
538 African birds to satisfy the cage-bird market demand—could have drastically reduced the  
539 risk of invasion of this species in Europe. Although this recommendation arrives too late  
540 for Europe, our approach could be applied to other countries and continents where the  
541 species is becoming widespread or has not yet become established. How can this  
542 valuable information be incorporated into trade regulations when these respond to  
543 complex ecological and socioeconomic drivers remains, however, a challenge. More  
544 attention should be placed on this issue in the future.

545         Here we dealt with a good study model for which a detailed picture of its recent  
546 invasion history has been obtained (Strubbe *et al.*, 2015; Jackson *et al.*, 2015; this  
547 study). However, how generalizable and feasible is our approach for predicting many  
548 other biological invasions? Sources of worldwide distribution data for a variety of taxa  
549 are increasingly available (e.g., eBird, GBIF), and CITES annually reports the origin  
550 and destination of internationally traded individuals from roughly 5 600 species of  
551 animals and 30 000 species of plants (www.cites.org). Therefore, our statistical

552 approach aimed to identify the relative contribution of habitat suitability, propagule  
553 origin and propagule pressure could be applied to a number of species that are or may  
554 become invasive due to their international trade. However, information on propagule  
555 pressure and geographic origin may be not available for many other globally traded  
556 species (e.g., those not listed by CITES). In such cases, at least projecting potential non-  
557 native distributions based on different geographic sources of propagules could lead to  
558 better risk assessments and to identify those international trade routes that are less safe  
559 in terms of potential alien invasions. Although more research is needed to fully  
560 understand invasions, differences in environmental constraints among propagules  
561 coming from different native ranges should be considered as important drivers of  
562 distribution of invasive species.

563

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565

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572

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## 742 SUPPORTING INFORMATION

743

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

745 **Appendix S1.** Supplementary Tables S1 and S2 and Figures S1-S3 showing exploratory  
746 analyses for pseudoabsence selection, occurrence characteristics and modelling outputs.

747 **Appendix S2.** Effect of sampling bias, sample size differences and MESS analyses in  
748 Maxent models.

749 **Appendix S3.** Description of CITES data.

750

751 **BIOSKETCH**

752

753 The research team was brought together by a shared interest in understanding the  
754 ecological factors affecting the spatial distribution of species, and particularly those that  
755 contribute to the invasion success of non-native species. All authors focus at least part  
756 of their research on biological invasions, using a variety of organisms as study models.

757

758 Author contributions: L.C., M.C., B.G. and J.L.T. conceived the ideas; L.C. and B.G.  
759 analysed the data with inputs from M.C. and J.L.T.; and L.C., M.C., B.G. and J.L.T.  
760 wrote the manuscript.

761

762 Editor: Joseph Veech

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**Table 1.** Results from univariate and multivariate GLMs (binomial error distribution; logit-link function) relating occurrence rate of ring-necked parakeets in European countries with environmental suitability, propagule pressure and geographic origin. The natural logarithm of country surface was included as an offset in all models. N = 25.

	<b>Intercept</b>	<b>Estimate</b>	<b>Z</b>	<b>P-value</b>
<b>Univariate models</b>				
Environmental suitability	-16.9 ± 0.17	1.93 ± 0.20	9.50	<0.001
Propagule pressure	-15.7 ± 0.06	5.1×10 <sup>-6</sup> ± 1.1×10 <sup>-6</sup>	4.74	<0.001
Geographic origin	-15.9 ± 0.08	1.15 ± 0.16	7.08	<0.001
Year of first importation	698 ± 57	-0.36 ± 0.03	-12.55	<0.001
<b>Multivariate model</b>				
Intercept	-18.0 ± 0.24			
Environmental suitability		2.43 ± 0.24	10.11	<0.001
Propagule pressure		-1.8×10 <sup>-6</sup> ± 0.7×10 <sup>-5</sup>	-0.26	0.8
Geographic origin		1.72 ± 0.21	6.78	<0.001
Prop press x Geogr origin		-3.8×10 <sup>-8</sup> ± 9.3×10 <sup>-6</sup>	-0.004	0.99
<b>Multivariate model (with year of first importation)</b>				
Intercept	592 ± 0.81			
Year of first importation		-0.31 ± 0.004	-7.50	<0.001
Environmental suitability		0.93 ± 0.33	2.82	0.005
Propagule pressure		-6.3×10 <sup>-6</sup> ± 8.1×10 <sup>-6</sup>	-0.79	0.432
Geographic origin		2.38 ± 0.32	7.35	<0.001
Prop press x Geogr origin		2.1×10 <sup>-6</sup> ± 1.0×10 <sup>-5</sup>	0.20	0.842

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**Table 2.** Results from multivariate GLMs (binomial error distribution; logit-link function) relating occurrence rate of ring-necked parakeets in European countries with environmental suitability and propagule pressure of Asian parakeets. The natural logarithm of country surface was included as an offset in all models. N = 25.

	Estimate	Z	P-value	Deviance explained
<b>Multivariate model</b>				22.57%
Intercept	-17.16 ± 0.19	-90.43	<0.001	
Environmental suitability	2.05 ± 0.22	9.49	<0.001	
Propagule pressure	$6.1 \times 10^{-6} \pm 1.3 \times 10^{-6}$	4.63	<0.001	
<b>Multivariate model (with year of first importation)</b>				44.26%
Intercept	826 ± 82.4	10.02	<0.001	
Year of first importation	-0.42 ± 0.04	-10.22	<0.001	
Environmental suitability	-0.28 ± 0.26	-1.08	0.28	
Propagule pressure	$7.0 \times 10^{-6} \pm 1.4 \times 10^{-6}$	4.98	<0.001	

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789 **Figure 1.** Occurrence density of African and Asian ring-necked parakeets along  
790 environmental gradients defined by Maxent models calibrated in (a) African range and  
791 (b) Asian range. Occurrence density is based on kernel smoothers. Dashed lines  
792 represent threshold values (fixed cumulative value 10 logistic threshold) above which  
793 environment is considered suitable for (a) African parakeets and (b) Asian parakeets  
794 according to Maxent models.

795 **Figure 2.** Predicted probabilities of occurrence of ring-necked parakeets in Europe  
796 according to Maxent models calibrated on native ranges. Continuous (a,b) and binary  
797 values of predictions (c,d) for models calibrated in Asia (a,c) and Africa (b,d) are  
798 shown.

799 **Figure 3.** Number and geographic origin of ring-necked parakeets exported to each  
800 European country according to CITES (1981-2011).

801 **Figure 4.** Partial response curves illustrating the relationships between modelled  
802 probability of occurrence of ring-necked parakeets across European countries and  
803 environmental suitability, propagule pressure and geographical origin of propagules  
804 (proportion of Asian importations). These curves show how the shape of the response  
805 changes for a particular predictor while all other predictors are held at their mean  
806 sample value. Observed frequencies of occurrences (points) in each country are also  
807 shown (N = 25).

808 **Figure 5.** Deviance partitioning analysis for the probability of occurrence of ring-  
809 necked parakeets across European countries. Results are expressed as a percentage of  
810 the total deviance explained by the model. Deviance is explained by three groups of  
811 predictors: propagule pressure, environmental suitability and geographic origin of  
812 propagules; (a), (b), and (c) are pure effects of propagule pressure, environmental

813 suitability and geographic origin, respectively; while (d), (e), (f) and (g) are fractions  
814 indicating their joint effects.

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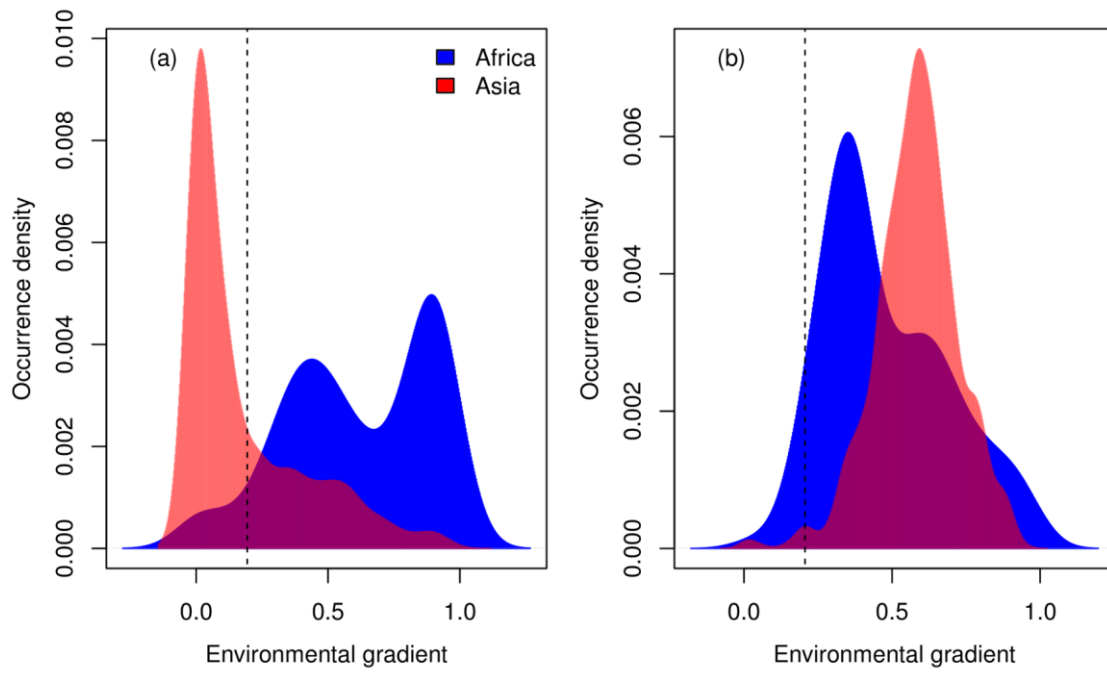
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839 Figure 1.



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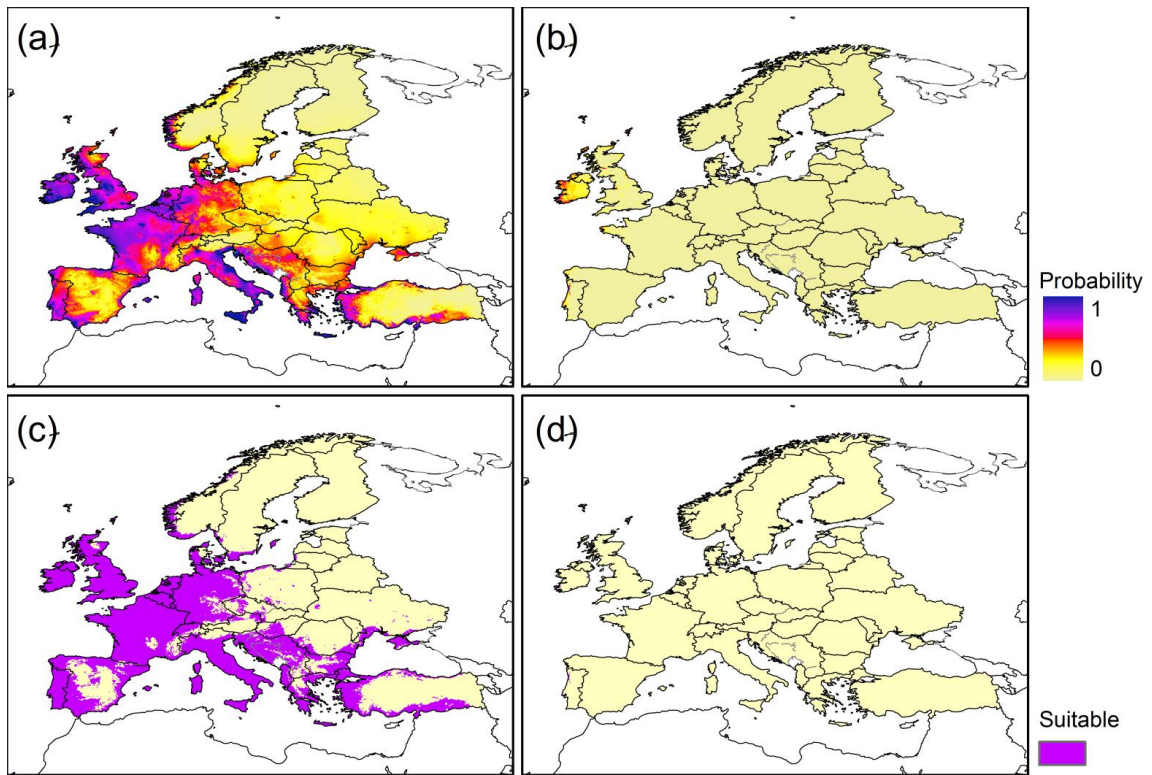
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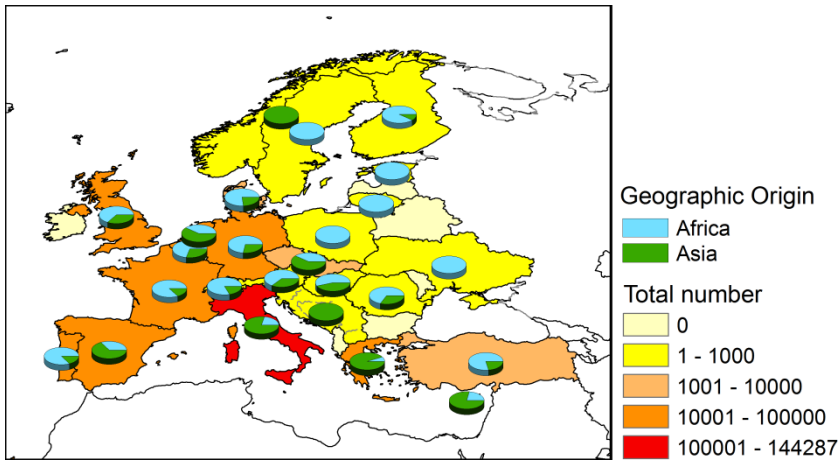
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872 Figure 3.



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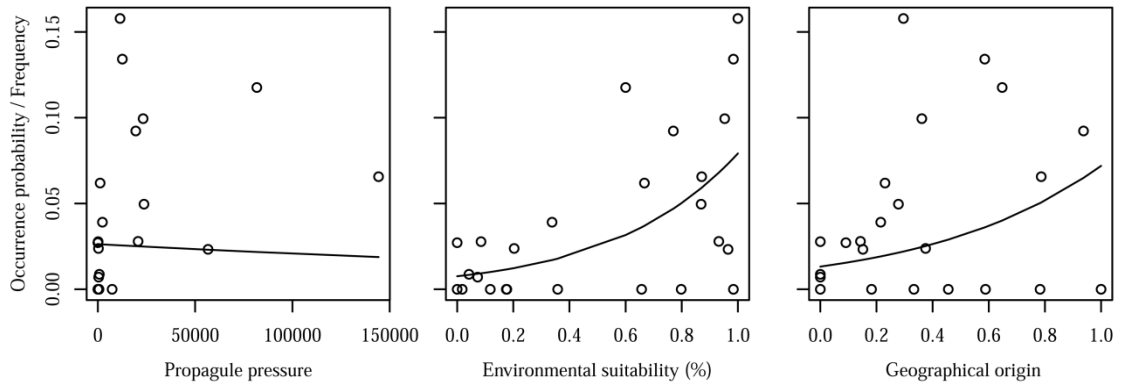
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892 Figure 4.



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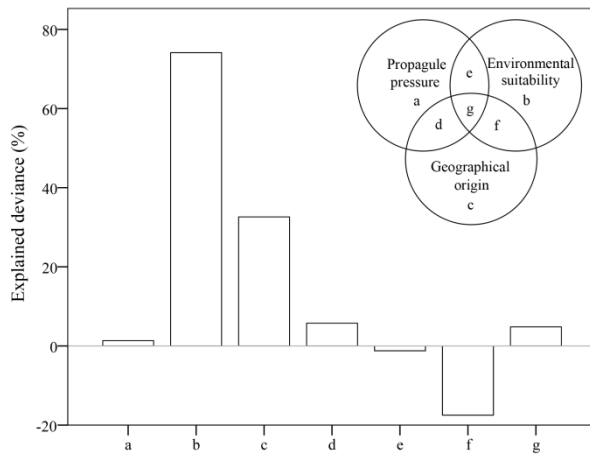
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913 Figure 5.

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