1   # Invasive alien mammals of European Union concern

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ABSTRACT

1. Biological invasions have emerged as one of the main drivers of biodiversity change and decline, and numbers of alien species are rapidly rising. The European Union established a dedicated regulation to limit the impacts of invasive alien species (IAS), which is focused on a Union List of IAS of particular concern. However, no previous study has specifically addressed the ecology of invasive alien mammals included in the Union List.

2. We performed a systematic review of published literature on these species. We retrieved 262 studies dealing with 16 species, and we complemented these with the most up-to-date information extracted from global databases on IAS.

3. We show that most of the study species reached Europe as pets that escaped from captivity or were intentionally released. On average, 1.2 species' new first records/year were documented in European countries in the period 1981-2020, and most species are still expanding their alien ranges colonising neighbouring territories. France, Germany, Italy, and The Netherlands are the most invaded nations, and the muskrat (*Ondatra zibethicus*), the raccoon dog (*Nyctereutes procyonoides*), and the American mink (*Neovison vison*) are the most widespread species, having invaded at least 27 countries each. Invasive mammals of European Union concern are threatening native biodiversity and human well-being: worryingly, 81.3% of the study species are implicated in the epidemiological cycle of zoonotic pathogens.

4. Containing the secondary spread to further countries is of paramount importance to avoid the establishment of new populations of invasive mammals and the related impacts on native communities, ecosystem services, and human health.

5. Our results offer the most updated compendium on the ecology of invasive mammals of European Union concern, that can be used to assist environmental policies, identify and subsequently fill knowledge gaps, and inform stakeholders.

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50   **Keywords**: biological invasions, environmental impact, pathways of introduction, spread, zoonotic

51   diseases.

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53   **Words count:** 8862

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INTRODUCTION

The human-mediated introduction of species to regions outside their native range has become one of the main drivers of biodiversity change and decline in recent human history (IPBES 2019). Despite a rise in awareness, and the adoption of legislation to reduce these introductions, the number of newly-introduced species has risen strongly in recent decades (Seebens et al. 2017) and is expected to continue to do so in the future (Seebens et al. 2020). International trade, global transportation networks (Hulme 2009), land-use change (Essl et al. 2020b), and climate change (Diez et al. 2012, Bellard et al. 2018) are the main drivers promoting species introduction and spread, and they continue to intensify. Many species introduced in new regions fail to establish self-sustaining populations or remain localised, whereas others become permanent additions to the receiving ecosystems and spread over substantial distances. In doing so, they can cause severe impacts on native biota (Blackburn et al. 2019) at different biological organisation levels (Hawkins et al. 2015), ecosystems services (Vilà & Hulme 2017), and human livelihoods (Bradshaw et al. 2016), i.e., they become invasive alien species (IAS).

The prevention and mitigation of biological invasions in Europe is a significant challenge, as policies are devoted to the free circulation of goods and people (Genovesi et al. 2015). To address this issue, the European Union (EU) adopted the Regulation (EU) No 1143/2014, aimed at the prevention of IAS introduction and spread (EU 2014). The Regulation, informed by years of invasion science research (Genovesi et al. 2015), called for the creation of a list of IAS of Union concern, the Union List. Each member state of the EU is required to collect information and take actions on introduction, detection, and eradication of these species and to mitigate their impact (EU 2014). Furthermore, this subset of IAS is subject to a ban on intentional importation and trade in the EU.

Out of the 66 species currently included in the Union List, 11 (~ 17%) are mammals, highlighting the perceived impact of this taxon across Europe. Indeed, mammals represent 60% of the worst invasive

82   terrestrial vertebrates in Europe (DAISIE 2009, Polaina et al. 2020) and, overall, more than 50 species

83   of mammals are currently established in this continent (Biancolini et al. 2021). Furthermore, seven

84   species with high invasive potential are in the initial phase of the invasion (i.e., restricted to the initial

85   location of introductions and without established populations in Europe): the four-toed hedgehog

86   (*Atelerix albiventris*), the American bison (*Bison bison*), the leopard cat (*Prionailurus bengalensis*), the

87   Northern palm squirrel (*Funambulus pennantii*), the striped skunk (*Mephitis mephitis*), the sugar glider

88   (*Petaurus breviceps*), and the Caucasian squirrel (*Sciurus anomalus*). Alarmingly, due to climate

89   change, suitable climatic space is projected to increase for most invasive mammals in Europe (Polaina

90   et al. 2020). For instance, this is the case for the coypu (*Myocastor coypus*; Schertler et al. 2020), the

91   raccoon (*Procyon lotor*; Louppe et al. 2019), and the small Indian mongoose (*Herpestes auropunctatus*;

92   Louppe et al. 2020). Invasive mammals exert negative impacts on biodiversity through competition

93   (Mazzamuto et al. 2017), disease transmission (Collins et al. 2014), habitat alteration (Nogales et al.

94   2014), hybridisation (McFarlane et al. 2020), and predation (Dahl & Åhlén 2019).

95   Here, we provide a comprehensive synthesis of the invasion process, current distribution, and impacts

96   of the invasive mammals of Union concern, by reviewing the literature for these species. Specifically,

97   we (1) analyse trends in the published literature regarding 16 mammal species of Union concern (and

98   candidate species to be included in the Union List) in the last 15 years (2005-2020), (2) summarise

99   pathways of introductions, (3) reconstruct the temporal trajectories of mammal invasions, (4)

100   illustrate geographic distribution patterns, (5) investigate environmental and (6) socio-economic

101   impacts, with a focus on human health. This review updates the current knowledge on a subset of

102   highly impacting mammals, that is crucial especially in the light of (and to accomplish the) recent

103   developments of international agreements to protect native biodiversity (EU 2014, CBD 2020), and

104   inform a wide audience of stakeholders and practitioners.

105

106   **METHODS**

107   We searched for relevant publications on invasive mammals of Union concern. To provide a wider

108   geographic context, the study area was not limited to the EU, but we considered the 47 member states

109   of the Council of Europe, including also the outermost regions of the EU located in the North Atlantic

110   (i.e., Azores, Madeira, and Canary Islands), but excluding the remaining ones (e.g., French Guiana,

111   Guadeloupe). We selected 10 mammal species of the 11 included in the Union List (thus excluding the

112   fox squirrel *Sciurus niger*, as no established populations are currently present in the study region);

113   further, based on the list from Carboneras et al. (2018), we included another six species recommended

114   for future inclusion in this list, excluding the species currently absent from Europe and species in the

115   initial phase of the invasion (not established). Therefore, a total of 16 species were included in this

116   review (Table 1).

117

118   **Literature search**

119   The literature search was carried out by the first author following the Preferred Reporting Items for

120   Systematic Reviews and Meta-Analyses (PRISMA) methodology (Appendix S1; Moher et al. 2009) in

121   August and September 2020. For each species, we downloaded available information from the EU

122   Commission CIRCA website (https://circabc.europa.eu/ui/welcome) in the form of the EU Non-Native

123   Risk Assessment Scheme or the Great Britain Non-Native Risk Assessment Scheme. In addition, we

124   downloaded   CABI   species   datasheets   (www.cabi.org)   and   the   NOBANIS   factsheets

125   (www.nobanis.org). Hereafter, for brevity, we will refer to all these documents as "datasheets". As

126   these datasheets were highly comprehensive on the scientific knowledge of the study species at the

127   time of completion, the time range of the search for additional articles was adapted for each species,

128   depending on the date of the most recent datasheet. If no prior datasheet was found, the search in

129   the literature databases was performed without a temporal filter.

130   Subsequently, we searched for additional recent information on the species in Scopus and Web of

131   Science (WoS). On Scopus, we conducted an advanced search refined for the sub-areas of Agricultural

132   and Biological Sciences and Environmental Sciences. On WoS, we performed a basic search without

133   sub-areas limitations, except for the American beaver, for which we filtered WoS results due to the

134   large literature retrieved on unrelated topics (such as engineering or fluid mechanics). For each species

135   we conducted a separate search with a combination of the scientific name and its synonyms, common

136   name(s) and the relevant keywords, linked by the Boolean operators AND/OR. The list of countries

137   encompassing the alien range, to be used as species-specific keywords, was obtained from the global

138   Distribution of Alien Mammals database (DAMA; Biancolini et al. 2021). Keywords were identified *a*

139   *priori* based on the known alien distribution of each species, European Regulation, invasion history,

140   characteristics linked to invasiveness and caused impacts (Appendix S1).

141   Two species are identified with different scientific names in the Union List and the IUCN Red List,

142   namely the small Indian mongoose (*Herpestes javanicus* changed in *Herpestes auropunctatus*) and the

143   Siberian chipmunk (*Tamias sibiricus* changed to *Eutamias sibiricus*). We are aware of the recent

144   taxonomic revision and, in this work, we choose to follow the IUCN taxonomy (IUCN 2020).

145

146   **Data extraction and preparation**

147   To be included in the review, literature results had to fulfil the following criteria: refer to the European

148   territory (defined as described above), be written in English and contain information related to at least

149   one of the following: (i) year(s) of first record of a study species, (ii) point(s) of first record, (iii)

150   pathway(s) of introduction, and/or (iv) impact(s).

151   A primary research topic was assigned to each publication, based on its aims, as follows: community

152   ecology, datasheet (sub-topics: CABI, NOBANIS), economic impacts, environmental impacts (sub-

153   topics: competition, disease transmission, habitat alteration, hybridisation, native species

154   replacement, predation), general ecology (sub-topics: activity pattern, behavioural responses, diet,

155   ecological modelling, reproduction, space use), genetics (sub-topics: genotyping, methodology,

156   phylogeny, population genetics), health status, management, population status, review, risk

157   assessment (sub-topics: EU NNRA, GB NNRA, other), social impacts, and systematics. A distinction was

158   made amongst species' pathogens studies, classifying them based on the threat posed to native fauna

159   (topic: environmental impacts/disease transmission), to humans (social impacts) or a general

160   investigation of species' pathogens (health status).

161   The same paper investigating two (or more) species was counted only once when illustrating trends

162   in the literature and was referred to the first species in alphabetical order (scientific name) to be

163   investigated. For instance, Bertolino and Lurz (2013) investigated both Pallas' squirrel and Finlayson's

164   squirrel, but the paper was counted for Pallas' squirrel. In such cases the relevant information (e.g.,

165   regarding pathways of introduction) was extracted for all the studied species.

166   In tables and figures, countries are indicated by their ISO country code. RU refers to the European part

167   of the Russian Federation. Species with occasional occurrences (i.e., not established) or with an

168   unknown status are indicated as "casual presences". Alien ranges for the study species were obtained

169   from DAMA (Biancolini et al. 2021), as well as the list of all established mammals in Europe, regardless

170   of their inclusion in the Union List, to get a more comprehensive picture of alien mammals' status in

171   Europe. Native zoogeographic realms (Holt et al. 2013) for the study species and all established

172   mammals in Europe were obtained based on species native ranges (IUCN 2020). Marginal parts of

173   native ranges occurring in less than 1% of a zoogeographic realm were not considered.

174   Capellini et al. (2015) and Blackburn et al. (2017) identified body size, litter size, litters per year, and

175   generation length as species' traits favouring introduction, establishment, and spread of invasive

176   mammals. We extracted these trait values from the recently developed Coalesced Mammal Database

177   of Intrinsic and Extrinsic traits database (COMBINE; Soria et al. 2021). Reproductive life span was

178   calculated as the difference between maximum longevity and age at first reproduction (Soria et al.

179   2021).

180   Each species was assigned to one or more pathway(s) of introduction following CBD categorization

181   (CBD 2014, Biancolini et al. 2021). First records of the species were mainly obtained from the Version

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182   2 (last updated in March 2021) of the Alien Species First Records Database (Seebens et al. 2017). For

183   first records obtained from articles encountered during the literature review, the earliest year was

184   retained in cases of multiple and/or continuous introduction in a country. Information regarding

185   species' pathogens (e.g., prevalence) was extracted both from original papers and from reviews

186   encountered during the literature search.

187

RESULTS

189   **Relevant literature and publication trends**

190   The literature search yielded 3322 papers published between 2005 and 2020 that were subjected to

191   screening by reading the title and abstract; if these elements did not provide definite information, the

192   full text was screened. All the species but one (Barbary ground squirrel) had at least one datasheet

193   available for download, for a total of 36 published datasheets. After this screening, 591 articles were

194   retained, and their full text assessed for eligibility. A backward reference search ("snowballing") was

195   performed on the reference list of each of these articles to identify other relevant publications, adding

196   further 30 studies. Duplicate records resulting from an overlap of the database outcomes were

197   removed. 26 articles could not be assessed due to access' restrictions or because they were not

198   written in English. Eventually, 262 publications were included in the review (Appendix S3).

199   Published information was available mostly for the raccoon (that accounted for 15% of all

200   publications), the American mink (14%), and the sika (12%) (Appendix S2). The majority of the

201   datasheets collected (88.2%) were published from 2009 to 2014 (Appendix S2) and, due to the

202   temporal filters adopted, for most of the study species the literature search supplied mainly papers

203   published after 2015. Accounting for these filters adopted in the literature search, mainly species'

204   environmental impacts were investigated (24.1% of all papers), with a peak of publications in 2017-

205   2018, followed by studies on health-related issues (17.6%) and social impacts (11.8%).

206

Taxonomic characterization, traits, and native ranges

208 The 16 study species belong to three orders and nine families. Half of them belong to the order

209 Rodentia (Appendix S2), whereas the remaining are either from Carnivora (31.3%) or Artiodactyla

210 (18.7%). The Sciuridae family is the most represented, accounting for 31.3% of all species, followed by

211 Cervidae (18.8%) and Procyonidae (12.5%). In comparison, the full ensemble of alien mammals

212 established in Europe is divided into seven orders and 17 families. The order Artiodactyla is the most

213 numerous (28.3%), followed by Rodentia (22.6%) and Carnivora (17%; Appendix S2). The most

214 represented family is Cervidae (15.1%), followed by Leporidae (13.2%) and Bovidae and Mustelidae

215 (11.3% each).

216 Adult body mass (in grams) for the study species varied between 85 for the Siberian chipmunk and

217 53000 for the sika (mean 9762.4; Appendix S2). Litter size was between 1 for sika and Reeves' muntjac

218 and 6.4 for the muskrat (mean 3.3). Litters per year ranged from 1 for American beaver, sika, American

219 mink, and raccoon to 2.6 for the muskrat (mean 1.5). Lastly, generation length (in days) fluctuated

220 between 2941 for the Barbary ground squirrel and 8504 for the sika (mean 5781).

221 The study species originate mainly from the Palearctic, Sino-Japanese, and Oriental zoogeographic

222 realms (Appendix S2). Similarly, the full ensemble of alien established mammals in Europe originate

223 mainly from Palearctic, Saharo-Arabian, and Sino-Japanese realms (Appendix S2).

224

Pathways of introduction to Europe

226 The main pathway of introduction for the study species in Europe was the pet trade (Fig. 1). A total of

227 68.8% of the species escaped after they were introduced at least once through pet trade (i.e., private

228 owners), 50% escaped from zoos (i.e., public exhibitions), and 37.5% escaped after they were

229 introduced to be bred in fur farms. One species was released in nature for biological control (the

230 mongoose in Croatia), and another one for conservation purposes (the American beaver in Finland).

10

231   The chital, introduced in Croatia, was the only species with an unknown introduction pathway,

232   although subsequent repeated introductions within Croatia were reported for hunting purposes

233   (Šprem & Zachos 2020). No study species was reported to be introduced as contaminant, stowaway,

234   or via a corridor.

235

236   **Temporal trajectories of mammal invasions in Europe**

237   The rate of first records (of both established and casual presences) of the study species in countries

238   of Europe increased on average from 1.4 new records/year over a 40-year period (1900-1940) to 2.3

239   records/year in 1941-1980, and then dropped to 1.2 records/year in 1981-2020 (Fig. 2, Appendix S4).

240   Overall, the American mink, the raccoon dog, and the muskrat accounted together for 47.1% of first

241   records.

242

243   **Geographic distribution patterns in Europe**

244   The United Kingdom and the Russian Federation first recorded three of the study species each, namely

245   the sika (1860), the Eastern gray squirrel (1876), and the Reeves' muntjac (1894) for the former, and

246   the Siberian chipmunk (1850), the American mink (1923), and the raccoon dog (1926) for the latter

247   (Appendix S4).

248   Considering the number of countries occupied, the most widespread species was the muskrat

249   (established in 32 countries and with casual presences in three countries; Appendix S2), followed by

250   the American mink (established in 28, casual in seven), the raccoon dog (established in 27, casual in

251   seven), and the coypu (established in 24, casual in four). However, with respect to the area occupied

252   only by the established species, the order slightly changes, with the raccoon dog becoming the most

253   widespread, followed by the muskrat, the American mink, and the raccoon (Fig. 3).

254   Fig. 4 illustrates the invasion waves of the four species that invaded most of the European territory

255   (the raccoon dog, the muskrat, the American mink, and the raccoon), including established presences

256   and casual records.

257

258   **Environmental and socio-economic impacts in Europe**

259   Among the studies retrieved during this search process, environmental impacts of invasive mammals

260   have been broadly investigated, as shown by the number of papers published on this topic (n = 63;

261   Appendix S2). Disease transmission was the most studied sub-topic (30.2% of the total number of

262   papers related to environmental impacts), followed by predation (23.8%) and habitat alteration

263   (14.3%). Studies on pathogens of invasive mammals (n = 19) revolved mainly around their

264   helminthofauna (50.6% of the papers on pathogens, Appendix S2). Some of these pathogens were

265   introduced in Europe with the study species, such as the nematode *Strongyloides callosciureus,*

266   introduced with Pallas' squirrel and potentially infecting the native red squirrel *Sciurus vulgaris* due to

267   spill-back and spill-over processes (Mazzamuto et al. 2016) or the Squirrelpox virus, which can be often

268   lethal for red squirrels and was introduced in UK and Ireland with gray squirrels (IUCN 2005, Invasive

269   Species Ireland 2012).

270   The study species were found to be infected by 224 pathogens, of which 143 (63.8%) have zoonotic

271   potential; 13 study species serve as potential reservoirs or are implicated in their epidemiological cycle

272   (Fig. 5; Appendix S5). Specifically, regarding the most widespread study species, 48.6% of the

273   pathogens known to infect the American mink have zoonotic potential; the percentage rises to 66.7%

274   for the raccoon dog, 77.8% for the raccoon, and 100% for the muskrat (Fig. 5). Overall, studies on

275   *Echinococcus multilocularis* (14 studies, three species), *Toxoplasma gondii* (nine studies, six species),

276   and *Baylisascaris procyonis* (nine studies, one species) were particularly abundant among the study

277   species (Appendix S5). Prevalence rates presented a high geographical and taxonomical variability: the

278   prevalence of *E. multilocularis* ranged between 0% (in the raccoon and the raccoon dog in various

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279   countries; Kornyushin et al. 2011, Wahlström et al. 2012, EFSA 2015, Karamon et al. 2016, Oksanen et

280   al. 2016, Duscher et al. 2017) and 28% (in the racoon dog in Slovakia; Oksanen et al. 2016); for *T.*

281   *gondii*, it ranged from 0% (in mink in Spain and the raccoon in the Czech Republic; Criado-Fornelio et

282   al. 2018, Kornacka et al. 2018) to 78.8% (in mink in Spain; Ribas et al. 2018); lastly, the prevalence of

283   *B. procyonis* in raccoons ranged from 1.9% in Poland (Karamon et al. 2014) to 80% in Germany

284   (Hohmann et al. 2002). Moreover, there are recent reports from Denmark and the Netherlands

285   regarding SARS-CoV-2 infection in minks (Oreshkova et al. 2020).

286   Regarding the second most investigated sub-topic (n = 15), the majority of studies analysed the

287   predatory effects of American minks (40% of the total number of papers related to predation), raccoon

288   dogs (26.7%), and Eastern gray squirrels (20%). Interestingly, 66.7% of American minks' studies were

289   performed in Poland, the whole of raccoon dogs' studies in Scandinavia, and 66.7% of Eastern gray

290   squirrels' studies were conducted in the UK. Lastly, regarding habitat alteration (n = 9), 55.5% of the

291   articles investigated the role of Barbary ground squirrels on native communities of the Canary

292   Archipelago, in Spain.

293

DISCUSSION

295   The majority of invasive mammals of Union concern reached Europe as pets that escaped from

296   captivity, or were intentionally released. Although introductions of alien mammals have declined in

297   Europe for more than 50 years, many study species are still expanding their alien ranges, colonising

298   neighbouring countries. France, Germany, Italy, and The Netherlands are the most invaded countries,

299   and the raccoon dog, the muskrat, the American mink, and the raccoon are the most widespread

300   species. Invasive mammals of Union concern are threatening native biodiversity and human health

301   with consequences largely overlooked in the past, such as new roles in epidemiological cycles of

302   zoonotic pathogens (Oreshkova et al. 2020).

13

303

Relevant literature and publication trends

305 Geographical and impact-related biases emerged from the reviewed literature. Charismatic,

306 widespread, and detrimental species received more attention – in terms of publication numbers –

307 than others, a trend already observed in invasion ecology (Pyšek et al. 2008). Apparently, documented

308 environmental or socio-economic impacts and alien range's size are also related to the number of

309 publications. For instance, species having localized alien distributions, such as island invaders (the

310 Barbary ground squirrel, the chital, the small Indian mongoose, and the South American coati) or

311 urban dwellers (Finlayson's squirrel) have been less investigated than more widespread species, such

312 as the raccoon or the coypu. The well-acknowledged invasive potential of this species urgently calls

313 for additional studies on their impacts and possible future spread. For example, the small Indian

314 mongoose is a devastating island invader across the World, which could irremediably harm native

315 biota in the Balkans mainland (Ćirović & Toholj 2016).

316 However, our results regarding publication trends shall be taken with caution, as our search did not

317 include grey literature nor articles in languages other than English; this language barrier may generate

318 biases and lead to knowledge gaps (Angulo et al. 2021).

319

Taxonomic characterization, traits, and native ranges

321 Humans pose an initial "filter" to introduction (Clout & Russell 2008), selecting mammal species based

322 on key traits (Blackburn et al. 2017), such as a large body mass, long reproductive lifespan, and large

323 litter size. These last two key traits have been shown to also promote the subsequent phases of

324 establishment and spread, along with frequent litters per year (Capellini et al. 2015). The mean adult

325 body mass for our species was high – especially if compared with the mean adult body mass for

326 mammals – but 75% of the study species not weighed much, as few of them (i.e., sika and chital)

327 heavily skewed the mean. Regarding litter size, it is interesting to note that the most widespread

328   species in Europe (both in terms of countries and area occupied) had also an above-average litter size,

329   confirming the importance of this trait in the invasion stages consecutive to introduction (Capellini et

330   al. 2015). As for the litters per year, the species above-average (more than 1.5 litter per year) were

331   mainly rodents. Accordingly, litter size is larger in these socially monogamous species (West & Capellini

332   2016). Although a longer reproductive life span promotes introduction and establishment in

333   mammals, apparently the study species with a higher value of this trait have rather localised

334   distributions (the sika, the Eastern gray squirrel, the Reeves' muntjac), possibly as an outcome of a

335   low colonization pressure. On the contrary, widespread species (like the muskrat and the American

336   mink) present a short reproductive life span. The discordance of some study species' traits (adult body

337   mass and reproductive life span) with what was found previously in the literature can be the result of

338   the relative over-representation of mammals introduced in the past for goods and services (hunting,

339   fur farming, transport; Blackburn et al. 2017), rather than a depiction of more recent introductions of

340   species used as pets (such as squirrels) or for other aesthetic purposes.

341   With regards to the provenience of the study species, the Palearctic, Sino-Japanese, and Oriental

342   realms were equally relevant. Previous studies (Genovesi et al. 2009, 2012) showed that the former

343   and the Nearctic were the realms harbouring native ranges of more introduced mammals. Similarly as

344   for species' traits, this could be linked to the over-representation of species introduced in the past to

345   be utilised by humans for other commercial purposes. Contrarily, the study species are mostly used

346   as pets, and originate from eastern realms.

347

348   **Pathways of introduction to Europe**

349   Overall, the study species were mainly kept in private or public collections or to be bred for fur, and

350   subsequently escaped or have been released. We showed that pet trade was still a relevant pathway

351   of introduction to Europe in the last 15 years: for instance, the Siberian chipmunk was first recorded

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352   in Ireland in 2007, probably released in nature by (or escaped from) private owners (Invasive Species

353   Ireland 2019). Indeed, all the Sciuridae have been introduced at least once for companionship,

354   enjoyment, recreation and/or trading. These species are charismatic and often released for "fauna

355   improvement" of urban parks (as in the case of Siberian chipmunks in Italy; Mori et al. 2018).

356   Higher rates of establishment and spread are related to multiple releases and, in general, to a higher

357   introduction effort (Clout & Russell 2008, Capellini et al. 2015). However, in the absence of accurate

358   introduction records it is often challenging to distinguish between the natural spread of a species from

359   invasion foci in adjacent countries and a deliberate release (for instance, from private owners) or an

360   escape, especially for highly vagile species such as ungulates and carnivores. For example, recent

361   genetic analyses have shown that new Eastern gray squirrel populations in Italy (supposedly originated

362   by natural dispersal of individuals) derived in fact from other populations established almost 200 km

363   far away (Signorile et al. 2016). Therefore, in the absence of clear evidence of unaided dispersal, it is

364   inappropriate to assign this pathway of introduction to some species (Pergl et al. 2020).

365

366   **Temporal trajectories of mammal invasions in Europe**

367   Despite the continuous alien range expansion throughout Europe, first records of alien mammals

368   declined from the 1960s onwards (Fig. 2). This pattern has already been recorded at a global level for

369   this taxon, and it is likely influenced by the most recent first records (Seebens et al. 2017). For instance,

370   there were almost no first records of the study species in the last 10 years. However, longer monitoring

371   is needed to assess the reliability of these trends (Seebens et al. 2017), especially to clarify if a

372   saturation has been finally reached or if these patterns depend on other factors. As a matter of fact,

373   the rapid decline in new introduction events can be attributed to the synergistic effects of increased

374   awareness and stricter regulations on alien mammals bred for fur, exploited as game species, or used

375   as pets across Europe (Seebens et al. 2017), especially since the implementation of the EU IAS

376   Regulation (EU 2014).

16

377   First records in Europe were not evenly distributed among countries, as the UK and the Russian

378   Federation first recorded three study species each. Interestingly, two of the most common species

379   (the American mink and the raccoon dog) were first recorded in the Russian Federation, where they

380   were introduced for fur farming. This comes as no surprise, as this country was one of the world's

381   largest producers and consumers of fur (Balakirev & Tinaeva 2001).

382

383   **Geographic distribution patterns in Europe**

384   In general, the introduction of a species into few localities, and subsequent further releases, can

385   rapidly lead to the colonisation of large parts of the European continent. We show that, in Europe, the

386   raccoon dog, the muskrat, the American mink, and the raccoon are the most widespread species (in

387   terms of area occupied with established presences), having invaded at least 19 countries each and

388   being present for at least 90 years in the European continent (the most recent invader was the

389   raccoon, introduced in 1927 in Germany). The wide distribution of these species can be attributed to

390   several factors, including adaptability and capacity of colonising different environments (Birnbaum

391   2013), wide trophic niches (Bartoszewicz 2011), and high reproduction potentials (Pitra et al. 2010).

392   It is of paramount importance to monitor the secondary spread (Essl et al. 2020a) of these species in

393   the European territory and to prevent the establishment of new populations of invasive mammals.

394   Secondary spread would foster alien ranges' expansion and would counteract the stringent

395   regulations adopted hitherto to prevent new introductions (and mitigate IAS impacts). In the EU, the

396   main drivers of potential impacts of biological invasions (trade and transport, climate change, and

397   socio-economy; Essl et al. 2020b) are highly relevant (Kovats et al. 2014). This, combined with the free

398   circulations of goods and people (Genovesi et al. 2015), may promote a rise of impacts of IAS.

399

400   **Environmental and socio-economic impacts in Europe**

401 The wide distribution of alien mammals in the European territory raises many concerns, as they can

402 also transmit diseases to native species, act as a reservoir, and introduce zoonotic pathogens. The

403 latter can be hosted by the majority of the study species and, worryingly, some widespread species

404 carry many of them. Associated infectious diseases such as echinococcosis, toxoplasmosis, and

405 baylisascariasis may pose a serious threat to human health. For comparison, only 11% of the IUCN list

406 of the 100 World's Worst Invasive Alien Species are reservoirs for zoonotic pathogens (Vila et al. *in*

407 *press*).

408 Studies on *E. multilocularis* (the pathogen most analysed among all the articles on disease

409 transmission) revolved mainly around raccoon dogs, as they are the definitive hosts (Bagrade et al.

410 2016), that is the host where the parasite attains sexual maturity. However, muskrats can be

411 intermediate hosts (i.e., a host in which a parasite passes one or more of its asexual stages), and only

412 two studies (out of 14) investigated the prevalence of the pathogen in this rodent. Dedicated health

413 surveillance, in general of these widespread species of invasive mammals, would be beneficial for

414 many people, as the study species are often found in cities or are bred in captivity for commercial

415 purposes.

416 In this context, the outbreaks of SARS-CoV-2 reported in the Netherlands and in Denmark in 2020

417 (Molenaar et al. 2020, Oreshkova et al. 2020) are notable. It is currently unknown which role American

418 minks and other wild animals (especially the ones that are regularly in contact with humans, such as

419 stray cats or their prey) may play in SARS-CoV-2 cycle and if they can spread new strains of the virus

420 (mutation affecting the spike protein have already been found in American minks; Molenaar et al.

421 2020, Oreshkova et al. 2020, WHO 2020) or act as a wild reservoir. This possibility could seriously

422 hinder the vaccination campaigns in Europe. American minks appear to be very susceptible to the

423 virus, and cases are being reported from further countries such as Spain, Sweden, Italy, and the United

424 States. Following the huge outbreaks of SARS-CoV-2, mink industry in the Netherlands and in Sweden

425 will be banned in 2021 (Human Society International 2020, 2021), while Italy and Denmark suspended

18

426   American mink fur farms activity until the end of 2021 (DW 2020, Ministero della Salute 2021).

427   Large-scale studies investigating zoonotic (and not) pathogen's prevalence and the possible roles of

428   invasive mammals of Union concern in their epidemiological cycles are still largely missing. The spread

429   of many pathogens follows similar invasion stages as animals and plants (Vila et al. *in press*). The

430   unknown role of these mammals as a reservoir in the wild could easily jeopardise the efforts in place

431   to prevent, manage or eradicate zoonotic diseases. Due to the many analogies between invasion

432   science and human emerging infectious diseases, the management of IAS can be very useful to tackle

433   future human epidemics (Vila et al. *in press*).

434   However, predation is probably the most well-known mechanism through which alien species are

435   infamously acknowledged for imperil native biodiversity. This is the case for the American mink, which

436   can exert a negative effect on endangered species such as the water vole (Mori & Mazza 2019) or

437   threaten genetically distinct populations of prey species (Flávio et al. 2020). Heavier egg-predation on

438   ground-nesting birds (compared to previous studies) has recently been reported for the raccoon dog

439   (Dahl & Åhlén 2019), and the muskrat was found to be a major threat to endangered freshwater

440   bivalves in Germany (Stoeckl et al. 2020).

441   Endangered species (e.g., endemic gastropods) have also been found to be a prey item for the Barbary

442   ground squirrel in the Canary Archipelago (López-Darias et al. 2008). Moreover, this African squirrel

443   disrupts seed dispersal of endemic plant species (Nogales et al. 2005), contributes to invasional

444   meltdown (i.e., an alien species facilitates one another's invasion; López-Darias & Nogales 2008), and

445   may consume endangered plant species (Bañares et al. 2003). However, all these environmental

446   impacts have been recorded, at present, only in the squirrel's alien range. The ecology of the other

447   species of invasive mammals in their alien ranges needs to be addressed as soon as possible (Gethöffer

448   & Siebert 2020, Polaina et al. 2020) to understand, contain, and reduce potential environmental

449   impacts.

450   To summarise, our review illustrates that pet trade is still the main pathway of introduction for alien

451 mammals into Europe. It is currently unclear if the recent decline in first records derived from the

452 stricter measures adopted by the European Union or if it is the result of a saturation effect. To answer

453 this question, longer and accurate monitoring of first records and secondary spread of the invasive

454 mammals of Union concern is necessary. Moreover, the eradication of the study species with a wide

455 distribution is likely unfeasible. However, alien species are not either "bad" or "good": it is rather the

456 population of the species that has become invasive, that can be problematic (Simberloff et al. 2013)

457 and that should be managed. In this context, the identification of problematic populations or invaded

458 areas may help to mitigate future impacts.

459

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466

REFERENCES

468 Angulo E, Diagne C, Ballesteros-Mejia L, Adamjy T, Ahmed DA, Akulov E et al. (2021) Non-English

469 languages enrich scientific knowledge: The example of economic costs of biological invasions. *Science*

470 *of The Total Environment*: 144441.

471 Bagrade G, Deksne G, Ozoliņa Z, Howlett SJ, Interisano M, Casulli A, Pozio E (2016) Echinococcus

472 multilocularis in foxes and raccoon dogs: an increasing concern for Baltic countries. *Parasites and*

473 *Vectors* 9: 1–9.

474 Balakirev NA, Tinaeva EA (2001) Fur Farming in Russia: the Current Situation and the Prospects.

475   *Scientifur* 25: 7–10.

476   Bañares A, Blanca G, Güemes J, Moreno JC, Ortiz S (2003) *Atlas y Libro Rojo de la Flora Vascular*

477   *Amenazada de España*. Dirección General de Conservación de la Naturaleza, Madrid.

478   Bartoszewicz M (2011) NOBANIS - Invasive Alien Species Fact Sheet - Procyon lotor. *Online Database*

479   *of the European Network on Invasive Alien Species - NOBANIS*: 1–9.

480   Bellard C, Jeschke JM, Leroy B, Mace GM (2018) Insights from modeling studies on how climate change

481   affects invasive alien species geography. *Ecology and Evolution* 8: 5688–5700.

482   Bertolino S, Lurz PWW (2013) Callosciurus squirrels: Worldwide introductions, ecological impacts and

483   recommendations to prevent the establishment of new invasive populations. *Mammal Review* 43: 22–

484   33.

485   Biancolini D, Vascellari V, Melone B, Rondinini C (2021) DAMA: the global Distribution of Alien

486   Mammals database. *Ecology*.

487   Birnbaum C (2013) NOBANIS - Invasive Alien Species Fact Sheet - Ondatra zibethicus. *Online Database*

488   *of the European Network on Invasive Alien Species - NOBANIS*: 1–11.

489   Blackburn TM, Bellard C, Ricciardi A (2019) Alien versus native species as drivers of recent extinctions.

490   *Frontiers in Ecology and the Environment* 17: 203–207.

491   Blackburn TM, Scrivens SL, Heinrich S, Cassey P (2017) Patterns of selectivity in introductions of

492   mammal species worldwide. *NeoBiota* 33: 33–51.

493   Bradshaw CJA, Leroy B, Bellard C, Roiz D, Albert C, Fournier A et al. (2016) Massive yet grossly

494   underestimated global costs of invasive insects. *Nature Communications* 7: 1–8.

495   Capellini I, Baker J, Allen WL, Street SE, Venditti C (2015) The role of life history traits in mammalian

496   invasion success. *Ecology Letters* 18: 1099–1107.

497   Carboneras C, Genovesi P, Vilà M, Blackburn TM, Carrete M, Clavero M et al. (2018) A prioritised list

498   of invasive alien species to assist the effective implementation of EU legislation. *Journal of Applied*

499   *Ecology* 55: 539–547.

500   CBD (2014) Pathways of introduction of invasive species, their prioritisation and management.

501   CBD (2020) Biodiversity and The 2030 Agenda for Sustainable Development - Policy Brief.

502   Ćirović D, Toholj D (2016) Distribution of Small Indian Mongoose (Herpestes auropunctatus) in the

503   Eastern Herzegovina – spreading inside mainland. *Balkan Journal of Wildlife Research* 2: 33–37.

504   Clout MN, Russell JC (2008) The invasion ecology of mammals: a global perspective. *Wildlife Research*

505   35: 180–184.

506   Collins LM, Warnock ND, Tosh DG, McInnes C, Everest D, Montgomery WI et al. (2014) Squirrelpox

507   virus: Assessing prevalence, transmission and environmental degradation. *PLoS ONE* 9: 1–8.

508   Criado-Fornelio A, Martín-Pérez T, Verdú-Expósito C, Reinoso-Ortiz SA, Pérez-Serrano J (2018)

509   Molecular epidemiology of parasitic protozoa and Ehrlichia canis in wildlife in Madrid (central Spain).

510   *Parasitology Research* 117: 2291–2298.

511   Dahl F, Åhlén PA (2019) Nest predation by raccoon dog Nyctereutes procyonoides in the archipelago

512   of northern Sweden. *Biological Invasions* 21: 743–755.

513   DAISIE (2009) *Handbook of Alien Species in Europe*, Invading N. Springer, New York.

514   Diez JM, D'Antonio CM, Dukes JS, Grosholz ED, Olden JD, Sorte CJB et al. (2012) Will extreme climatic

515   events facilitate biological invasions? *Frontiers in Ecology and the Environment* 10: 249–257.

516   Duscher T, Hodžić A, Glawischnig W, Duscher GG (2017) The raccoon dog (Nyctereutes procyonoides)

517   and the raccoon (Procyon lotor)—their role and impact of maintaining and transmitting zoonotic

518   diseases in Austria, Central Europe. *Parasitology Research* 116: 1411–1416.

519   DW (2020) Danish lawmakers ban mink farming until 2022 amid coronavirus outbreak.

520   EFSA (2015) Scientific opinion – Update on oral vaccination of foxes and raccoon dogs against rabies.

521   *EFSA Journal* 13: 70.

522   Essl F, Latombe G, Lenzner B, Pagad S, Seebens H, Smith K, Wilson JRU, Genovesi P (2020a) The

22

523   Convention on Biological Diversity (CBD)'s Post-2020 target on invasive alien species – what should it

524   include and how should it be monitored? *NeoBiota* 121: 99–121.

525   Essl F, Lenzner B, Bacher S, Bailey S, Capinha C, Daehler C et al. (2020b) Drivers of future alien species

526   impacts: An expert-based assessment. *Global Change Biology* 26: 4880–4893.

527   EU (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October

528   2014 on the prevention and management of the introduction and spread of invasive alien species.

529   *Official Journal of the European Union* L317: 35–55.

530   Flávio H, Caballero P, Jepsen N, Aarestrup K (2020) Atlantic salmon living on the edge: Smolt behaviour

531   and survival during seaward migration in River Minho. *Ecology of Freshwater Fish*: 1–12.

532   Genovesi P, Bacher S, Kobelt M, Pascal M, Scalera R (2009) Handbook of Alien Species in Europe. *Alien*

533   *Mammals of Europe*.

534   Genovesi P, Carboneras C, Vilà M, Walton P (2015) EU adopts innovative legislation on invasive

535   species: a step towards a global response to biological invasions? *Biological Invasions* 17: 1307–1311.

536   Genovesi P, Carnevali L, Alonzi A, Scalera R (2012) Alien mammals in Europe: Updated numbers and

537   trends, and assessment of the effects on biodiversity. *Integrative Zoology* 7: 247–253.

538   Gethöffer F, Siebert U (2020) Current knowledge of the Neozoa Nutria and Muskrat in Europe and

539   their environmental impacts. *Journal of Wildlife and Biodiversity* 4: 1–12.

540   Hawkins CL, Bacher S, Essl F, Hulme PE, Jeschke JM, Kühn I et al. (2015) Framework and guidelines for

541   implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). *Diversity*

542   *and Distributions* 21: 1360–1363.

543   Hohmann U, Voigt S, Andreas U (2002) Racoons take the offensive. A current assessment. *Biologische*

544   *Invasionen. Herausforderung zum Handeln?*: 191–192.

545   Holt BG, Lessard JP, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D et al. (2013) An Update of

546   Wallace's Zoogeographic Regions of the World. *Science* 339: 74–79.

547   Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of

548   globalization. *Journal of Applied Ecology* 46: 10–18.

549   Human Society International (2020) Dutch mink fur farms to be permanently closed by March 2021

550   following 41 COVID-19 farm infections.

551   Human Society International (2021) Sweden suspends mink fur farming in wake of COVID-19.

552   Invasive Species Ireland (2012) Squirrel pox virus alert.

553   Invasive Species Ireland (2019) Siberian Chipmunk.

554   IPBES (2019) *Summary for policymakers of the global assessment report on biodiversity and ecosystem*

555   *services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.*

556   IPBES Secretariat, Bonn, Germany.

557   IUCN (2005) *Datasheet on Sciurus carolinensis.* Wallingford, United Kingdom.

558   IUCN (2020) IUCN Red List of Threatened Species.

559   Karamon J, Kochanowski M, Cencek T, Bartoszewicz M, Kusyk P (2014) Gastrointestinal helminths of

560   raccoons (Procyon lotor) in western Poland (Lubuskie province) - with particular regard to Baylisascaris

561   procyonis. *Bulletin of the Veterinary Institute in Pulawy* 58: 547–552.

562   Karamon J, Samorek-Pieróg M, Moskwa B, Rózycki M, Bilska-Zajac E, Zdybel J, Włodarczyk M (2016)

563   Intestinal helminths of raccoon dogs (Nyctereutes procyonoides) and red foxes (Vulpes vulpes) from

564   the Augustów Primeval Forest (north-eastern Poland). *Journal of Veterinary Research (Poland)* 60:

565   273–277.

566   Kornacka A, Cybulska A, Popiołek M, Kuśmierek N, Moskwa B (2018) Survey of Toxoplasma gondii and

567   Neospora caninum in raccoons (Procyon lotor) from the Czech Republic, Germany and Poland.

568   *Veterinary Parasitology* 262: 47–50.

569   Kornyushin V V., Malyshko EI, Malega AM (2011) The Helminths of wild predatory mammals of

570   Ukraine. Cestodes. *Vestnik Zoologii* 45: 4–11.

571 Kovats RS, Valentini R, Bouwer LM, Georgopoulou E, Jacob D, Martin E, Rounsevell M, Soussana JF

572 (2014) Europe. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE et al. (eds)

573 *Climate Change 2014: Impacts, Adaptation and Vulnerability: Part B: Regional Aspects: Working Group*

574 *II Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*,

575 1267–1326. Cambridge University Press, Cambridge, United Kingdom, and New York, NY, USA.

576 López-Darias M, Nogales M (2008) Effects of the invasive Barbary ground squirrel (Atlantoxerus

577 getulus) on seed dispersal systems of insular xeric environments. *Journal of Arid Environments* 72:

578 926–939.

579 López-Darias M, Lobo JM, Gouat P (2008) Predicting potential distributions of invasive species: The

580 exotic Barbary ground squirrel in the Canarian archipelago and the west Mediterranean region.

581 *Biological Invasions* 10: 1027–1040.

582 Louppe V, Leroy B, Herrel A, Veron G (2019) Current and future climatic regions favourable for a

583 globally introduced wild carnivore, the raccoon Procyon lotor. *Scientific Reports* 9: 1–13.

584 Louppe V, Leroy B, Herrel A, Veron G (2020) The globally invasive small Indian mongoose Urva

585 auropunctata is likely to spread with climate change. *Scientific Reports* 10: 1–11.

586 Mazzamuto MV, Bisi F, Wauters LA, Preatoni DG, Martinoli A (2017) Interspecific competition between

587 alien Pallas's squirrels and Eurasian red squirrels reduces density of the native species. *Biological*

588 *Invasions* 19: 723–735.

589 Mazzamuto MV, Pisanu B, Romeo C, Ferrari N, Preatoni D, Wauters LA, Chapuis J-L, Martinoli A (2016)

590 Poor Parasite Community of an Invasive Alien Species: Macroparasites of Pallas's Squirrel in Italy.

591 *Annales Zoologici Fennici* 53: 103–112.

592 McFarlane SE, Hunter DC, Senn H V., Smith SL, Holland R, Huisman J, Pemberton JM (2020) Increased

593 genetic marker density reveals high levels of admixture between red deer and introduced Japanese

594 sika in Kintyre, Scotland. *Evolutionary Applications* 13: 432–441.

595 Ministero della Salute (2021) Proroga sospensione delle attività degli allevamenti di visoni.

596   *Comunicato n. 4.*

597   Moher D, Liberati A, Tetzlaff J, Altman DG, Altman D, Antes G et al. (2009) Preferred reporting items

598   for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine* 6.

599   Molenaar RJ, Vreman S, Hakze-van der Honing RW, Zwart R, de Rond J, Weesendorp E et al. (2020)

600   Clinical and Pathological Findings in SARS-CoV-2 Disease Outbreaks in Farmed Mink (Neovison vison).

601   *Veterinary Pathology* 57: 653–657.

602   Mori E, Mazza G (2019) Diet of a semiaquatic invasive mammal in northern Italy: Could it be an

603   alarming threat to the endemic water vole? *Mammalian Biology* 97: 88–94.

604   Mori E, Zozzoli R, Mazza G (2018) Coming in like a wrecking-ball: are native Eurasian red squirrels

605   displacing invasive Siberian chipmunks? A study from an urban park. *Urban Ecosystems* 21: 975–981.

606   Nogales M, Nieves C, Illera JC, Padilla DP, Traveset A (2014) Effect of native and alien vertebrate

607   frugivores patterns of Rubia fruticosa viability and germination in the eastern Canary Islands

608   (Rubiaceae). *Functional Ecology* 19: 429–436.

609   Nogales M, Nieves C, Illera JC, Padilla DP, Traveset A (2005) Effect of native and alien vertebrate

610   frugivores on seed viability and germination patterns of Rubia fruticosa (Rubiaceae) in the eastern

611   Canary Islands. *Functional Ecology* 19: 429–436.

612   Oksanen A, Siles-Lucas M, Karamon J, Possenti A, Conraths FJ, Romig T et al. (2016) The geographical

613   distribution and prevalence of Echinococcus multilocularis in animals in the European Union and

614   adjacent countries: A systematic review and meta-analysis. *Parasites and Vectors* 9: 1–23.

615   Oreshkova N, Moelnaar RJ, Vreman S, Harders F, Munnink BBO, Van Der Honin RWH et al. (2020) SARS-

616   CoV-2 infection in farmed minks, the Netherlands, April and May 2020. *Euro Surveillance* 25 (23): 1–7.

617   Pergl J, Brundu G, Harrower CA, Cardoso AC, Genovesi P, Katsanevakis S et al. (2020) Applying the

618   Convention on Biological Diversity Pathway Classification to alien species in Europe. *NeoBiota* 62: 333–

619   363.

620   Pitra C, Schwarz S, Fickel J (2010) Going west-invasion genetics of the alien raccoon dog Nyctereutes

621   procynoides in Europe. *European Journal of Wildlife Research* 56: 117–129.

622   Polaina E, Pärt T, Recio MR (2020) Identifying hotspots of invasive alien terrestrial vertebrates in

623   Europe to assist transboundary prevention and control. *Scientific Reports*: 1–11.

624   Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic

625   biases in invasion ecology. *Trends in Ecology and Evolution* 23: 237–244.

626   Ribas MP, Almería S, Fernández-Aguilar X, De Pedro G, Lizarraga P, Alarcia-Alejos O et al. (2018)

627   Tracking Toxoplasma gondii in freshwater ecosystems: interaction with the invasive American mink

628   (Neovison vison) in Spain. *Parasitology Research* 117: 2275–2281.

629   Schertler A, Rabitsch W, Moser D, Wessely J, Essl F (2020) The potential current distribution of the

630   coypu (Myocastor coypus) in Europe and climate change induced shifts in the near future. *NeoBiota*

631   58: 129–160.

632   Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, Dullinger S et al. (2020) Projecting the

633   continental accumulation of alien species through to 2050. *Global Change Biology*: 1–13.

634   Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM et al. (2017) No saturation in

635   the accumulation of alien species worldwide. *Nature Communications* 8.

636   Signorile AL, Reuman DC, Lurz PWW, Bertolino S, Carbone C, Wang J (2016) Using DNA profiling to

637   investigate human-mediated translocations of an invasive species. *Biological Conservation* 195: 97–

638   105.

639   Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J et al. (2013) Impacts of biological

640   invasions: What's what and the way forward. *Trends in Ecology and Evolution* 28: 58–66.

641   Soria CD, Di Marco M, Pacifici M, Butchart SHM, Rondinini C (2021) COMBINE: A Coalesced Mammal

642   Database of Intrinsic and Extrinsic traits. *Ecology*.

643   Šprem N, Zachos FE (2020) Axis Deer Axis axis Erxleben, 1777. In: Hackländer K, Zachos FE (eds)

644   *Handbook of the Mammals of Europe*, 1–9. Springer Nature Switzerland.

645   Stoeckl K, Denic M, Geist J (2020) Conservation status of two endangered freshwater mussel species

646   in Bavaria, Germany: Habitat quality, threats, and implications for conservation management. *Aquatic*

647   *Conservation: Marine and Freshwater Ecosystems* 30: 647–661.

648   Vila M, Dunn A, Essl F, Gòmez-Dìaz E, Hulme PE, Jeschke JM et al. Viewing emerging human infectious

649   disease epidemics through the lens of invasion science. *BioScience*.

650   Vilà M, Hulme PE (eds) (2017) *Impact of biological invasions on ecosystem services*, Invading N.

651   Springer.

652   Wahlström H, Lindberg A, Lindh J, Wallensten A, Lindqvist R, Plym-Forshell L et al. (2012) Investigations

653   and actions taken during 2011 due to the first finding of echinococcus multilocularis in Sweden.

654   *Eurosurveillance* 17: 1–7.

655   West HER, Capellini I (2016) Male care and life history traits in mammals. *Nature Communications* 7.

656   WHO (2020) SARS-CoV-2 mink-associated variant strain – Denmark.

657

658   **FIGURES LEGEND**

659   **Fig. 1.** The CBD's pathways of introduction of the study species in Europe (n = 50). Each species was

660   assigned to one or more pathways. Pathways with zero occurrences and nomenclature not relevant

661   for terrestrial mammals are not shown. Pathways names are abbreviated following CBD (2014).

662   .... **Errore. Il segnalibro non è definito.**

663   **Fig. 2.** Temporal distribution of first records of the study species in the countries of Europe (n = 197).

664   Point sizes represent the number of records per species and time period...32

665   **Fig. 3.** Established presences of the study species in Europe: (a) heat map showing study species'

666   richness in the study area; (b) area (log scale, km^2) occupied by the study species. 33

674

TABLES LEGEND

676   **Table 1.** The 16 species included in this review. Scientific name, common name, native

677   zoogeographic realms (following Holt et al. 2013), year of first record in Europe, and country of first

678   record in Europe are indicated. Native zoogeographic realms are given for each species in decreasing

679   order, based on the percentage of native range located in each realm.   6

680

SUPPORTING INFORMATION

682   Additional supporting information may be found in the online version of this article at the publisher's

683   web-site.

684   **Appendix S1.** Process of literature search and keywords used.

685   **Appendix S2.** Figures illustrating the trends in the published literature, species' taxonomy, traits,

686   native zoogeographic realms, and pathogens classification.

687   **Appendix S3.** List of the papers obtained through the literature search process for each study species

688   in Europe.

689   **Appendix S4.** Year of first record and presences for the study species in Europe.

690   **Appendix S5.** List of pathogens known to have been recorded to infect the study species in Europe

691   and list of additional references.

692

693   **GRAPHICAL ABSTRACT**

694
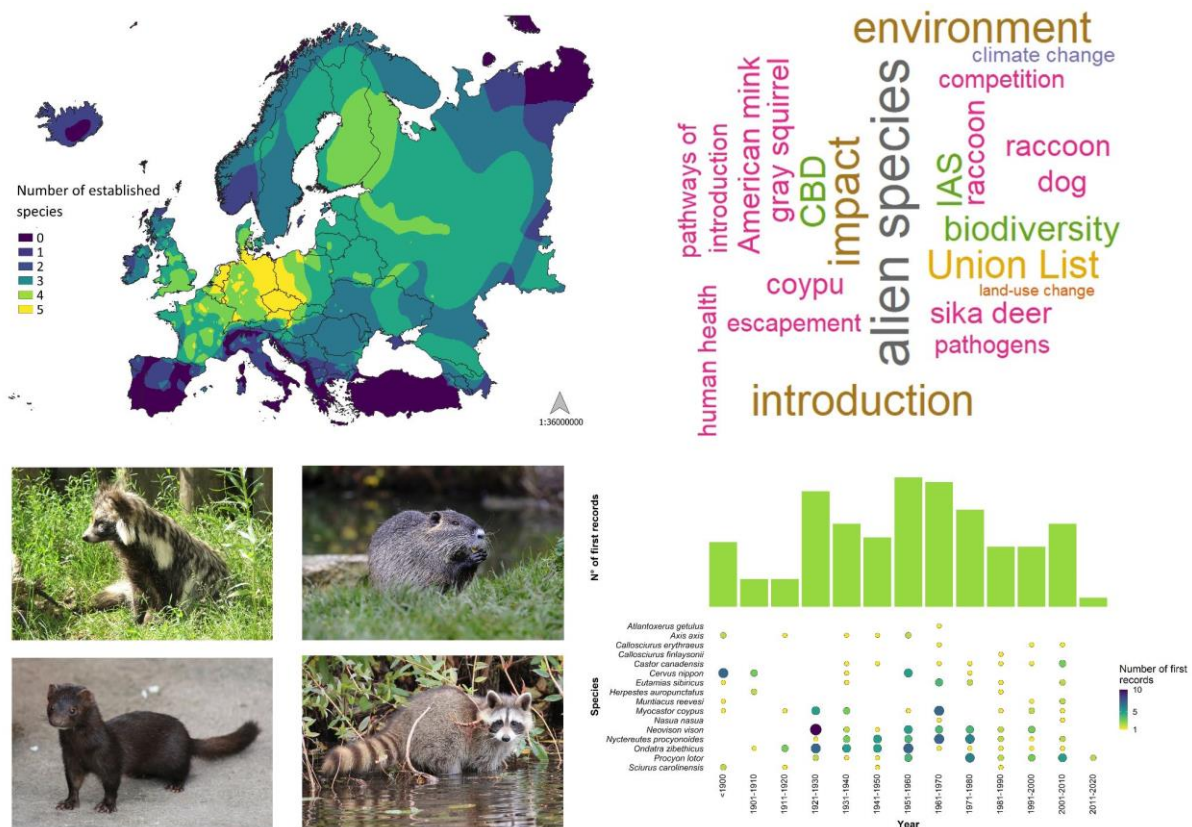
695   Graphical abstract: Invasive alien mammals of European Union concern.

696   The figure illustrates how the introduction of a species in few new areas, followed by a lag phase of

697   adaptation and sometimes enriched by further subsequent releases, can rapidly lead to the

698   colonisation of large parts of a continent. On the top left, a heat map with species' richness in countries

699   of Europe. On the top right, a word cloud with the main keywords of our literature search and some

700   of the study species' names. On the bottom left, four out of 16 study species: in clockwise order, the

701   raccoon dog (*Nyctereutes procyonoides*), the muskrat (*Ondatra zibethicus*), the American mink

702   (*Neovison vison*), and the raccoon (*Procyon lotor*). On the bottom right, the temporal distribution of

30

703   the first records of the study species in the countries of Europe.
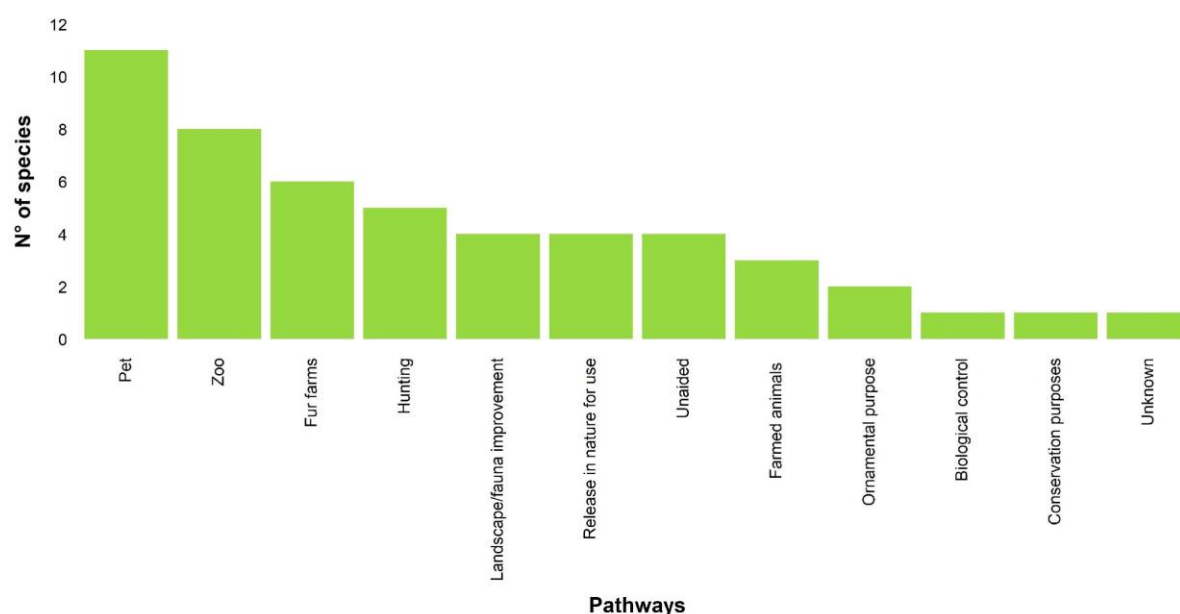
704

705   **FIGURES**

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707

708   **Fig. 1.** The CBD's pathways of introduction of the study species in Europe (n = 50). Each species was assigned to one or more

709   pathways. Pathways with zero occurrences and nomenclature not relevant for terrestrial mammals are not shown. Pathways
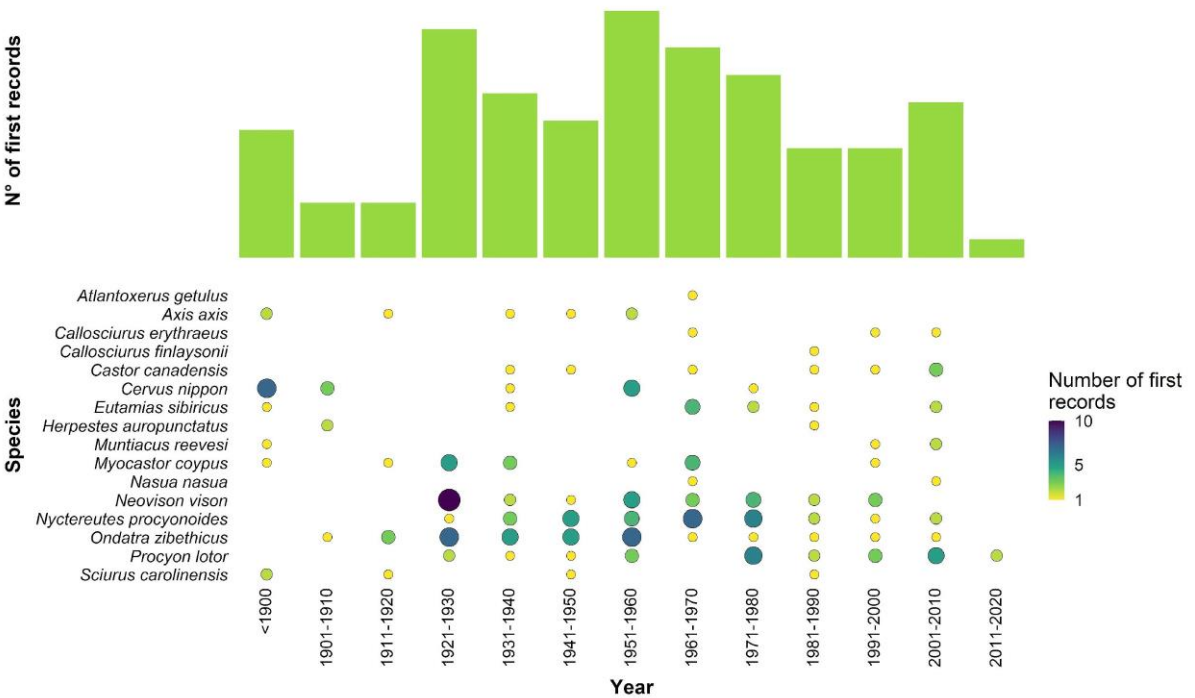
710   names are abbreviated following CBD (2014).

711

712   **Fig. 2.** Temporal distribution of first records of the study species in the countries of Europe (n = 197). Point sizes represent
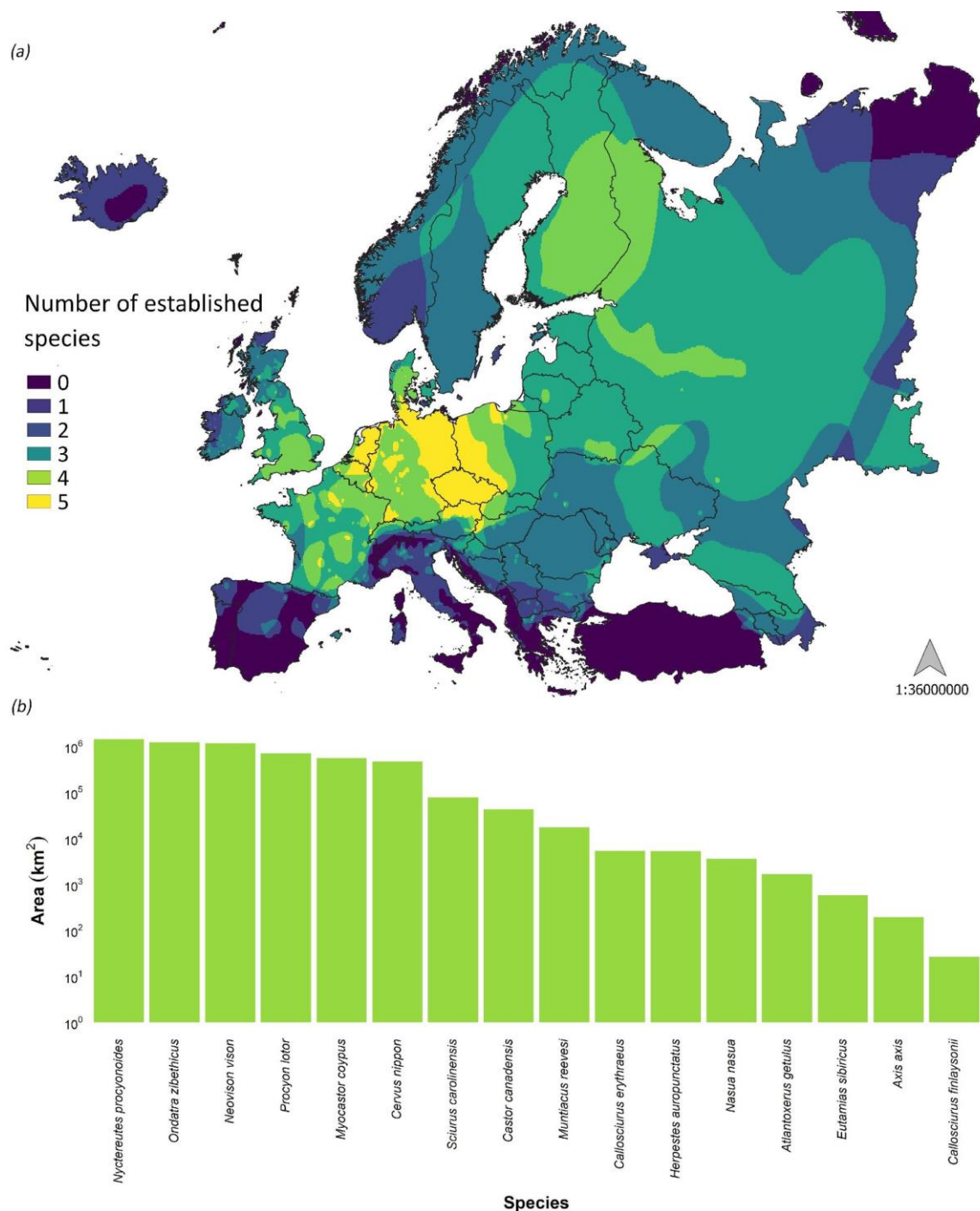
713   the number of records per species and time period.

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Fig. 3. Established presences of the study species in Europe: (a) heat map showing study species' richness in the study area;

(b) area (log scale, km^2) occupied by the study species.

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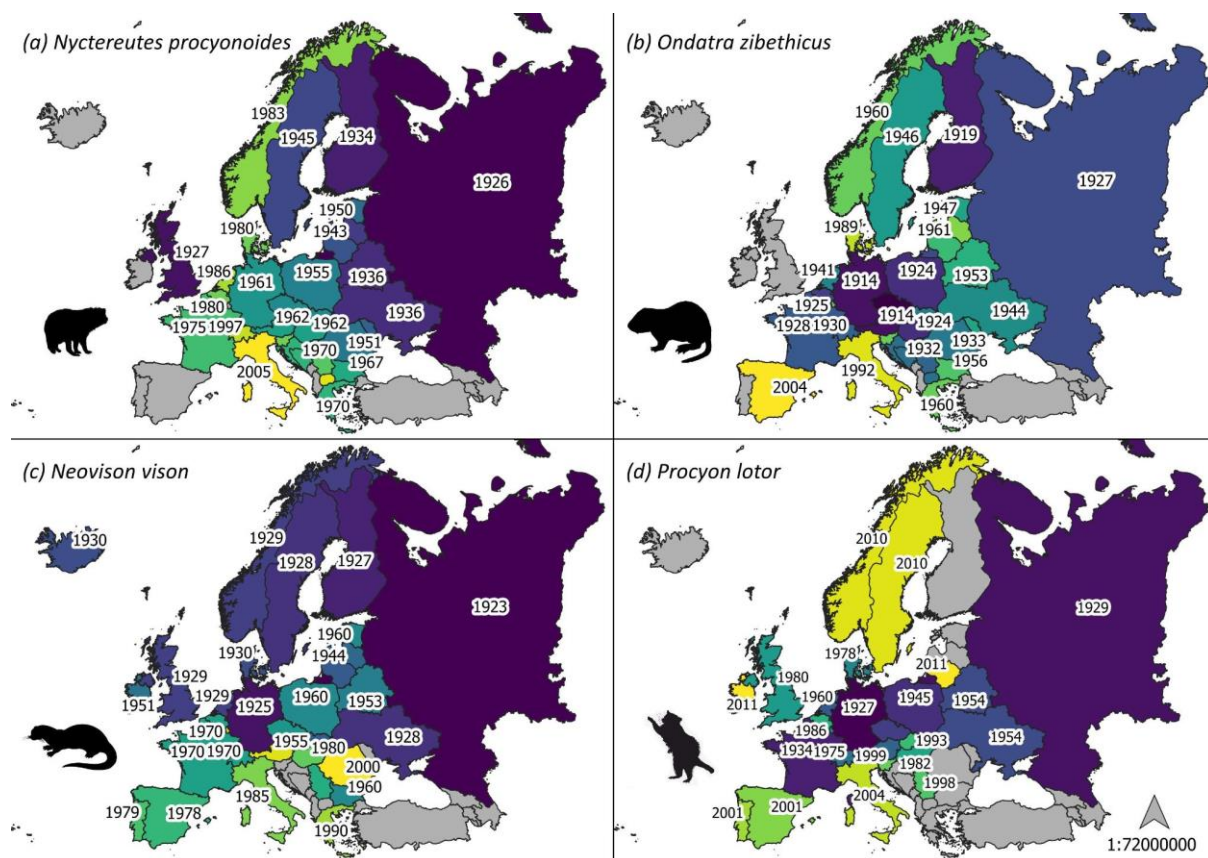
720 **Fig. 4.** The spread trajectories of the four species that invaded most of the European territory: (a) the raccoon dog, (b) the

721 muskrat, (c) the American mink, and (d) the raccoon. Countries are graded from the country invaded earliest (darker) to the

722 latest (lighter). Year of the first record (when available) is shown. Countries without presences (established or casual) of the

723 species are shown in grey.

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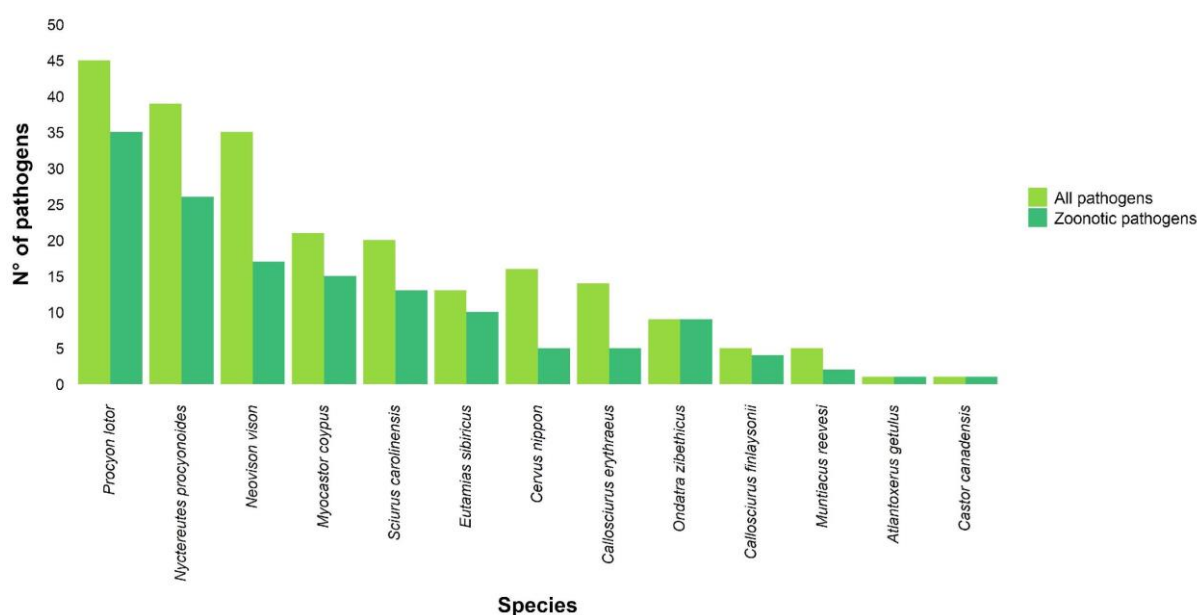
726 **Fig. 5.** Total number of pathogens known to be infecting the study species (all pathogens) and pathogens with zoonotic

727 potential (zoonotic pathogens). Species without recorded pathogen infections are not shown.

728

729 **Table 1.** The 16 species included in this review. Scientific name, common name, native zoogeographic realms (following Holt

730 et al. 2013), year of first record in Europe, and country of first record in Europe are indicated. Native zoogeographic realms

731 are given for each species in decreasing order, based on the percentage of native range located in each realm.

Scientific name	Common name	Native zoogeographic realms	First record	Country of first record
Axis axis (Erxleben, 1777)	Chital	Oriental, Sino-Japanese	1750	Germany
Eutamias sibiricus (Laxmann, 1769)	Siberian chipmunk	Palearctic, Sino-Japanese	1850	Russia
Cervus nippon (Temminck, 1838)	Sika	Sino-Japanese, Palearctic, Oriental	1860	United Kingdom
Sciurus carolinensis (Gmelin, 1788)	Eastern gray squirrel	Nearctic	1876	United Kingdom
Myocastor coypus (Molina, 1782)	Coypu	Neotropical	1882	France

Muntiacus reevesi (Ogilby, 1839)	Reeves' muntjac	Oriental, Sino-Japanese, Palearctic	1894	United Kingdom
Ondatra zibethicus (Linnaeus, 1766)	Muskrat	Palearctic, Nearctic	1905	Czech Republic
Herpestes auropunctatus (É. Geoffroy Saint-Hilaire, 1818)	Small Indian mongoose	Oriental, Saharo-Arabian, Sino-Japanese	1910	Croatia
Neovison vison (Schreber, 1777)	American mink	Palearctic, Nearctic	1923	Russia
Nyctereutes procyonoides (Gray, 1834)	Raccoon dog	Sino-Japanese, Palearctic, Oriental	1926	Russia
Procyon lotor (Linnaeus, 1758)	Raccoon	Panamanian, Nearctic	1927	Germany
Castor canadensis (Kuhl, 1820)	American beaver	Palearctic, Nearctic	1935	Finland
Atlantoxerus getulus (Linnaeus, 1758)	Barbary ground squirrel	Saharo-Arabian	1965	Spain
Callosciurus erythraeus (Pallas, 1979)	Pallas' squirrel	Oriental, Sino-Japanese	1974	France
Callosciurus finlaysonii (Horsfield, 1823)	Finlayson's squirrel	Oriental	1981	Italy
Nasua nasua (Linnaeus, 1766)	South American coati	Neotropical	2003	Spain

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