

# A global picture of biological invasion threat on islands

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2	A global picture of biological invasion threat on islands
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### 37 Introductory paragraph

Biological invasions are one of the main drivers of biodiversity losses. As threats from biological invasions increase, one of the most urgent tasks is to identify areas of high vulnerability. However, the lack of comprehensive information on the impacts of invasive alien species (IAS) is especially a problem on islands, where most recorded extinctions associated with IAS have occurred. Here we provide a global, network-oriented analysis of IAS on islands. Using network analysis, we structured 27,081 islands and 437 threatened vertebrates into 21 clusters, based on their profiles in term of invasiveness and shared vulnerabilities. These islands are mainly located in the southern hemisphere and many are in biodiversity hotspots. Some of them share similar characteristics regarding their connectivity that could be useful in understanding their response to invasive species. The major invaders found in these clusters of islands are feral cat, feral dog, pigs and rats. Our analyses reveal those IAS that systematically act alone or in combination, and the pattern of shared IAS among threatened species, providing new information to implement effective eradication strategies. Combined with further local, contextual information this can contribute to global strategies to deal with IAS. 

64 Islands harbour a significant portion of the Earth's species and have an unusually high rate of 65 endemism<sup>1</sup>. However, many species on islands are now recorded as threatened, and most recorded extinctions of vertebrate species have occurred on islands<sup>2</sup>. Invasive alien species 66 67 (IAS) are considered the second most important driver of species extinctions on islands, and are associated with nearly 25% of birds and amphibians currently threatened worldwide<sup>3</sup>. 68 Island ecosystems are particularly vulnerable to biological invasions<sup>2</sup>. To date, there have 69 been over 700 attempted eradications of invasive alien mammals<sup>4</sup>, which have benefited to 70 600 local populations, leading to larger populations or increased distributional areas<sup>4</sup>. 71 72 Specifically, 236 species have benefited from those eradication programs, including 62 73 species that are at risk of extinction, and four species had their extinction risk reduced as a direct result of these eradications<sup>4</sup>. Despite these encouraging results, the threat posed by 74 75 invasive alien species (IAS) remains significant and widespread for native species<sup>3</sup>. Thus, prioritization of research efforts and eradication strategies needs to be more effective<sup>5</sup> and 76 77 there are many more opportunities to decrease extinction risk for island species by eradicating 78 IAS. 79 Because funding allocated to conservation is limited, it is important that these interventions 80 target islands where the conservation benefit will be highest. Efforts to prioritize research, 81 management, and policy for IAS have traditionally relied on expert judgments, and have been

82 limited to either single IAS<sup>6</sup> or subsets of islands<sup>7,8</sup>. In the absence of a systematic analysis of

83 IAS impacts, it is difficult to see how an efficient and comprehensive strategy can be

84 developed. While several recent papers have examined the threats posed by IAS globally<sup>9</sup> or

85 for entire taxonomic groups (e.g., mammals<sup>10</sup>), all of these studies implicitly assume that the

86 distribution of IAS reflects their impacts (e.g., in terms of the decline in native species

87 populations they cause). However, there is much evidence that the impacts of IAS are context

dependent<sup>3,11,12</sup>, and spatially variable. Other large-scale studies have analyzed IAS impact on

89	specific archipelagoes <sup>13</sup> or on a particularly problematic subset of IAS <sup>14</sup> . But all these
90	approaches are piecemeal and cannot deliver the evidence needed to support an efficient
91	approach to focus IAS research and action at a global scale.
92	Here we use the comprehensive data compiled by the International Union for the
93	Conservation of Nature (IUCN) database, BirdLife International database and the Global
94	Invasive Species Database (GISD) to extract information about vertebrates threatened by IAS,
95	and the identity of the threatening IAS to address the three following questions: (i) How are
96	the impacts of IAS distributed among islands and threatened species? (ii) Are there
97	combinations of IAS for which targeted actions may have high conservation impacts? (iii)
98	Within the targeted areas what are the characteristics of the network between IAS and IAS-
99	threatened species that can improve strategies to deal with IAS?
100	Some species occur on multiple islands while others are endemic to a single island. Moreover,
101	some IAS are shared as threats by multiple species on the same or different groups of islands,
102	while others are very localized and specific. To gain insights into the structure of this complex
103	interconnected system we apply network approaches. Many systems can be represented as
104	networks of interconnected nodes. Networks are mathematical objects where a node is linked
105	(connected) to zero, one or several other nodes. The links highlight a relationship between
106	two nodes. For instance, each inhabitant of the world can be represented as a node in a
107	network graph and each email sent by those inhabitants to others can be represented as a link.
108	Of course with increasing node and link number, the complexity of network graphs grows
109	exponentially and limits our ability to identify structure. Network theory aims at extracting
110	significant patterns from networks.
111	In our study, we built two kinds of networks. In the first, the nodes are either species or
112	islands and the links represent the presence of a species on a given island. We clustered this
113	network to identify islands that are highly interconnected by the co-occurrence of many IAS-

threatened species, and selected the clusters with highest number and densities of IASthreatened species. The aim of this clustering approach is to identify group of islands that share similar pattern of threatened species based on biogeographical knowledge. In the second set of networks the IAS and their threatened species were linked, and related to the island clusters identified in the first analysis (Methods and Materials for details). This allowed us to determine the IAS that are mostly responsible of threats in those clusters of islands and we used this to provide insights to deal with IAS threat.

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124

#### 122 Results

123 How are the impacts of different IAS distributed among islands and threatened species?

125 species. First, we selected islands for which we could expect high return in investment for

The second s

126 conservation program. Specifically, we selected islands that harbour more than 1% of the total

We analyzed more than 73,515 islands where the IUCN Red List recorded IAS-threatened

127 number of IAS-threatened species, and those with a high ratio of the number of threatened

species to area. We identified a total of 21 clusters (labeled in supplementary table 2) that

129 include a total of 437 IAS-threatened species on the 27,081 islands across the world that met

130 our criteria (figure 1, for the complete network see supplementary figure 1). These clusters

131 represent the groups of islands that are highly inter-connected by the co-occurrence of IAS-

threatened species (Figure 1) i.e., insular regions harbouring similar patterns of threatened

133 vertebrates by IAS. Most of these islands detected, vulnerable to invasions, are located in the

southern hemisphere and encompass most of the Caribbean and Pacific archipelagos

135 (including Hawaï), Madagascar and islands at southern of the coasts of Africa, Indonesia, the

136 coast of America, New Zealand and Australia (Figure 1a). The majority of the islands found

137 in the 21 clusters are included in the insular biodiversity hotspots<sup>15</sup>.

138 Some clusters are fully isolated (i.e., disconnected to others in terms of IAS-threatened

139 species: e.g., Puerto Rico islands; Okinawa islands and Seychelles) because their IAS-

140 threatened species are found nowhere else. Two of the Caribbean clusters (including 141 Hispaniola and Jamaica islands), and Malaysia, Philippines, and South of east indies islands 142 are connected only to each other (Figure 1b). Overall, the clusters that share a high number of 143 threatened species with other clusters are Polynesia and Micronesia, North America Pacific 144 coast islands, as well as the South American, Antarctic, sub-Antarctic and Australian islands. 145 Our analysis revealed that most of the connections between clusters are due to bird species, 146 but amphibians, mammals and reptiles are also responsible for connections between the 147 southern part of New Zealand, Australia and southern-hemisphere islands, Caribbean clusters, 148 and African islands (supplementary figure 1). Some clusters are particularly noticeable due to 149 their high number of threaned species by IAS: New Caledonia, Hawaian islands and 150 Madagascar and African southeastern coast for reptiles, birds, and amphibians, respectively. 151 The 21 identified clusters vary in terms of number of threatened species (see size of the taxa 152 nodes of the outer circle Figure 1b), number of islands (size of the inner circle nodes, Figure 153 1b) and total area. Specifically, the number of threatened species ranges from 7 (the cut-off 154 point we selected that corresponds to at least 1% of the total number of insular threatened 155 vertebrates) to 61 species, while the number of islands ranges from 1 (i.e., Puerto Rico) to 156 7,460 (Table 1). Most of the threatened species found in these clusters are birds (51%), 157 followed by reptiles (18%), amphibians (17%) and mammals (14%), which is consistent with 158 the taxonomic groups that have been identified as threatened by IAS worldwide<sup>3</sup>. 159 Are there combinations of IAS for which targeted actions may have high conservation 160 *impacts?* 161 In a second step, we analyzed the patterns of interactions between IAS and the vertebrate 162 species they threaten for the whole network and for the 21 identified clusters (Figure 2a, for 163 the complete network see supplementary figure 1). We built interaction networks with IAS 164 and IAS-threatened species as nodes. The links between nodes represent the vulnerability of a 165 given species to a known IAS (see supplementary figure 2 for each IAS-threatened species) 166 within a cluster (Figure 2a). The global interaction network revealed that most IAS are 167 threatening numerous species across different taxonomic groups. The top threatening IAS is 168 the feral cat (*Felis catus*), followed by other IAS such as rat (*Rattus spp*), feral dog (*Canis* 169 *familiaris*) and pig (Sus scrofa). Some IAS are more specialized, such as Eucalyptus spp. that 170 predominantly threatens vertebrates located in clusters of Madagascar and African 171 southeastern coast islands, the little fire ant (Wasmannia auropunctata) that affects reptiles in the New Caledonia cluster (see also <sup>16</sup>) and the Chytrid Bd (*Batrachochytrium dendrobatidis*) 172 173 that mainly threatens amphibians in the Caribbean clusters. 174 The network approach can, in theory, help to identify the best strategies for combating IAS 175 that maximise the number of threatened species that will benefit from any eradications. For 176 example, the feral cat and feral dog eradicated alone would directly benefit to 10 and 6 177 species respectively, but targeted together could benefit up to 27 species (because 11 others 178 species are simultaneously threatened by those two IAS). Therefore, both need to be 179 controlled to achieve the highest overall conservation benefit. Note that other threatened 180 species will also benefit from such eradications because the IAS pressure on them will be 181 reduced even if other IAS are still threatening them. The control or eradication of the Chytrid 182 *Bd*, feral cats and feral dogs together could fully benefit at least 41 threatened island species 183 worldwide (Figure 2B), assuming that no other threats are significant for these species. 184 Within the targeted areas what are the characteristics of the network between IAS and IAS-185 threatened species that can improve strategies to deal with IAS?

186 The characteristics of IAS and IAS-threatened species interaction networks within each

187 cluster can also be used to focus actions to deal with the IAS threat. In each cluster, we

188 identified the top-IAS that affect the most species (i.e., highest number of links with

threatened species), and the connectivity of IAS and threatened species. We also determined

190 which IAS or combinations of IAS should be targeted, in theory, to maximize the number of 191 threatened species that will fully benefit from IAS eradications per cluster. We found that the 192 top-IAS that threatens most of the native species is not necessarily the same as the IAS that 193 should in theory be eradicated to maximize the number of species that fully benefit (Table 1). 194 For most of the clusters, we found that a targeted combination of IAS will result in a better 195 outcome for threatened species than controlling only the most important invader. For instance, 196 the native species in the Polynesia and Micronesia cluster are highly threatened by feral cats. 197 Yet, targeting only feral cats would, in theory, lead to only one species fully benefiting, 198 because the other species threatened by cats are also threatened by others IAS. The combined 199 control of black rat (R. rattus), pacific rat (R. exulans) and feral cats could, in theory, fully 200 benefit to 13 species of IAS (Figure 3a). A specific example is Okinawa islands cluster. This 201 insular region might also offer good opportunities as the removal of IAS from the family 202 Herpestidae (e.g., H. javanicus) could directly benefit to at least 6 species and decrease 203 pressure for 6 additional species that are also threatened by other IAS (Figure 3a). The 204 number of links in the Okinawa cluster is quite low, so we can expect that the control of a low 205 number of IAS would result in a high benefit for native species. In addition, most of the 206 threatened species located in this cluster are found nowhere else (Figure 1b), so they have a 207 particularly high value for biodiversity. Note that neither the potential feasibility nor the cost-208 effectiveness of such programs has been evaluated here and so our findings should be 209 complemented with local prioritization analyses at the island and IAS level. 210 We also identified some clusters where the networks share similar properties that could be 211 helpful in understanding their response to IAS. For example, two clusters (i.e., Papua New 212 Guinea cluster, and the South of east indies islands cluster) share both a high-density value (a 213 high ratio of the number of links per node to the number of possible links) and a relatively 214 low number of IAS in their clusters (Figure 3b). This means that the threatened species within

215 these two clusters are threatened by few IAS but these few IAS threaten most of the species in 216 this cluster. Hence, the control or eradication of this small number of IAS may offer great 217 opportunity for conservation, especially as the number of IAS-threatened species is important 218 (Figure 3a). Because these two clusters are highly disconnected from other clusters as well 219 (Figure 1b), protecting their species might be particularly significant globally. We observed 220 similar characteristics for Solomon, New Britain and New Ireland islands that may also offer 221 significant opportunities for conservation (Table 1). We also observed that the Hispaniola, 222 Jamaica and Puerto Rico clusters share similar characteristics in terms of the average number 223 of links, and density values. Some other interaction networks are particularly distinctive and 224 should be studied individually. For instance, Madagascar and Africa southeastern coast 225 clusters harbour a larger number of IAS-threatened species and New Caledonia cluster more 226 interconnections than any other clusters.

227

#### 228 Discussion

229 We have identified 21 clusters of islands harbouring threatened vertebrates species that are 230 highly significant sites of IAS threat and where focusing resources, for both research and 231 conservation action should be most efficient. The spatial distribution of the 21 identified 232 clusters overlaps with the majority of global biodiversity hotspots (except some coastal 233 islands, see brown polygons represented in Figure 1a) that are priorities in terms of endemic plants threatened by habitat loss<sup>17</sup>. Over \$1 billion has been spent protecting the remaining 234 natural vegetation of these biodiversity hotspots<sup>18</sup>. We identified other areas important for 235 236 conservation, including many small islands and island groups that may offer high return on 237 investment. Specifically, we were able to identify clusters that harbour a unique part of 238 vertebrate species diversity threatened by IAS. These island clusters that include Caribbean, 239 Okinawa, Seychelles islands, and also Malaysia, Philippines, some of the Indonesian islands and South of East Indies islands would qualify as priorities on their own while clusters that

are inter-connected (i.e., where IAS-threatened species are shared) will require also trans-

242 national efforts for conservation to be fully effective.

243 We also reaffirm here the role played by major invaders such as rats, cats, and the Chytrid *Bd*,

which are already known to cause widespread threats to species on islands  $^{19-21, 22}$ . Feral cats

are well-known to drive numerous extinctions of endemic vertebrates ( $>175^6$ ). Yet, our

analysis quantifies their roles whether they are the only invader responsible of population

247 decline in islands or if they act in combination with other IAS on islands.

248 Most of the current eradication programs focus on single species, which may be ineffective

when multiple IAS are involved<sup>23</sup>. On the basis of our results, we suggest that targeting

250 multiple IAS simultaneously would be a more efficient strategy for species conservation<sup>23</sup> and

should be achievable as eradication programmes increase in coverage and complexity<sup>24</sup>.

252 In our analyses we have identified the co-occurrences of IAS threat on islands and quantified

the potential number of species that, in theory, could benefit through the eradication of these

254 IAS. However, we do not account for predator release effect that could further threaten

species<sup>25,26</sup> or other unanticipated events (e.g., changes of vegetation or trophic webs that

could follow IAS eradication). In addition, we assume that all IAS have the same effect on

threatened species, which may not be a safe assumption but there is currently too little

258 information on which to improve this aspect of the analysis. Moreover, we did not assess the

259 potential for reintroductions or the feasibility of eradication events.

260 The eradication of the Chytrid *Bd* could, for example, be quite challenging. Indeed, we lack of

261 efficient methods to systematically eradicate the Chytrid *Bd*, although two recent advances

have greatly improved our understanding of amphibian-chytridiomycosis dynamics<sup>27</sup>. First,

the recognition that Bd is not one species but distinct lineages that vary in distribution and

virulence and, second, that species have been infected for much longer than initially thought

with some species co-evolving without any impact (see <sup>27</sup> for a review). Thus, preventing 265 266 measures to avoid further propagation of the Chytrid Bd in nearby clusters should be a 267 priority. In contrast, eradication attempts for vertebrates have been quite efficient for cats or rats with failure rates of only  $12\%^{28}$  as well as for invasive ants<sup>29</sup>. 268 269 In general we argue that network approaches should complement local prioritization schemes 270 including eradication feasibility information to target regions and IAS for which actions should be undertaken<sup>8,30</sup>. For example, a recent study analyzed conservation opportunities for 271 272 sea-bird populations in most of the 800 small, uninhabited, and high-middle-income countries islands<sup>31</sup>. Our analyses also revealed that in some clusters it might be quite challenging to 273 274 protect native species from extinctions, because of the high number of IAS combinations that 275 threaten native species as shown by their high values of connectivity. Yet, local removals of 276 IAS could prevent local extirpations of native populations and therefore benefit biodiversity. 277 This is particularly the case of the Polynesia and Micronesia cluster. 278 There are some limitations of our approach that are discussed in the following. First, we 279 considered the impacts of IAS as a reduction in population size or distribution range 280 determined by the IUCN Red list of threatened species, but other type of impacts on 281 functional or genetic diversity through hybridization or ecosystem services might also be 282 important. Our network-based analyses only accounted for the existence of an impact between 283 IAS and IAS-threatened species, but not the types of impact (predation, competition, habitat 284 modification) nor the population abundance of IAS-threatened species. Moreover, we focused 285 on IAS threat, but many IAS threatened species are also affected by habitat loss or 286 overexploitation, and these threats might prevent full recovery of populations even if IAS are controlled or eradicated<sup>32</sup>. Our work considered only IAS-threatened vertebrate species, for 287 288 which data are most comprehensively available, but invertebrate species are also known to be 289 particularly affected by IAS. In addition, IUCN and BirdLife provide comprehensive data for

some regions and taxa, but are far from being comprehensive in some regions (e.g., Africa).

291 Regarding these limitations, the analyses here should be considered as a first step to inform

about the combination of IAS that, in theory, might offer high return for species conservation.

293 In spite of these limitations, our results have the potential to help mitigate the impacts of

invasive species in insular habitats known for their remarkably rich biodiversity.

295 Concluding remarks

296 Our network-oriented analysis of threats posed by IAS on islands allowed us (i) to structure

297 27,081 islands and 437 threatened vertebrates into 21 clusters that could be used to define

298 priorities for conservation research and actions to address threats from biological invasion,

and (ii) to identify the major invaders that threaten a large number of vertebrate species. We

300 suggest that an approach based on networks that take into account islands, IAS and their

301 impacts has been largely missing from biological invasion studies, despite its potential to

302 guide effective responses. The clusters of islands with similar profiles in terms of IAS impacts

303 represents an efficient and innovative way to determine priorities for both areas and species

and then to better understand and mitigate the IAS threat. Continuous investment to

305 understand, eradicate, control or prevent new invasions in islands could benefit a high number

306 of endemic species that are predicted to be extirpated (e.g., <sup>10</sup>), and the high phylogenetic and

307 functional richness located on those islands offering an unique opportunity to mitigate the loss

308 of biodiversity and contribute to achieve international conservation commitments such as the309 Aichi Targets 9.

310

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318	CB and JFR conceived the study designed with the contribution of GM M. JFR and CB did
319	the analyses, BL provided initial version of computing code. CB and JFR wrote the first draft
320	of the manuscript and all authors significantly contributed to interpreting and writing the
321	manuscript.
322	
323	Competing Financial Interests statement
324	The authors declare no competing financial interests.
325	
326	
327	Material & Method
328	Data
329	Information about vertebrate species threatened by invasive species was extracted from the
330	International Union for the Conservation of Nature (IUCN Red List <sup>33</sup> ), and the BirdLife
331	International database <sup>34</sup> . We used the Global Invasive Species Database (GISD <sup>35</sup> ) for
332	information on the identity of invasive alien species responsible for the threat and the Global
333	islands database from IUCN <sup>33</sup> website to obtain spatial data on islands worldwide
334	
335	Vertebrates threatened by IAS
335 336	<i>Vertebrates threatened by IAS</i> The species assessments of the IUCN Red List classify the risk of species extinction into one
335 336 337	Vertebrates threatened by IAS The species assessments of the IUCN Red List classify the risk of species extinction into one of the following categories: extinct (EX), extinct in the wild (EW), critically endangered

339 deficient (DD). These categories are based on quantitative criteria that indicate the extinction 340 risk including the rate of population decline (criterion A), the size and decline of the 341 geographical range (criterion B), the population size, its fragmentation and decline rate (criteria C and D) or quantitative analyses (criterion E)<sup>36</sup>. Prior to 2001, Red List assessments 342 343 were based on expert opinion but now all assessments use the standard quantitative Red List 344 Categories and Criteria, so they are objective, transparent, and repeatable. As part of the species assessment process, factors associated with decline are collated for each species<sup>37</sup>. 345 346 Specifically, the IUCN and BirdLife International have classified these factors into 11 main 347 threat categories (i.e. the IUCN threat classification scheme v. 3.0). These threats are: (1) 348 residential and commercial development; (2) agriculture and aquaculture; (3) energy 349 production and mining; (4) transportation and service corridors; (5) biological resource use; 350 (6) human intrusion and disturbance; (7) natural system modifications; (8) invasive and other 351 problematic species, genes and diseases; (9) pollution; (10) geological events; and (11) climate change and severe weather<sup>37</sup>. We extracted information for terrestrial vertebrates (i.e., 352 353 mammals, reptiles, amphibians and birds) that classified under (8) and identified those 354 threatened by IAS to be included our analysis. 355 We selected vertebrates that were classified into one of the threatened categories (i.e., CR, EN 356 and VU; N=1.324) and extracted their spatial distributions (spatial polygons) from IUCN spatial data for mammals, amphibians and reptiles, and from the BirdLife database<sup>34</sup> for birds 357 358 (resulted in a total N= 1,291). Spatial data were missing for 4 mammals and 29 reptiles. Note 359 that in our analyses any IAS-threat associated with a species is a binary response - either an 360 invasive alien species does impact a species or it does not; we do not consider different 361 intensities of invasive species impact (but see supplementary figure 3-4). In this way we were 362 able to identify which vertebrates are threatened by any IAS among islands. 363 Information about invasive alien species

- 364 We used the Global Invasive Species Database (GISD) which interlinks the IUCN Red List
- 365 with IAS information<sup>35</sup>. The information in the GISD has been compiled from many sources
- 366 including scientific papers and regional databases that have been reviewed by international
- 367 expert contributors. Specifically, for vertebrate species identified as threatened by IAS, we
- 368 collected information about the identity of IAS responsible.
- 369

370 Island data

371 We used the Global islands database from IUCN website

372 (http://www.iucnredlist.org/technical-documents/red-list-training/iucnspatialresources), a

- 373 spatial dataset of more than 180,488 islands <sup>33</sup>. We overlaid the spatial polygon of islands and
- the polygon of vertebrate species distributions to derive a set of 73,515 islands where
- vertebrate species are threatened by IAS (see supplementary methods for more details). When
- an overlap between an island and the polygon of species distribution was indistinct, we
- 377 visually checked the species distribution. In order to restrict the analysis to insular vertebrates
- 378 (persisting only on islands), we excluded species that were both on continental coastal areas
- and islands. The resulting dataset includes 97 amphibians threatened by IAS on 903 islands,
- 120 reptiles on 2,340 islands, 336 birds on 72,433 islands and 110 mammals on 9,709 islands.
- 381

#### 382 **Bipartite networks**

- 383 We first built an island and IAS-threatened species network that we clustered into groups of
- islands on the basis of shared IAS-threatened species. Then, for each of the clusters, we
- 385 conducted analyses of IAS and IAS-threatened species interaction networks.
- 386 *Analyses of the island IAS-threatened species network*
- 387 Recently, geographical relationships between species and localities has been abstracted as a
- 388 bipartite association network, where links are the occurrences of species within geographical
- 389 locations<sup>38</sup>. Similarly, the occurrence of species on islands worldwide can be represented as a

390 network for which nodes are either species or islands. When a species is present on a given 391 island, a connection between this species and the island is established in the network. As 392 species never connect to species, and islands never connect to islands (i.e., links only connect 393 species to island in the network), such a network is called a bipartite network. This network 394 provides information on co-occurrences of species on islands, the number of times species co-395 occur, and the number of species shared by particular groups of islands. In this study, we built 396 the network with all vertebrate species threatened by IAS on islands. We chose a 397 biogeographical approach to represent connections between islands, IAS-threatened species 398 and invasive without any *a priori* knowledge of political jurisdiction or geographical 399 proximity. Indeed, native and invasive species do not respect political boundaries, but mostly 400 environmental boundaries. Thus, it makes more biological sense to use biogeography of 401 species (spatial distribution of species) to delimit the impact of invasive species across islands 402 as it will better reflect the processes of dispersion among islands than other types of 403 boundaries. 404 Since such an interconnected network has a high degree of complexity (663 species, 73,515 405 islands), numerous techniques have been developed to synthesize information by clustering nodes (e.g., the map equation minimization approach<sup>39</sup> and the modularity maximization 406 approach<sup>40</sup>). Among these techniques, the map equation algorithm<sup>39</sup> has been proven 407 particularly well suited for cluster networks in comparative studies<sup>41,42,38</sup>. This technique 408 409 allows us to extract meaningful ecological structure composed of islands and species that are 410 similar. Specifically, this technique will allow us to cluster our bipartite network based on 411 biogeographical knowledge (species distribution) and detect common patterns of threatened 412 species among islands.

The map equation algorithm is iterative: first it chooses a random node, and then randomlyselects a second node that is connected to the first one. This process is repeated a random

415	number of times. Then another node is chosen randomly and the same process repeated. If
416	some nodes are strongly interconnected, this process tends to frequently select the same
417	nodes, which are then attached to a cluster. In groups of islands with marked structure (high
418	connectivity), the algorithm will focus mostly within clusters, crossing only when a cross-
419	cluster species is selected. Once the algorithm go through all the nodes of the system, it will
420	provide the list of clusters where it spent more time <sup>38</sup> . This technique allows us to extract
421	meaningful ecological structure composed of islands and species that are connected.
422	We expected a hierarchical structure in the dataset – due to the nested nature of species
423	distribution - as species may be located on specific islands, which are encompass in
424	archipelagos, and on larger regions. Consequently, we applied the multiple-level
425	implementation of the map equation, which produces hierarchically nested groups of clusters.
426	Thus, the algorithm hierarchically partition the groups of nodes into clusters <sup>43,44</sup> .
427	In this study, a three-step approach was used to identify clusters of islands and species that are
428	of high interest for conservation.
429	(1) We applied the map equation algorithm to define clusters of island based on IAS-
430	threatened species co-occurrences, and attributed hierarchical levels into clusters that
431	correspond to a subset of the original network in which species and islands are strongly inter-
432	connected to each other, but weakly linked to species and islands outside the group <sup>45</sup> .
433	(2) We selected clusters with high conservation interest defined as those that harbour at least
434	1% of all IAS-threatened species (>6 IAS-threatened species, see supplementary figure 6 for
435	sensitivity analyses of this parameter).
436	(3) We then selected, for each branch in the hierarchy, clusters that maximize the ratio of the
437	number of IAS threatened species to the total area. In this way we identify islands with a high
438	density of threatened species. Specifically, we chose to maximize the ratio between number of
439	threatened species and total area for a given unit area (km2 here), so the eradication events

succeed on a small area<sup>46</sup> than large ones. We made the assumptions here that all species have 441 442 the same value and interest for conservation, without any distinctions of their originality or 443 role for the community or ecosystem Therefore, we attempted with this criterion to consider 444 the opportunity for eradication to protect many species as possible. 445 The application of those criteria results in the exclusion of 226 species (24 amphibians, 111 446 birds, 50 mammals, and 41 reptiles) (black nodes in Figure 1b) as they did not meet the 447 criteria detailed below. Note that 14 of the excluded IAS-threatened species could offer 448 particular opportunities for research and eradication programs as 4 birds, 5 reptiles and 5 449 amphibians are both located on single islands and are threatened by only one identified IAS

could benefit to a high number of species. Indeed, eradications outcome are more likely to

450 (see list in the supplementary table 1).

451 From these three steps we obtained 21 clusters that correspond to groups of strongly inter-

452 connected species and islands with a high density of IAS-threatened species (see

453 supplementary figure 5 for illustration of the 3-step approach). For each cluster we document

- 454 the number of IAS-threatened species, number of islands, total area (km<sup>2</sup>), and identities of
- 455 IAS-threatened species (Table 1).

456

440

457 *IAS - IAS-threatened species interaction network* 

458 Thereafter, for each of the 21 clusters, we constructed an interaction network between IAS-

459 threatened species and their associated IAS. This relationship is based on the IUCN GISD

460 information that identified which IAS threatens which species. The majority of IAS-

threatened species are threatened by several invasive alien species. Using a network to

- describe the relationships between IAS-threatened species and IAS provides the means to list
- all species threatened by a given IAS and how they are linked to other IAS.

464 For each of the 21 interaction networks we identified the (i) top-IAS per cluster (*i.e.*, IAS with

the highest number of links to threatened species), (ii) number of nodes (total number of IAS

and threatened vertebrates included in the cluster), (iii) number of links (total number of 466 467 interactions between IAS and threatened vertebrates), (iv) the connectivity of IAS and their 468 threatened species nodes (i.e., the average number of links (interactions) per IAS and their 469 threatened species) and (v) graph density: a ratio of the number of links per node to the 470 number of possible links. Knowing a network's property regarding connectivity is important 471 here for two reasons. First, it will help us to identify if control of certain IAS in the network 472 will have positive effects on a number of threatened species. Conversely, knowing the number 473 of connections of IAS-threatened species will help determine which IAS should primarily be 474 controlled or eradicated. Indeed, the connectivity of IAS and their threatened species nodes 475 will help us to identify how IAS and threatened species are connected. It can be used to 476 identify which IAS threaten a large number of species and if those threatened species share 477 the same IAS or not. This can indicate how eradication of any IAS will benefit different 478 threatened species. We also measured whether the network is close to saturation (density 479 value close to 1, indicating that all the possible interactions have been achieved). In a 480 saturated network where the threatened species are threatened by many IAS it will be very 481 difficult to release significant pressure on threatened species, as most IAS would have to be 482 removed to release significant pressure on threatened species. Yet, in a saturated network, 483 where the threatened species are threatened by a low number of IAS, it will be highly 484 beneficial to conduct eradication campaings, especially if the number of threatened species is 485 high.

486

Maximising the number of IAS-threatened species that may benefit from IAS eradication
Finally we calculated, for the whole network (n=21 clusters), the combination of IAS for
which control or eradication programs could theoretically benefit the largest number of
threatened species. Specifically, for each potential combination of invasive species (from 1 to

491 5 IAS), we calculated the number of species that would be invasive free after eradication of 492 that combination of IAS. We found the best strategy by testing every possible eradication 493 scenario (see Fig. 2b). Any IAS-threatened species could benefit from the eradication of one 494 or several of its associated IAS, but the highest conservation benefit would require all of its 495 known IAS (according to the IUCN-GISD data) to be eradicated. For this analysis, we assume 496 that a threatened species only benefits from the eradication, if all invasive species that affect it 497 are eradicated. Obviously, this assumption does not necessarily reflect of real ecological 498 situations because other native species might also benefit from such eradications. But, it is not 499 possible to predict the effect of eradication for partially benefited species (such data do not 500 exist at the global scale). In addition it is worth noting that many other factors, such as Allee 501 effects or the existence of other threats may limit recovery, even if all invasive species are 502 eradicated. Consequently, for the purposes of the analyses, we define conservation success as 503 the eradication all of the known IAS threatening a given species. Note that eradicating any 504 IAS may also benefit others species by releasing pressure on them, even if other IAS are still 505 threatening them. For example if a species<sub>A</sub> is threatened only by a IAS<sub>B</sub> the eradication of 506 this IAS<sub>B</sub> in the cluster will theoretically allow species<sub>A</sub> to recover. But, if species<sub>A</sub> is 507 threatened by IAS<sub>B</sub>, IAS<sub>C</sub>, IAS<sub>D</sub>, the removal of IAS<sub>B</sub> will not be sufficient to permit the full 508 recovery of the species, it will only release some pressure. We report the top 5 IAS whose 509 eradication would most benefit IAS-threatened species across the whole network. 510 We conducted the same analysis for each cluster. We kept the identity of the IAS or the 511 combination of IAS that maximize the ratio of the number of invasive-free species to the 512 number of necessary eradicated IAS per cluster. All analyses were carried out with R version 3.2.4 using ggplot2<sup>47</sup> maptools<sup>48</sup>, igraph<sup>49</sup>, 513 infomap version 0.18.2<sup>41</sup> and dplyr<sup>50</sup> packages, and gephi software<sup>51</sup> under Debian-Linux 514

515 operating system.

516									
517	Data	availability:							
518	The dataset of the co-occurrence of species on islands is available in Zenodo data repository								
519	( <u>http://doi.org/10.5281/zenodo.884886</u> ). The code to create the network is available on								
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#### 666 Figure legends

667 Figure 1: Bipartite IAS-threatened species/islands network. A - The map represents the 668 location of the 27,081 islands included in the 21 clusters coded using ID number and colour 669 (see legend). Brown areas show the location of biodiversity hotspots originally defined by Mixers and then updated to 35 hotspots<sup>17,52</sup>. B- Graphical summary of the 21 clusters; each 670 671 cluster is defined by islands and IAS-threatened species, and distinguished using the same 672 colour as in (a). with the ID numbers shown (see the legend for the labels). The size of the 673 nodes in the inner circle is log-proportional to the number of islands in the cluster, and the 674 size of the nodes in the outer circle is log-proportional to the number of species of each taxon 675 in a cluster. Shapes representing the higher taxa are shown in the circle when possible. The 676 width of the grey links is log-proportional to the number of species that are located in two 677 given clusters. Nodes (islands and IAS-threatened species) represented in black on the right-678 hand side of the figure show the species and islands that were not included the analysis (see 679 *Materials and Methods*)

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681

682 *Figure 2*: A- Global interaction network between IAS in black (n=169) and individual

683 threatened species (n=397; green = mammals, red = birds, purple = amphibians, blue =

684 *reptiles).* Node size of the IAS is proportional to the number of species that it is reported to

685 threaten, while the node size for higher taxa is log-proportional to the number of species

686 *threatened by IAS. Some IAS shapes are represented: rats (including R. exulans, R.* 

687 norvegicus, R. rattus, and R. unspecified), pig (Sus scrofa), ant (Wasmannia auropunctata),

688 feral dogs (Canis familiaris), Chytrid Bd, and feral cat (Felis catus) **B**- Barplot of the

689 theoretical number of vertebrate species that would fully benefit from the removal of the top

690 (*Chytrid Bd*) to top 5 IAS in the network.

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Figure 3: A-Representation of two networks between IAS (in black) and IAS-threatened species (in color, green = mammals, red = birds, purple = amphibians, blue = reptiles) for ID 1 and ID 18. Some IAS shapes are represented: ant, pig, rats and feral cat for ID1, Herpestidae family and cat for ID 18. Note that Herpestes sp. appears twice because one node represens the whole Herpestidae family and the other represents species identified as H. javanicus B- Radarplot showing the network characteristics for Caribbean clusters (ID 13, 14, 15), and the Indonesian region clusters (ID 17, 20). All the variables (number of threatened species, total number of nodes, total number of links, density, average number of
links per threatened species, average number of links per IAS, and number of islands) have
been normalized for comparison.

**Table 1:** Characteristics of the 21 clusters based on the two types of networks: the network of IAS-threatened species and islands, and the interaction network between IAS and their threatened species. The table reports the cluster ID, the number of IAS-threatened species, the number of islands, the total area in km2, the top invaders, the percentage of IAS included in the network, the average number of links per IAS-threatened species and per IAS, the density of the network, the combination of IAS that in theory could benefit to the highest number of vertebrate species, and the number of vertebrate species free of IAS. The latter quantity is defined as the number of threatened species for which all known IAS in the cluster are eradicated based on the stated combination of IAS. Note that when the ratio between the number of targeted IAS and the number of vertebrates free of IAS is less than 1, we did not include it in the table. 

### **Table 1:**

Ð	Nb. of IAS- threatene	Nb. of Islands	Area (km²)	Top-1st IAS	% of IAS	Mean nb. of link per IAS- threatene d sp.	Mean nb. of link per IAS	Density	Combinat ion of IAS to target	Nb. of full benefit
1	54	6011	52488	F. catus	42,3	3,3	4,5	0,1	R. rattus+F. catus+R. exulans	13
2	20	4836	106070	F. catus	67,2	3,9	1,9	0,1	F. catus+R. norvegicus	3
3	7	7460	124150	F. catus	60	2,8	1,9	0,31	R. rattus	1
4	15	1034	3004	Rattus spp.	46,1	2	2,3	0,17	F. catus	2
5	28	263	266420	M. erminea	62,2	5,3	3,2	0,12	Chytrid Bd	1
6	7	741	48737	F. catus	36,4	1,9	3,2	0,46	C. familiaris+F. catus+Rattus spp.	6
7	28	70	16891	P. relictum	63,2	8,1	4,7	0,17	-	-
8	55	56	16700	Family rodentia	24,7	3,7	11,4	0,21	-	-
9	8	31	983	F. catus	61,9	4	2,5	0,31	-	-
10	10	56	1523	B. irregularis	64	3,8	2,1	0,24	B. irregularis	1
11	16	24	8081	R. rattus	62,5	4,7	2,8	0,19	M. musculus+R. Rattus	4
12	8	13	1894	L. robustum	74,2	6,25	2,2	0,27	-	-
13	11	63	74555	Chytrid Bd	41,2	1,6	2,3	0,23	Chytrid Bd	6
14	11	5	11028	Rattus spp. + others	54,2	1,7	1,5	0,13	-	-
15	12	1	8761	Chytrid Bd	36,9	1,6	2,7	0,23	Chytrid Bd	7
16	61	387	598629	Eucalyptus spp.	30,9	2,1	4,7	0,08	-	-
17	8	256	823053	R. rattus + others	40	1,2	1,7	0,29	C. familiaris	2
18	18	64	3091	F. catus	54,2	1,9	3,6	0,21	family herpestidae	6
19	30	5566	1656400	F. catus	40	1,6	2,4	0,10	Rattus spp.	4
20	10	126	196869	C. familiaris	36,4	1,7	3	0,43	C. familiaris + F. catus	5
21	20	18	250	F. catus	53,9	2,9	2,5	0,21	T. ecaudatus	2





a

#### **ID** Main location

- 1 Polynesia and Micronesia
- 2 South America, Antartic, sub-Antarctic and Australian islands
- **3** North America Pacific Coast
- 4 Southeastern Brazil and South Africa 16
- 5 New Zealand
- 6 Solomon, New Britain and
  - New Ireland islands
- 7 Hawaiian islands
- 8 New Caledonia islands
- 9 New Zealand and Chatham islands
- 10 Mariana Islands
- 11 Galápagos Islands



Islands and species outside of the 21 clusters

- **12** Mauritius and Trindade
- 13 Hispaniola
- 14 Jamaica
  - Puerto Rico
  - 5 Madagascar and Africa southeastern coast
- 17 Papua New Guinea
- 18 Okinawa Islands
- 19 Malaysia, Philippines and Indonesian islands
- 20 South of east indies islands
- 21 Seychelles





## **Table 1:**

₽	Nb. of IAS- threatene	Nb. of Islands	Area (km²)	Top-1st IAS	% of IAS	Mean nb. of link per IAS- threatene d sp.	Mean nb. of link per IAS	Density	Combinat ion of IAS to target	Nb. of full benefit
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3	7	7460	124150	F. catus	60	2,8	1,9	0,31	R. rattus	1
4	15	1034	3004	Rattus spp.	46,1	2	2,3	0,17	F. catus	2
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6	7	741	48737	F. catus	36,4	1,9	3,2	0,46	C. familiaris+F. catus+Rattus spp.	6
7	28	70	16891	P. relictum	63,2	8,1	4,7	0,17	-	-
8	55	56	16700	Family rodentia	24,7	3,7	11,4	0,21	-	-
9	8	31	983	F. catus	61,9	4	2,5	0,31	-	-
10	10	56	1523	B. irregularis	64	3,8	2,1	0,24	B. irregularis	1
11	16	24	8081	R. rattus	62,5	4,7	2,8	0,19	M. musculus+R. Rattus	4
12	8	13	1894	L. robustum	74,2	6,25	2,2	0,27	-	-
13	11	63	74555	Chytrid Bd	41,2	1,6	2,3	0,23	Chytrid Bd	6
14	11	5	11028	Rattus spp. + others	54,2	1,7	1,5	0,13	-	-
15	12	1	8761	Chytrid Bd	36,9	1,6	2,7	0,23	Chytrid Bd	7
16	61	387	598629	Eucalyptus spp.	30,9	2,1	4,7	0,08	-	-
17	8	256	823053	<i>R. rattus</i> + others	40	1,2	1,7	0,29	C. familiaris	2
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19	30	5566	1656400	F. catus	40	1,6	2,4	0,10	Rattus spp.	4
20	10	126	196869	C. familiaris	36,4	1,7	3	0,43	C. familiaris + F. catus	5
21	20	18	250	F. catus	53,9	2,9	2,5	0,21	T. ecaudatus	2