

1 **Title:**

2 **A global picture of biological invasion threat on islands**

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37 **Introductory paragraph**

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

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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  
66 recorded extinctions of vertebrate species have occurred on islands<sup>2</sup>. Invasive alien species  
67 (IAS) are considered the second most important driver of species extinctions on islands, and  
68 are associated with nearly 25% of birds and amphibians currently threatened worldwide<sup>3</sup>.  
69 Island ecosystems are particularly vulnerable to biological invasions<sup>2</sup>. To date, there have  
70 been over 700 attempted eradications of invasive alien mammals<sup>4</sup>, which have benefited to  
71 600 local populations, leading to larger populations or increased distributional areas<sup>4</sup>.  
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  
74 direct result of these eradications<sup>4</sup>. Despite these encouraging results, the threat posed by  
75 invasive alien species (IAS) remains significant and widespread for native species<sup>3</sup>. Thus,  
76 prioritization of research efforts and eradication strategies needs to be more effective<sup>5</sup> and  
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  
88 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-

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

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## 122 **Results**

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

124 We analyzed more than 73,515 islands where the IUCN Red List recorded IAS-threatened  
125 species. First, we selected islands for which we could expect high return in investment for  
126 conservation program. Specifically, we selected islands that harbour more than 1% of the total  
127 number of IAS-threatened species, and those with a high ratio of the number of threatened  
128 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-  
132 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  
134 southern hemisphere and encompass most of the Caribbean and Pacific archipelagos  
135 (including Hawaiï), 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, Hawaiian 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  
172 the New Caledonia cluster (see also <sup>16</sup>) and the Chytrid Bd (*Batrachochytrium dendrobatidis*)  
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  
189 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  
234 plants threatened by habitat loss<sup>17</sup>. Over \$1 billion has been spent protecting the remaining  
235 natural vegetation of these biodiversity hotspots<sup>18</sup>. We identified other areas important for  
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

240 and South of East Indies islands would qualify as priorities on their own while clusters that  
241 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*,  
244 which are already known to cause widespread threats to species on islands<sup>19–21, 22</sup>. Feral cats  
245 are well-known to drive numerous extinctions of endemic vertebrates (>175<sup>6</sup>). Yet, our  
246 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  
249 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  
251 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  
253 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  
255 species<sup>25,26</sup> or other unanticipated events (e.g., changes of vegetation or trophic webs that  
256 could follow IAS eradication). In addition, we assume that all IAS have the same effect on  
257 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  
262 have greatly improved our understanding of amphibian-chytridiomycosis dynamics<sup>27</sup>. First,  
263 the recognition that *Bd* is not one species but distinct lineages that vary in distribution and  
264 virulence and, second, that species have been infected for much longer than initially thought

265 with some species co-evolving without any impact (see<sup>27</sup> for a review). Thus, preventing  
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  
268 rats with failure rates of only 12%<sup>28</sup> as well as for invasive ants<sup>29</sup>.

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  
271 should be undertaken<sup>8,30</sup>. For example, a recent study analyzed conservation opportunities for  
272 sea-bird populations in most of the 800 small, uninhabited, and high-middle-income countries  
273 islands<sup>31</sup>. Our analyses also revealed that in some clusters it might be quite challenging to  
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  
287 controlled or eradicated<sup>32</sup>. Our work considered only IAS-threatened vertebrate species, for  
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

290 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  
292 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  
294 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,  
299 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  
304 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 the  
309 Aichi Targets 9.

310

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316

### 317 **Author Contributions**

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.

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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*

336 The species assessments of the IUCN Red List classify the risk of species extinction into one  
337 of the following categories: extinct (EX), extinct in the wild (EW), critically endangered  
338 (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC) and data

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  
342 (criteria C and D) or quantitative analyses (criterion E)<sup>36</sup>. Prior to 2001, Red List assessments  
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  
345 species assessment process, factors associated with decline are collated for each species<sup>37</sup>.  
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)  
352 climate change and severe weather<sup>37</sup>. We extracted information for terrestrial vertebrates (i.e.,  
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  
357 spatial data for mammals, amphibians and reptiles, and from the BirdLife database<sup>34</sup> for birds  
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  
374 the polygon of vertebrate species distributions to derive a set of 73,515 islands where  
375 vertebrate species are threatened by IAS (see supplementary methods for more details). When  
376 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  
379 and islands. The resulting dataset includes 97 amphibians threatened by IAS on 903 islands,  
380 120 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  
384 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  
406 nodes (e.g., the map equation minimization approach<sup>39</sup> and the modularity maximization  
407 approach<sup>40</sup>). Among these techniques, the map equation algorithm<sup>39</sup> has been proven  
408 particularly well suited for cluster networks in comparative studies<sup>41,42,38</sup>. This technique  
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.

413 The map equation algorithm is iterative: first it chooses a random node, and then randomly  
414 selects 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 (km<sup>2</sup> here), so the eradication events

440 could benefit to a high number of species. Indeed, eradications outcome are more likely to  
441 succeed on a small area<sup>46</sup> than large ones. We made the assumptions here that all species have  
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  
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

#### 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-  
461 threatened species are threatened by several invasive alien species. Using a network to  
462 describe the relationships between IAS-threatened species and IAS provides the means to list  
463 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  
465 the highest number of links to threatened species), (ii) number of nodes (total number of IAS

466 and threatened vertebrates included in the cluster), (iii) number of links (total number of  
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 campaigns, especially if the number of threatened species is  
485 high.

486

487 *Maximising the number of IAS-threatened species that may benefit from IAS eradication*

488 Finally we calculated, for the whole network (n=21 clusters), the combination of IAS for  
489 which control or eradication programs could theoretically benefit the largest number of  
490 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<sub>A</sub>, 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.

513 All analyses were carried out with R version 3.2.4 using ggplot2<sup>47</sup> maptools<sup>48</sup>, igraph<sup>49</sup>,  
514 infomap version 0.18.2<sup>41</sup> and dplyr<sup>50</sup> packages, and gephi software<sup>51</sup> under Debian-Linux  
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 (<http://doi.org/10.5281/zenodo.884886>). The code to create the network is available on  
520 request.

521

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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  
670 Myers and then updated to 35 hotspots<sup>17,52</sup>. B- Graphical summary of the 21 clusters; each  
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)

680

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.

691

692 **Figure 3:** A-Representation of two networks between IAS (in black) and IAS-threatened  
693 species (in color, green = mammals, red = birds, purple = amphibians, blue = reptiles) for  
694 ID 1 and ID 18. Some IAS shapes are represented: ant, pig, rats and feral cat for ID1,  
695 Herpestidae family and cat for ID 18. Note that *Herpestes* sp. appears twice because one  
696 node represens the whole Herpestidae family and the other represents species identified as *H.*  
697 *javanicus* B- Radarplot showing the network characteristics for Caribbean clusters (ID 13,  
698 14, 15), and the Indonesian region clusters (ID 17, 20). All the variables (number of

699 *threatened species, total number of nodes, total number of links, density, average number of*  
700 *links per threatened species, average number of links per IAS, and number of islands) have*  
701 *been normalized for comparison.*

702

703 **Table 1:** *Characteristics of the 21 clusters based on the two types of networks: the network of*  
704 *IAS-threatened species and islands, and the interaction network between IAS and their*  
705 *threatened species. The table reports the cluster ID, the number of IAS-threatened species, the*  
706 *number of islands, the total area in km<sup>2</sup>, the top invaders, the percentage of IAS included in*  
707 *the network, the average number of links per IAS-threatened species and per IAS, the density*  
708 *of the network, the combination of IAS that in theory could benefit to the highest number of*  
709 *vertebrate species, and the number of vertebrate species free of IAS. The latter quantity is*  
710 *defined as the number of threatened species for which all known IAS in the cluster are*  
711 *eradicated based on the stated combination of IAS. Note that when the ratio between the*  
712 *number of targeted IAS and the number of vertebrates free of IAS is less than 1, we did not*  
713 *include it in the table.*

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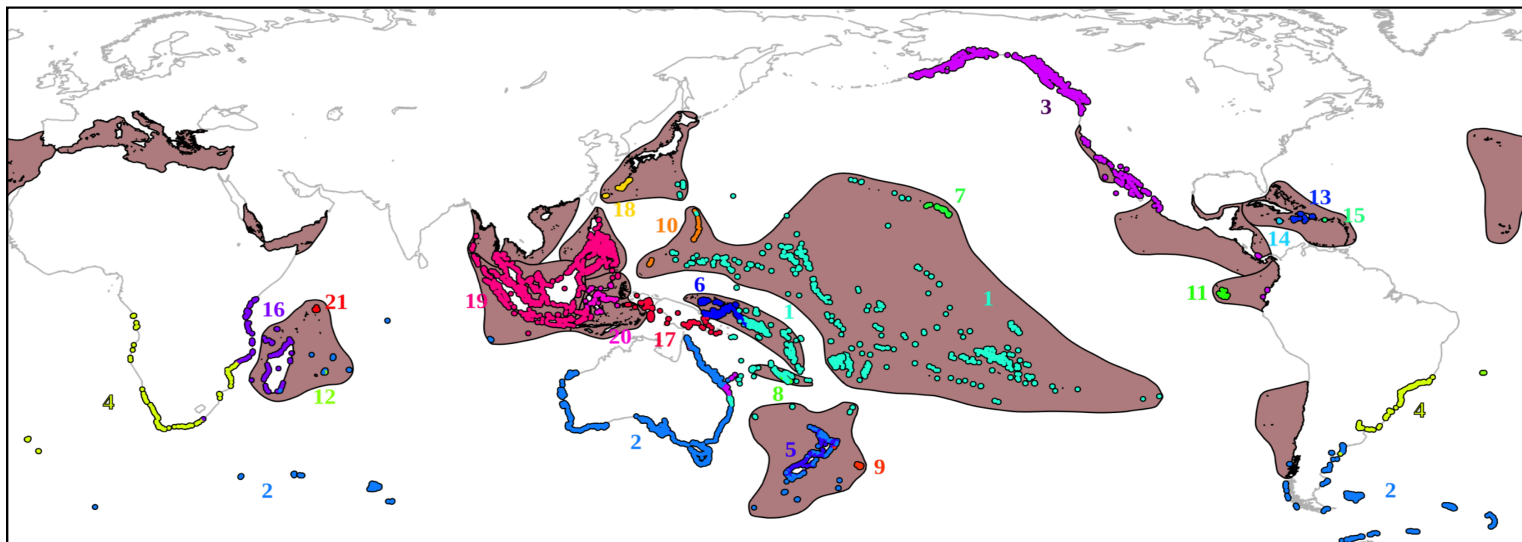
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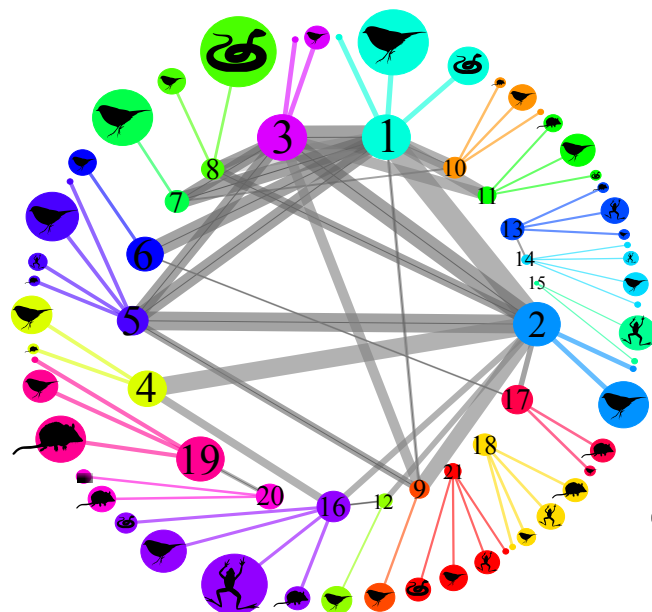
733 **Table 1:**

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

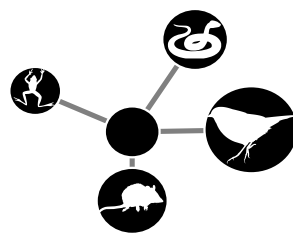
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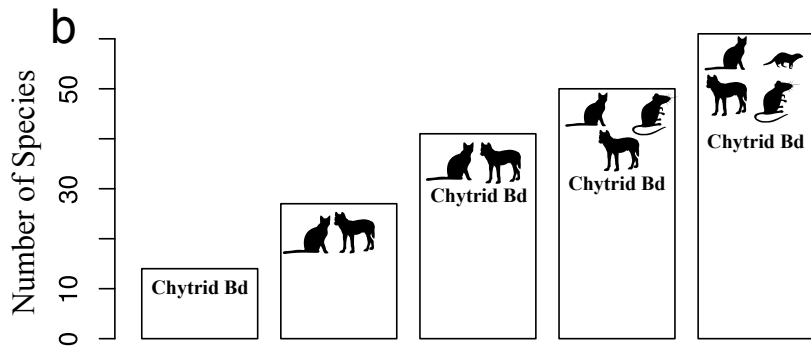
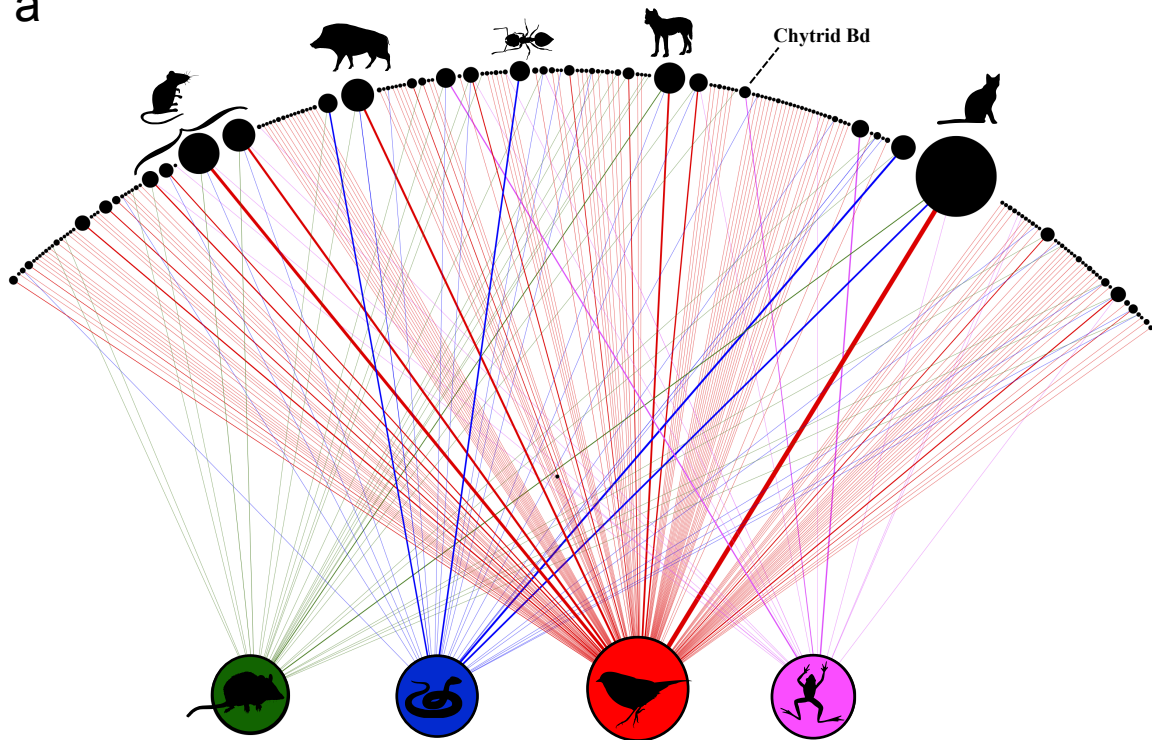
b

**ID Main location**

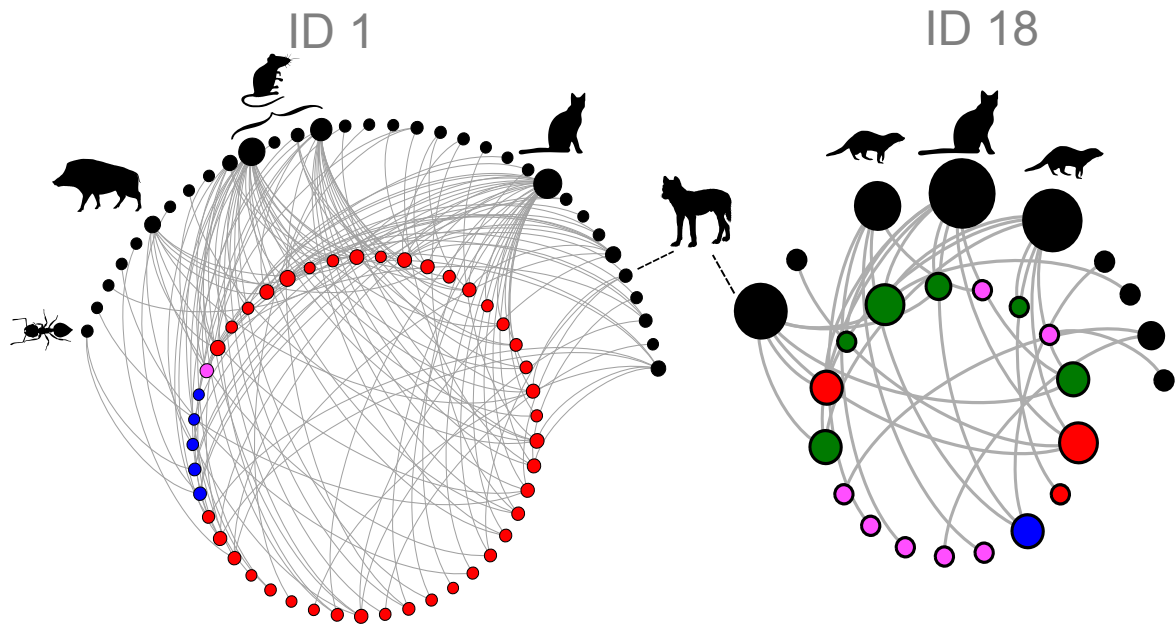
- |    |   |    |  |
|----|---|----|--|
| 1  | Polynesia and Micronesia                                      | 12 | Mauritius and Trindade                       |
| 2  | South America, Antartic, sub-Antarctic and Australian islands | 13 | Hispaniola                                   |
| 3  | North America Pacific Coast                                   | 14 | Jamaica                                      |
| 4  | Southeastern Brazil and South Africa                          | 15 | Puerto Rico                                  |
| 5  | New Zealand   | 16 | Madagascar and Africa southeastern coast     |
| 6  | Solomon, New Britain and New Ireland islands                  | 17 | Papua New Guinea                             |
| 7  | Hawaiian islands  | 18 | Okinawa Islands                              |
| 8  | New Caledonia islands   | 19 | Malaysia, Philippines and Indonesian islands |
| 9  | New Zealand and Chatham islands                               | 20 | South of east indies islands                 |
| 10 | Mariana Islands   | 21 | Seychelles                                   |
| 11 | Galápagos Islands   |    |  |



Islands and  
species outside  
of the 21 clusters

**a**

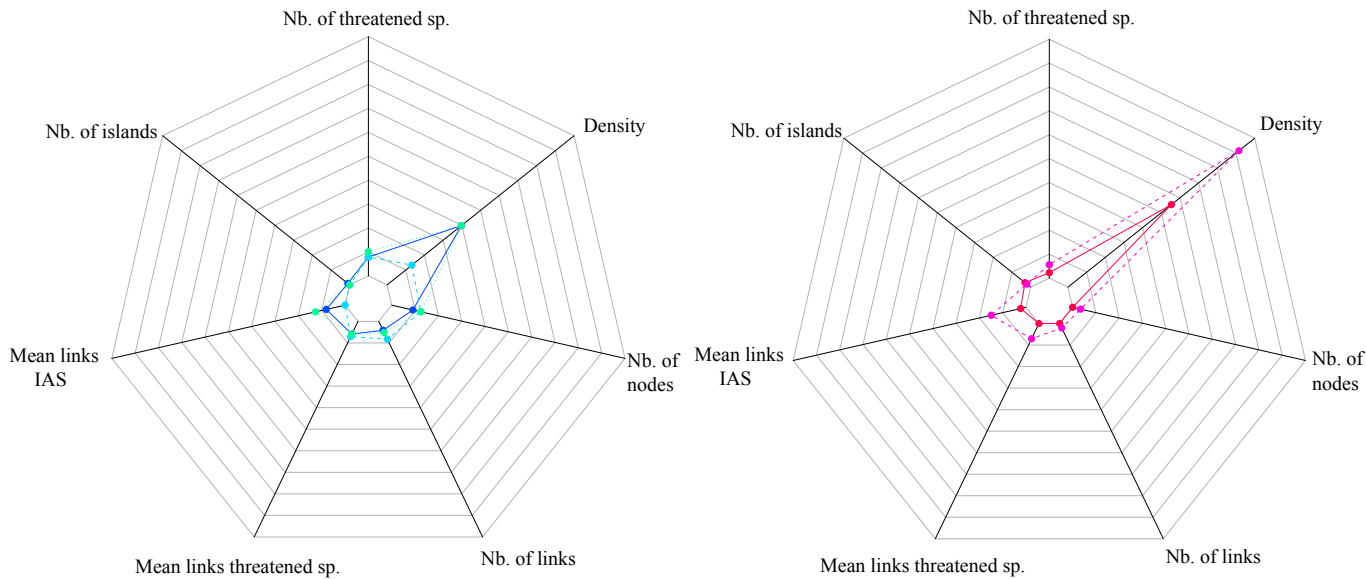
a



b

ID 13 14 15 (Hispaniola, Jamaica, Puerto rico)

ID 17 20 (Papua New Guinea, South of east indies islands)





1 **Table 1:**

ID	Nb. of IAS-threatened	Nb. of Islands	Area (km <sup>2</sup> )	Top-1st IAS	% of IAS	Mean nb. of link per IAS-threatened sp.	Mean nb. of link per IAS	Density	Combination of IAS to target	Nb. of full benefit
1	54	6011	52488	<i>F. catus</i>	42,3	3,3	4,5	0,1	<i>R. rattus</i> + <i>F. catus</i> + <i>R. exulans</i>	13
2	20	4836	106070	<i>F. catus</i>	67,2	3,9	1,9	0,1	<i>F. catus</i> + <i>R. norvegicus</i>	3
3	7	7460	124150	<i>F. catus</i>	60	2,8	1,9	0,31	<i>R. rattus</i>	1
4	15	1034	3004	<i>Rattus spp.</i>	46,1	2	2,3	0,17	<i>F. catus</i>	2
5	28	263	266420	<i>M. erminea</i>	62,2	5,3	3,2	0,12	Chytrid Bd	1
6	7	741	48737	<i>F. catus</i>	36,4	1,9	3,2	0,46	<i>C. familiaris</i> + <i>F. catus</i> + <i>Rattus spp.</i>	6
7	28	70	16891	<i>P. relictum</i>	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	<i>F. catus</i>	61,9	4	2,5	0,31	-	-
10	10	56	1523	<i>B. irregularis</i>	64	3,8	2,1	0,24	<i>B. irregularis</i>	1
11	16	24	8081	<i>R. rattus</i>	62,5	4,7	2,8	0,19	<i>M. musculus</i> + <i>R. Rattus</i>	4
12	8	13	1894	<i>L. robustum</i>	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	<i>Rattus spp.</i> + 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	<i>Eucalyptus spp.</i>	30,9	2,1	4,7	0,08	-	-
17	8	256	823053	<i>R. rattus</i> + others	40	1,2	1,7	0,29	<i>C. familiaris</i>	2
18	18	64	3091	<i>F. catus</i>	54,2	1,9	3,6	0,21	family herpestidae	6
19	30	5566	1656400	<i>F. catus</i>	40	1,6	2,4	0,10	<i>Rattus spp.</i>	4
20	10	126	196869	<i>C. familiaris</i>	36,4	1,7	3	0,43	<i>C. familiaris</i> + <i>F. catus</i>	5
21	20	18	250	<i>F. catus</i>	53,9	2,9	2,5	0,21	<i>T. ecaudatus</i>	2

2

3