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1 **Title:**

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

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20 **Words:**

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22 **Keywords**

23 Insular ecosystems, biological invasions, prioritization, conservation

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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 endemism¹. However, many species on islands are now recorded as threatened, and most
66 recorded extinctions of vertebrate species have occurred on islands². 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 worldwide³.
69 Island ecosystems are particularly vulnerable to biological invasions². To date, there have
70 been over 700 attempted eradications of invasive alien mammals⁴, which have benefited to
71 600 local populations, leading to larger populations or increased distributional areas⁴.
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 eradications⁴. Despite these encouraging results, the threat posed by
75 invasive alien species (IAS) remains significant and widespread for native species³. Thus,
76 prioritization of research efforts and eradication strategies needs to be more effective⁵ 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 IAS⁶ or subsets of islands^{7,8}. 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 globally⁹ or
85 for entire taxonomic groups (e.g., mammals¹⁰), 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^{3,11,12}, and spatially variable. Other large-scale studies have analyzed IAS impact on

89 specific archipelagoes¹³ or on a particularly problematic subset of IAS¹⁴. 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.

121

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 hotspots¹⁵.

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 worldwide³.

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 ¹⁶) 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 loss¹⁷. Over \$1 billion has been spent protecting the remaining
235 natural vegetation of these biodiversity hotspots¹⁸. 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^{19–21, 22}. Feral cats
245 are well-known to drive numerous extinctions of endemic vertebrates (>175⁶). 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 involved²³. On the basis of our results, we suggest that targeting
250 multiple IAS simultaneously would be a more efficient strategy for species conservation²³ and
251 should be achievable as eradication programmes increase in coverage and complexity²⁴.

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^{25,26} 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 dynamics²⁷. 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 (see²⁷ 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%²⁸ as well as for invasive ants²⁹.

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^{8,30}. 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 islands³¹. 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 eradicated³². 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., ¹⁰), 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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315 the manuscript.

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.

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 List³³), and the BirdLife
331 International database³⁴. We used the Global Invasive Species Database (GISD³⁵) for
332 information on the identity of invasive alien species responsible for the threat and the Global
333 islands database from IUCN³³ 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)³⁶. 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 species³⁷.
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 weather³⁷. 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 database³⁴ 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 information³⁵. 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 islands³³. 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 locations³⁸. 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 approach³⁹ and the modularity maximization
407 approach⁴⁰). Among these techniques, the map equation algorithm³⁹ has been proven
408 particularly well suited for cluster networks in comparative studies^{41,42,38}. 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 time³⁸. 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^{43,44}.

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 group⁴⁵.

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

440 could benefit to a high number of species. Indeed, eradications outcome are more likely to
441 succeed on a small area⁴⁶ 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 (km²), 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_A is threatened only by a IAS_B the eradication of
506 this IAS_B in the cluster will theoretically allow species_A to recover. But, if species_A is
507 threatened by IAS_B, IAS_C, IAS_D, the removal of IAS_B will not be sufficient to permit the full
508 recovery of the species_A, 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 ggplot2⁴⁷ maptools⁴⁸, igraph⁴⁹,
514 infomap version 0.18.2⁴¹ and dplyr⁵⁰ packages, and gephi software⁵¹ 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^{17,52}. 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. unspcified*), 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 km², 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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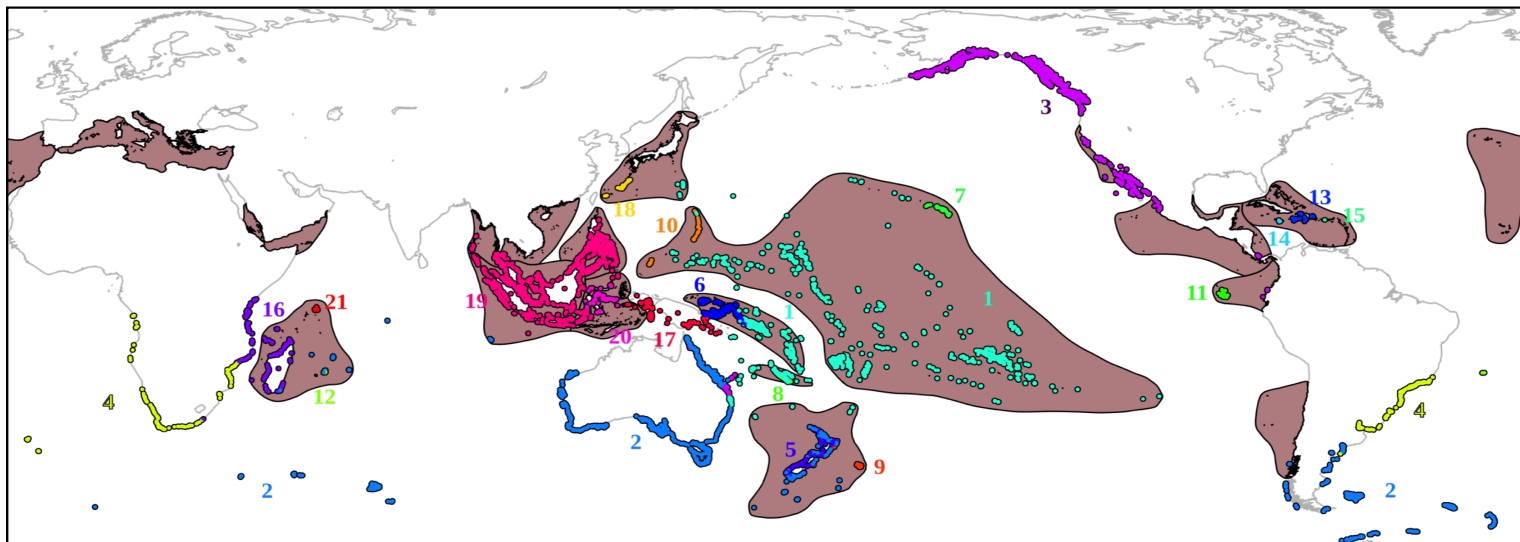
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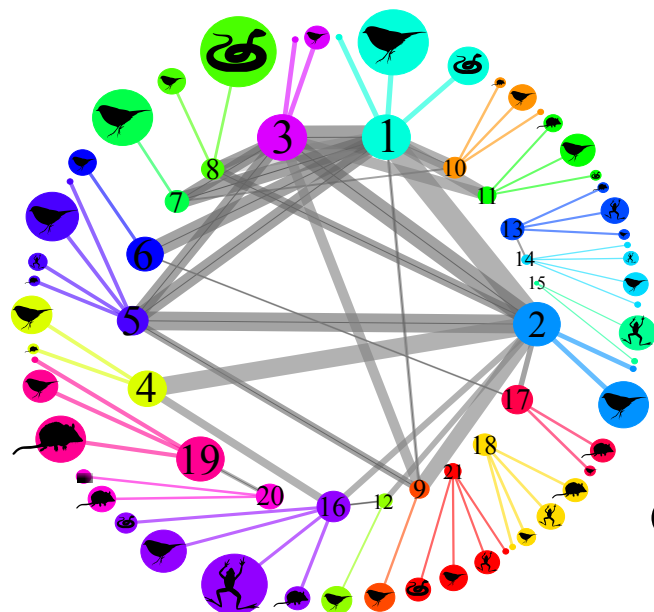
733 **Table 1:**

ID	Nb. of IAS- threatene	Nb. of Islands	Area (km ²)	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	<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

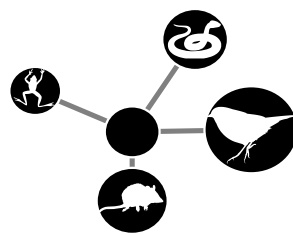
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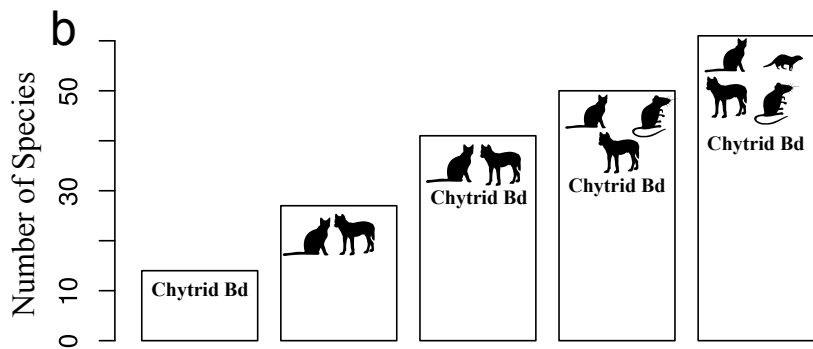
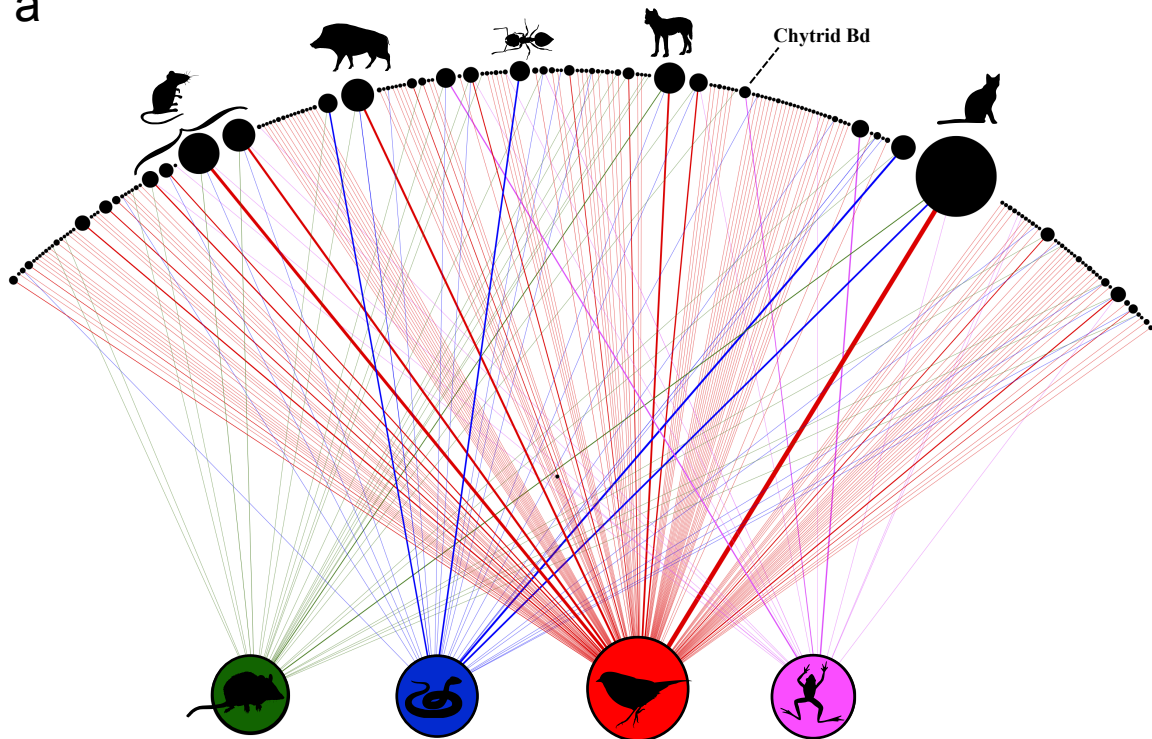
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ID Main location

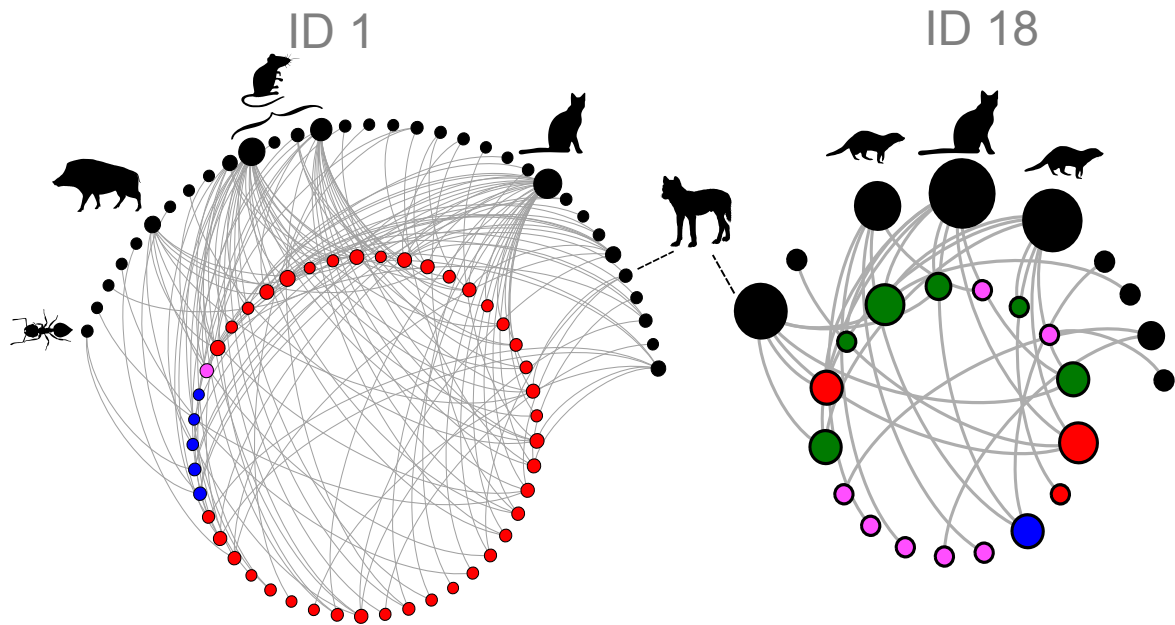
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|----|---|----|--|
| 1 | Polynesia and Micronesia | 12 | Mauritius and Trindade |
| 2 | South America, Antartic, sub-Antarctic and Australian islands | 13 | Hispaniola |
| 3 | North America Pacific Coast | 14 | Jamaica |
| 4 | Southeastern Brazil and 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

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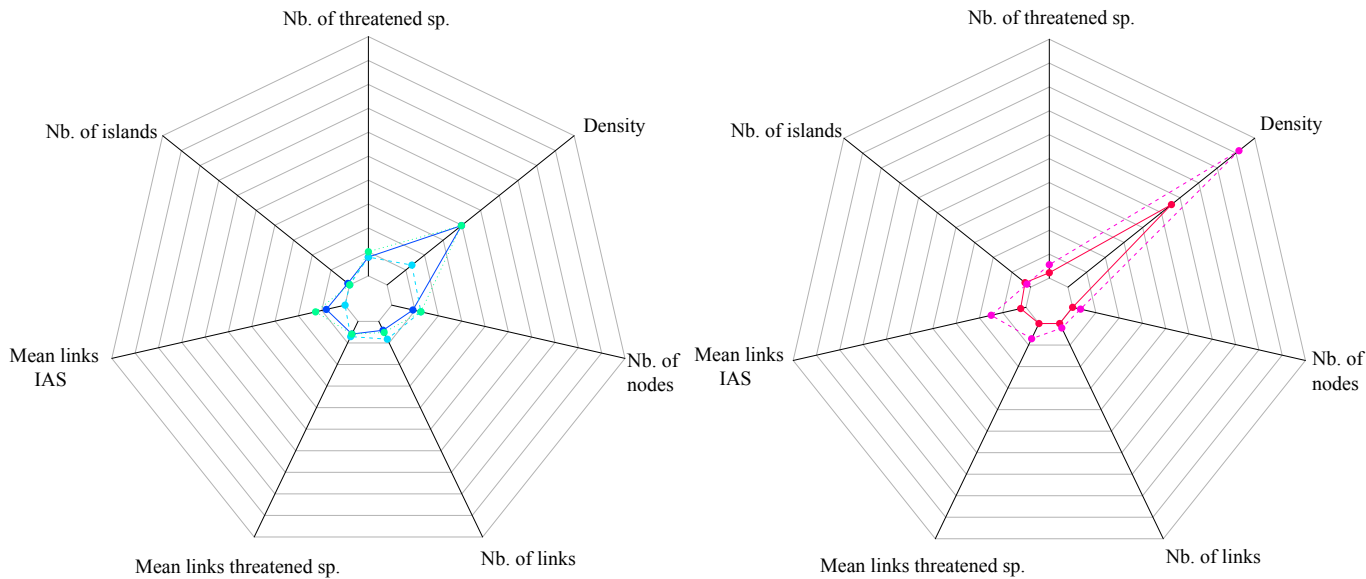
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ID 13 14 15 (Hispaniola,
Jamaica, Puerto rico)

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



1 **Table 1:**

ID	Nb. of IAS-threatened	Nb. of Islands	Area (km ²)	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. + others</i>	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 + others</i>	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 <i>herpestidae</i>	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 + 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

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