

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

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## **Title:**

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## **Introductory paragraph**

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

64 Islands harbour a significant portion of the Earth's species and have an unusually high rate of 65 endemism<sup>1</sup>. However, many species on islands are now recorded as threatened, and most 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  $IAS^6$  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

65 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



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

### **Results**

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

We analyzed more than 73,515 islands where the IUCN Red List recorded IAS-threatened species. First, we selected islands for which we could expect high return in investment for

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

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

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

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

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

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

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

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

southern hemisphere and encompass most of the Caribbean and Pacific archipelagos

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

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>.

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

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

threatened species are found nowhere else. Two of the Caribbean clusters (including Hispaniola and Jamaica islands), and Malaysia, Philippines, and South of east indies islands are connected only to each other (Figure 1b). Overall, the clusters that share a high number of threatened species with other clusters are Polynesia and Micronesia, North America Pacific coast islands, as well as the South American, Antarctic, sub-Antarctic and Australian islands. Our analysis revealed that most of the connections between clusters are due to bird species, but amphibians, mammals and reptiles are also responsible for connections between the southern part of New Zealand, Australia and southern-hemisphere islands, Caribbean clusters, and African islands (supplementary figure 1). Some clusters are particularly noticeable due to their high number of threaned species by IAS: New Caledonia, Hawaian islands and Madagascar and African southeastern coast for reptiles, birds, and amphibians, respectively. The 21 identified clusters vary in terms of number of threatened species (see size of the taxa nodes of the outer circle Figure 1b), number of islands (size of the inner circle nodes, Figure 1b) and total area. Specifically, the number of threatened species ranges from 7 (the cut-off point we selected that corresponds to at least 1% of the total number of insular threatened vertebrates) to 61 species, while the number of islands ranges from 1 (i.e., Puerto Rico) to 7,460 (Table 1). Most of the threatened species found in these clusters are birds (51%), 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>. *Are there combinations of IAS for which targeted actions may have high conservation impacts?*  In a second step, we analyzed the patterns of interactions between IAS and the vertebrate species they threaten for the whole network and for the 21 identified clusters (Figure 2a, for the complete network see supplementary figure 1). We built interaction networks with IAS and IAS-threatened species as nodes. The links between nodes represent the vulnerability of a

given species to a known IAS (see supplementary figure 2 for each IAS-threatened species) 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 the feral cat (*Felis catus*), followed by other IAS such as rat (*Rattus spp*), feral dog (*Canis familiaris*) and pig (*Sus scrofa*). Some IAS are more specialized, such as *Eucalyptus* spp. that predominantly threatens vertebrates located in clusters of Madagascar and African 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*) that mainly threatens amphibians in the Caribbean clusters. The network approach can, in theory, help to identify the best strategies for combating IAS that maximise the number of threatened species that will benefit from any eradications. For example, the feral cat and feral dog eradicated alone would directly benefit to 10 and 6 species respectively, but targeted together could benefit up to 27 species (because 11 others species are simultaneously threatened by those two IAS). Therefore, both need to be controlled to achieve the highest overall conservation benefit. Note that other threatened species will also benefit from such eradications because the IAS pressure on them will be reduced even if other IAS are still threatening them. The control or eradication of the Chytrid *Bd*, feral cats and feral dogs together could fully benefit at least 41 threatened island species worldwide (Figure 2B), assuming that no other threats are significant for these species. *Within the targeted areas what are the characteristics of the network between IAS and IAS-threatened species that can improve strategies to deal with IAS?* 

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

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

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

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

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

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

#### **Discussion**

We have identified 21 clusters of islands harbouring threatened vertebrates species that are highly significant sites of IAS threat and where focusing resources, for both research and conservation action should be most efficient. The spatial distribution of the 21 identified clusters overlaps with the majority of global biodiversity hotspots (except some coastal 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 conservation, including many small islands and island groups that may offer high return on investment. Specifically, we were able to identify clusters that harbour a unique part of vertebrate species diversity threatened by IAS. These island clusters that include Caribbean, Okinawa, Seychelles islands, and also Malaysia, Philippines, some of the Indonesian islands and South of East Indies islands would qualify as priorities on their own while clusters that

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

national efforts for conservation to be fully effective.

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  $(>175^6)$ . Yet, our

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

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

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>.

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

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

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

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

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

information on which to improve this aspect of the analysis. Moreover, we did not assess the potential for reintroductions or the feasibility of eradication events.

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

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,

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

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

265 with some species co-evolving without any impact (see for a review). Thus, preventing measures to avoid further propagation of the Chytrid *Bd* in nearby clusters should be a 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 ants<sup>29</sup>. In general we argue that network approaches should complement local prioritization schemes 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 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 protect native species from extinctions, because of the high number of IAS combinations that threaten native species as shown by their high values of connectivity. Yet, local removals of IAS could prevent local extirpations of native populations and therefore benefit biodiversity. This is particularly the case of the Polynesia and Micronesia cluster. There are some limitations of our approach that are discussed in the following. First, we considered the impacts of IAS as a reduction in population size or distribution range determined by the IUCN Red list of threatened species, but other type of impacts on functional or genetic diversity through hybridization or ecosystem services might also be important. Our network-based analyses only accounted for the existence of an impact between IAS and IAS-threatened species, but not the types of impact (predation, competition, habitat modification) nor the population abundance of IAS-threatened species. Moreover, we focused on IAS threat, but many IAS threatened species are also affected by habitat loss or 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 which data are most comprehensively available, but invertebrate species are also known to be particularly affected by IAS. In addition, IUCN and BirdLife provide comprehensive data for

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

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

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

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

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

*Concluding remarks* 

Our network-oriented analysis of threats posed by IAS on islands allowed us (i) to structure 27,081 islands and 437 threatened vertebrates into 21 clusters that could be used to define

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

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

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

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

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

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

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

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

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

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

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deficient (DD). These categories are based on quantitative criteria that indicate the extinction risk including the rate of population decline (criterion A), the size and decline of the 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 were based on expert opinion but now all assessments use the standard quantitative Red List Categories and Criteria, so they are objective, transparent, and repeatable. As part of the species assessment process, factors associated with decline are collated for each species<sup>37</sup>. Specifically, the IUCN and BirdLife International have classified these factors into 11 main threat categories (i.e. the IUCN threat classification scheme v. 3.0). These threats are: (1) residential and commercial development; (2) agriculture and aquaculture; (3) energy production and mining; (4) transportation and service corridors; (5) biological resource use; (6) human intrusion and disturbance; (7) natural system modifications; (8) invasive and other 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., mammals, reptiles, amphibians and birds) that classified under (8) and identified those threatened by IAS to be included our analysis. 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 (resulted in a total N= 1,291). Spatial data were missing for 4 mammals and 29 reptiles. Note that in our analyses any IAS-threat associated with a species is a binary response - either an invasive alien species does impact a species or it does not; we do not consider different intensities of invasive species impact (but see supplementary figure 3-4). In this way we were able to identify which vertebrates are threatened by any IAS among islands. *Information about invasive alien species* 

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

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

- 373 spatial dataset of more than 180,488 islands <sup>33</sup>. We overlaid the spatial polygon of islands and
- the polygon of vertebrate species distributions to derive a set of 73,515 islands where

vertebrate species are threatened by IAS (see supplementary methods for more details). When

- an overlap between an island and the polygon of species distribution was indistinct, we
- visually checked the species distribution. In order to restrict the analysis to insular vertebrates
- (persisting only on islands), we excluded species that were both on continental coastal areas
- and islands. The resulting dataset includes 97 amphibians threatened by IAS on 903 islands,
- 120 reptiles on 2,340 islands, 336 birds on 72,433 islands and 110 mammals on 9,709 islands.
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### **Bipartite networks**

- We first built an island and IAS-threatened species network that we clustered into groups of
- islands on the basis of shared IAS-threatened species. Then, for each of the clusters, we
- conducted analyses of IAS and IAS-threatened species interaction networks.
- *Analyses of the island IAS-threatened species network*
- Recently, geographical relationships between species and localities has been abstracted as a
- 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

network for which nodes are either species or islands. When a species is present on a given island, a connection between this species and the island is established in the network. As species never connect to species, and islands never connect to islands (i.e., links only connect species to island in the network), such a network is called a bipartite network. This network provides information on co-occurrences of species on islands, the number of times species co-occur, and the number of species shared by particular groups of islands. In this study, we built the network with all vertebrate species threatened by IAS on islands. We chose a biogeographical approach to represent connections between islands, IAS-threatened species and invasive without any *a priori* knowledge of political jurisdiction or geographical proximity. Indeed, native and invasive species do not respect political boundaries, but mostly environmental boundaries. Thus, it makes more biological sense to use biogeography of species (spatial distribution of species) to delimit the impact of invasive species across islands as it will better reflect the processes of dispersion among islands than other types of boundaries. Since such an interconnected network has a high degree of complexity (663 species, 73,515 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 allows us to extract meaningful ecological structure composed of islands and species that are similar. Specifically, this technique will allow us to cluster our bipartite network based on biogeographical knowledge (species distribution) and detect common patterns of threatened species among islands.

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



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 the same value and interest for conservation, without any distinctions of their originality or role for the community or ecosystem Therefore, we attempted with this criterion to consider the opportunity for eradication to protect many species as possible. The application of those criteria results in the exclusion of 226 species (24 amphibians, 111 birds, 50 mammals, and 41 reptiles) (black nodes in Figure 1b) as they did not meet the

criteria detailed below. Note that 14 of the excluded IAS-threatened species could offer

particular opportunities for research and eradication programs as 4 birds, 5 reptiles and 5

amphibians are both located on single islands and are threatened by only one identified IAS

(see list in the supplementary table 1).

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

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

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  $(km^2)$ , and identities of
- IAS-threatened species (Table 1).

*IAS - IAS-threatened species interaction network* 

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

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

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

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

describe the relationships between IAS-threatened species and IAS provides the means to list

all species threatened by a given IAS and how they are linked to other IAS.

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

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

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

*Maximising the number of IAS-threatened species that may benefit from IAS eradication*  Finally we calculated, for the whole network (n=21 clusters), the combination of IAS for which control or eradication programs could theoretically benefit the largest number of threatened species. Specifically, for each potential combination of invasive species (from 1 to 5 IAS), we calculated the number of species that would be invasive free after eradication of that combination of IAS. We found the best strategy by testing every possible eradication scenario (see Fig. 2b). Any IAS-threatened species could benefit from the eradication of one or several of its associated IAS, but the highest conservation benefit would require all of its known IAS (according to the IUCN-GISD data) to be eradicated. For this analysis, we assume that a threatened species only benefits from the eradication, if all invasive species that affect it are eradicated. Obviously, this assumption does not necessarily reflect of real ecological situations because other native species might also benefit from such eradications. But, it is not possible to predict the effect of eradication for partially benefited species (such data do not exist at the global scale). In addition it is worth noting that many other factors, such as Allee effects or the existence of other threats may limit recovery, even if all invasive species are eradicated. Consequently*,* for the purposes of the analyses, we define conservation success as the eradication all of the known IAS threatening a given species. Note that eradicating any 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 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  $IAS<sub>B</sub>$ ,  $IAS<sub>D</sub>$ , 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 eradication would most benefit IAS-threatened species across the whole network. We conducted the same analysis for each cluster. We kept the identity of the IAS or the combination of IAS that maximize the ratio of the number of invasive-free species to the number of necessary eradicated IAS per cluster. 513 All analyses were carried out with R version 3.2.4 using ggplot $2^{47}$  maptools<sup>48</sup>, igraph<sup>49</sup>, 514 infomap version  $0.18.2^{41}$  and dplyr<sup>50</sup> packages, and gephi software<sup>51</sup> under Debian-Linux

operating system.





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#### **Figure legends**

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

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

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

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

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

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

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

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

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

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

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

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

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## 733 **Table 1:**







#### **ID Main location**

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



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





## 1 **Table 1:**



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