Saul, Wolf-Christian; Roy, Helen E.; Booy, Olaf; Carnevali, Lucilla; Chen, Hsuan-Ju; Genovesi, Piero; Harrower, Colin A.; Hulme, Philip E.; Pagad, Shyama; Pergl, Jan; Jeschke, Jonathan M. 2017. **Assessing patterns in introduction pathways of alien species by linking major invasion data bases**. *Journal of Applied Ecology*, 54 (2). 657-669. 10.1111/1365-2664.12819

Received Date: 30-may-2016
Revised Date : 01-sep-2016
Accepted Date : 12-oct-2016
Article Type : Standard Paper
Handling Editor: Jacqueline Beggs

Assessing patterns in introduction pathways of alien species by linking major invasion databases

Wolf-Christian Saul[1,2,3,4] (saul@igb-berlin.de), Helen E. Roy[5] (hele@ceh.ac.uk), Olaf Booy[6] (olaf.booy@apha.gsi.gov.uk), Lucilla Carnevali[7] (lucilla.carnevali@gmail.com), Hsuan-Ju Chen[8] (hjc870111@gmail.com), Piero Genovesi[9] (piero.genovesi@isprambiente.it), Colin A. Harrower[5] (corr@ceh.ac.uk), Philip E. Hulme[10] (philip.hulme@lincoln.ac.nz), Shyama Pagad[11] (s.pagad@auckland.ac.nz), Jan Pergl[12] (jan.pergl@ibot.cas.cz), Jonathan M. Jeschke[1,2,3,4] (jonathan.jeschke@gmx.net)

[1] Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany

[2] Freie Universität Berlin, Department of Biology, Chemistry, Pharmacy, Institute of Biology, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

[3] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, 14195 Berlin, Germany

[4] Technische Universität München, Department of Ecology and Ecosystem Management, Restoration Ecology, Emil-Ramann-Str. 6, 85354 Freising, Germany

[5] NERC Centre for Ecology & Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire, OX10 8BB, UK

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2664.12819

[6] GB Non-Native Species Secretariat, Animal and Plant Health Agency, Sand Hutton, York, YO41 1LZ, UK

[7] Institute for Environmental Protection and Research (ISPRA), Via Vitaliano Brancati 44, 00144 Roma, Italy

[8] Ludwig-Maximilians-Universität München, Department of Biology II, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

[9] Institute for Environmental Protection and Research (ISPRA), Via Vitaliano Brancati 48, 00144 Roma, Italy, and Chair IUCN SSC Invasive Species Specialist Group

[10] Bio-Protection Research Centre, Lincoln University, PO Box 85084, Lincoln 7647 Christchurch, New Zealand

[11] University of Auckland, School of Biological Sciences, Centre for Biodiversity and Biosecurity, P.B. 92019, Auckland 1142, New Zealand, and Programme Officer IUCN SSC Invasive Species Specialist Group

[12]Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic

Corresponding author: W.-C. Saul, Freie Universität Berlin, Department of Biology, Chemistry, Pharmacy, Institute of Biology, Königin-Luise-Str. 1-3, 14195 Berlin, Germany; Phone: +49-30-83857296; Email: saul@igb-berlin.de

Running title: Patterns in introduction pathways of alien species

Summary

1. Preventing the arrival of invasive alien species (IAS) is a major priority in managing biological invasions. However, information on introduction pathways is currently scattered across many databases that often use different categorisations to describe similar pathways. This hampers the identification and prioritisation of pathways in order to meet the main targets of recent environmental policies.

2. Therefore, we integrate pathway information from two major IAS databases, IUCN's Global Invasive Species Database (GISD) and the DAISIE European Invasive Alien Species Gateway, applying the new standard categorisation scheme recently adopted by the Convention on Biological Diversity (CBD). We describe the process of mapping pathways from the individual databases to the CBD scheme and provide, for the first time, detailed descriptions of the standard pathway categories. The combined dataset includes pathway information for 8323 species across major taxonomic groups (plants, vertebrates, invertebrates, algae, fungi, other) and environments (terrestrial, freshwater, marine).

3. We analyse the data for major patterns in the introduction pathways, highlighting that the specific research question and context determines whether the combined or an individual dataset is the better information source for such analyses. While the combined dataset provides an improved basis for direction-setting in invasion management policies on the global level, individual datasets often better reflect regional idiosyncrasies. The combined dataset should thus be considered in addition to, rather than replacing, existing individual datasets.

4. Pathway patterns derived from the combined and individual datasets show that the intentional pathways 'Escape' and 'Release' are most important for plants and vertebrates, while for invertebrates, algae, fungi and micro-organisms unintentional transport pathways prevail. Differences in pathway proportions among marine, freshwater and terrestrial environments are much less pronounced. The results also show that IAS with highest impacts in Europe are on average associated with a greater number of pathways than other alien species and are more frequently introduced both intentionally *and* unintentionally.

5. *Synthesis and applications.* Linking databases on invasive alien species by harmonising and consolidating their pathway information is essential to turn dispersed data into useful knowledge. The standard pathway categorisation scheme recently adopted by the Convention on Biological Diversity may be crucial to facilitate this process. Our study demonstrates the value of integrating major invasion databases to help managers and policymakers reach robust conclusions about patterns in introduction pathways and thus aid effective prevention and prioritisation in invasion management.

Key-words: biosecurity, escape, introduction pathways, invasion management, invasive non-native species, prevention, prioritisation, release, standard pathway categorisation, transport

Introduction

Alien species, introduced by humans beyond their native range, are arriving in new regions at unprecedented rates worldwide (Essl *et al.* 2015; van Kleunen *et al.* 2015), and a proportion, the so called invasive alien species (IAS), have negative consequences for the economy and environment in the recipient region (Millennium Ecosystem Assessment 2005). Effective prevention and management of IAS requires a detailed knowledge of the ways in which they are transported from their native range to new regions ('introduction pathways'; CBD 2010), as well as a framework that allows prioritisation of pathways in management and legislation (Mack 2003;

Hulme *et al.* 2008; Hulme 2009, 2015; McGeoch *et al.* 2016). Indeed, a number of policies are emerging for which this information is critical to underpin implementation, as for instance the new EU regulation on IAS (EU 2014; Genovesi *et al.* 2015) and Aichi Biodiversity Target 9 (CBD 2010).

Our ability to prioritise introduction pathways has remained limited despite intensified research in the last decade (Hulme *et al.* 2008; Hulme 2009, 2015; Essl *et al.* 2015; Nunes *et al.* 2015). A difficulty of particular practical importance is that relevant information is scattered across different databases that utilise disparate terminology and categorisations for documenting pathways (Gatto *et al.* 2013; Essl *et al.* 2015). Paraphrasing Naisbitt (1982), we are beginning to drown in information but starving for knowledge. Thus, linking databases by harmonising and consolidating their pathway information is critical to turn accumulating and dispersed data into useful knowledge. This will underpin understanding and inform research and policy (Gatto *et al.* 2013; CBD 2014). The benefits and challenges of linking IAS databases have been previously discussed (e.g. Ricciardi *et al.* 2000; Crall *et al.* 2006; Simpson *et al.* 2006; Graham *et al.* 2008; Gatto *et al.* 2013), but without detailed considerations of how best to consolidate pathway data. General benefits of integrated data repositories include: (i) efficient management of comprehensive data including avoidance of duplicate work and standardised review routines that secure consistent data quality; (ii) improved accessibility and dissemination of data, (iii) synergies between otherwise incomplete datasets (e.g. species may be recorded with different pathways in different databases due to the databases' particular foci); and (iv) analyses with increased sample sizes and across different taxonomic groups, environments and spatiotemporal scales are made possible.

Our study focuses on linking two major alien species databases widely used by researchers and policy makers: IUCN's Global Invasive Species Database (GISD, www.iucngisd.org) and DAISIE (European Invasive Alien Species Gateway, www.europe-aliens.org). GISD and DAISIE are two of the few comprehensive databases that cover, based on peer-reviewed information, both aquatic and terrestrial environments as well as high numbers of taxa recorded at large spatial scales. We therefore envision their linkage to be a critical first step towards the building of a global IAS pathway data repository, possibly as part of a larger distributed IAS web portal that allows drawing information from multiple sources (cf. the European Alien Species Information Network EASIN, Katsanevakis *et al.* 2012). The general feasibility of harmonising the pathway information from GISD and DAISIE has been preliminarily confirmed using a shared standard pathway categorisation scheme based on the general framework proposed by Hulme *et al.* (2008). This standard categorisation was recently adopted by the Convention on Biological Diversity (CBD 2014). Essl *et al.* (2015) reported that 99% of GISD pathway data and 79% of DAISIE pathway data directly matched with the available categories of the CBD scheme. The present study builds on this existing mapping introducing some modifications where additional interpretation and work was necessary for the analysis of pathway patterns. We provide detailed information about the mapping process as well as descriptions of the standard pathway categories (Appendix S1 in Supporting Information). Since GISD and DAISIE differ in several aspects (worldwide *vs.* European coverage, *ad hoc vs.* mainly systematic approach for assessing species, taxonomic composition and species numbers; see Methods section), we report pathway patterns for the combined dataset as well as the individual datasets. The comparison of these patterns allows assessing whether the data from these databases can and should actually be combined.

In summary, this study assesses the integration of available pathway information from different databases into a single data repository and analyses these data, to support countries and institutions to meet major targets in environmental policy like the CBD Aichi Biodiversity Target 9. To this end, it (i) links the two large databases GISD and DAISIE and (ii) identifies major patterns in the introduction pathways recorded therein. The specific questions we address are:

1. Can pathway information in GISD and DAISIE be pooled? To elucidate this, we complement the existing mapping to the CBD scheme and then ask: (a) are pathway classifications of shared species congruent between the datasets, and (b) are possible mismatches in the classification of shared species caused by systematic deviations between the datasets (which would speak against pooling the datasets)?
2. If the two datasets can be pooled, the following question is addressed for the combined dataset and each dataset independently, otherwise only for each dataset independently: what are the relative proportions of the standardised pathways in different taxonomic groups and environments, and what are important differences between pathway patterns at global (GISD) and European (DAISIE) scale?

Finally, we also investigate the pathway patterns of high-impact IAS, focusing on those that have been classified as Europe's 'worst IAS' (EEA 2007).

Materials and methods

In our study, GISD pathway information is considered in combination with global pathway records for additional species using the prototype Invasive Alien Species Pathway Management Resource (IASPMR, www.pathway-toolbox.auckland.ac.nz).

This pathway tool was developed within the framework of the Global Invasive Alien Species Information Partnership (GIASIPartnership, www.giasipartnership.myspecies.info) and includes all GISD pathway data. We therefore refer to this dataset as 'GISD/IASPMR' hereafter.

Pathway categorisation in GISD, DAISIE and the CBD standard scheme

The pathway categorisation originally used in the GISD database comprised 34 categories without any hierarchical structuring (Fig. 1; the recently relaunched GISD website now implements the CBD standard categorisation). The DAISIE categorisation, in turn, includes a hierarchical approach with six broad categories comprising 22 subcategories of pathways (Fig. 1). The CBD standard categorisation comprises six broad categories (Release in nature, Escape from confinement, Transport–Contaminant, Transport–Stowaway, Corridor and Unaided) and 44 subcategories (Fig. 1; Appendix S1). In our analyses, 'Release' and 'Escape' were considered pathways of intentional introduction, while the remaining categories were considered pathways of unintentional introduction.

The schematic representation in Figure 1 illustrates the pathway mapping process between the DAISIE and GISD categorisations on one hand and the CBD standard categorisation on the other, as conducted for testing purposes during the development of the CBD scheme (Essl *et al.* 2015; see Appendix S2 for further details about the mapping). As a result of these previous mapping efforts, the pathway information in the GISD/IASPMR dataset that was used in the present study already largely complied with the CBD scheme. As the only exceptions, the category 'Unaided' was not (yet) implemented in the dataset and a non-standard category 'Other' (with 10 records) existed. These two categories did thus not form part of our analyses. In relation to some DAISIE categories, the existing mapping (Fig. 1) was revised for the purpose of this study as described in Appendix S2. Ultimately, all species transported as commodity contaminants or stowaways were pooled for the analyses in a combined category 'Contaminant & Stowaway'. Such pooling was necessary since differentiating between the two individual transport pathways was not possible with sufficient certainty for a considerable number of species within the DAISIE dataset (927 spp., i.e. 15% of DAISIE species; Appendix S2). By inspecting numerous randomly sampled individual species, we confirmed that these additional mappings resulted in reasonable classifications. Records in the few remaining unmapped DAISIE categories were excluded from all analyses.

Datasets for the analysis of pathway patterns

The following datasets were used in the analyses of pathways across taxonomic groups (plants, vertebrates, invertebrates, algae, fungi, other) and environments (terrestrial, freshwater, marine) (more details on the datasets and general data handling are provided in Appendix S2 and Table S1).

GISD/IASPMR dataset

The GISD/IASPMR dataset comprised 2413 species (Table S1): 493 plants, 1663 vertebrates, 215 invertebrates, 12 algae, 9 fungi, 21 other (the latter category comprising mostly micro-organisms). Four taxa with records at genus level could not be assigned unequivocally to one of the environment categories (Table S1), their records were thus excluded from the respective analysis. Original data (including all GISD pathway data) were retrieved from IASPMR in February 2014. They contained information on main introduction pathways for all species with records eligible to be included in the analyses of this study (see Appendix S2), and on pathway subcategories for all but seven species.

DAISIE dataset

The DAISIE dataset comprised 6370 species (Table S1): 3636 plants, 377 vertebrates, 2040 invertebrates, 167 algae, 77 fungi, 73 other. Original data were retrieved from DAISIE in May 2014 and comprised records potentially eligible to be included in the analyses of this study (Appendix S2) for 7315 species. Within these, however, information about main pathway categories was lacking for 945 species, and about pathway subcategories for 2782 species, i.e. for 13% and 38%, respectively (for more details on these species see Appendix S2).

Combined dataset

For combined analyses, the GISD/IASPMR and DAISIE datasets were collated into one single dataset. The combined dataset comprised over 10000 pathway records for 8323 species (Table S1): 3950 plants, 1822 vertebrates, 2203 invertebrates, 174 algae, 85 fungi, 89 other. 460 species were shared by GISD/IASPMR and DAISIE when considering records that contain main pathway information (179 plants, 218 vertebrates, 52 invertebrates, 5 algae, 1 fungus, 5 other).

Analyses and statistics

The congruence between GISD/IASPMR and DAISIE in their pathway classification (after mapping to the CBD standard pathways) of species that were present in both datasets was assessed with Simple Matching Coefficients (SMC; Krebs 1999). The SMC is a similarity coefficient with values ranging from 0 (no similarity) to 1 (complete congruence). Matches between the datasets were defined as shared presences and shared absences of pathway recordings, whereas mismatches comprised those cases in which a particular pathway was recorded for a certain species in either one dataset but not in the other. For pathway categories with SMC ≤ 0.8, we checked whether the mismatches in the pathway classification were caused by systematic, recurring deviations between the datasets, which would speak against pooling the datasets. Such systematic pattern could consist, for instance, in a certain pathway always being recorded in dataset A but not in dataset B, in mismatches between dataset A and B always occurring in the same pathway category regardless of the taxonomic group, or in a mismatched but consistently recurring pairing between a certain pathway in dataset A and a particular pathway in dataset B.

For identifying major pathway patterns, relative proportions of the different pathway categories within each taxonomic group and environment were calculated based on the number of species with corresponding pathway records. For instance, 3242 of the 3950 plant species in the combined dataset have been introduced by 'Escape from confinement', i.e. approximately 82%. Relative proportions were also calculated for grouped intentional and unintentional pathways. For all proportions, we calculated 95% Wilson confidence intervals, which have distinctive advantages over ordinary confidence intervals for proportions (Brown, Cai & DasGupta 2001). The analyses were carried out for the combined dataset as well as separately for the individual datasets of GISD/IASPMR and DAISIE.

We also investigated, on a general level, pathway patterns of invaders with high impacts and other alien species by splitting the DAISIE dataset into two subsamples: the first ('EEA Worst IAS') included 157 species (143 when considering pathway subcategories) that due to their high impacts have been classified by the European Environment Agency (EEA) as 'Worst invasive alien species threatening biodiversity in Europe' (EEA 2007). This list has been compiled by the EEA through an extensive consultative process with experts, the scientific community and national environmental authorities (EEA 2007). It is based on a transparent set of criteria and has been used by the EEA within the European biodiversity indicator 10 for changes in biological diversity caused by IAS (EEA 2007, 2009). We compared these species with a second subsample ('Other alien species') which included all other species of the DAISIE dataset.

Results

Data compatibility between GISD/IASPMR and DAISIE

Congruence in the assigned CBD pathways was high (SMC > 0.8) regarding most main pathway categories in plant, vertebrate and invertebrate species shared between both databases, i.e. in those taxonomic groups that comprised the vast majority of species in this study (Fig. 2; for congruence on subcategory level see Fig. S1). In these taxonomic groups, reduced SMC values (≤ 0.8) at the main pathway level were only found for 'Release' or 'Escape'. This resulted from mismatches in the respective pathway records of 56 of the 179 shared plants (31%), 53 of the 218 shared vertebrates (24%) and 13 of the 52 shared invertebrates (25%). For plants, the relatively low matching value in the 'Release' pathway (SMC = 0.69) primarily originated from shared species having been assigned to this pathway in DAISIE but not in GISD/IASPMR (i.e. there were 39 species with unmatched 'Release' records in DAISIE, but only 17 such species in GISD/IASPMR; Table S2). For vertebrates (SMC = 0.76), this was the other way round (38 spp. in GISD/IASPMR, 15 spp. in DAISIE). For invertebrates, there was a good match in 'Release' (SMC = 0.85) but not for 'Escape' (SMC = 0.75): these mismatches originated primarily from species having been assigned to this pathway in DAISIE but not in GISD/IASPMR (9 spp. in DAISIE, 4 spp. in GISD/IASPMR). In plants and vertebrates, the unmatched 'Release' records were predominantly mismatched with 'Escape'; in invertebrates, the unmatched

'Escape' records were predominantly mismatched with transport pathways 'Contaminant & Stowaway' (Table S2). These pairings occurred in either direction (e.g. in plants and vertebrates, an unmatched 'Release' record in dataset A was often mismatched with an 'Escape' record for the same species in dataset B, but this was found regardless of which of the two datasets was DAISIE and which GISD/IASPMR; Table S2).

Introduction pathways in different taxonomic groups and environments

The analyses of all 8323 species in the combined dataset (Fig. 3a), as well as the separate analyses for the GISD/IASPMR (Fig. 3b) and DAISIE (Fig. 3c) datasets, revealed that for plants and vertebrates, introduction via the intentional pathways 'Escape' and (to a lesser extent) 'Release' is dominant, while for invertebrates, algae, fungi and micro-organisms unintentional pathways prevail (particularly, 'Contaminant & Stowaway'). 'Release' and 'Escape' are also of some importance for invertebrates, for instance biocontrol agents that are intentionally released directly into the wild, or which may escape from a more confined area of release (e.g. the ladybird *Harmonia axyridis*; Roy and Wajnberg 2008). 'Contaminant & Stowaway' is common for invertebrates, algae, fungi and micro-organisms, while the 'Corridor' pathway is of importance for algae, invertebrates and vertebrates, primarily in aquatic environments (Fig. 4; see also Hulme *et al.* 2008; Nunes *et al.* 2014). The 'Unaided' pathway fell out of the analyses since the IASPMR tool lacks this category, and no analogous category of DAISIE (or individual records) had yet been mapped to it.

Pathway proportions differ much more distinctly among taxonomic groups (Fig. 3) than among environments (Fig. 4). In fact, across environments patterns of pathway proportions were generally very similar and noticeably resembled the proportion patterns found for plants and vertebrates: high for 'Escape' (approx. 60-80%), intermediate for 'Release' (approx. 15-40%), low to intermediate for 'Contaminant & Stowaway' (approx. 5-50%), and low for 'Corridor' (approx. 0-20%). In the marine environment, unintentional pathways gain in importance relative to pathways of intentional introduction (Fig. 4). Comparing the individual datasets in this respect, 'Contaminant & Stowaway' and 'Corridor' gain more importance for marine introductions in DAISIE than in the GISD/IASPMR dataset (Fig. 4b/c). In GISD/IASPMR, in turn, 'Escape' (e.g. of aquaculture stock) represents a significant marine pathway, with almost 70% of species being introduced in this way (Fig. 4b).

'EEA Worst IAS' vs. 'Other alien species'

The comparison between the two subsamples of the DAISIE dataset shows that 'EEA Worst IAS' are on average introduced via a significantly larger number of pathway subcategories than 'Other alien species' (Fig. 5). Also, on main pathway level a substantially higher proportion of 'EEA Worst IAS' as compared to 'Other alien species' is being introduced both intentionally *and* unintentionally in most taxonomic groups (Fig. 6). Similar results are found in the corresponding analysis regarding environments (see Fig. S2).

Discussion

The present study clearly demonstrates the capacity of the CBD standard pathway scheme to accommodate the categorisations of two major IAS databases, GISD and DAISIE. At the same time, the process of mapping provided useful insights into potential issues regarding standardisation of pathway information and its analysis. For example, we were not able to discriminate between the transport pathways 'Contaminant' and 'Stowaway' due to differences between the schemes of DAISIE and CBD in how pathway categories are assigned to species (see Appendix S2). A common feature of both individual databases is their failure to adequately capture the 'Unaided' pathway, probably resulting in a substantial underestimation (e.g. in invasion management) of the role of alien species moving by natural means from one introduced region to another (Hulme 2015). Furthermore, some DAISIE categories still remain unmapped. A more detailed documentation of the CBD categories, extending the descriptions provided here for the first time (Appendix S1), and provision of complementary pathway information for each species in addition to their original classification would certainly facilitate the mapping process.

Compatibility between data from GISD/IASPMR and DAISIE is indicated by the relatively high congruence between the two individual datasets in the pathways recorded for shared species. Experts contributing data on the same species but to different databases are thus largely consistent in their judgments. Recurring pairings between certain mismatching pathways of shared species were found (Release–Escape in plants and vertebrates, Release–Transport in invertebrates), but irrespective of whether a record was found in DAISIE and not in GISD/IASPMR, or *vice versa*. It seems unlikely that intrinsic incompatibilities between the two databases (e.g. related to geographic coverage or data-input methodology) would result in such a symmetric mismatch pattern. Rather, it may be related to categories overlapping in their applicability to certain introductions. For instance, it is conceivable that a clear-cut differentiation may at times be difficult between subcategories 'Biological control' (Release) and 'Agriculture' (Escape), 'Landscape improvement' (Release) and 'Ornamental' (Escape), or 'Horticulture' (Escape) and 'Nursery material' (Transport). Such blurring between categories can never be avoided completely, representing practical limitations of categorisation schemes *per se*.

Data compatibility is also supported by the fact that pathway patterns of the individual datasets are very similar at least when looking at taxonomic groups (Fig. 3). Yet, this is somewhat less so when differentiating between environments (Fig. 4). In particular, the proportions of unintentional introductions in marine environments are higher in the European DAISIE compared to the global GISD/IASPMR. This may be due to the combined effect of the Suez canal and Europe's central role in marine transport (Katsanevakis *et al.* 2013; Seebens, Gastner & Blasius 2013; Nunes *et al.* 2014). Thus, the answer to whether the combined dataset or an individual dataset is the better information source seems to depend on the question and context one is interested in. The combined dataset provides an improved basis for direction-setting in invasion management policies on the global level (see also section on implications for management below). It contains comprehensive information on globally recorded pathways by which species have been introduced into non-native areas, and comes with a substantial increase in sample size for analysing pathway patterns of taxonomic groups. This allows, for instance, the identification of significant differences in pathway proportions where the global but smaller GISD dataset does not provide enough discriminatory power (e.g. compare difference in the proportions of unintentional pathways between invertebrates and algae in Figs. 3a and 3b). Individual datasets like DAISIE, on the other hand, often better reflect regional idiosyncrasies such as the importance of the Suez canal. Also, a species might be an escape in one region but may have been deliberately released in another, with different management implications in each region (e.g. *Pinus contorta* in Great Britain and New Zealand, McGregor *et al.* 2012). But information about the region where pathways were observed need not be discarded in the combined dataset so that the possibility of analyses with a region-specific focus is maintained. In summary, we suggest that a combined dataset in addition to, rather than replacing, existing individual datasets is a valuable tool for analysing and better understanding introduction pathways.

Regarding the observed pathway patterns, we found that 'Escape' is the most important pathway for plants and vertebrates. This highlights the need for continued efforts to improve the effectiveness of containment measures and increase public awareness about the potential negative consequences of species escaping people's custody. The relatively high proportions of 'Release' for plants and vertebrates reflect the importance of these organisms in human activities such as e.g. establishing game animals in the wild, aquaculture, pasture improvement, or 'improving' local flora and fauna for aesthetic reasons (e.g. Driscoll *et al.* 2014). Invertebrates, algae, fungi and micro-organisms are frequently introduced via transport pathways, which is not surprising given the widespread abundance and inconspicuousness of these organisms. For instance, pathogens and parasites are often introduced as contaminants with their hosts (Perkins *et al.* 2008). Many marine invertebrates arrive as stowaways with ballast water or as ship fouling (Katsanevakis *et al.* 2013; Nunes *et al.* 2014). A considerable proportion of plants is also introduced via unintentional transport, which may happen for instance as seed contaminants in crop seeds or as stowaways in soil attached to machinery and vehicles (Mack 2003). Finally, the prevalent association in our data of the 'Corridor' pathway with aquatic environments emphasises the role of large-scale canals that connect river catchments, waterways, basins and seas; yet, it possibly underestimates the importance of terrestrial corridors such as tunnels and land bridges.

Between environments, differences in pathway proportions are less pronounced. This may be explained by the fact that depending on which dataset and environment we look at, plants and/or vertebrates are most times far more numerous than species of the other taxonomic groups (Table S1). Thus, their pattern of largely intentional pathways seems to be replicated across most environments. This superimposition is least obvious in the marine environment (especially in the DAISIE dataset), possibly because the marine data is in fact less dominated by plants and vertebrates. Another reason could be that due to the continuously increasing global trade and transport, the unintentional contaminant and stowaway pathways (e.g. ballast water, hull fouling and contamination of aquaculture stock) actually play a particularly important role in the marine environment (Katsanevakis *et al.* 2013; Nunes *et al.* 2014). It is also worth noting that the opening of marine corridors has been almost as important as the pathways 'Contaminant' and 'Stowaway' combined (Fig. 4a). Thus, much effort has rightly focused on unintentional marine pathways (e.g. IMO 2004), but the observed high proportions of the 'Escape' pathway indicate that we must not overlook the risk of marine species escaping from containment into which they initially have been introduced on purpose (e.g. for aquaculture).

Implications for management

For a standard pathway categorisation to be a useful tool for invasion management, it needs to balance comprehensiveness with utility (Hulme *et al.* 2008). A hierarchical approach with main and subordinate levels seems most promising for achieving this goal (cf. Essl *et al.* 2015). Clustering a large number of pathway subcategories into standardised main categories promotes utility. It facilitates pathway classification of species and its comparison between different data sources and thus helps understanding the main drivers and general principles of invader introductions across taxa and environments. However, to ensure effective management it is critical that comprehensiveness is also achieved and that subcategories are not discarded. For instance, plants, vertebrates and invertebrates make use of a large proportion of the spectrum of subcategories within each main pathway (see supplementary information in Table S3). Each subcategory stands for specific conditions under which introduction occurs and which require due consideration for tailored management responses. Complementary to our results, there is great need to increase our capacity to differentiate between pathways of primary introduction (e.g. intercontinental introductions to major ports) and of subsequent secondary introduction (e.g. intracontinental transport to smaller towns or natural spread of introduced species) in order to use limited management resources most efficiently. This is again also related to the urgent need of increasing our efforts to gain more information about unaided introductions, i.e. secondary natural dispersal across borders.

The pronounced differences in pathway proportions among taxonomic groups indicate the need for a differentiated legislative regulation and management (see also Hulme 2015). As a first step, discriminating between pathways of intentional and unintentional introduction provides an immediate idea about adequate management priorities for different taxonomic groups: for preventing the introduction of species from taxonomic groups that arrive mainly via intentional pathways, i.e. in particular plants and vertebrates, prevention focused on regulatory approaches at the species level can be highly effective, as explicit bans of intentional introductions can be implemented and monitored. However, for species that are unintentionally introduced (i.e. mainly invertebrates, algae, fungi and micro-organisms), strategies are necessary that target entire pathways, applying approaches like for example those developed under the International Plant Protection Convention for regulating potential introduction vectors of pests, such as wood packaging material and pallets (FAO 2011).

Our results also underscore that the management of IAS with highest impacts (represented by the ‘EEA Worst IAS’ subsample) is more demanding than that of 'Other alien species'. The former seem to get introduced via a greater variety of pathways and more frequently both intentionally and unintentionally. Again, this indicates the need that prevention strategies combine species-specific approaches (e.g. by way of impact scoring and blacklisting approaches; see e.g. Blackburn *et al.* 2014; Hawkins *et al.* 2015) with effective management of the pathways of unintentional introduction, including extensive surveillance and monitoring. However, a word of caution is warranted here: although the species on the EEA list have been selected to represent the worst IAS in Europe (EEA 2007), several species in the ‘Other’ subsample may also have strong impacts. For a rigorous testing of the hypothesis that the observed pathway patterns are indeed associated with the degree of impact, a more detailed assessment of species’ impacts will be necessary in future studies. Such studies will also have to consider that high-impact invaders are typically studied in greater detail than other alien species. Hence, the higher average number of pathways reported here for Europe’s ‘Worst IAS’ could be partly due to them being better studied.

Overall, the pathway patterns and data presented in this study have strong potential to increase our understanding of introductions as well as our ability to predict and manage them. For example, looking at pathway information of species listed in GISD/IASPMR but not in DAISIE may help horizon-scanning approaches in that we can anticipate how those species may arrive in Europe. Further, combining findings on the most relevant pathways with knowledge about the most harmful IAS seems a particularly promising approach to enhance prioritisation of prevention and management actions. Shifts in the importance of pathways over time and what implications this may have for future invasions should be considered therein (Hulme *et al.* 2008; Wilson *et al.* 2009; Essl *et al.* 2015). Finally, identifying frequent combinations of introduction pathways (what may be called 'pathway syndromes'; see Table S4) may help making management more effective, for instance when the discovery of introductions through one pathway automatically triggers the monitoring of associated pathways.

Conclusions

Knowledge about the pathways of introduction is crucial for prevention and early detection of invasive species. Missing pathway data (e.g. in this study for a considerable number of species in DAISIE) and non-standardised pathway categorisations constitute regrettable obstacles in this endeavour. Our study demonstrates the feasibility and usefulness of linking pathway information from two major IAS databases, GISD/IASPMR and DAISIE, providing insights relevant to standardised database design, aiding effective prevention and management, and informing IAS legislation. The proposed approach could be applied more broadly, integrating other databases (e.g. CABI's Invasive Species Compendium, www.cabi.org/isc, EASIN, or national inventories) to prioritise pathways at different geographic scales, including at the national level.

Importantly, identifying the most relevant pathways of introduction is only a first step. It needs to be followed by: (1) the development of adequate policies, regulations and management measures; (2) fully enforcing the relevant legislations; and (3) monitoring the effectiveness of these legislations. Managing pathways involves regulating trade and other economic activities (e.g. the National Environmental Management Biodiversity Act No. 10/2004 of South Africa prohibits the import of 168 vertebrates and 240 plants into the country, Faulkner *et al*. 2016). Such regulations need to be solidly justified based on rigorous scientific assessments and have to comply with the principles of the Agreement on Sanitary and Phytosanitary Measures under the World Trade Organisation (e.g. Perrings *et al*. 2010). The new EU regulation may be able to provide a pilot approach to pathway management, and it is thus essential that the efficacy of this tool is carefully evaluated for producing guidance to other regions of the world.

Acknowledgements

We thank the ERA-Net BiodivERsA (project FFII) with the national funder German Research Foundation DFG (JE 288/7-1) for financial support (part of the 2012-13 BiodivERsA call for proposals); JMJ was additionally supported by the DFG project JE 288/9-1. HER and CH were funded by the Joint Nature Conservation Committee and the Natural Environment Research Council (via National Capability funding to the Centre for Ecology & Hydrology, project NEC04932). We thank the COST Association for funding the COST Action (TD1209) ALIEN Challenge, which has facilitated our collaboration. JP was supported by long-term research development project RVO 67985939 (Academy of Sciences of the Czech Republic) and P504/11/1028 from the Czech Science Foundation. We would like to acknowledge the Secretariat of the Convention on Biological Diversity (CBD) and the Global

Invasive Alien Species Information Partnership (GIASIPartnership) for their support in the development of the IASPMR. SP would like to acknowledge the University of Auckland, School of Biological Sciences, New Zealand, and Lua Andrea Alvas who worked on the development of the IASPMR dataset.

Data accessibility

All data used in this study are accessible online: Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.m93f6 (Saul *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of the CBD standard pathway categories.

Appendix S2. Details of the pathway mapping, general data handling and datasets.

Figure S1. Congruence in pathway classification (Simple Matching Coefficient, SMC) for species shared between GISD/IASPMR and DAISIE.

Figure S2. Intentionality of pathways across environments, comparing 'Other alien species' and 'EEA Worst IAS' in DAISIE.

Table S1. Numerical description of GISD/IASPMR, DAISIE and combined datasets.

Table S2. Mismatch analysis for main pathway categories with SMC ≤ 0.8 for species shared between GISD/IASPMR and DAISIE.

Table S3. Ratios between recorded and possible pathway subcategories in the combined dataset.

Table S4. Frequencies and proportions of combinations of pathway subcategories ('pathway syndromes') in the combined dataset.

Figure legends

Figure 1. Schematic representation of the mapping process between the categorisation schemes of DAISIE and GISD and the CBD standard categorisation. Thick lines indicate cases where records in a DAISIE or GISD subcategory also mostly fall into one single subcategory in the CBD scheme. Dotted lines indicate a less direct comparability of subcategories, i.e. when records of a DAISIE or GISD subcategory split between several categories of the CBD scheme (see e.g. DAISIE subcategories 'Leisure' and 'Vessels').

Figure 2. Simple Matching Coefficient (SMC) values, indicating the congruence between GISD/IASPMR and DAISIE in the recorded main pathway categories for

those plants (179 spp.), vertebrates (218 spp.), and invertebrates (52 spp.) that are shared by both datasets. Algae, fungi and micro-organisms are not shown separately due to low species numbers, but are included in 'All species' (460 spp.). SMC values can range from 0 to 1, the latter denoting a perfect match.

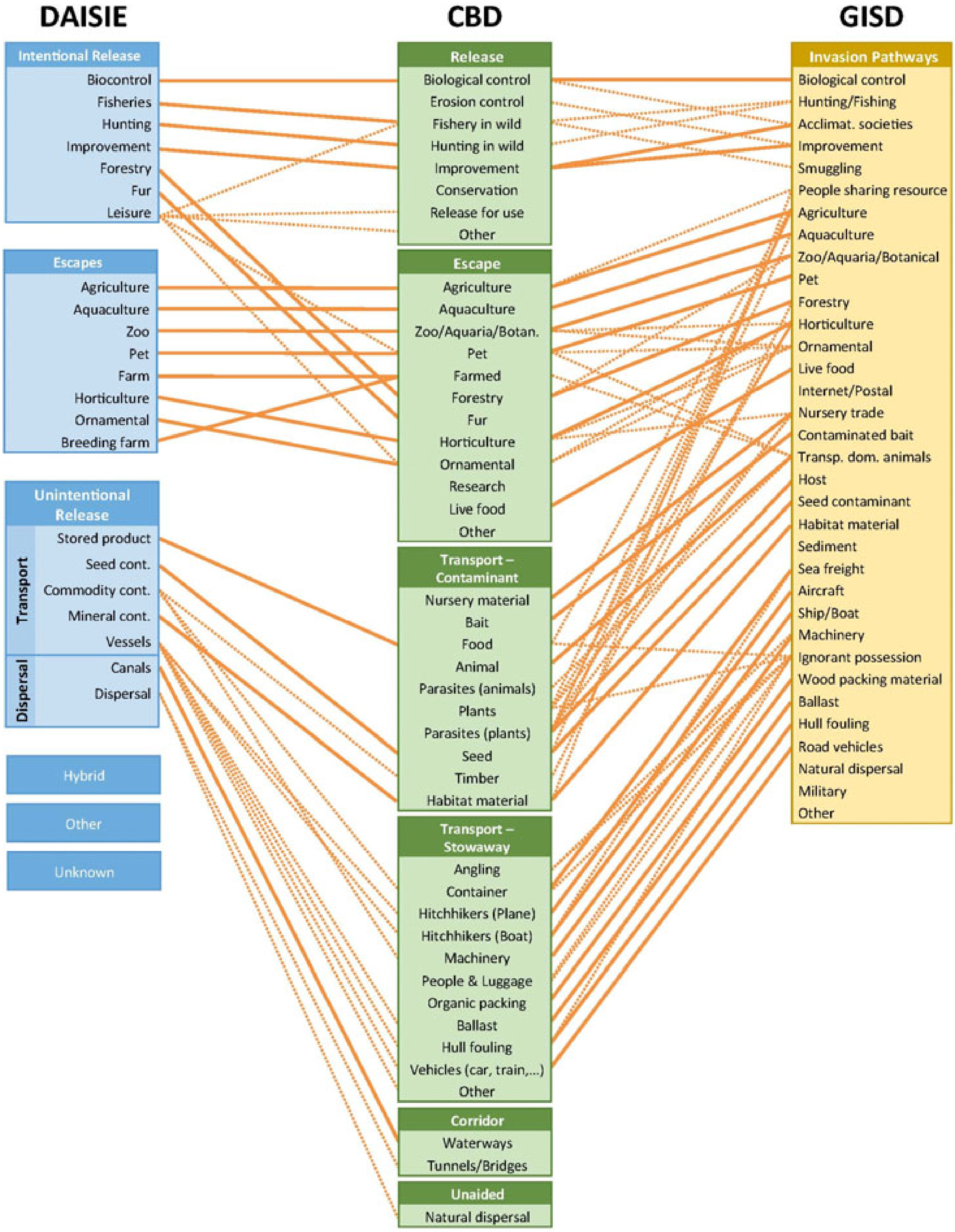
Figure 3. Main introduction pathways according to taxonomic groups in (a) the combined dataset (8323 spp.), (b) GISD/IASPMR (2413 spp.) and (c) DAISIE (6370 spp.). Left-hand side graphs show individual proportions of pathways (the sum of proportions is larger than 100% in all taxonomic groups and environments since species can be introduced via more than one pathway). Right-hand side graphs show the difference in accumulated proportions of intentional and unintentional pathways (excluding species that fall into both categories). Error bars indicate 95% Wilson confidence intervals.

Figure 4. Main introduction pathways according to environments in (a) the combined dataset (8319 spp.), (b) GISD/IASPMR (2409 spp.) and (c) DAISIE (6370 spp.). Left-hand side graphs show individual proportions of pathways (the sum of proportions is larger than 100% in all taxonomic groups and environments since species can be introduced via more than one pathway). Right-hand side graphs show the difference in accumulated proportions of intentional and unintentional pathways (excluding species that fall into both categories). Error bars indicate 95% Wilson confidence intervals.

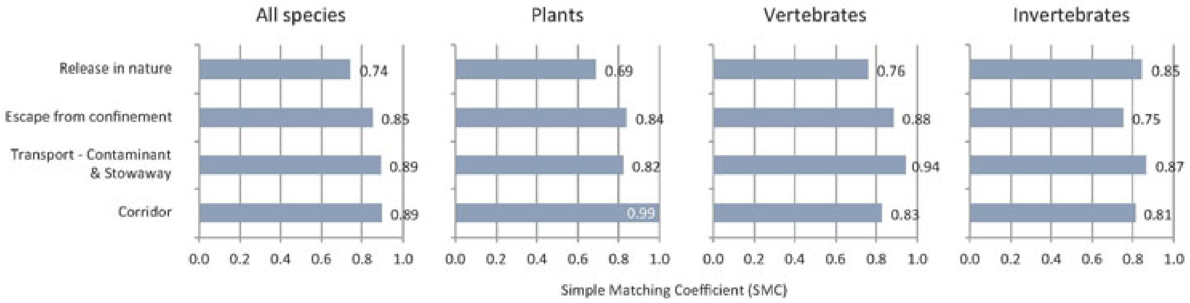
Figure 5. Average number of observed pathway subcategories per species in the DAISIE dataset for the subsamples 'Other alien species' (4390 spp.: 2697 plants, 321 vertebrates, 1168 invertebrates, 152 algae, 14 fungi, 38 other) and 'EEA Worst IAS'

(143 spp.: 38 plants, 35 vertebrates, 51 invertebrates, 15 algae, 4 other). Error bars indicate 95% confidence intervals.

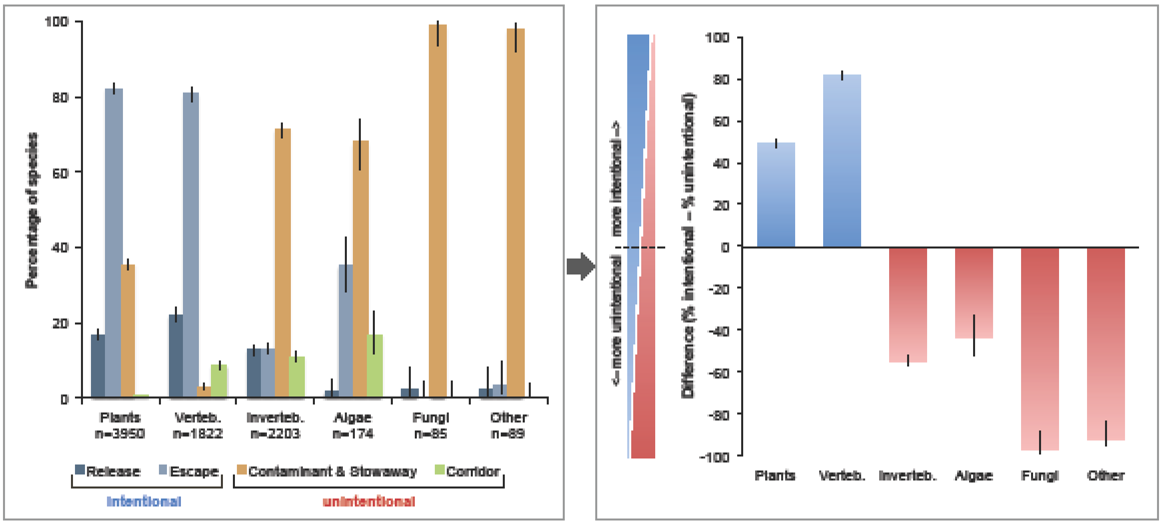
Figure 6. Proportion of species introduced via intentional or unintentional main pathways, or via both, in different taxonomic groups, comparing 'Other alien species' and 'EEA Worst IAS' in the DAISIE dataset (6213 Other alien species vs. 157 EEA Worst IAS). Error bars indicate 95% Wilson confidence intervals.



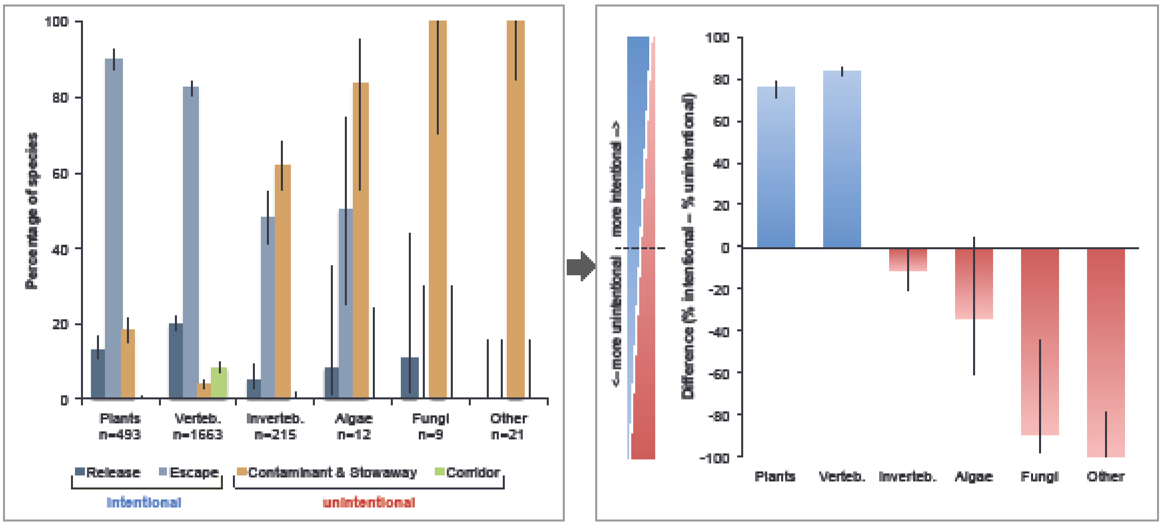
DAISIE
CBD
GISD
Intentional Release
Biocontrol
Fisheries
Hunting
Improvement
Forestry
Fur
Leisure
Escapes
Agriculture
Aquaculture
Zoo
Pet
Farm
Horticulture
Ornamental
Breeding farm
Unintentional Release
Transport
Stored product
Seed cont.
Commodity cont.
Mineral cont.
Vessels
Dispersal
Canals
Dispersal
Hybrid
Other
Unknown
Release
Biological control
Erosion control
Fishery in wild
Hunting in wild
Improvement
Conservation
Release for use
Other
Escape
Agriculture
Aquaculture
Zoo/Aquaria/Botan.
Pet
Farmed
Forestry
Fur
Horticulture
Ornamental
Research
Live food
Other
Transport – Contaminant
Nursery material
Bait
Food
Animal
Parasites (animals)
Plants
Parasites (plants)
Seed
Timber
Habitat material
Transport – Stowaway
Angling
Container
Hitchhikers (Plane)
Hitchhikers (Boat)
Machinery
People & Luggage
Organic packing
Ballast
Hull fouling
Vehicles (car, train,...)
Other
Corridor
Waterways
Tunnels/Bridges
Unaided
Natural dispersal
Invasion Pathways
Biological control
Hunting/Fishing
Acclimat. societies
Improvement
Smuggling
People sharing resource
Agriculture
Aquaculture
Zoo/Aquaria/Botanical
Pet
Forestry
Horticulture
Ornamental
Live food
Internet/Postal
Nursery trade
Contaminated bait
Transp. dom. animals
Host
Seed contaminant
Habitat material
Sediment
Sea freight
Aircraft
Ship/Boat
Machinery
Ignorant possession
Wood packing material
Ballast
Hull fouling
Road vehicles
Natural dispersal
Military
Other


All species
Plants
Vertebrates
Invertebrates
Release in nature
Escape from confinement
Transport - Contaminant & Stowaway
Corridor
0.74
0.85
0.89
0.89
0.69
0.84
0.82
0.99
0.76
0.88
0.94
0.83
0.85
0.75
0.87
0.81
0.0 0.2 0.4 0.6 0.8 1.0
Simple Matching Coefficient (SMC)

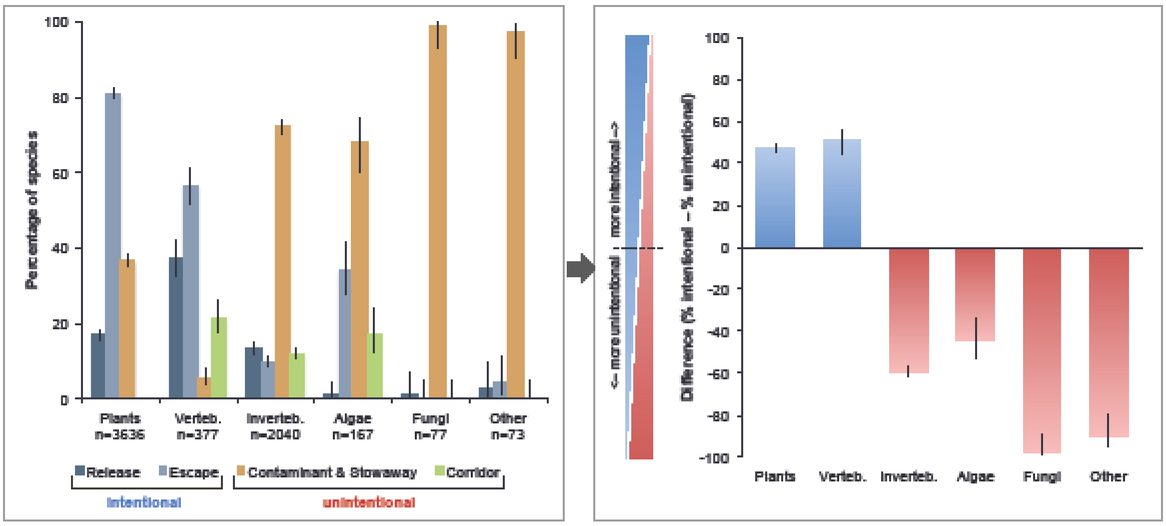
(a) Combined dataset

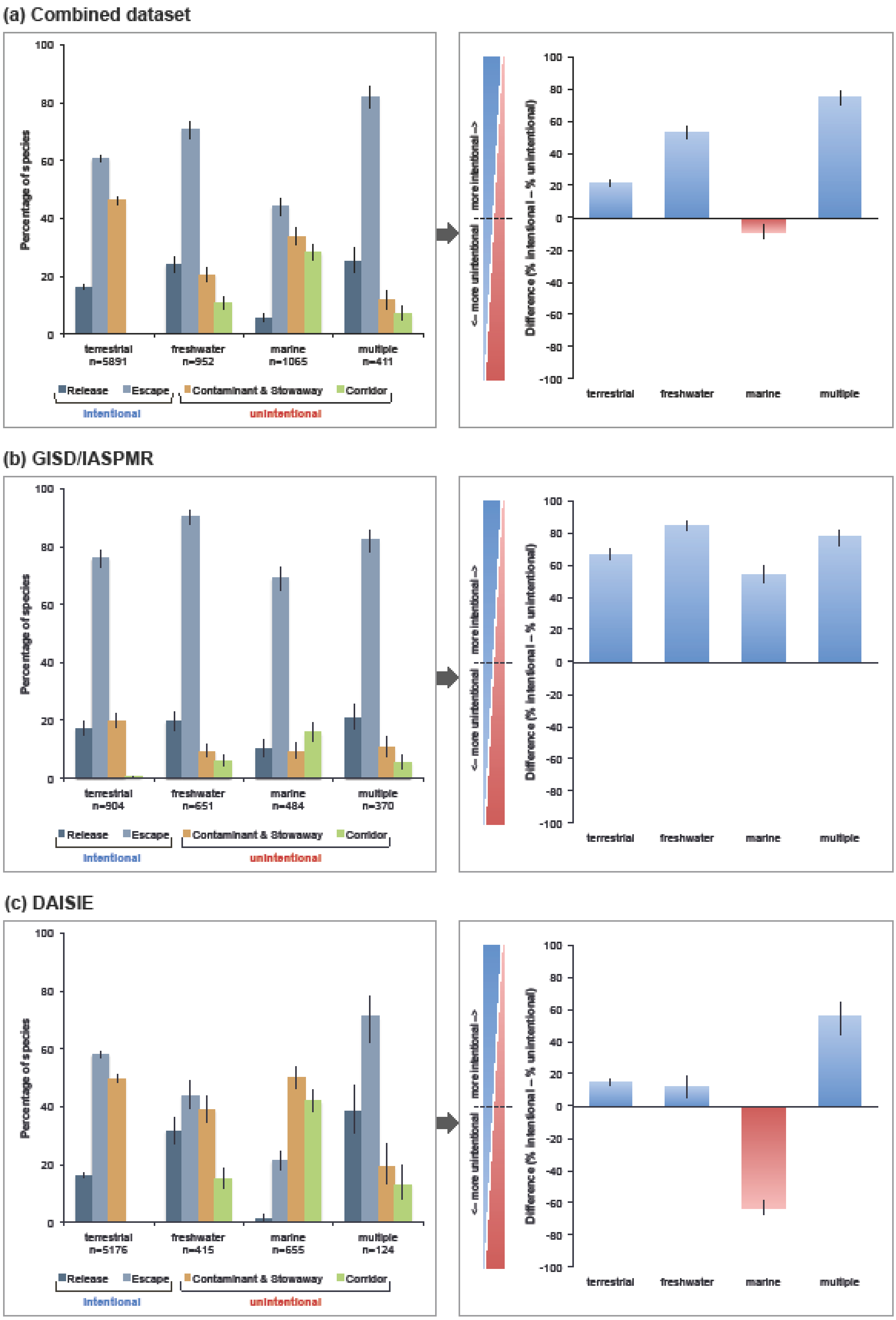


(b) GISD/IASPMR

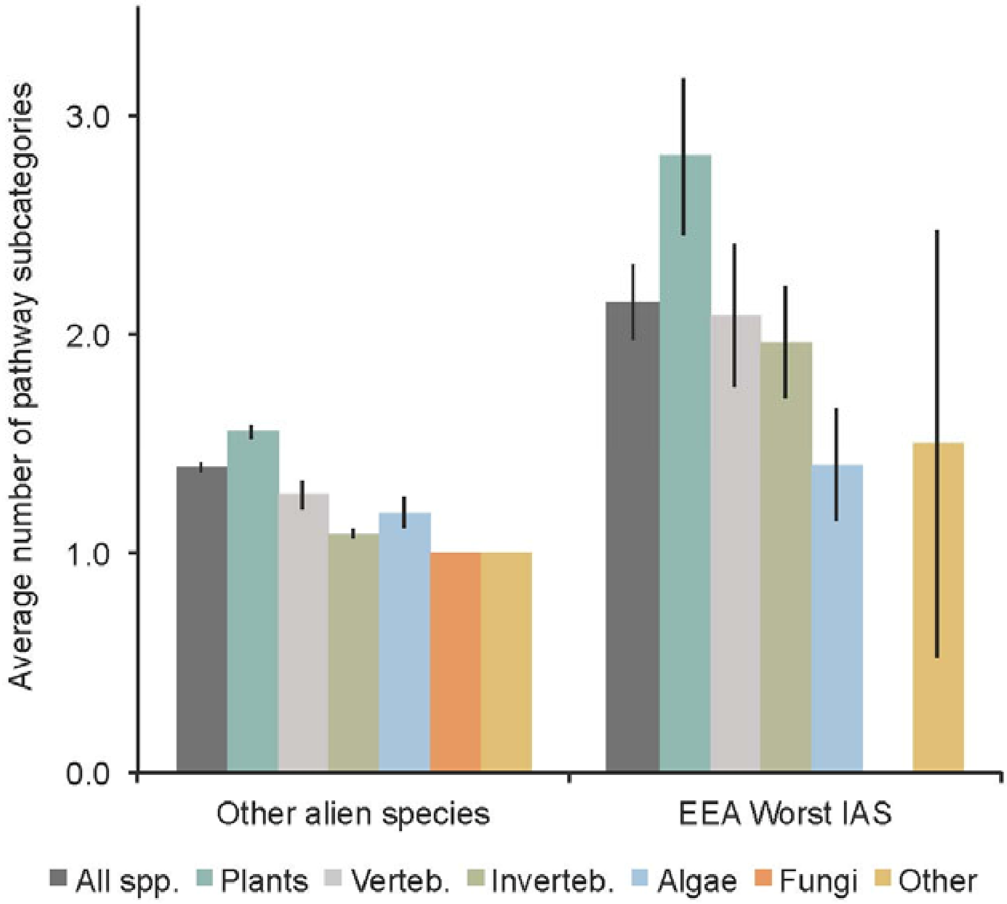


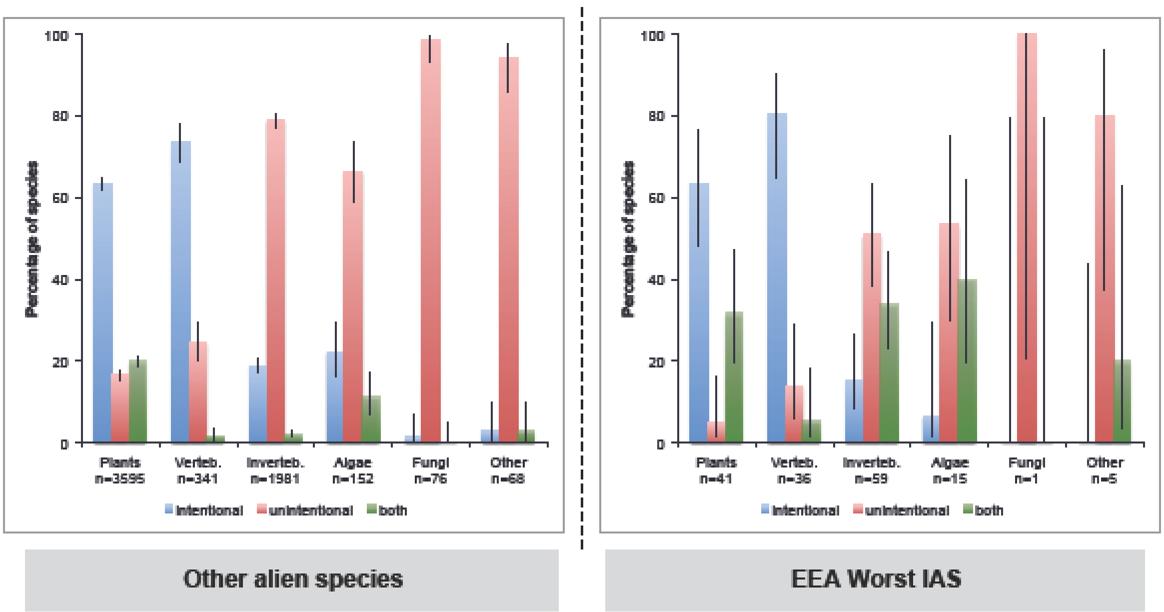
(c) DAISIE





(a) Combined dataset
(b) GISD/IASPMR
(c) DAISIE
Percentage of species
terrestrial n=5891
freshwater n=952
marine n=1065
multiple n=411
terrestrial n=904
freshwater n=651
marine n=484
multiple n=370
terrestrial n=5176
freshwater n=415
marine n=655
multiple n=124
Release
Escape
Contaminant & Stowaway
Corridor
intentional
unintentional
<- more unintentional
more intentional ->
Difference (% intentional - % unintentional)
terrestrial
freshwater
marine
multiple


Average number of pathway subcategories
0.0
1.0
2.0
3.0
Other alien species
EEA Worst IAS
All spp. Plants Verteb. Inverteb. Algae Fungi Other


Percentage of species
0
20
40
60
80
100
Plants n=3595
Verteb. n=341
Inverteb. n=1981
Algae n=152
Fungi n=76
Other n=68
intentional unintentional both
Other alien species
Plants n=41
Verteb. n=36
Inverteb. n=59
Algae n=15
Fungi n=1
Other n=5
EEA Worst IAS