Received: 18 March 2022 | Accepted: 5 September 2022

DOI: 10.1111/1365-2664.14287

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Pathways of introduction of alien species in Norway: Analyses of an exhaustive dataset to prioritise management efforts

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Funding information
Miljødirektoratet, Grant/Award Number: 19087428

Handling Editor: Joseph Bennett

Abstract

1. Alien species constitute one of the major threats to global biodiversity. Stopping alien species at an early stage, preferably before establishment, is crucial for the effectiveness of management actions. To enable early detection and prevent future introductions, knowledge of pathways of introduction and their absolute and relative importance is crucial.
2. Based on an exhaustive impact assessment of alien species in Norway (all multicellular neobiota), the relations of taxonomy, lifestyle and ecological impact of alien species to their pathways of introduction are investigated. This taxonomically and ecologically unbiased dataset contains 2267 unique pathways of 1180 alien species.
3. Ecological and taxonomic patterns indicate that terrestrial organisms were predominantly introduced by means of escape (mainly perennial plants escaped from gardens), parasites as contaminants (mainly fungi and insects parasitising plants), freshwater organisms by release (mainly vertebrates) and marine organisms as stowaways (mainly invertebrates and algae). Unaided introductions were most common among insects and marine organisms.
4. Alien species with high ecological impact were mainly introduced along the same pathways as other alien species. In relative terms, high-impact species were overrepresented among released species, even though this pathway was subordinate in absolute terms. The number of pathways and the overall introduction pressure were important predictors of ecological impact, especially of the species' invasion potential, and area of occupancy.
5. Introduction rates of novel alien species have seen recent increases in all taxa and along almost all pathways. This acceleration was especially pronounced for insects and fungi introduced as contaminants and for marine organisms introduced as stowaways. In absolute terms, introduction rates were highest for plant escapes, reaching more than five novel species per year.
6. *Synthesis and applications*. Introductions of new alien species cannot be prevented by closing one or two introduction pathways, since none can be singled out as the main pathway of high-impact alien species. Yet each pathways closed

makes a difference, as this reduces the overall introduction pressure. The highest priorities for management are the pathways that are easiest to address, such as release, and those with the highest volumes, such as plant trade.

KEYWORDS
ecological impact, escape, introduction pathway, invasive species, spread, stowaway

1 | INTRODUCTION

Alien species constitute one of the five major threats to global biodiversity (IPBES, 2019). In recent decades, efforts against alien species have shifted from a focus on documenting the distribution and ecological effects of alien species (Powell et al., 2011; Vilà et al., 2010) to prevention of introductions (e.g. Hulme, 2015; Perrings et al., 2005) as well as early detection and rapid response (Genovesi, 2005; Simberloff, 2003). Stopping alien species at an early stage, preferably before establishment, is crucial for the effectiveness of management actions (Pluess et al., 2012) and more cost-effective than implementing actions once the species have become a problem (Bogich et al., 2008; Genovesi, 2005; Leung et al., 2002; Scalera, 2010). To enable early detection or preferably prevent future introductions, knowledge of pathways of introduction of alien species is crucial (Hulme et al., 2008; Perrings et al., 2005; Pyšek et al., 2011).

Pathways of introduction are 'the processes that result in the introduction of alien species from one location to another' (Hulme et al., 2008). These processes have been classified into six main categories of introduction pathways: intentional release, escape from confinement, contaminants of commodities, stowaways on transport vectors, spread through human-made corridors and unaided dispersal via natural means from alien populations elsewhere (Hulme et al., 2008). Previous studies have shown that taxonomic groups vary with respect to the processes that lead to their introduction as alien species (Essl et al., 2015; Hulme et al., 2008; Saul et al., 2017), that the risk of adverse ecological effects of alien species varies between pathways of introduction (Essl et al., 2015; Pergl et al., 2017) and that changes in human habits and practices, like fluctuations in the economy or changes in the transport sector, may alter the relative and absolute importance of the different pathways (Pyšek et al., 2011; Seebens et al., 2017, 2018; Zieritz et al., 2017).

Knowing which pathways of introduction lead to the dispersal of high-risk alien species is therefore important for distributing management resources effectively between different pathways (McGeoch et al., 2016). However, detailed and exhaustive datasets about pathways are rare, because most datasets are biased towards certain taxonomic groups or certain biomes, or do not contain all relevant information for all species (Pergl et al., 2017, 2020). As a remedy for missing data, assessments often have used proxies such as trade routes, import statistics and population density (Essl et al., 2015), which implies a weaker causality in the evaluation of pathways and may hamper the effectiveness of derived management actions and resource distributions. Other studies have had to rely on mining data from a range of databases (Faulkner et al., 2016; Pyšek et al., 2011; Zieritz et al., 2017). However, national standardised meta-databases would enable more reliable quantitative assessments of the risk of alien species associated with the different pathways and provide a sounder, and more direct, basis for management actions.

Norway has conducted a complete impact assessment of alien species, which covers all multicellular neobiota (Sandvik et al., 2020a). As a part of the assessment, the known and assumed pathways have been listed for every species, resulting in an extensive dataset with unique opportunities for analysing the correlation between pathways of introduction and a number of traits associated with different groups of alien species. In order to better inform management actions against novel introductions of alien species, we have analysed this dataset focusing on the following research questions:

- What are the most important pathways of introduction for alien species to Norway?
- Do pathways differ according to the taxonomy, ecology, geographical origin and environmental impact of the species introduced?
- Have introductions of novel species along different pathways been accelerating or decelerating over recent decades?

Norwegian management authorities aim at reducing novel introductions (KLD et al., 2020). Answering the above questions is important for prioritising management efforts towards the most relevant pathways, both for evaluating the success of existing measures and for designing new ones.

2 | MATERIALS AND METHODS

2.1 | Data sources

The data analysed in this paper were collected in connection with the impact assessments of alien species in Norway, which were carried out by the Norwegian Biodiversity Information Centre (Artsdatabanken, 2018; Sandvik et al., 2020a, 2020b; Sandvik, Dolmen, et al., 2019). Our study data contained all 1183 multicellular species that are alien to mainland Norway (for further details, see Appendix S1, p. 6). Impact assessments of alien species in Norway follow the GEIAA protocol (Sandvik, Hilmo, et al., 2019; summarised in Appendix S1). In connection with GEIAA assessments, a number of variables are recorded for each species (Table 1). Pathways are among the information collected, and several details are recorded for each

TABLE 1 Information collected about each species during impact assessments of alien species in Norway and utilised in this paper

Category of information	Information provided, i.e. possible answers [or units]
Taxonomy	Scientific names of species, genus, family, order, class, phylum and kingdom
Impact category	No known (NK), low (LO), potentially high (PH), high (HI), severe (SE)
Ecological effect	Integer score between 1 and 4
Invasion potential	Integer score between 1 and 4
Area of occupancy	[km^2]
Pathways	See Table 2
Year of first observation	Integer between 1750 and 2017
Environment	Freshwater, marine, terrestrial, parasitic
Ecosystems	Ecological systems according to *Nature in Norway* (Halvorsen et al., 2020)
Area of origin	Continents and climate zones or oceans
Generation time	[years]

TABLE 2 Information collected about each species–pathway (i.e. for each unique combination of species and pathway)

Variable	Information provided, i.e. possible answers [and units]
Kind of spread	Introduction (to Norwegian nature), secondary spread (within Norwegian nature)
Category	Release, escape, contamination, stowaway, corridor, unaided
Subcategory	See Table 3
Frequency	<1, 1–8, 9–19, >19, unknown [incidents per decade]
Abundance	1, 2–10, 11–100, 101–1000, >1000, unknown [individuals per incident]
Timing	Historical (ceased and will not happen again), discontinued (but may happen again), current, in the future, unknown

species–pathway, that is, for each unique combination of species and pathway (Table 2). Most of the latter details are based on expert judgement rather than actual empirical estimates. All data analysed are freely available (Artsdatabanken, 2018; Sandvik et al., 2020b, 2022).

2.2 | Definitions of pathways

The categorisation of pathways used in Norwegian impact assessments followed Hulme et al. (2008) and CBD (2014). The subcategories were operationalised in a way that was compatible with Saul et al.'s (2017) interpretation, but had some minor inconsistencies with Harrower et al. (2020). Details are provided in Appendix S2.

2.3 | Analyses

Pearson's χ^2 tests were used to test whether the proportions of alien species, grouped according to several criteria, differed across pathways of introduction. Species were grouped according to (i) frequency of introductions, (ii) taxonomy (land plants [Embryophyta, i.e. Bryophyta + Marchantiophyta + Tracheophyta], insects [Hexapoda], 'fungi' [Ascomycota + Basidiomycota + Oomycota], vertebrates [Vertebrata] and 'other animals' [remaining Metazoa]; 'algae' [Chlorophyta + Ochrophyta + Rhodophyta] had too few species and were omitted from contingency tables), (iii) lifecycle (only plants: annual, biennial, perennial), (iv) lifestyle (freshwater, marine, terrestrial, parasitic), (v) ecosystem (only terrestrial species: open lowlands, semi-natural systems, wetlands, woodlands; the few purely alpine species were omitted from contingency tables), (vi) continent of origin (Asia, Europe, North America, Southern Hemisphere) and (vii) ecological impacts (high + severe impact vs. the remaining three categories). Because species can occur in several habitats and originate in more than one continent, they were assigned to the most specialised and/or least frequent lifestyle (parasitic > marine > freshwater > terrestrial) and the closest and/or climatically most similar continent (Europe > Asia > North America > Southern Hemisphere).

The associations between the number of pathways or the introduction pressure and measures of ecological risk (scores for ecological effect, invasion potential and overall ecological impact; see Appendix S1) were assessed using Kendall's rank correlation tests. 'Introduction pressure' for a given species was defined as the cumulative number of introduction events per year across all relevant pathways (log-transformed). Ideally, the abundance of individuals introduced per event should be included in introduction pressure as well (so as to yield propagule pressure sensu Lockwood et al., 2005), but this measure was unavailable for most species.

The associations between the number of pathways or the introduction pressure and (log-transformed) areas of occupancy were assessed using linear models. Differences in area of occupancy between species introduced along different pathways were tested using *t*-tests. Area of occupancy is the specific area that is inhabited by a species, excluding cases of vagrancy (IUCN, 2012, p. 12); see Appendix S1 (Box S1 and p. 5) for further details.

Temporal trends in the prominence of pathways were estimated based on the cumulative number of alien species observed in Norway up to a given year. For each species, only the year of the first reported observation was considered. Negative binomial regression models were used to test whether introduction frequencies had been accelerating or decelerating during the most recent 25-year interval. For each combination of pathway and taxon, a model was fitted to annual count data (the number of novel introductions per year), omitting years before the first record and after the last record. As explanatory variable, we used a categorical covariate that differed between two time periods (1800–1992 vs. 1993–2017). If the null model (intercept only) was rejected, this indicated that rates of novel introductions along a pathway in the most recent 25-year interval differed from the preceding years. Negative binomial regression was chosen because the count data were overdispersed.

All analyses were carried out in the **R** environment (R Core Team, 2020). To take multiple testing and the exploratory nature of our analyses into account, we applied a statistical significance level of $\alpha = 0.001$, corresponding to Bonferroni correction for 50 tests (this paper contains a total of 43 statistical tests). We regarded as biologically significant rank correlations of $\tau > 0.3$, coefficients of determination of $R^2 > 0.1$ and standardised χ^2 residuals of >+5 or <−5.

3 | RESULTS

Information on introduction pathways was available for 1156 (98%) of the 1183 alien species that have been risk assessed. For these species, a total of 2286 introduction pathways were described, corresponding to an average of 2.0 pathways per species. Regarding secondary spread within the country, such pathways were available for 561 species (47%), and a total of 768 pathways were described, corresponding to an average of 1.4 per species. The lower numbers are mainly due to the fact that not all alien species in Norway are able, or have started, to spread, although underreporting cannot be ruled out. The dominant timing of introductions was 'current' (78%). The remaining timings were historical (i.e. ceased and will not happen again, 9%), discontinued (but may happen again, 5%), future (1%) and 'unknown' (8%).

The number of species introduced along the different pathway subcategories varied between 1 (e.g. release for biological control) and 560 (escape from gardens; Table 3). All pathway categories and subcategories have been reported for at least one species (Table 3), with the single exception of the 'tunnels and land bridges' subcategory in the 'corridor' category. The second 'corridor' subcategory ('interconnected waterways') was only reported for three species, and only for secondary spread.

The remaining analyses focus on actual introductions to Norway. This means that secondary spread, including corridors, and likely future introductions were excluded from analyses, leaving 2267 unique pathways of introduction.

The frequency of introduction events was scored as unknown in 16% of the cases. The answer 'unknown' was chosen more often for unaided dispersers (60%), stowaways (30%) and contaminants (24%) than for other pathways. After the exclusion of these 'unknowns', the frequency of introduction events differed between pathways ($\chi^2_{12} = 136$, $p = 10^{-23}$). The annual frequency of introduction events (mean ± standard error) decreased in the order unaided (6.7 ± 0.8) > escape (2.5 ± 0.1) > contaminants (2.0 ± 0.2) > release (1.5 ± 0.4) ≥ stowaway (1.3 ± 0.2). The abundance of individuals per introduction event was scored as unknown in 97% of the cases. It was therefore not analysed further.

3.1 | Taxonomy, ecology and origin

Pathways differed significantly between taxonomic groups ($\chi^2_{16} = 636$, $p = 10^{-124}$; Table 4). Land plants were predominantly introduced by means of escape (mainly from horticulture, i.e. gardens, Table 3), fungi and insects as contaminants (mainly in plant trade), insects also unaidedly, vertebrates by release and other animals as stowaways (Figure 1a). Algae were omitted from Table 4 because of low sample size (10 species, all of which have been introduced as stowaways, and 5 of which also unaidedly).

Land plants constituted the majority of alien species in Norway (76%) and could be analysed in greater detail, revealing that different lifecycles were associated with different pathways ($\chi^2_8 = 313$, $p = 10^{-62}$; Table 4). Annual, and to a somewhat lesser degree biennial, plants were predominantly introduced as contaminants (78%, mainly of seeds and habitat material, Table 3) and stowaways (55%, mainly with ballast sand), whereas escape was the predominant pathway of introduction for perennial plants (83%; Table 4).

The ecology of alien species also influenced their most prominent pathways ($\chi^2_{12} = 365$, $p = 10^{-70}$; Table 4). Whereas terrestrial organisms were mainly introduced by means of escape, freshwater organisms were predominantly released, marine organisms were introduced unaidedly or as stowaways and parasites as contaminants (Figure 2a).

A finer grained analysis of terrestrial species revealed further differences ($\chi^2_{12} = 151$, $p = 10^{-25}$). Whereas escape was the main pathway for most ecosystems, in cultivated land and urban areas, a larger proportion than expected by chance was introduced as stowaways (Figure 2a). This mainly applied to alien plants (95%).

Differences in pathways between areas of origin were somewhat less pronounced ($\chi^2_{12} = 98.9$, $p = 10^{-15}$; Table 4). The only biologically significant finding was that Asian species were introduced by escape more often than expected by chance.

3.2 | Ecological impact

Alien species that were assessed to have a high (HI) or severe (SE) ecological impact were mainly introduced by means of escape (64%), followed by contaminants (27%) and stowaways (24%; Table 4). This was due to the total volume of species introduced along these pathways (Figure 3a). In relative terms, HI + SE species were strongly overrepresented among species that had been intentionally released, even though this pathway only accounted for 18% of the introductions (Table 4). In addition, HI + SE species were somewhat underrepresented among species introduced as contaminants. Accordingly, they differed in their pathways from the remaining impact categories ($\chi^2_4 = 37.0$, $p = 10^{-7}$; Table 4). In terms of taxonomy, ecology and origin, pathways along which many HI + SE species were introduced were mostly identical to the pathways along which many alien species were introduced in total (Figures 1b and 2b, Appendix S3).

Measures of ecological risk were positively associated with measures of the importance of pathways (Table 5). Correlations with the number of pathways were below our threshold for biological significance, but the introduction pressure of alien species was strongly correlated with their ecological impact category. When splitting ecological impact into its two components, introduction pressure was strongly correlated with invasion potential, but less so with ecological effect (Table 5).

TABLE 3 Prevalence of categories and subcategories of pathways of alien species in Norway. The table includes both introductions to and secondary spread within Norwegian nature. For introductions, numbers of species are provided both as a total (irrespective of ecological impact) and for species with high (HI) or severe (SE) ecological impact.

		Introd.		
Category	Subcategory	Total	HI + SE	Sec. spread
(1) Release in nature	Other (or unknown) intentional release	55	14	0
	Landscape/flora/fauna 'improvement' in the wild	17	11	0
	Fishery in the wild (including game fishing)	8	5	2
	Hunting	5	3	0
	Erosion control/dune stabilisation	4	4	0
	Release in nature for (other/commercial) use	3	0	0
	Biological control	1	1	0
	Introduction for conservation/wildlife management	1	0	0
(2) Escape from confinement	Horticulture	560	91	0
	Other (or unknown) escape from confinement	299	51	0
	Ornamental purpose other than horticulture	253	63	0
	Botanical gardens/zoos/aquaria	31	6	0
	Forestry (including afforestation or reforestation)	27	7	0
	Agriculture	26	9	0
	Live food and live bait	5	2	0
	Aquaculture/mariculture	4	4	0
	Farmed animals	3	1	0
	Pet/aquarium/terrarium species (including live food)	2	0	0
	Research and ex situ breeding (in facilities)	2	0	0
	Fur farms	1	1	0
(3) Contaminant	Seed contaminant	172	18	1
	Transportation of habitat material (soil, …)	114	16	110
	Contaminant on plants (except parasites)	68	7	11
	Parasites on plants	65	5	23
	Timber trade	62	3	1
	Contaminant nursery material	31	4	12
	Other (or unknown) contaminants	21	1	3
	Contaminated bait	21	3	2
	Parasites on animals	13	6	9
	Food contaminant (including of live food)	7	0	0
	Contaminant on animals (except parasites)	3	1	5
(4) Stowaway	Ship/boat ballast water or ballast sand/soil	155	26	4
	Vehicles (car, train, …)	64	18	71
	Other means of transport	19	3	8
	Container/bulk	18	4	4
	Ship/boat hull fouling	17	6	8
	Angling/fishing equipment	11	6	5
	People and their luggage/equipment	9	1	15
	Organic packing material	5	1	5
	Hitchhikers on ship/boat	5	3	1
	Machinery/equipment	1	0	8
	Hitchhikers in or on airplane	1	1	0
(5) Corridor	Interconnected waterways/basins/seas	0	0	3
	Tunnels and land bridges	0	0	0
(6) Unaided	Natural dispersal across borders	88	18	455

TABLE 4 Prevalence of pathways of introduction for different sets of alien species to Norway. Bold (italic) percentages indicate that the standardised χ^2 residuals within a section of the table are >+5 (<−5 respectively). Only past and present pathways of introduction (no secondary spread) are included. Percentages within a row sum to more than 100% because species can be introduced along several pathways. Decimals are provided only if $N > 150$.

Set of species	*N*	Release	Escape	Contaminant	Stowaway	Unaided
Taxonomy						
Land plants	892	7.3%	**72.8%**	*29.0%*	18.6%	*2.0%*
Insects	95	0%	*1%*	**91%**	18%	**32%**
Fungi	71	0%	*0%*	**89%**	4%	20%
Vertebrates	24	**75%**	54%	0%	0%	29%
Other animals	61	10%	*5%*	39%	**54%**	20%
Lifecycle (plants)						
Annual	102	1%	*18%*	**85%**	**57%**	3%
Biennial	49	8%	*27%*	**78%**	55%	4%
Perennial	741	8.1%	**83.4%**	*18.1%*	*10.9%*	1.8%
Lifestyle						
Terrestrial organisms	1048	6.8%	**62.6%**	36.5%	18.6%	*6.2%*
Parasites	45	0%	*0%*	**98%**	7%	7%
Marine organisms	35	6%	*9%*	*6%*	**74%**	**51%**
Freshwater organisms	25	**64%**	28%	12%	20%	0%
Ecosystem (terr.)						
Open lowlands	852	7.0%	64.3%	36.4%	19.6%	5.8%
Semi-natural systems	623	4.7%	66.8%	37.9%	**26.6%**	2.1%
Woodlands	452	8.8%	**79.9%**	*19.0%*	*6.0%*	7.5%
Wetlands	74	18%	77%	19%	14%	11%
Origin						
Europe	697	6.5%	54.2%	44.5%	22.8%	4.4%
Asia	209	9.1%	**75.6%**	21.1%	8.1%	11.0%
North America	195	12.3%	62.6%	33.3%	11.3%	5.1%
Southern hemisphere	20	0%	30%	55%	30%	25%
Impact category						
'Low' (NK–PH)	974	*5.7%*	56.6%	39.4%	19.1%	7.1%
'High' (HI + SE)	179	**18.4%**	64.2%	26.8%	24.0%	9.5%
All species	1153	*7.7%*	**57.8%**	**37.5%**	19.9%	*7.5%*

Finally, the number of pathways and introduction pressure explained 15% and 34% of the variation in the total areas of occupancy of alien species respectively (Table 5, Figure 3b). Species that were introduced unaidedly had an area of occupancy (median 670 km^2, interquartile range 81–3100 km^2) that was roughly five times larger than the remaining species' ($t = 5.01$, $p = 0.000003$). Species introduced by means of release (120, 16–1900), escape (160, 36–850), as contaminants (120, 24–800) or as stowaways (240, 32–1900) did not differ in their area of occupancy (all estimates in km^2; all $|t| < 4$, $p > 0.002$).

3.3 | History

The frequency of introductions of novel alien species changed over time, with magnitudes and patterns of these changes differing between pathways and taxa (Figure 4; Table S3-2). For insects (Figure 4b) and fungi (Figure 4c), introductions as contaminants have strongly accelerated (c. fivefold) in the most recent 25 years, averaging more than one new species per year. For marine species, an equally strong recent acceleration was evident for introductions as stowaways (Figure 4d). For plants (Figure 4a), patterns were mixed: escapes and releases accelerated in the most recent 25 years, escapes accounting for more than five new introductions per year (all $z > 3$, $p < 0.0005$; Table S3-2). Plant introductions as contaminants and stowaways levelled off early in the 20th century (Figure 4), albeit with a recent, non-significant increase for contaminants ($z = 2.06$, $p = 0.039$). The early levelling off was due to the (near-)cessation of two historically important pathways for plants, namely ballast soil/sand (68% of 189 alien plants introduced as stowaway prior to 1930) and seed contamination (52%

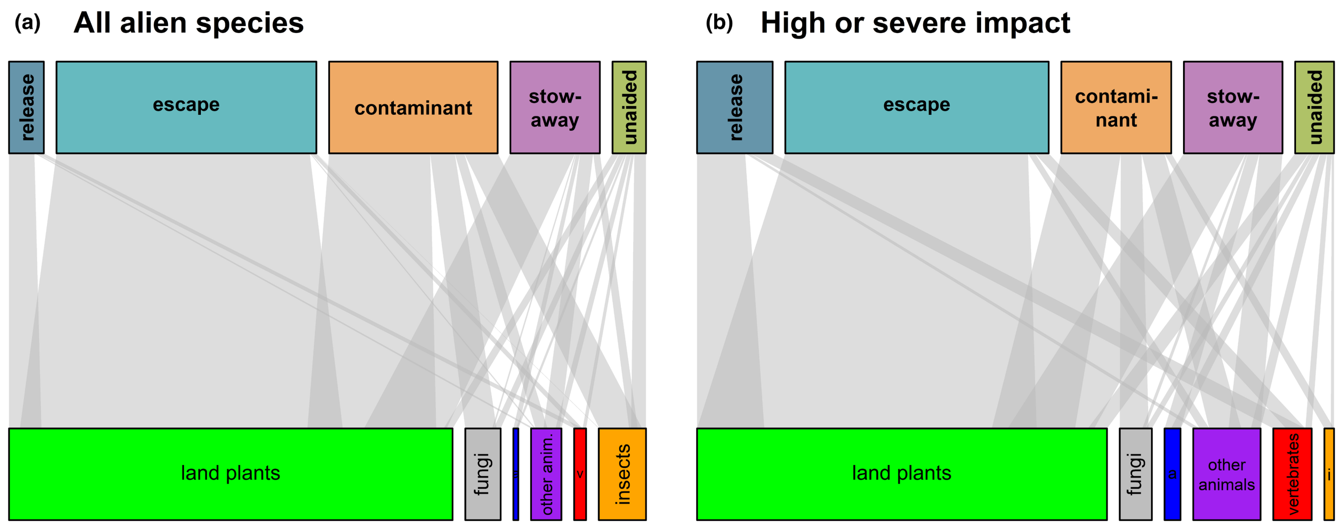

FIGURE 1 Pathways of introduction of alien species to Norway according to taxonomy. (a) All alien species (N = 1145 species and 1489 species–pathways). (b) Only alien species with high or severe ecological impact (N = 179 species and 254 species–pathways). Pathways are (from left to right) release, escape, contaminant, stowaway, unaided. Taxonomic groups are (from left to right) land plants, 'fungi', 'algae', 'other animals', vertebrates, insects. A species can have more than one pathway, which is why pathways may overlap; the graph is somewhat simplified in that the overlap area may not be correct for a specific pair of pathways (whereas the total overlap area is)

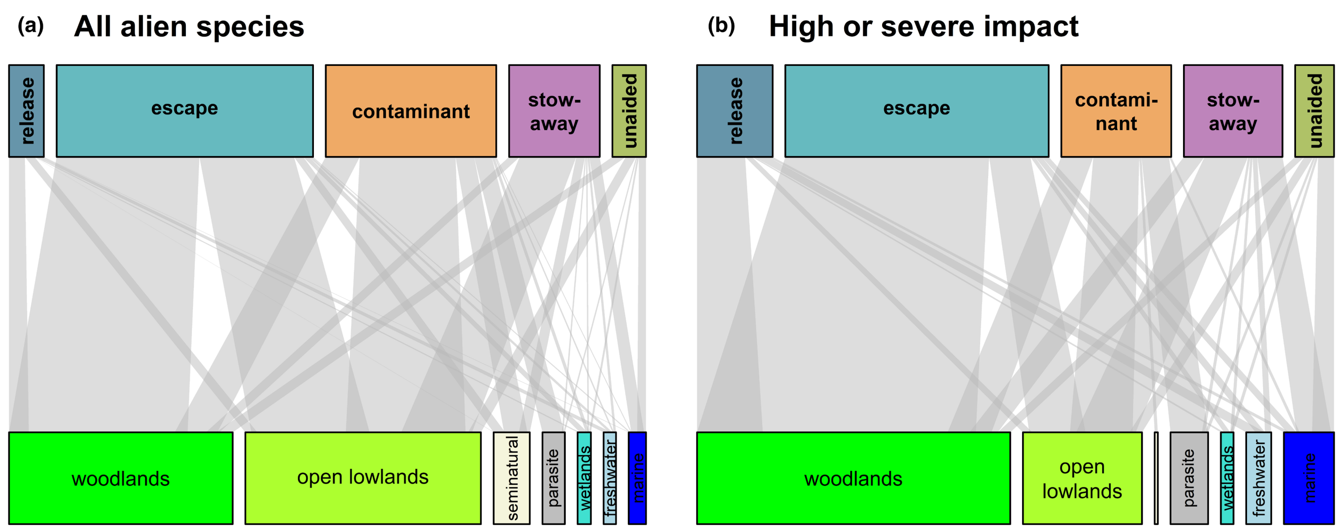

FIGURE 2 Pathways of introduction of alien species to Norway according to ecosystem. (a) All alien species (N = 1125 species and 1468 species–pathways). (b) Only alien species with high or severe ecological impact (N = 179 species and 254 species–pathways). Ecosystems are (from left to right) woodlands, open lowlands, semi-natural systems, parasites, wetlands, freshwater, marine. See Figure 1 for further explanations.

of 287 alien plants introduced as contaminants prior to 1930). For the remaining taxa and pathways, data were too sparse to indicate recent shifts, although most tendencies were compatible with recent increases.

The proportion of introductions of species that originated in Asia has been steadily increasing over the past 200 years (Figure 5a). This increase was mainly due to releases and escapes (Figure 5b,c). Species from the Southern Hemisphere have been increasing, too, but constituted a minor fraction of all introductions (Figure 5f). For contaminants and stowaways, continents of origin have been remarkably stable for the past century (Figure 5d,e).

4 | DISCUSSION

The prevention of new establishments of alien species is highly prioritised both internationally, for example, by the European Union (EU, 2014), and nationally by Norwegian authorities (KLD et al., 2020). In order to reach this goal, authorities need accurate and updated information on which pathways to prioritise. This paper provides a scientific basis for management actions against introduction of alien species. In our study, we analysed a dataset containing 2267 unique pathways of introduction of alien species to Norway. By covering all 1183 known alien species (multicellular neobiota) in Norway, all of which have been risk assessed (Sandvik et al., 2020a),

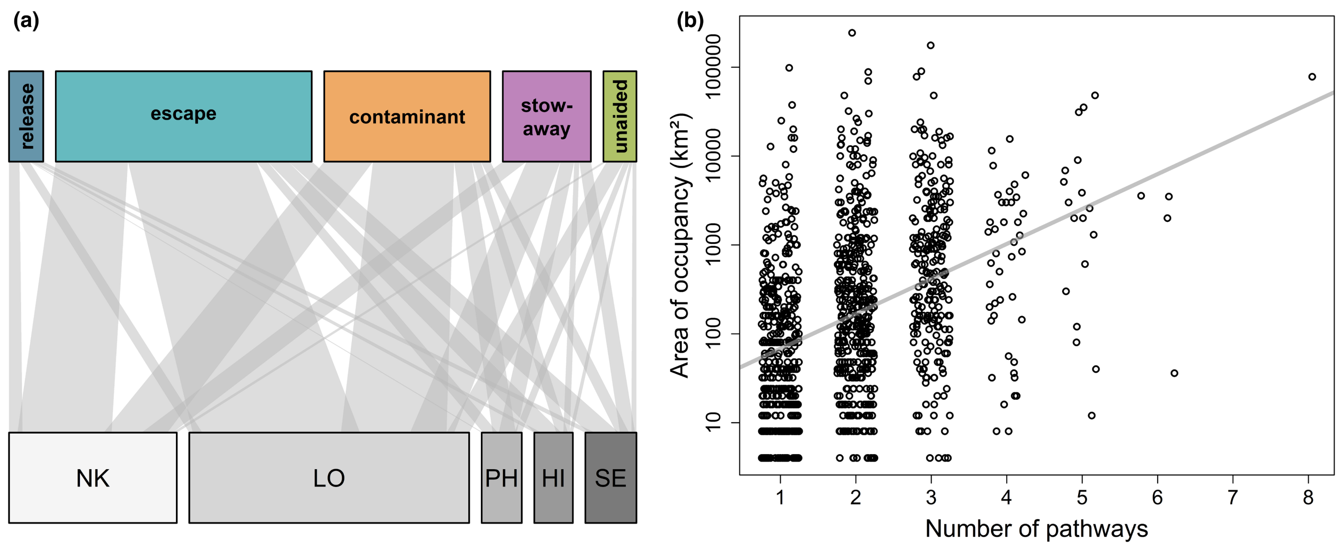

FIGURE 3 (a) Pathways of introduction of alien species to Norway according to ecological impact ('NK' = no known, 'LO' = low, 'PH' = potentially high, 'HI' = high, 'SE' = severe impact; $N = 1145$ species and 1489 species–pathways). See Figure 1 for further explanations. (b) Correlation between the number of pathway subcategories and the area of occupancy of alien species in Norway ($R^2 = 0.148$, $F_{1,1150} = 199$, $p = 10^{-41}$ excluding the outlier to the right). Note the logarithmic *y*-axis. Points are spread out horizontally ±0.25 units using random noise.

TABLE 5 Associations between pathways of alien species and different measures of their ecological risk. Introduction pressure is the sum of introduction events across all pathways of a species (see Section 2.3). Scores for ecological impact can be disaggregated into ecological (per-locality) effect and invasion potential (see Appendix S1). Introduction pressure and area of occupancy were log-transformed. Tests are Kendall's rank correlation test or linear models. $N = 1153$ alien species, all $p < 10^{-8}$. Bold statistics are regarded as biologically significant (see Section 2.3)

	Number of pathways	Introduction pressure
Ecological impact	$\tau = 0.243$, $z = 9.69$	**$\tau = 0.388$, $z = 16.77$**
Ecological effect	$\tau = 0.156$, $z = 6.00$	$\tau = 0.246$, $z = 10.29$
Invasion potential	$\tau = 0.261$, $z = 10.60$	**$\tau = 0.421$, $z = 18.49$**
Area of occupancy	**$R = 0.384$, $F = 199$**	**$R = 0.584$, $F = 595$**

this dataset constitutes a taxonomically and ecologically unbiased source of information.

The most frequent pathways of introduction were escape, contaminants and stowaways, which reflects the main alien species pathways in Europe (Hulme et al., 2008). Also the taxonomic patterns were in line with several earlier studies (Essl et al., 2015; McGrannachan et al., 2021; Pergl et al., 2017, 2020; Saul et al., 2017), in that plants were predominantly introduced by means of escape (mainly perennial garden plants, less so annual weeds), fungi and insects as contaminants (mainly of plants), remaining invertebrates as stowaways and vertebrates by release.

The importance of pathways varied between alien species depending on their impact. Alien species with high ecological impact (impact categories 'high' and 'severe') were strongly overrepresented in the 'release' category (Table 4). The main reason for this pattern is that intentional introductions focus on species that are expected to be able to survive and reproduce in the new environment (Blackburn et al., 2009). The set of released species is therefore biased towards species that in fact will be able to establish (and potentially expand). However, this pathway accounted for only 18% of the introductions of high-impact species. The distribution across the remaining pathways was rather similar to the other alien species. In absolute terms, most high-impact species were thus introduced as escapees, contaminants and stowaways. These findings suggest that several pathways, not just release, must be addressed in order to prevent introductions of species with high ecological impact.

The overall introduction pressure, that is, the cumulative frequency of introduction events across pathways for a species, was an important predictor of ecological impact (Foxcroft et al., 2019; Pergl et al., 2017; Saul et al., 2017). Following Parker et al. (1999), the impact categories of GEIAA assessments are composed of a spatial component (invasion potential) and a per-site ecological effect component (Sandvik, Hilmo, et al., 2019; see Appendix S1). Introduction pressure was strongly related to invasion potential, but only weakly so to ecological effect. In particular, the strong correlation found between a species' introduction pressure and its area of occupancy indicates that the likelihood of a species to become invasive increased with the number of introductions. This may either be caused by an increase in the probability of establishment when a species gets more chances (Blackburn et al., 2009; Lockwood et al., 2009), because it can obtain a higher density or larger range (Pergl et al., 2017), or because of a greater genetic diversity (Smith et al., 2020). Our results thus imply that preventing new introductions is important also for already established alien species, in order to limit their ecological impact.

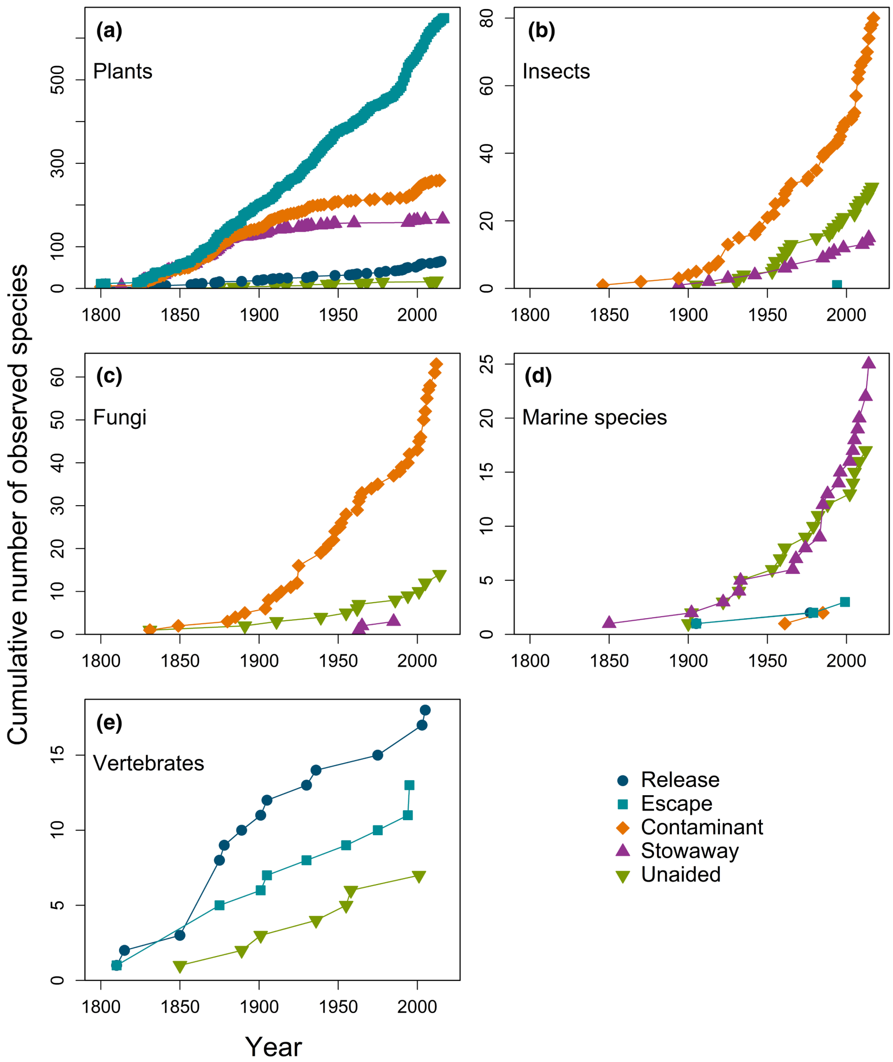

FIGURE 4 Temporal trends for the cumulative number of alien species observed in Norway according to their pathways of introduction and taxonomy/ecology. Only novel introductions are included, meaning that each alien species is counted only once, viz. in the year it is first reported. Note that *y*-axes differ. (a) Plants, (b) insects, (c) fungi, (d) marine species, (e) vertebrates

It is also significant that species introduced unaidedly attained a median area of occupancy that was five times greater than for alien species not introduced unaidedly. The most likely explanation is that species capable of reaching Norway unaidedly are well equipped to spread effectively across the country, or along its coast, afterwards. For such species, early detection and rapid-response management regimes are especially important.

The significance of different pathways may change temporally (Essl et al., 2015; Faulkner et al., 2016; Wilson et al., 2009). Detecting such changes is crucial for understanding the human processes underlying alien species introductions, and for designing management schemes to contain them. In Norway, almost all pathways with sufficient data exhibited recent increases in introduction rates of novel alien species. This acceleration was especially pronounced for insects and fungi introduced as contaminants and for marine organisms introduced as stowaways (Figure 4; cf. McGrannachan et al., 2021). In absolute terms, introduction rates were highest for plants, reaching more than five novel species per year for escape, and almost two species per year for contaminants. As introduction rates were based on records of novel alien species, these figures clearly underestimate the overall magnitude of introduction pressure, since the volume of introductions may increase also in alien species that have already been reported. However, in the absence of saturating introduction curves, one can assume that the introduction of novel species is indicative of the total import volume (Seebens et al., 2017, 2018). The introduction trends along most pathways show that ongoing measures to prevent introductions, such as ballast water management (IMO, 2004) or bans on the import of certain species (KLD, 2015), although important, have been insufficient to decelerate introductions.

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our national study clearly illustrates the power of combining taxonomically and ecologically unbiased data on all alien species and their known pathways of introduction with ecological impact assessments. Our results point to two important aspects for guiding national and international management strategies against the further spread of alien species and their impact on autochthonous nature: ecological impact and total numbers.

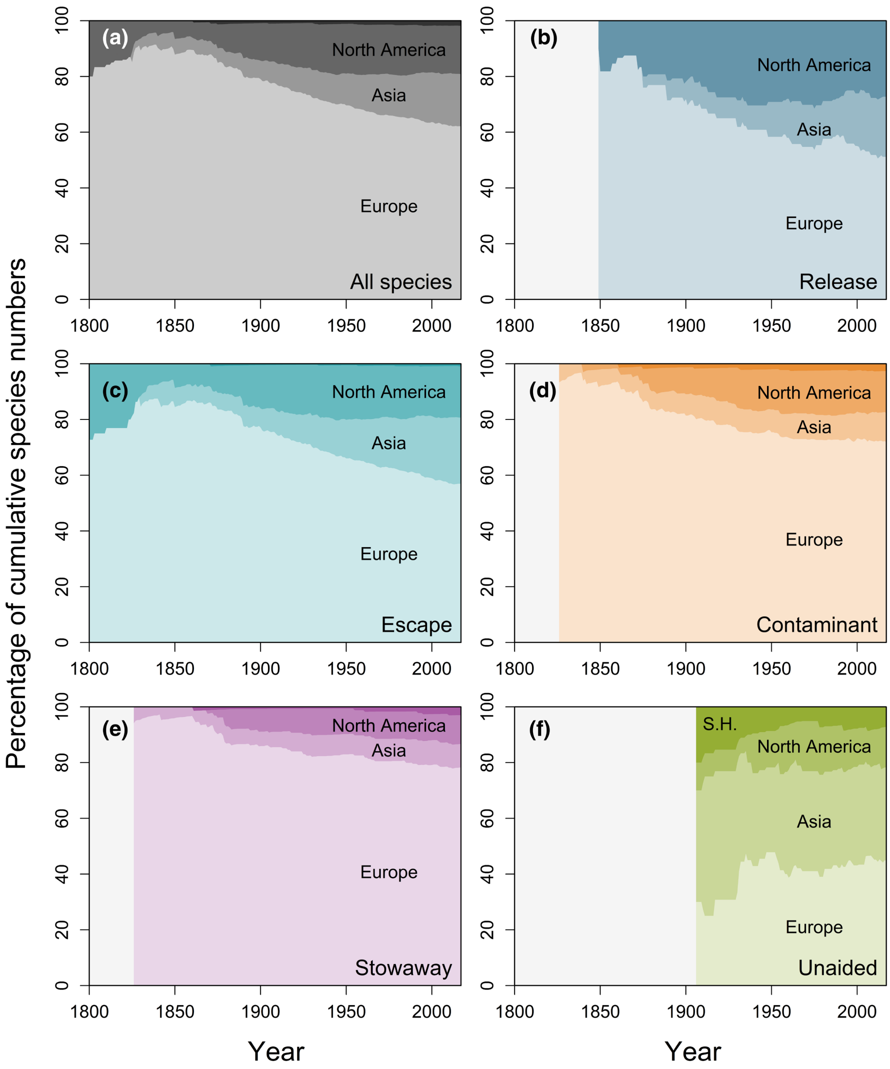

FIGURE 5 Temporal trends for the percentages of the cumulative number of alien species observed in Norway according to their pathways of introduction and continents of origin. The dark colours above North America represent species from the Southern Hemisphere ('S.H.'). In the light grey areas, there are too few species (<10) to present percentages. (a) All species, (b) releases, (c) escapes, (d) contaminants, (e) stowaways, (f) unaided spread

Release is a pathway of subordinate importance in terms of total numbers, but it has introduced many high-impact species and is comparatively easy to address: When species are introduced intentionally, one can, in principle, also stop doing so. Plant trade is the most important pathway in absolute terms, both through escape of imported plants and through parasites or contaminants of plants or of habitat material (see Table 3). These pathways can be addressed by better regulations of plant import as well as awareness-raising campaigns directed at garden owners (KLD et al., 2020). Other important pathways in terms of volume are seed contamination, timber trade, forestry, agriculture, ballast water, containers/bulk and hull fouling. These pathway subcategories should thus be obvious targets of management efforts. Aquaculture may be added to this list, not because many species have escaped into Norwegian nature (4), but because all of them have a high ecological impact.

Although we analysed what is probably the first nationally exhaustive dataset on introduction pathways of alien species, there are still knowledge gaps. For instance, the frequency of introductions and the abundance of individuals introduced per event were unknown for many species. Moreover, expert judgements are still a major source of information regarding alien species introductions. Filling these knowledge gaps would further improve the scientific basis for the management of alien species.

Together, our findings allow a pessimistic and an optimistic conclusion. The pessimistic one is that it does not suffice to close one or two introduction pathways, if the goal is to avoid the introduction of potentially harmful alien species. All of them must be addressed, since none can be singled out as the main pathway of invasives. The cumulative introduction pressure seems to be an important determinant of ecological impact, and one which can be reduced one pathway at a time. Thus, the optimistic conclusion is that each pathways closed does make a difference. The pathway subcategories with the greatest volume of introductions, as well as those with particularly large proportions of high impact species, suggest themselves as the highest priorities.

AUTHOR CONTRIBUTIONS

Hanno Sandvik, Siri L. Olsen and Joachim P. Töpper conceived and designed the study; Olga Hilmo and Hanno Sandvik prepared the dataset; Hanno Sandvik analysed the data; Hanno Sandvik, Siri L. Olsen and Joachim P. Töpper wrote the manuscript; all authors approved the final version.

ACKNOWLEDGEMENTS

This study was financed by the Norwegian Environment Agency (contract number 19087428). We are grateful to Ditte K. Hendrichsen's contributions to the conception and design of the study.

CONFLICT OF INTEREST

The authors state that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data analysed are available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.8sf7m0cjc (Sandvik et al., 2020b) and at https://doi.org/10.5061/dryad.4b8gthtg7 (Sandvik et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Sandvik, H., Olsen, S. L., Töpper, J. P., & Hilmo, O. (2022). Pathways of introduction of alien species in Norway: Analyses of an exhaustive dataset to prioritise management efforts. *Journal of Applied Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2664.14287