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Biological invasions: a global assessment of geographic distributions, long-term trends, and data gaps

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ABSTRACT

Biological invasions are one of the major drivers of biodiversity decline and have been shown to have far-reaching consequences for society and the economy. Preventing the introduction and spread of alien species represents the most effective solution to reducing their impacts on nature and human well-being. However, implementing effective solutions requires a good understanding of where the species are established and how biological invasions develop over time. Knowledge of the status and trends of biological invasions is thus key for guiding research efforts, informing stakeholders and policymakers, for targeted management efforts, and preparing for the future. However, information about the status and trends of alien species is scattered, patchy, and highly incomplete, making it difficult to assess. Published reports for individual regions and taxonomic groups are available, but large-scale overviews are scarce. A global assessment therefore requires a review of available knowledge with careful consideration of sampling and reporting biases. This paper provides a comprehensive global assessment of the status and trends of alien species for major taxonomic groups [Bacteria, Protozoa, Stramenopila, Alveolata, and Rhizaria (SAR), fungi, plants, and animals] for Intergovernmental Panel of Biodiversity and Ecosystem Services (IPBES) regions.

The review provides irrefutable evidence that alien species have been introduced to all regions worldwide including Antarctica and have spread to even the most remote islands. The numbers of alien species are increasing within all taxa and across all regions, and are often even accelerating. Large knowledge gaps exist, particularly for taxonomic groups other than vascular plants and vertebrates, for regions in Africa and Central Asia, and for aquatic realms. In fact, for inconspicuous species, such as Bacteria, Protozoa, and to some degree SAR and fungi, we found records for very few species and regions. Observed status and trends are thus highly influenced by research effort. More generally, it is likely that all lists for alien species of any taxonomic group and region are incomplete. The reported species numbers therefore represent minima, and we can expect additions to all lists in the near future. We identified six key challenges which need to be addressed to reduce knowledge gaps and to improve our ability to assess trends and status of biological invasions.

Key words: Neobiota, invasive species, non-native, alien, biogeography, time series, worldwide, future projections, knowledge gaps, IPBES.

CONTENTS

I. INTRODUCTION

The introduction of alien and invasive alien species (see definitions in Section II below) can have far-reaching consequences (Pyšek *et al.*, 2020) for the distribution of life on Earth (Leroy *et al.*, 2023; Aulus-Giacosa, Ollier & Bertelsmeier, 2024), biodiversity conservation (Pyšek *et al.*, 2012b) and native species survival (Blackburn, Bellard & Ricciardi, 2019; Bellard, Bernery & Leclerc, 2021), ecosystem functioning (Linders *et al.*, 2019; Pérez, Vilà & Gallardo, 2022), human well-being and plant and animal health (Lazzaro *et al.*, 2018), and the economy (Diagne *et al.*, 2021). The rate of new alien species introductions has risen continuously for centuries (Seebens *et al.*, 2017) and is expected to keep rising (Seebens *et al.*, 2021a). The ongoing accumulation and spread of alien species poses distinct challenges to assessing the current status of biological invasions. Comprehensive and regularly updated assessments of available knowledge about alien species distributions are essential for elucidating the underlying dynamics of biological invasions globally, for assessing current trends and data needs, and for informing and supporting managers and policymakers (Latombe *et al.*, 2017; Meyerson *et al.*, 2022).

The high dynamism of alien species introductions and spread complicates the task of providing up-to-date and accurate assessments of the status of biological invasions across the world. The establishment of new alien species is reported frequently worldwide (Seebens *et al.*, 2021b). For example, the regularly updated alien flora of the Czech Republic reported an increase of the total number of alien plants from 1378 in 2002 to 1576 in 2022 (Pyšek *et al.*, 2022). Fluctuations in alien species numbers result from a multitude of factors, such as the intensity of introductions of new species, environmental changes, or local disturbances (Pyšek *et al.*, 2020). However, changes may also arise from the deployment of new technologies (Meyerson *et al.*, 2022) and effective alien species management and eradication (Simberloff, 2011; Pluess *et al.*, 2012a,b; Spatz *et al.*, 2022). Further uncertainty arises from the highly variable intensity of research and the notorious inconsistency in reporting (Hughes *et al.*, 2021; Meyerson *et al.*, 2022). It is therefore necessary to conduct regular assessments of alien species' distributions, and their temporal trends, to integrate the most comprehensive available information, as well as taking data gaps into account.

Here, we present results of a comprehensive assessment of the historical trends and current distributions of alien species across geographic regions worldwide. This effort builds on the report of the Intergovernmental Panel of Biodiversity and Ecosystem Services of invasive alien species and their control (IPBES, 2023). This IPBES report presents a broad overview and assessment of the current situation of biological invasions, their impacts, management, and policy options. Chapter 2 of the report focuses on the trends and status of alien species (Seebens *et al.*, 2023), which has been updated and revised here by assessing: (*i*) the levels of invasions by established alien Bacteria, Protozoa, SAR (monophyletic group consisting of Stramenopila, Alveolata, and Rhizaria; partly considered as Chromista), fungi, plants, and animals across all IPBES regions, both in terms of overall quantitative patterns and individual examples; (*ii*) the trends in the accumulation of established alien taxa and associated invasion dynamics that have resulted in their current distributions; and (*iii*) taxonomic and geographic data gaps, where future research efforts should be directed. We provide overviews of the trends and status of established alien species at the global scale, including an assessment of gaps (Section IV), for individual IPBES regions (Sections V–IX), and future trends (Section X), followed by recommendations for improving the level of knowledge (Section XI).

II. METHODS

We define key terms in this article as used in IPBES (2023) (Table 1). The information provided herein was collated in two ways: through comprehensive literature reviews and by generating a database of alien species occurrences to provide

Table 1. Definitions of key terms following IPBES (2023).

Key terms	Definitions
Trends	Temporal changes in established alien species numbers over decades to centuries.
Status	Currently observed and reported distribution patterns of alien species.
Gap	Absence of information on alien species occurrences, also called the Wallacean shortfall (Lomolino, 2004). A gap usually arises from low sampling effort, but might also be due to other reasons, such as the lack of accessibility of information, underreporting, unresolved taxonomies, or linguistic barriers.
Alien species	Species transported beyond the limits of their native range through human agency and that occur in the new region outside cultivation or captivity. We here refer to 'established' alien species, representing those alien species that form self-sustaining populations in the wild (Richardson *et al.*, 2000). This corresponds to category 'C3' in the framework proposed by Blackburn *et al.* (2011), and is a synonym of the term 'naturalised' (e.g. Richardson *et al.*, 2000; Pyšek *et al.*, 2017). For the sake of readability, we use 'alien species' in the main text although the numbers and examples refer to established alien species.
Invasive alien species	A subset of established alien species that spread and have a negative impact on biodiversity and local ecosystems following the definition of IPBES (2023) and IUCN (2000). We note that neither spread nor negative impact have agreed-upon quantitative definitions.

a quantitative basis for assessing the distribution of alien species.

The database underlying this article represents a collection of standardised checklists of alien species for regions worldwide and has been generated by applying a published workflow called 'Standardisation and Integration of Alien Species distribution data' (SInAS) (Seebens *et al.*, 2020). This workflow standardises information available in checklists (i.e. lists of species per region) and integrates data into a single combined database. The R code for applying the workflow has been published previously (Seebens *et al.*, 2020); the generation of the final database is thus fully transparent and reproducible. Standardisation included the harmonisation of taxonomic names according to the backbone taxonomy of the Global Biodiversity Information Facility (GBIF, www.gbif.org), the harmonisation of key terms according to Groom *et al.* (2019), matching the spatial resolution of all checklists, and the standardisation of years of first records according to rules defined in the workflow and outlined in Seebens *et al.* (2020). Once all the data were standardised, the checklists were combined, and duplicates removed. Conflicting entries from different databases that could not be resolved were retained and are flagged as such in the database.

To ensure transparency and achieve comprehensiveness, we sought published and freely accessible global databases of alien species checklists. Seven databases (Table 2) met these criteria; these together collate more than 4000 individual sources of information including scientific publications, reports, and regional databases. Integrating these sources resulted in the single database underlying this article that is called 'SInAS database 2.5'. The integration achieved by applying the SInAS workflow to the seven databases resulted in the largest currently available single database of alien species, with 175,980 occurrences in 264 regions of 37,591 established alien species worldwide. The database is freely available (https://doi.org/10.5281/zenodo.10038256) and follows the data principles of being findable, accessible, interoperable, and reusable (FAIR).

As the spatial delineation of the study, we adopted the classification of IPBES regions and subregions (IPBES, 2021), as used in their recent biodiversity reports (IPBES, 2019, 2023). This classification recognises five IPBES regions ('Africa', 'Asia & the Pacific', 'The Americas', 'Europe & Central Asia', and 'Antarctica') and 18 subregions (3–5 subregions for each region except Antarctica, which is not subdivided). We do not cover Antarctica in the same detail as the other IPBES regions as it has far fewer reported alien species. We used the IPBES classification for providing overviews in the text and tables, while the maps shown in the main text keep the regional and national categorisation of the underlying databases.

To provide overviews of status and trends, we grouped taxa according to their taxonomic classification following the GBIF backbone taxonomy with two exceptions: We included the group algae, which is a paraphyletic group including red algae (Rhodophyta), green algae (Chlorophyta, Charophyta), cryptophytes (Chryptophyta), and haptophytes (Haptophyta). The GBIF taxonomy includes the kingdom Chromista, which is an outdated classification. Instead, we used the supergroup SAR, which is a monophyletic group consisting of Stramenopila, Alveolata, and Rhizaria.

III. ACKNOWLEDGEMENT OF INCOMPLETE KNOWLEDGE AND DATA

We acknowledge the likelihood that none of the alien species checklists used here can be considered complete or unbiased. Reasons for the lack of data include low sampling effort, lack of detection, underreporting, inaccessible literature and reports, lack of expertise, inconsistent use of definitions

Table 2. Databases of alien species used for generating the database underlying the figures and tables herein. In these databases, regions correspond to countries, administrative units in case of large countries, and islands, and a 'regional record' denotes a record of an established alien species in such a region.

Database	Content used here	Citation and source
Global Naturalised Alien Flora (GloNAF)	Regional records of alien vascular plants	van Kleunen *et al.* (2019) https://idata.idiv.de/DDM/Data/ShowData/257
Global Avian Invasions Atlas (GAVIA)	Regional records of alien birds	Dyer *et al.* (2017b) https://doi.org/10.1038/sdata.2017.41
Distribution of Alien Mammals (DAMA)	Regional records of alien mammals	Biancolini *et al.* (2021) https://doi.org/10.6084/m9.figshare.13014368
Alien amphibians and reptiles	Regional records of alien amphibians and reptiles	Capinha *et al.* (2017) https://doi.org/10.1111/ddi.12617
MacroFungi	Regional records of alien macrofungi	Monteiro *et al.* (2020) https://doi.org/10.15468/2qky1q
Alien Species First Records (FirstRecords)	First records of alien species in regions across taxonomic groups	Seebens *et al.* (2017) https://doi.org/10.5281/zenodo.4632335
GRIIS	Regional records of alien and invasive alien species across taxonomic groups	Pagad *et al.* (2022) https://doi.org/10.5281/zenodo.6348164

and concepts, time lags in the process of biological invasions, delays in reporting, taxonomic uncertainty, and language barriers, among others. Consequently, species numbers reported here are conservative minima, and actual numbers of alien species are likely higher in all cases.

Knowledge and data availability varied highly across taxa, regions, and over time. Data were especially scarce for certain taxonomic groups, particularly for invertebrates, fungi, SAR, protozoans, and prokaryotes. Maps and time series for these groups were highly influenced by the availability of reports rather than true distributions. Furthermore, while much information is available for some regions of the world, it is largely lacking for others, which influenced our presentation of status and trends. While we tried our best to provide information for all groups and regions, sections inevitably vary in comprehensiveness. We provided more detailed evaluations, including figures, only for data-rich groups and regions, but could not cover all taxonomic groups and regions in the same detail. We therefore assessed the reported numbers and distributions of species in the context of data availability. We included a section on knowledge gaps (Section IV.2), where we provided an overview of knowledge gaps across regions and taxonomic groups, but to avoid repetition, we did not address knowledge gaps for each region–taxon combination.

IV. A GLOBAL OVERVIEW

(1) Historical trends and current status

The number of alien species records has increased since 1700 CE consistently across all taxonomic groups and regions (Fig. 1). Between 1700 and 1850, the number of alien species was comparatively low and increased only slightly for all taxa. Numbers of alien species records rose markedly during the 19th century, and that trend continues today. The onset of the acceleration in alien species numbers varied slightly among taxonomic groups with a tendency of earlier onsets for mammals, birds, and vascular plants, and a later acceleration for invertebrates (Fig. 1). However, this may partly be an effect of lower research intensity and data availability for the latter group, which resulted in more delayed detections (Seebens *et al.*, 2017; Muñoz-Mas *et al.*, 2023). The time series of alien species numbers were very similar for all IPBES regions except Africa, which shows lower values, perhaps in part due to lower data availability. In addition to cumulative numbers, the rates of newly recorded alien species have risen continuously for all taxonomic groups and nearly all regions except for mammals, which peaked around 1950 (Fig. 1). The declining trend in rates of alien mammal introductions is likely due to more stringent regulation of trade, their higher detectability compared to smaller organisms, the comparatively small pool of potential candidate species, and some successful eradications (Simberloff *et al.*, 2013; Seebens *et al.*, 2017).

Currently observed numbers of alien species vary across IPBES regions, with the highest numbers recorded for Europe & Central Asia followed by The Americas, Asia & the Pacific, and Africa (Fig. 2, Table 3). Countries with particularly high numbers of alien species include the USA and Australia, which are also geographically large areas, and New Zealand, France, and the UK. Hawaii stands out as being a group of remote islands with invasion levels comparable to countries, such as Japan or Belgium, which are distinctly larger in area.

Despite the larger area, Asia & the Pacific harbour similar numbers of alien amphibians and reptiles to Europe & Central Asia (Table 3), which is possibly a result of stringent biosecurity measures in some areas such as Australia, New Zealand, and Japan (Brenton-Rule, Barbieri & Lester, 2016; Chapple *et al.*, 2016; García-Díaz *et al.*, 2017; Toomes *et al.*, 2020). Uneven sampling and reporting likely affect the reported total numbers of alien taxa, particularly in Africa, South America, Central Asia & the Pacific (Henriksen *et al.*, 2024). In addition, articles not written in English and grey literature were more difficult for us to include in our analyses, resulting in a bias towards English sources.

Using comprehensive and well-curated taxon-specific databases (Table 2), we calculated the range of species numbers for mammals, birds, and vascular plants in the individual taxon-specific databases compared to the full database (Table 3). The differences in numbers are high with nearly 30% more species reported in the full database compared to the taxon-specific ones. The difference among databases is likely an effect of using different criteria for adding species by, for example, selecting information that is more or less robust. Thus, absolute numbers of species should be treated with caution and considered as estimates and often minimum numbers of true alien species levels.

Across taxonomic groups, vascular plants are by far the largest contributors to global alien species numbers, followed by insects and fishes (Table 3). For many taxonomic groups, all regions except Africa report similar numbers of established alien species. For instance, the numbers of vascular plant species reported for The Americas, Asia & the Pacific, and Europe & Central Asia are similar, while the number for Africa is much lower. Similar patterns are observed for alien bird, fish, and mammal species. By contrast, algae show a different pattern, with Europe & Central Asia harbouring the highest alien species numbers, followed by Asia & the Pacific, The Americas, and Africa. However, some of the observed patterns are certainly influenced by variation in survey intensity and availability of information around the world.

(2) Biases and information availability

Patterns of the distribution of alien species are influenced by the uneven sampling of alien species occurrences across the globe and the uneven availability of information. For example, hotspots of alien species occurrences (i.e. areas of high

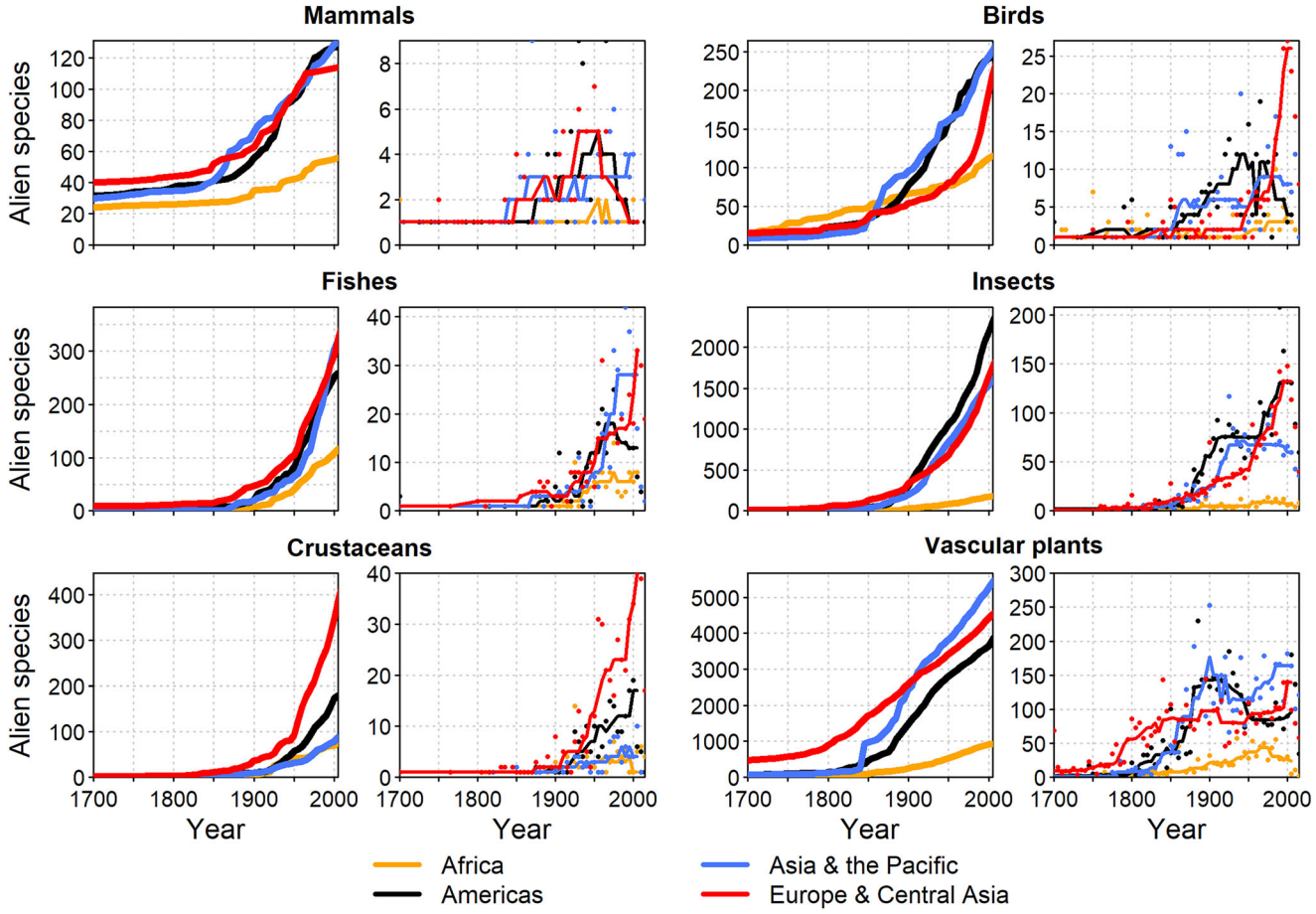

Fig. 1. Trends in numbers of established alien species for Intergovernmental Panel of Biodiversity and Ecosystem Services (IPBES) world regions. Panels by taxon show cumulative numbers (left panels, thick lines) and numbers of new alien species per five-year intervals (right panels, thin lines). Lines in right panels indicate smoothed trends calculated as running medians. Note that the range of the *y*-axes differs among panels.

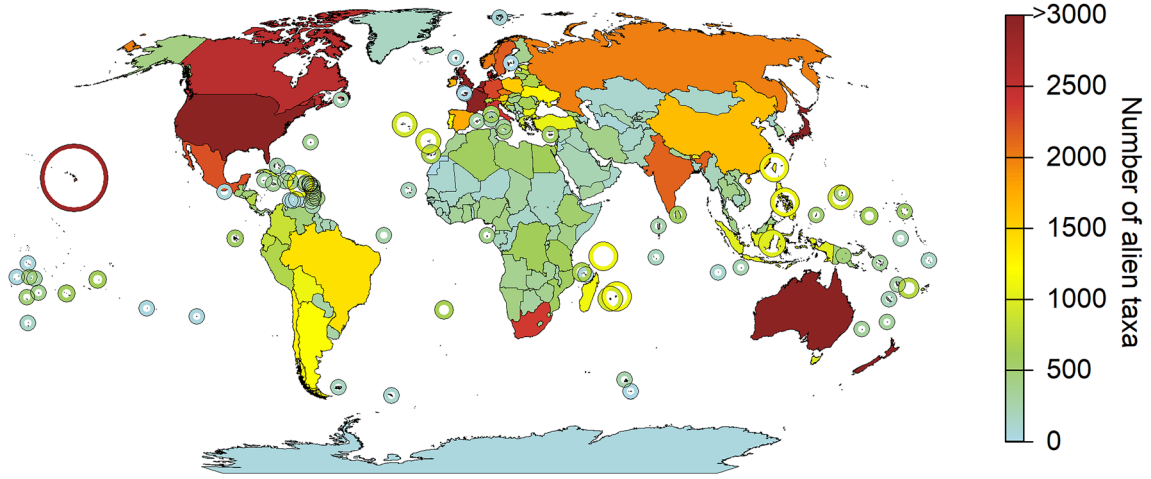

Fig. 2. Numbers of established alien species per region. Species from all realms (marine, freshwater, and terrestrial) were considered if they could be assigned to one of the regions used in this study. Species only recorded for the open sea are not included in this map. Note that numbers may deviate from those reported in the text due to variation among data sources.

alien species numbers relative to other regions; Dawson *et al.*, 2017) coincide with global hotspots of data availability and study sites (Martin, Blossey & Ellis, 2012; Meyer *et al.*, 2015), which influence our knowledge of species distributions (Hughes *et al.*, 2021). This conclusion is confirmed by the information provided here: mapping the number of available studies used to generate the underlying database of this study revealed that regions with the most information on alien species occurrences (Fig. 3) were also the hotspots of alien species occurrences (Fig. 2). Hence, knowledge of alien species occurrences is biased towards well-sampled regions, such as Europe and North America, and taxonomic groups, such as vertebrates and plants, with most studies conducted in recent decades (Pyšek *et al.*, 2008; Jeschke *et al.*, 2012; Bellard & Jeschke, 2016). It remains unclear how much the distribution of alien species and documented hotspots are affected by spatial variation in research intensity and data availability, and how much represents the 'true' distributional pattern of alien species. Such biases need to be taken into consideration when assessing the trends and status of alien species (McGeoch *et al.*, 2023).

Table 3. Numbers of established alien species for the Intergovernmental Panel of Biodiversity and Ecosystem Services (IPBES) regions. The numbers are extracted from the SInAS database (see Section II) and may deviate from those reported in regional studies. The numbers should be considered as minimum values as the true level of invasion is likely higher. For mammals, birds, and vascular plants, ranges of values indicate variation among databases. Duplicated taxa for the same region and Totals were removed. SAR, Stramenopila, Alveolata, Rhizaria.

	Africa	The Americas	Asia & the Pacific	Europe & Central Asia	Totals
Mammals	30–80	83–164	97–163	72–164	197–368
Birds	121–133	249–287	287–336	221–630	495–877
Fishes	187	803	633	469	1451
Reptiles	158	192	103	98	411
Amphibians	12	62	43	43	135
Insects	344	2636	2017	2747	6795
Arachnids	94	207	129	289	500
Molluscs	142	255	261	584	826
Crustaceans	125	248	158	563	813
Vascular plants	3109–4498	8005–9325	6141–9101	5146–8519	13,081–18,543
Algae	40	55	66	212	270
Bryophytes		61	44	37	118
Fungi	122	363	363	609	1149
SAR	22	150	103	373	534
Bacteria and protozoans	4	14	12	23	38
Totals	4510 – 5961	13,383–14,822	10,457–13,532	11,486–15,360	26,813–32,828

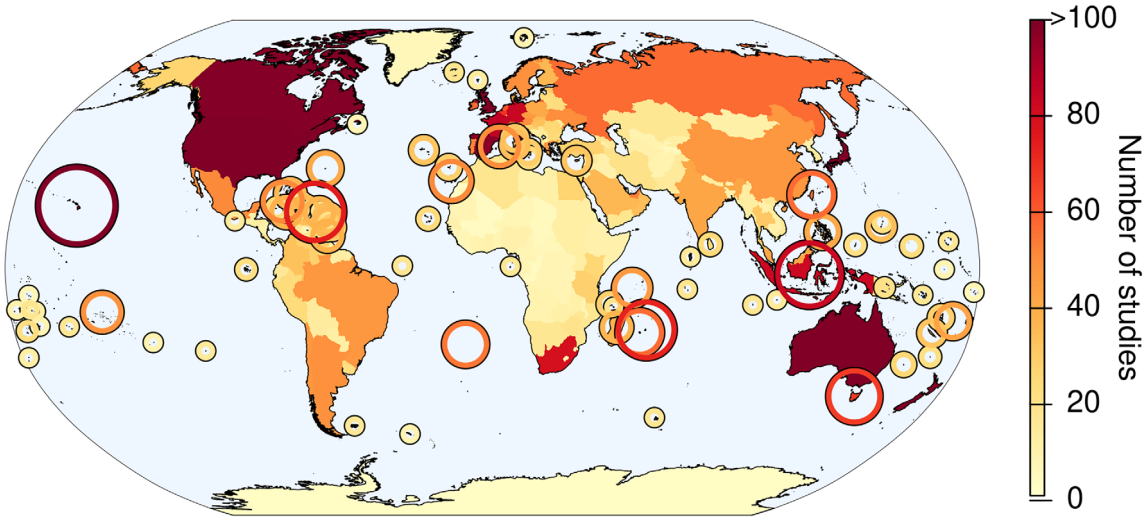

Fig. 3. Research intensity and data gaps for global alien species distribution records. Research intensity is indicated by the number of studies available for individual regions as listed in the database of this study. Islands are indicated by circles. Circle sizes increase with increasing numbers of studies.

There are conspicuous areas of low research intensity (i.e. fewer studies), particularly over large parts of Africa, Asia, and Antarctica (Fig. 3). Some islands or archipelagos have been thoroughly studied, while information is scarce for many small and remote islands. In addition to regional biases, research intensity varies across taxonomic groups. Considerably more information is available on the distribution of alien vertebrates, particularly mammals and birds, and vascular plants than for other taxa. The reasons for these knowledge gaps include undersampling, underdeveloped taxonomies, incomplete knowledge about invasion status and distributions of alien species (Hughes *et al.*, 2021; Carlton & Schwindt, 2024). Very little information is available for alien microorganisms or small invertebrates (e.g. Annelida, Porifera, or Nematoda) worldwide and recorded distributions often reflect the availability of studies rather than true species distributions. Moreover, even when such information is available, it is often highly incomplete.

V. AFRICA

(1) Bacteria and Protozoa

Among alien prokaryotes and protozoans, most records represent agents of infectious diseases either in humans or plants. *Vibrio cholerae* (cholera) is a famous example of alien Bacteria and one of the few prokaryotes with good distributional data. This species, originating from South India, was introduced to Africa in the early 19th century and is considered established in several African countries. As another example, the plant pathogen *Erwinia amylovora* (fire blight) was reported for Egypt in the 1960s and other mostly North African countries (Vanneste, 2008). No records of alien protozoans exist for Africa in the SInAS database.

(2) SAR

Altogether, 22 species of SAR have been reported in the SInAS database (Table 4), including eight species from South Africa, five from Egypt, and three from Libya. A majority of these are aquatic species, such as Phaeophyceae (brown algae), Tubothalamea (Foraminifera), and Dinophyceae (dinoflagellates). The ciliate *Mirofolliculina limnoriae* is reported as being alien for South Africa (Mead *et al.*, 2011) and two species of the genus *Sargassum* (brown algae) were found in Sierra Leone (Norman *et al.*, 2021). First records are often missing, but two of the earliest records of alien SAR in Africa stem from Libya with *Padina boryana* (brown alga), reported in 1974 (Zenetos *et al.*, 2022) and the dinoflagellate *Dinophysis acuminata* in 1991 in South Africa (Mead *et al.*, 2011). Several oomycete species, especially of the genus *Phytophthora*, have been recorded across Africa. For example, *P. infestans* (potato blight) was reported first in 1941 in Kenya, from where it spread to other African countries (Njoroge *et al.*, 2019). Other species of that genus widespread in Africa are *P. cinnamomi* (root rot), *P. nicotianae* (black shank), and *P. palmivora* (coconut budrot) (Barwell *et al.*, 2020). *Plasmopara viticola*, the downy mildew of grapevine, was introduced from North America to other wine-producing regions of the world and recorded in South Africa for the first time in 1907 (Koopman *et al.*, 2007).

(3) Fungi

A comparatively low number of 122 alien fungal species is available for Africa according to the SInAS database, while true numbers are likely much higher (Table 4). One of the earliest reported introductions to Africa was *Armillaria mellea* (honey fungus) in South Africa (Cape Town region), which presumably was introduced in the early 17th century by European settlers (Coetzee *et al.*, 2001). The plant pathogen *Claviceps africana* (ergot) was first reported in Kenya in 1924 and spread particularly in the 1980s, since when it has been recorded from several sub-Saharan countries from Ghana to Lesotho (CABI, 2009). *Batrachochytrium dendrobatidis* (chytrid fungus), likely originating from Asia, has caused amphibian declines worldwide, including in Africa (Scheele *et al.*, 2019). The trend of recording new alien fungi increased until the 1980s, while new detections of alien fungal plant pathogens in Africa have been declining more recently relative to reported increases in other regions of the world (Waage *et al.*, 2008). This is likely a consequence of low research effort rather than true decline, because new records of alien fungi are increasing worldwide (Seebens *et al.*, 2017; Sandvik *et al.*, 2019; Fuentes *et al.*, 2020).

In South Africa, nine alien fungal species are known to infect native plants, while 23 host-specific fungi of alien plant species have likely been introduced together with their hosts (Wood, 2017). In addition, 11 alien saprotrophic species, and 61 species of alien fungi forming ectomycorrhizae have been reported (Wood, 2017). Furthermore, seven host-specific alien pathogens have been introduced for the biological control of invasive alien plants (Wood, 2017). *Ceratocystis fimbriata* (ceratocystis blight) was found as an alien plant pathogen in several countries of Central and Southern Africa (CABI, 2022).

Compared to other regions of the world, Africa, with 107 species, has the lowest number of known alien macrofungi (Monteiro *et al.*, 2020), possibly because of lower research intensity. Of these, 40% of species belong to Agaricales, 29% to Boletales, and 13% to Russulales. The most widespread macrofungal species are *Pyrrhoderma noxium*, *Amanita muscaria* (fly agaric), *Pisolithus albus* (white dye-ball fungus), *Rhizopogon luteolus* (yellow false truffle), and *Suillus granulatus* (weeping bolete mushroom), recorded in eight or more countries. The highest numbers of alien macrofungi are reported for South Africa (65), Tanzania (25), Morocco (10), and Kenya (10).

(4) Plantae

(a) *Historical trends*

The number of alien plant species in Africa has increased continually for centuries as reported for multiple African

Table 4. Numbers of established alien species for subregions of Africa. The numbers are extracted from the SInAS database (see Section II) and may deviate from those reported in regional studies. The numbers should be considered as minimum values as the true level of invasion is likely much higher. For mammals, birds, and vascular plants, ranges of values indicate variation among databases. Duplicated taxa for the same region and Totals were removed. SAR, Stramenopila, Alveolata, Rhizaria.

	Central Africa	East Africa and adjacent islands	North Africa	Southern Africa	West Africa	Totals
Mammals	4–17	17–35	5–17	9–54	1–9	30–80
Birds	13–16	77–79	17–20	71–74	14–23	121–133
Fishes	26	56	130	46	17	187
Reptiles	2	33	8	124	9	158
Amphibians		5	2	2	5	12
Insects	33	143	71	227	48	344
Arachnids	9	29	10	70	11	94
Molluscs	2	11	75	67	7	142
Crustaceans	1	11	82	47	3	125
Vascular plants	880–1071	1738–2570	485–1162	1754–2292	645–818	3109–4498
Algae	1	4	30	7	1	40
Bryophytes						
Fungi	19	44	18	82	9	122
SAR	2	1	12	8		22
Bacteria and protozoans	1	2	1	2	1	4
Totals	993–1200	2171–3023	946–1638	2516–3102	771–961	4510–5961

countries (Henderson, 2006; Maroyi, 2012; Senan *et al.*, 2012; Brundu & Camarda, 2013; Shaltout *et al.*, 2016). Southern Africa experienced a steady increase in numbers of alien plant species during the entire 19th century, which was the most rapid rise of all African regions; this trend appeared to slow down only towards the end of that century (Fig. 4). By contrast, alien plant numbers in East Africa showed a marked acceleration starting in the final quarter of the 20th century and have not yet slowed down, whereas in North Africa, the numbers of alien plants increased slowly but steadily towards the end of the 19th century. No readily apparent trends could be detected for West Africa. However, trends are certainly affected by data availability and research intensity (Pyšek *et al.*, 2008, 2020; Richardson *et al.*, 2022).

(*b*) *Current status*

For most of Africa, very little information is available on the status of alien plants. Although lists of alien plant species have been published for Algeria, Angola, Eswatini, Chad, Ghana, Lesotho, Madagascar, Namibia, and Zimbabwe (many in the last decade; references in Richardson *et al.*, 2022), only for South Africa is detailed information of the status of species available – with 759 alien plant species (Richardson *et al.*, 2020). The limited data for the rest of the continent summarised in Richardson *et al.* (2022) suggest that seven other countries harbour over 300 alien plant species: Congo (522), Ethiopia (421), Morocco (410), Mozambique (396), Benin (333), Algeria (328), and Eswatini (315). South Africa also has the highest number of invasive alien species (374). Species that are widely distributed over large parts of the continent include *Lantana camara* (lantana), *Tithonia diversifolia* (Mexican sunflower), *Pontederia crassipes* (water hyacinth), *Chromolaena odorata* (Siam weed), *Leucaena leucocephala* (leucaena), *Prosopis juliflora* (mesquite), and *Parthenium hysterophorus* (parthenium weed) (Richardson *et al.*, 2022).

Many tree species used in forestry and agroforestry, especially from the genera *Acacia*, *Eucalyptus*, and *Pinus*, have been introduced throughout Africa, and some shrubs and trees, such as *Acacia melanoxylon* (Australian blackwood), *Broussonetia papyrifera* (paper mulberry), and *Calliandra houstoniana* (calliandra), are well established in many parts of the continent (Richardson *et al.*, 2022). Australian *Acacia* species are actively promoted for agroforestry in several parts of the continent (Richardson, Binggeli & Botella, 2023) and areas at higher altitudes have been heavily invaded by *A. melanoxylon*, *A. mearnsii* (black wattle), *Pinus patula* (Mexican weeping pine), and *P. radiata* (radiata pine). Pines are particularly invasive in the Southwestern mountains of South Africa and *Acacia* species invade many ecosystems in the country (Holmes *et al.*, 2005). *Prosopis juliflora* (mesquite) is common in semi-arid and arid areas of Southern and Eastern Africa. Other tree and shrub invaders with impacts include several *Rubus* (bramble) species and *Biancaea decapetala* (Mysore thorn). *Azadirachta indica* (neem tree), *Lantana camara* (lantana), and *Leucaena leucocephala* (leucaena) are abundant invaders along the coastline of much of Africa, preferring hot and humid conditions. *Chromolaena odorata* (Siam weed) is now common in many countries in Central and Southern Africa, being abundant in open savanna grasslands, woodlands, riparian zones, forest gaps, and edges (Richardson *et al.*, 2022).

La Réunion is estimated to have over 2000 alien plant species, with more than 100 of these classified as invasive, e.g. *Leucaena leucocephala* (leucaena), *Hiptage benghalensis* (hiptage), and *Ulex europaeus* (gorse) (Baret *et al.*, 2006; Soubeyran

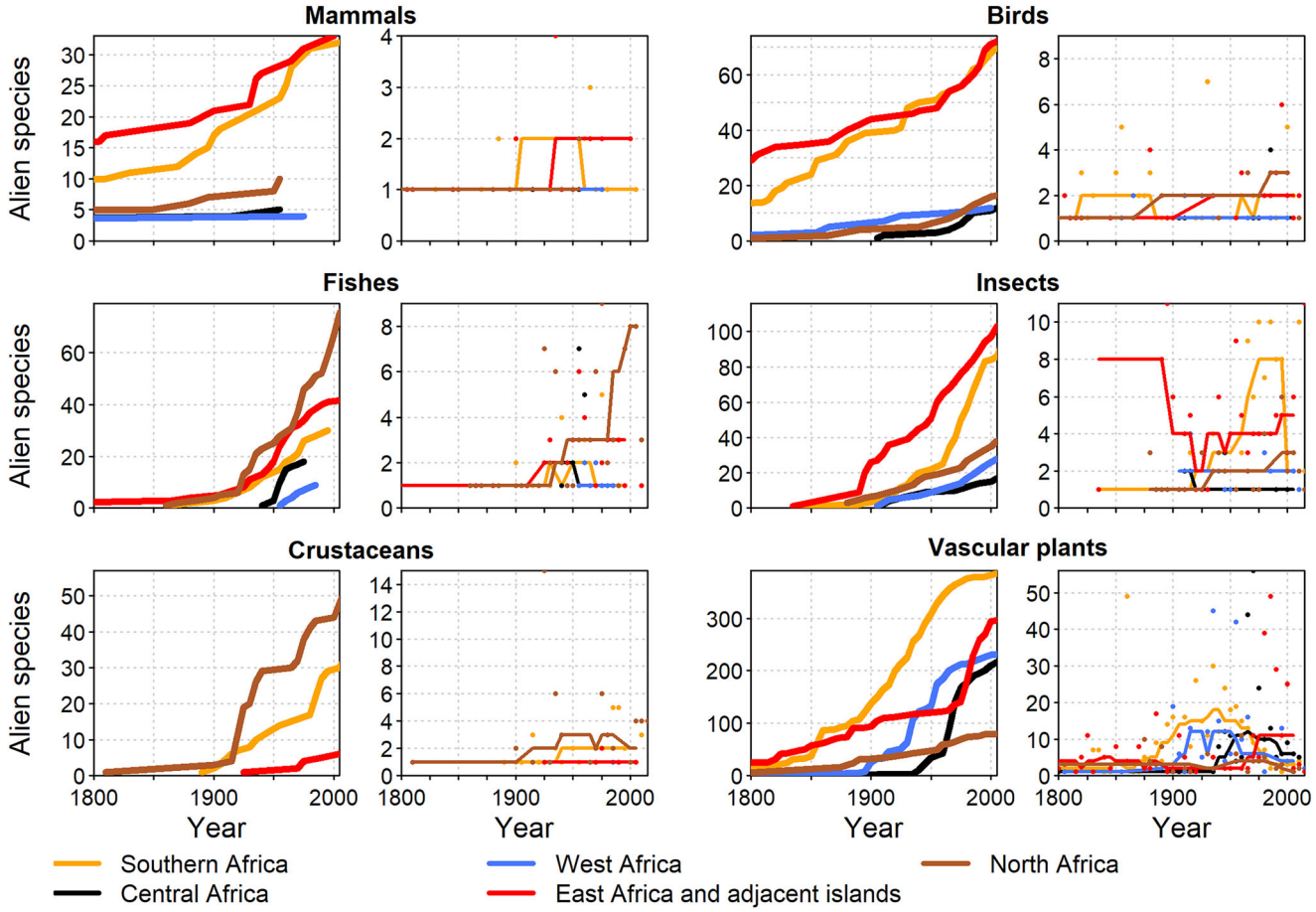

Fig. 4. Trends in numbers of established alien species for Africa. Panels by taxon show cumulative numbers (left panels, thick lines) and numbers of new alien species per five-year intervals (right panels, thin lines). The actual numbers of alien species occurrences are underestimated due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians. Note that presented numbers may deviate from those reported in the text due to variation among data sources.

et al., 2015). On Socotra, 88 alien plants have been recorded (Senan *et al.*, 2012). A total of 28 major alien aquatic plants has been recorded in African waters, 16 of which are alien to the whole of Africa, and 12 are native to other parts of the continent (Howard & Chege, 2007; Sghaier *et al.*, 2011). A recent review records the existence of 19 alien freshwater plants only in South Africa, mainly introduced through trade and hitchhiking *via* boating and angling (Hill *et al.*, 2020). In South Africa, the most important alien freshwater macrophyte remains *Pontederia crassipes* (water hyacinth). The marine alien seagrass *Halophila stipulacea* is native to the East African coast, yet is invasive along the Mediterranean coast from Egypt to Tunisia, an early introduction through the Suez Canal (Winters *et al.*, 2020).

(5) Animalia

(*a*) *Historical trends*

The number of alien animal species has increased continuously for all taxonomic groups in all African regions (Fig. 4), similar to the observed global patterns (Fig. 1). European acclimatisation societies were very active, particularly in South Africa, and introduced many plant, bird, and mammal species to 'improve' landscape aesthetics to conform with European preferences around the mid-1800s (Osborne, 2000; van Wilgen *et al.*, 2020). Several islands off the African coasts, such as St. Helena, Mauritius, and La Réunion, played important strategic roles for international shipping and ocean crossings during colonial times (Cheke & Hume, 2008), and consequently have many early records of species introductions (Fuller & Boivin, 2009). In São Tomé and Príncipe, species introductions by Europeans began in the 1470s with 14 alien mammal species established on São Tomé and 12 on Príncipe (Dutton, 1994). In the 20th century, increasing global trade accelerated alien species introductions across Africa and, combined with the advent of the game-farming industry and ecotourism, resulted in a striking rise in introductions of alien vertebrates and invertebrates (Picker & Griffiths, 2017; Measey, Hui & Somers, 2020; van Wilgen *et al.*, 2020; Muñoz-Mas *et al.*, 2023).

For mammals, birds, and insects, documented increases tended to be higher in East Africa and adjacent islands,

mostly because of many early species introductions on the islands of Mauritius and La Réunion that were not recorded elsewhere. For fishes and crustaceans, particularly high increases of new alien species were recorded in North Africa after 1869 (Fig. 4) when the Suez Canal opened and initiated the Erythraean invasion of marine species (Galil, 2023), a trend that continues until today (Fig. 4). In South Africa, the overall rate of introductions of alien freshwater animals accelerated sharply after 1880 and generally increased over time, with unintentional introductions of invertebrates playing a relevant role (Weyl *et al.*, 2020). Only freshwater fish introductions decreased significantly after the 1950s, probably due to new legislation regulating such introductions, which decreased demand for new angling species (Faulkner, Robertson & Wilson, 2020). In general, the number of invertebrate introductions to South Africa rose over time (Faulkner *et al.*, 2020), this pattern being reported for freshwater (Weyl *et al.*, 2020), terrestrial (Janion-Scheepers & Griffiths, 2020), and marine invertebrate introductions (Robinson, Peters & Brooker, 2020). The observed rise in alien species seems affected by increased sampling intensity: while only four marine alien species were reported before 1900 (Robinson *et al.*, 2020), several other species were likely introduced much earlier (Carlton & Schwindt, 2024).

(*b*) *Current status*

The African continent currently harbours 44 alien mammals (Biancolini *et al.*, 2021), although there is a range of 30–80 reported alien mammals depending on the source (Table 4). These alien species are mainly concentrated along the Western Mediterranean coast, South Africa, and Madagascar. Alien mammals can be found on each group of the 28 island groups in the Western Indian Ocean, with an average richness of five species per island group (Russell *et al.*, 2016). There are 12 invasive alien mammal species on La Réunion and six of them on the nearby Îles Éparses (Russell & Le Corre, 2009). Most alien bird species in Africa are found in the far south of the continent, although *Corvus splendens* (house crow) is distributed from Sudan to South Africa along the East coast. The islands of East Africa are important hubs of alien reptiles and amphibians globally: Mauritius and La Réunion are inhabited by 17 and 15 alien species, respectively (Kraus, 2009; Capinha *et al.*, 2017; Telford, Channing & Measey, 2019).

Although insects have the highest species richness in general, their proportional representation in Table 4 is still less than expected (344 alien insects out of at least 4510 alien species; Table 4), likely due to under-reporting of alien insects in the African continent. South Africa is the only African country with a comprehensive list of alien insect species, comprising 300 out of 571 alien animal species in South Africa (Picker & Griffiths, 2017). Most alien arthropods (including insects) in Africa are terrestrial, with the Hemiptera comprising the largest fraction, followed by the Coleoptera (Janion-Scheepers & Griffiths, 2020). Most insects are introduced accidentally and the Hemiptera are known to be common contaminants of plants that are shipped internationally for propagation in agriculture, forestry or horticulture (Liebhold *et al.*, 2012). Some of the most impactful insect invaders, which are widely distributed in Africa, include *Spodoptera frugiperda* (fall armyworm) and *Tuta absoluta* (tomato leafminer), both of which have severe impacts on food production in many African countries (Day *et al.*, 2017; Rwomushana *et al.*, 2019).

East Africa and its adjacent islands have the second highest numbers of alien fishes, probably because of introductions in the many lakes of the Rift Valley area, including the three largest, Lakes Victoria, Tanganyika, and Malawi (Craig, 1992; Pitcher & Hart, 1995), and Lake Naivasha (Kenya), where the rates of introductions have increased steadily since the 1950s (Gherardi *et al.*, 2011). Twenty-one alien freshwater fishes have been established in South Africa (Ellender & Weyl, 2014; Weyl *et al.*, 2020), while 16 alien fish species have been introduced in Central Africa (Brooks, Allen & Darwall, 2011) (26 alien fishes have been reported in total, Table 4). In Madagascar, one quarter of the freshwater fish fauna consists of alien species, with 26 alien species present (Šimková *et al.*, 2019). On La Réunion, six species of fish and one decapod crustacean, *Macrobrachium rosenbergii* (giant freshwater prawn) were introduced by 2002, but only four were established by then (Keith, 2002).

Five freshwater alien crayfish have established populations in the wild, of which three have spread widely across Africa: *Procambarus clarkii* (red swamp crayfish), *P. virginalis* (marbled crayfish), and *Cherax quadricarinatus* (redclaw crayfish) (Madzivanzira *et al.*, 2021). Seventy-seven alien freshwater animals, with numbers largely dominated by fishes, molluscs, and crustaceans, are currently established in South Africa, most of which were intentionally introduced (Picker & Griffiths, 2017; Weyl *et al.*, 2020). Many species of alien molluscs have been recorded in African fresh waters, with 14 species of gastropods reported by 2011, some of which were released for the biological control of the intermediate hosts of schistosomiasis (Appleton & Brackenbury, 1998; Appleton, 2003). Only a few alien freshwater bivalves have been recorded in African waters, such as *Corbicula fluminea* (Asian clam) and *Sinanodonta woodiana* (Chinese pond mussel), both probably related to fish stocking (Darwall *et al.*, 2011; Clavero *et al.*, 2012; Mabrouki & Taybi, 2022). Among alien freshwater jellyfish, the cnidarian *Craspedacusta sowerbii* (peach blossom jellyfish) has been recorded in South Africa and Morocco (Oualid *et al.*, 2019; Weyl *et al.*, 2020).

Information about marine alien species is mostly limited to certain coasts, mainly in South Africa and North Africa: high numbers of marine alien species had been reported by 2020 along Mediterranean and Red Sea coasts of Northern African countries, such as Morocco (24), Algeria (41), Tunisia (166), Libya (77), and Egypt (266) (Galanidi *et al.*, 2023). Numbers have since increased to 39 species in Moroccan Mediterranean waters (Mghili *et al.*, 2024). Erythraean species are clearly expanding their distribution westwards along the African coast, with over 60% of alien species recorded in Tunisian waters considered to have been introduced through

the Suez Canal (Ounifi-Ben Amor *et al.*, 2015). A strong positive relationship between the time elapsed since Erythraean species' first record in the Mediterranean and its westward spread calls attention to a considerable invasion debt advancing westwards (Galil *et al.*, 2021). Along the South African coast, which includes two large marine ecosystems, the Agulhas current in the East and the Benguela current in the West (Mead *et al.*, 2011; Robinson *et al.*, 2020), 95 alien marine species have been reported, of which 56 are considered invasive. A variety of taxa are represented, from small protists (e.g. *Mirofolliculina limnoriae*) and dinoflagellates (e.g. *Alexandrium minutum*) to the most conspicuous macroalgae, molluscs, crustaceans, bryozoans, and tunicates. The most common taxa are ascidians (e.g. *Ciona robusta* and *Botryllus schlosseri*; Peters, Sink & Robinson, 2017). Populations of *Diadumene leucolena* (sea anemone) have been recorded from Senegal (Glon *et al.*, 2020).

VI. THE AMERICAS

(1) Bacteria and Protozoa

Among Bacteria, 14 alien Proteobacteria have been reported in the SInAS database for The Americas. A well-known case is the introduction of *Vibrio cholerae*, causing cholera in humans, which has been introduced repeatedly and to different regions of The Americas (Colwell, 1996; Louis *et al.*, 2003). The introduction of *V. cholerae* through ballast water was considered the cause of a severe cholera outbreak in South America (Colwell, 1996) but it has also been detected in the Chesapeake Bay, USA (Louis *et al.*, 2003). The introduction of *Yersinia pestis*, the agent of bubonic plague, which has been reported from multiple countries in South America, is another example. Agents of infectious diseases, such as the variola virus (smallpox virus; now eradicated globally), *Measles morbillivirus* (measles virus), Bacteria causing typhus, and *Vibrio cholerae* (cholera), were introduced through European colonisation mostly accidentally, although in some cases diseases were intentionally introduced to decimate populations of Native Americans (Oldstone, 2020). Other alien prokaryotes represent plant pathogens, including different species of the genus *Xanthomonas* (*X. campestris* and *X. axonopodis*), which have been reported from various countries throughout The Americas. Among protozoans, three species have been recorded as alien in Canada, USA, and Mexico, namely *Haplosporidium nelsoni*, *H. costale*, and *Glugea hertwigi* (Mills *et al.*, 1993; Pederson *et al.*, 2017; Simpson *et al.*, 2018). These species are pathogens of oysters and fish.

(2) SAR

For The Americas, a total of 150 species of SAR are included in the SInAS database (Table 5). One of the earliest records is the oomycete *Phytophthora cinnamomi* from 1850 in the USA (Aukema *et al.*, 2010). This species is considered as one of the most devastating plant pathogens globally, with a widespread distribution and a broad host range of around 5000 known plant hosts (Hardham & Blackman, 2018). Several other species of the same genus have been reported. For example, the sudden oak death pathogen, *P. ramorum*, has infected ecologically, economically, and culturally important genera in North America including *Quercus* and *Notholithocarpus* spp. (McPherson *et al.*, 2005). *Phytophthora lateralis* caused declines in the Port-Orford-Cedar, endemic to the Eastern USA, with first reports in natural stands from the 1950s (Jung *et al.*, 2018).

Table 5. Numbers of established alien species for subregions of The Americas. The numbers are extracted from the SInAS database (see Section II) and may deviate from those reported in regional studies. The numbers should be considered as minimum values as the true level of invasion is likely much higher. For mammals, birds, and vascular plants, ranges of values indicate variation among databases. Duplicated taxa for the same region and Totals were removed. SAR, Stramenopila, Alveolata, Rhizaria.

	Caribbean	Mesoamerica	North America	South America	Totals
Mammals	35–62	8–34	49–95	25–77	83–164
Birds	110–113	29–41	210–211	53–114	249–287
Fishes	91	226	619	144	803
Reptiles	60	60	121	56	192
Amphibians	20	8	41	16	62
Insects	153	163	2116	640	2636
Arachnids	33	36	168	76	207
Molluscs	26	60	212	68	255
Crustaceans	10	64	173	79	248
Vascular plants	1402–1761	1600–2242	6571–7424	2492–3099	8005–9325
Algae	2	14	32	21	55
Bryophytes			40	32	61
Fungi	17	15	174	219	363
SAR	4	93	40	34	150
Bacteria and protozoans	1	4	6	5	14
Totals	1964–2353	2380–3060	10,572–11,472	3960–4680	13,383–14,822

Other widespread SAR are marine species, such as the brown algae *Sargassum muticum* (wireweed), *S. fluitans*, and *Undaria pinnatifida*, or the dinoflagellate *Gymnodinium catenatum* (Williams, 2007; Simpson *et al.*, 2018). A high number of 94 alien SAR was reported in Mexico according to the GRIIS database (González Martínez *et al.*, 2020), followed by the USA (Simpson *et al.*, 2018), and Argentina (Zalba *et al.*, 2021). For a few countries comprehensive assessments of alien species have been conducted, which also list SAR. For example, five marine SAR have been reported for Chile (Fuentes *et al.*, 2020) and 12 for the USA (Simpson *et al.*, 2018), most of them being members of Ochrophyta (brown algae).

(3) Fungi

While it is difficult to trace its initial introduction date, one early introduction was black stem rust of wheat (*Puccinia graminis*) with an epidemic in the USA in 1878. A colony in Rio Grande do Sul, Brazil, reported yield losses due to stem rust already in the 1700s (CABI, 2021). Earlier introductions of other fungal species likely occurred unnoticed. First reports of a cacao disease matching the infestation by *Moniliophthora roreri* (frosty pod rot of cacao) appeared in 1817 in Colombia, which is outside its presumed native range (Bailey *et al.*, 2018). Two important forest pathogens are *Cronartium ribicola* (white pine blister rust), first reported in the USA in 1906 (Geils, Hummer & Hunt, 2010), and *Cryphonectria parasitica* (chestnut blight), first reported in the USA in 1904 (Rigling & Prospero, 2018), both having caused significant impacts to native biota. *Cryphonectria parasitica* has rendered *Castanea dentata* (American chestnut) functionally extinct in North America (Dutech *et al.*, 2012). *Ophiostoma ulmi* (Dutch elm disease), introduced to North America in 1928, and followed by the more aggressive *O. novo-ulmi*, severely impacted *Ulmus americana* (American elm) in the USA and Canada (Copeland *et al.*, 2023). In South America, *Hemileia vastatrix* (coffee leaf rust) was successfully intercepted in 1903 in Puerto Rico, but established in Brazil in the 1970s, marking the onset of the third great pandemic of coffee rust globally (McCook, 2006). First records of alien fungi in Chile were documented beginning in the early 20th century and have shown a continuous increase until the present (Fuentes *et al.*, 2020).

Altogether, 363 alien fungi are reported in the SInAS database for The Americas (Table 5). The USA has the highest number of alien fungi (136), followed by Chile (81), Brazil (80), and Argentina (65) (see also Simpson *et al.*, 2018; Fuentes *et al.*, 2020). Two widespread and well-known alien fungal pathogens in The Americas are *Batrachochytrium dendrobatidis* (chytrid fungus), which has caused massive population declines and extinctions in amphibian species since the 1960s (Fisher, Garner & Walker, 2009), and *Claviceps africana* (ergot).

The Americas harbour at least 199 alien macrofungi species, with approximately 36% belonging to the order Agaricales, 32% to Boletales and 11% to Russulales (Monteiro *et al.*, 2020). Some of the most widely distributed are ectomycorrhizal fungi, such as *Suillus luteus*, *Rhizopogon roseolus*, and *Suillus granulatus* (weeping bolete), which seemed to play a key role in pine invasions of the Southern Hemisphere (Policelli *et al.*, 2019). South American countries with high numbers of known alien fungi include Brazil (75), Argentina (60), and Chile (40) (Monteiro *et al.*, 2020). In the remaining IPBES subregions, higher numbers of alien macrofungi were recorded in the USA (50), Canada, and Mexico (seven each).

(4) Plantae

(a) *Historical trends*

The first explorers of the eastern coast of The Americas introduced *Lolium perenne* (perennial ryegrass), and *Trifolium repens* (clover) among others; these alien species were fully established prior to colonisation by Europeans (Crosby, 1986). English colonisation of the North American east coast in the 17th century led to deforestation and the establishment of farms where many European species were cultivated for ornamental [e.g. *Taraxacum officinale* (dandelion)] or medicinal [*Verbascum thapsus* (common mullein)] purposes, directly sown in pastures [*Poa pratensis* (smooth meadow-grass)], or brought in as weeds [*Capsella bursa-pastoris* (shepherd's purse)] (Crosby, 1986), or in ship's solid ballast [*Phragmites australis* (common reed)] (Saltonstall, 2002). Over the last two centuries, North America has had the most rapid cumulative rate of increase of alien plant species, accelerating at the end of the 19th century (Fig. 5) (Lavoie *et al.*, 2012; Pyšek *et al.*, 2019), with macrophytes such as *P. australis* invading across the continent in less than 200 years (Meyerson *et al.*, 2025). South America exhibited a slower cumulative increase, likely due to lower research intensity relative to North America (Frehse *et al.*, 2016; Schwindt & Bortolus, 2017; Schwindt *et al.*, 2020). Nevertheless, as early as 1877, an impressive number of plant species were recorded as introduced in Argentina from Europe through the port of Buenos Aires, from where they rapidly dispersed up to the southernmost end of Patagonia (Berg, 1877; Bortolus & Schwindt, 2022). The rates of newly recorded alien plants began decreasing in the mid-20th century, particularly in North America (Fig. 5). The magnitude of introductions in the Caribbean and Mesoamerica was much lower, but showed increases similar to those observed in North and South America (Fuentes *et al.*, 2008; Ugarte, Fuentes & Klotz, 2010; Rojas-Sandoval & Acevedo-Rodríguez, 2015).

(b) *Current status*

North America has the highest number of recorded alien plant species in the world with at least 5958 established taxa (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017), while South America harbours 2667 alien plant species (Pyšek *et al.*, 2019). Globally, California is richest in alien vascular plants, with 1753 taxa recorded and Florida is another

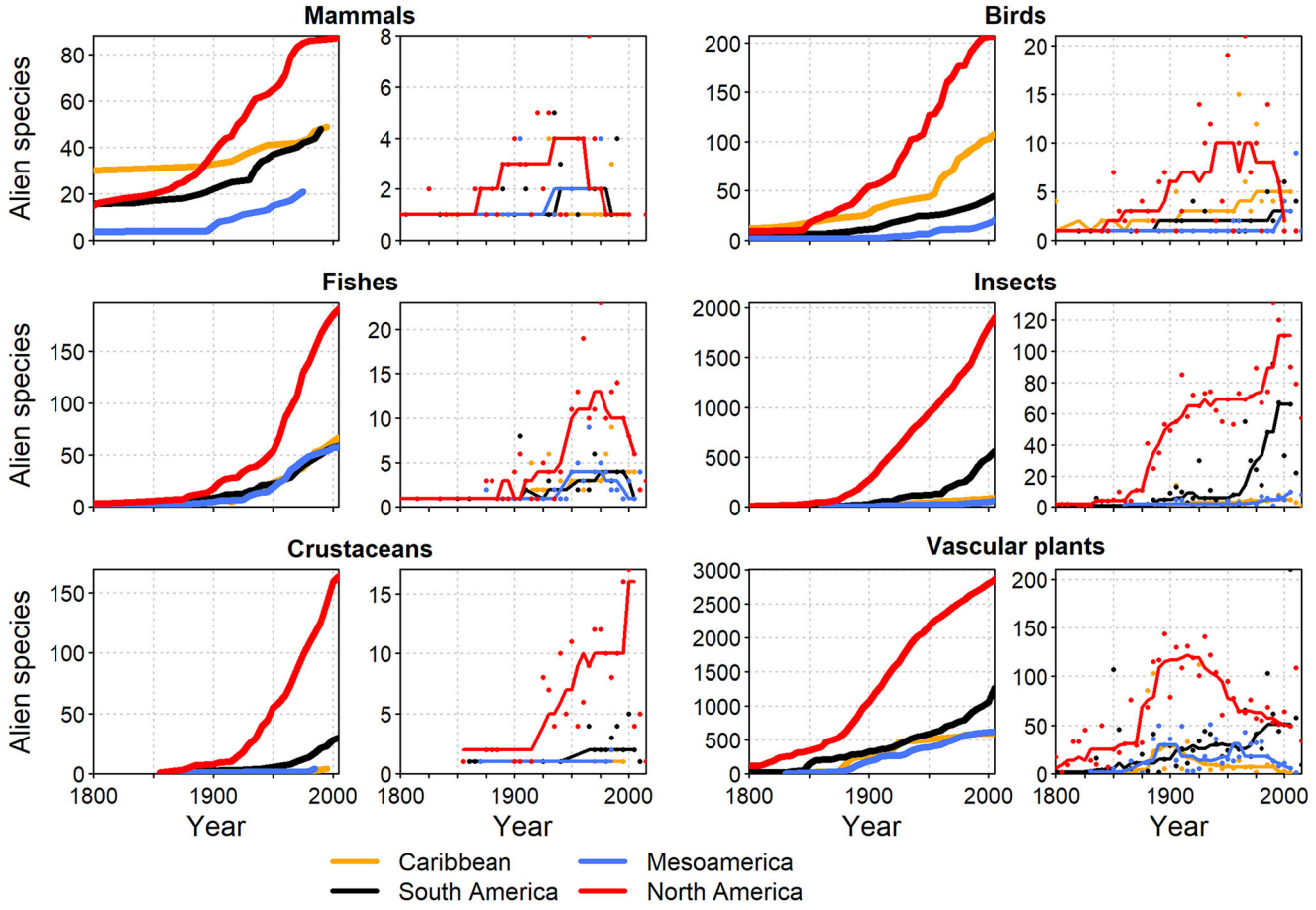

Fig. 5. Trends in numbers of established alien species for The Americas. Panels by taxon show cumulative numbers (left panels, thick lines) and number of new alien species per five-year intervals (right panels, thin lines). Numbers shown here underestimate the real extent of alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians. Note that presented numbers may deviate from those reported in the text due to variation among data sources.

invasion hotspot harbouring 1473 alien plants (Kartesz, 2015). According to Pyšek *et al.* (2017), countries in Mesoamerica also harbour many alien plants (Nicaragua: 671, Mexico: 519, Costa Rica: 280, Panama: 263), but due to their high native diversity, alien plants make up only 2.0–2.8% of the total floras, the exception being Nicaragua with 10.4% (Correa A., Galdames & De Stapf, 2004; Chacón & Saborío, 2012; Pyšek *et al.*, 2017). Some regions in the Caribbean are heavily invaded by alien plants, both in terms of actual species numbers (Cuba: 542, Bahamas: 356) and the proportion of alien plants in the national floras (Bahamas 24%, Barbados 14%). Other countries in the Caribbean harbour 20–110 alien plants and contributions to national floras do not exceed 8% (Acevedo-Rodríguez & Strong, 2008; Kartesz, 2015; Pyšek *et al.*, 2017).

Alien species are widespread on islands along both the Pacific and Atlantic coasts of The Americas, notably the Caribbean islands (Kairo *et al.*, 2003; Van der Burg *et al.*, 2012; Rojas-Sandoval & Acevedo-Rodríguez, 2015). As an example, parts of Caribbean island forests are dominated by alien tree species (Chinea & Helmer, 2003; Brandeis *et al.*, 2009; Helmer *et al.*, 2012), some of which are shade tolerant and could permanently change forest species composition (Brown *et al.*, 2006). In addition, several alien species invade forest plantations, livestock pastures, and abandoned agricultural fields causing both economic and environmental impacts. Such is the case for *Dichrostachys cinerea* (sickle bush), an alien species of African origin that occurs across almost 800,000 hectares in Cuba (Hernández, Lahmann & Pérez-Gil Salcido, 2002).

An example of a widespread marine plant is *Halophila stipulacea* (broadleaf seagrass; native to the Indian Ocean and Red Sea), which invaded the coasts of the Mediterranean Sea as early as 1895 (Winters *et al.*, 2020), and then the Caribbean Sea by 2002 (Willette *et al.*, 2014). Compared to the slow spread of this seagrass across the Mediterranean from Egypt to Tunisia (~120 years), it invaded coasts from Puerto Rico to Venezuela in just 15 years (Winters *et al.*, 2020), becoming the world's first circumglobal marine alien angiosperm. The seagrass *Zostera japonica* (dwarf eelgrass) was

introduced to the Pacific northwest in the mid-1900s likely *via* oyster aquaculture and has since spread and negatively impacted native *Zostera marina* (eelgrass) and ecosystem processes (Shafer, Kaldy & Gaeckle, 2014).

The Galapagos Archipelago harbours an estimated 1700 alien species with *Rubus niveus* (Mysore raspberry) being among the most common (Toral-Granda *et al.*, 2017), posing a serious threat to the foundation species of native forest, endemic daisy tree *Scalesia pedunculata* (Riegl *et al.*, 2023) and, together with *Cestrum auriculatum* and *Tradescantia fluminensis*, to the entire forest (Jäger *et al.*, 2024). Between the 1980s and 1990s, the number of alien plants has nearly doubled on the Galapagos Islands, reaching nearly 900 species (Torres & Mena, 2018). A study of the residence time and human-mediated propagule pressure of plants suggests that this archipelago is still in an early stage of plant invasions, due to the booming tourism industry and increasing human population size (Trueman *et al.*, 2010).

(5) Animalia

(a) *Historical trends*

The number of alien animals in The Americas has continuously increased across all taxonomic groups, especially post-1850, and across all subregions (Fig. 5). Particularly sharp increases were observed for North America, followed by South America, while alien birds steeply increased in the Caribbean. The first introductions of alien mammals date to pre-Columbian times in the Caribbean islands, e.g. *Didelphis marsupialis* (common opossum) and *Dasyprocta leporina* (agouti) (Long, 2003; Giovas, LeFebvre & Fitzpatrick, 2012; Biancolini *et al.*, 2021). The number of alien species introductions began surging in the 15th century with European colonisation, peaked in the 20th century with many introduced game species, and more recently, *via* the pet trade (Long, 2003; Biancolini *et al.*, 2021). Since 1900, rates of increase have declined in a few cases, particularly for mammals and fishes (Fig. 5). The number of alien amphibians and reptiles in The Americas has increased since the 1950s with new alien species introductions *via* the pet trade projected to remain steady or accelerate (Kraus, 2009; Powell *et al.*, 2011; Stringham & Lockwood, 2018; Lockwood *et al.*, 2019; Perella & Behm, 2020).

Several studies indicate increasing numbers of alien insects in North America (Mattson *et al.*, 1994; Aukema *et al.*, 2010; Nealis *et al.*, 2016). Some of the earliest alien insect introductions were ground-dwelling beetles, such as Carabidae, accidentally transported from Europe with rocks used as ship ballast (Lindroth, 1954). During the early 1900s, many insect species, such as *Quadraspidiotus perniciosus* (San Jose scale), were accidentally introduced with plants imported for agriculture and horticulture (Liebhold & Griffin, 2016). In South America, the number of reported alien aquatic organisms is rapidly increasing (e.g. Fuentes *et al.*, 2020; Schwindt *et al.*, 2020; Vitule *et al.*, 2021). The first alien aquatic species introductions occurred in the 1500s in conjunction with European colonisation. The number of introductions remained low in the 1800s and 1900s, but increased thereafter (Vitule *et al.*, 2021). Beginning in the 2000s, both the number of records and the number of studies on alien organisms increased continuously (e.g. Frehse *et al.*, 2016; Vitule *et al.*, 2021), with no sign of slowing down, both in terms of alien species numbers and new spatiotemporal records (e.g. Vitule *et al.*, 2021).

For marine alien species, seminal studies have highlighted rising numbers in American waters (Cohen & Carlton, 1998; Carlton & Eldrege, 2015; Carlton & Schwindt, 2024). For example, in temperate coastal waters of The Americas, new data show an increase in the total number of alien species detected, while the rate of new detections of alien species has stabilised (Bailey *et al.*, 2020). Following a distinct intensification of research efforts on marine alien species in South America between 1997 and 2014 (Schwindt & Bortolus, 2017), the number of introduced species increased by 160% between 2009 and 2019 in Brazil (Teixeira & Creed, 2020). In Argentina and Uruguay, marine alien species numbers increased by a factor of 4.5 between 2001 and 2019, with one new species estimated to arrive every 178 days (Schwindt *et al.*, 2020).

(b) *Current status*

The Americas host 96 species of alien mammals with particularly high species numbers on the East coast of North America, Alaskan islands, Southern USA, the Caribbean Archipelago, Patagonia, and Falkland Islands (Malvinas) (Biancolini *et al.*, 2021). The number of reported alien mammals ranges from 83 to 164, depending on the source (Table 5). One of the most widespread alien mammals in The Americas is *Urva auropunctata* (small Indian mongoose) which has established on many islands in the Caribbean (Hays & Conant, 2007; Louppe *et al.*, 2020; Biancolini *et al.*, 2021). North America is particularly rich in alien bird species, notably in Florida and California where several alien parrot species have established populations (Dyer, Redding & Blackburn, 2017b). The Americas have the highest number of alien reptiles and amphibians in the world with several hotspots in the USA (Kraus, 2009; Krysko *et al.*, 2011, 2016; Capinha *et al.*, 2017), including Florida, California, and Puerto Rico (Meshaka, 2011; Powell *et al.*, 2011; Perella & Behm, 2020). Other Caribbean islands, such as Cuba and the Bahamas, are also important global alien amphibian hotspots (Kraus, 2009; Knapp *et al.*, 2011; Powell *et al.*, 2011; Borroto-Páez *et al.*, 2015). In South America, Brazil has the highest number of alien amphibian and reptile species (136), of which at least seven have established wild populations (Kraus, 2009; Fonseca, Both & Cechin, 2019). Globally, North America has the most alien insect species (Liebhold *et al.*, 2016) with the largest concentration of species in Northeastern North America (Liebhold *et al.*, 2013). Even though there are more described species of Coleoptera than any other order, there are slightly more alien Hemiptera species established in North America

(Yamanaka *et al.*, 2015; Liebhold *et al.*, 2016) and Chile (López *et al.*, 2023). The over-representation of the Hemiptera is most likely the result of the ease with which they are accidentally introduced with imported plants.

The most recent studies of freshwater fishes in South America indicate that more than 75 alien species have been translocated between different basins within South America (Bezerra *et al.*, 2019; Vitule *et al.*, 2019) and more than 80 alien fish species from other regions of the world (Vitule *et al.*, 2019, 2021; Doria *et al.*, 2021). A famous example of an alien aquatic invertebrate is *Limnoperna fortunei* (golden mussel) (Schwindt & Bortolus, 2017). North America has a long history of aquatic species introductions, particularly for fish, such as *Salmo trutta* (brown trout) or *Cyprinus carpio* (common carp) (Moyle, 1986; Courtenay & Meffe, 1989; Fuller, Nico & Williams, 1999), as well as many crustaceans and molluscs, such as *Bythotrephes longimanus* (spiny waterflea), *Dreissena* spp. (zebra and quagga mussels), and *Corbicula* spp. (basket clams). The Laurentian Great Lakes have been invaded by nearly 190 alien species (Ricciardi, 2006; Ricciardi & MacIsaac, 2022), more than any other freshwater ecosystem in the world. These species include several invasive alien animals of Ponto-Caspian origin, mostly introduced through ballast water (Ricciardi & MacIsaac, 2000; Ricciardi, 2001, 2006; Vanderploeg *et al.*, 2002). Many species native to small regions of The Americas, such as *Faxonius rusticus* (rusty crayfish), *Gambusia* spp. (mosquitofishes), and salmonids, such as *Oncorhynchus mykiss* (rainbow trout), have been widely introduced throughout The Americas and elsewhere (Marr *et al.*, 2013; Schwindt *et al.*, 2018; Muñoz-Mas *et al.*, 2023). A spectacular case is the North American beaver (*Castor canadensis*), which was introduced to the Tierra del Fuego Archipelago in 1946 and negatively impacts *Nothofagus* forests; subsequently, abandoned beaver ponds become hotspots for the spread of alien pasture plants (Skewes *et al.*, 2006).

Studies of marine alien species across The Americas are geographically and taxonomically patchy. Spatial and temporal surveys are scarce, even in well-studied regions, such as the USA, making it difficult to draw general conclusions (Bailey *et al.*, 2020). The first comprehensive assessment was for the continental coasts of the USA, finding 298 marine alien species (Ruiz *et al.*, 2000), but by 2006, 257 marine alien species were identified in California alone (Ruiz *et al.*, 2011). In South America, the Southwestern Atlantic region is the most-investigated area for marine invasive alien species, with fish and molluscs represented in the largest numbers of studies, species, and spatiotemporal occurrence records (Frehse *et al.*, 2016; Schwindt & Bortolus, 2017; Bezerra *et al.*, 2019). Brazil has the highest number with 138 marine alien species (Teixeira & Creed, 2020), followed by Argentina and Uruguay with 129 alien species in total (Schwindt *et al.*, 2020). On the Pacific coast, Chile reported 51 marine alien species (Castilla & Neill, 2009; Villaseñor-Parada, Pauchard & Macaya, 2017) and Colombia four (Gracia *et al.*, 2011). As with essentially all coasts worldwide, the numbers of introductions are distinctly under-estimated due to an absence of historical baselines and a lack of research (Schwindt & Bortolus, 2017; Carlton & Schwindt, 2024). For example, the number of marine alien species in Chile is likely to be much higher than the reported 51 (Stowhas Salinas *et al.*, 2023).

VII. ASIA & THE PACIFIC

(1) Bacteria and Protozoa

Little is known about alien prokaryotes with very few reports in Asia & the Pacific. Chen, Sun & Zhan (2017b) reported three Proteobacteria in China, *Pseudomonas syringae*, *Acidovorax avenae*, and *Xanthomonas oryzae* (leaf blight), which are known for their role as plant pathogens, and one marine cyanobacterium *Trichodesmium erythraeum*. The proteobacterium and plant pathogen *Xanthomonas axonopodis* has been recorded across multiple Pacific Islands from Australia to the Hawaiian Islands (EPPO, 2016; Nahrung & Carnegie, 2020). *Erwinia amylovora* (fire blight) has been recorded for multiple countries mostly on mainland Asia (Vanneste, 2008).

(2) SAR

The SInAS database includes 103 taxa of SAR for Asia & the Pacific (Table 6). While the earliest record is *Phytophthora infestans* (potato blight) from 1900 (APASD, 2024), the number of records showed a strong increase starting in the 1970s and continuing until today. Soilborne plant pathogens like *P. cinnamomi*, which originates from Southeast Asia (Hardham & Blackman, 2018; Thakur *et al.*, 2019), and *P. ramorum* (sudden oak death) are also widely distributed and occur on several hosts in most countries in Asia (Davison, 2022; Garbelotto & Frankel, 2020) including several Australian islands (Auld & Hutton, 2004; Pickering, Bear & Hill, 2007), Hawaii (Davison, 2022), Fiji, Samoa, Tuvalu, and New Zealand (Campbell, 2010; Thaman, 2011; Thaman & O'Brien, 2011). Other frequently recorded species are the brown alga *Undaria pinnatifida* and the dinoflagellate *Alexandrium minutum*. A large number of the taxa reported in the SInAS database are marine (96 species), including species of the genus *Alexandrium*, *Sargassum*, and *Rhizosolenia*. For China alone, 60 species of SAR (in all realms) have been reported with the majority being Ochrophyta (31 species), such as five species of the genus *Rhizosolenia*, followed by Myzozoa (21) (Xu *et al.*, 2012; Chen *et al.*, 2017b). For Australia, 13 species have been recorded in the SInAS database, of which six were identified as forest pests (Nahrung & Carnegie, 2020).

(3) Fungi

For Asia & the Pacific, the highest numbers of alien fungi are reported in New Zealand (180 species) and Australia (132) according to the SInAS database. However, the database *Biota of New Zealand* lists more than 2000 alien fungi just for New Zealand, indicating the huge discrepancy among

Table 6. Numbers of established alien species for subregions of Asia & the Pacific. The numbers are extracted from the SInAS database (see Section II) and may deviate from those reported in regional studies. The numbers should be considered as minimum values as the true level of invasion is likely much higher. For mammals, birds, and vascular plants ranges of values indicate variation among databases. Duplicated taxa for the same region and Totals were removed. SAR, Stramenopila, Alveolata, Rhizaria.

	Northeast Asia	Oceania	South Asia	Southeast Asia	Western Asia	Totals
Mammals	28–53	50–105	12–28	38–54	5–20	97–163
Birds	119–129	169–175	29–38	84–85	84–139	287–336
Fishes	287	95	90	296	125	633
Reptiles	41	41	7	35	13	103
Amphibians	24	13	4	12	1	43
Insects	607	1521	111	89	101	2017
Arachnids	67	83	13	18	6	129
Molluscs	81	119	15	24	89	261
Crustaceans	43	75	12	19	63	158
Vascular plants	2219–2454	4631–6747	1055–3142	1313–1598	271–562	6141–9101
Algae	5	37	4	7	27	66
Bryophytes	3	43				44
Fungi	59	303	17	20	1	363
SAR	59	31	6	7	20	103
Bacteria and protozoans	7	4	3	2	4	12
Totals	3649–3919	7215–9392	1378–3490	1964–2266	810–1171	10,457–13,532

databases (Manaaki Whenua – Landcare Research, 2024). One of the earliest reports was *Hemileia vastatrix* (coffee leaf rust), which caused an epidemic in Southern India and Sri Lanka (Ceylon) in 1869 and spread further across coffee-producing regions in the Indian Ocean and Pacific (McCook, 2006). Data from China indicate that of the 27 known alien fungi, only two new additions were reported after 2000 (Xu & Qiang, 2018). Fifteen alien fungal pathogens were intercepted by plant quarantine in India (Akhtar *et al.*, 2019, 2021; Dubey *et al.*, 2021) between 2015 and 2020. Another significant plant pathogen is *Ceratocystis lukuohia*, the causal agent of Rapid ʻŌhiʻa Death (ROD), reported since 2010 and causing high mortality in Hawaii's endemic keystone tree species *Metrosideros polymorpha* (Fortini *et al.*, 2019).

As for other regions in the Southern Hemisphere, the extensive cultivation of eucalypts and pines led to the co-invasion of a suite of associated fungi (Vellinga, Wolfe & Pringle, 2009). Ectomycorrhizal fungal communities of *Pinus contorta* in New Zealand were dominated by alien fungi, highlighting co-invasion as an important process (Dickie *et al.*, 2010). In tropical Asia, pathogens of alien eucalypts, such as species of the genera *Mycosphaerella*, *Teratosphaeria*, and *Aulographina eucalypti* and *Cryphonectria cubensis*, were apparently co-introduced from Australia (Sankaran & Hussain, 2019). Ectomycorrhizal fungi of eucalypts, such as *Laccaria fraterna*, *Pisolithus albus*, and *P. arrhizus*, are alien species introduced into the region. The myrtle rust, *Austropuccinia psidii* (originally from South America), has been recorded in China, Indonesia, Japan, New Zealand, Australia, Singapore (Carnegie & Giblin, 2022), and New Caledonia (Soewarto *et al.*, 2018). Other alien fungi recorded from the region include *Ceratocystis fimbriata sensu lato* (wilt of several hosts), *Melampsora medusae* (leaf rust of poplars), and *Puccinia horiana* (white rust) (Akhtar *et al.*, 2019; CABI, 2022; EPPO, 2024). Twenty-seven invasive alien fungal pathogens were recorded from China (Xu & Qiang, 2018), 21 from India (Government of India, 2005; Akhtar *et al.*, 2019, 2021; Dubey *et al.*, 2021), 30 from the Maldives (Shafia & Saleem, 2003), and 15 from the Lao People's Democratic Republic (Nhoybouakong & Khamphouke, 2003). Of the 42 powdery mildew species (*Erysiphales*) found in Australia, all are classified as introduced, mainly since the European colonisation of the continent (Kiss *et al.*, 2020). However, it is clear from studies by Fisher *et al.* (2020) that several new alien fungi may have been introduced to the region from across the globe and the numbers are grossly underestimated. In addition, limited historical data on fungi hinder the identification of native and alien status with any degree of certainty.

A comparatively high number of alien macrofungi have been reported for Asia & the Pacific, which harbours at least 235 alien species (Monteiro *et al.*, 2020). The majority belong to the order Agaricales (54%), followed by Boletales (21%), and Russulales (10%). The most widespread alien macrofungus is *Pyrrhoderma noxium*. Available data indicate that the highest numbers of alien macrofungi are known in New Zealand (170 species) followed by Australia (40 species).

(4) Plantae

(a) *Historical trends*

First records of alien plant species in Asia & the Pacific date back more than 1000 years (Wijesundara, 2010) and consistent increases in the number of alien species have been recorded for several Asian and Pacific countries

(Wijesundara, 2010; Wu *et al.*, 2010; Lazkov & Sultanova, 2011; Jaryan *et al.*, 2013; Shrestha, 2016; Vinogradov & Kupriyanov, 2016; Chen *et al.*, 2017a; Pant *et al.*, 2021; Cáceres-Polgrossi *et al.*, 2023). The strongest increase in the cumulative number of alien plant species is recorded for Oceania, including Australia, New Zealand, and the Pacific Islands (Fig. 6). Introduction rates peaked around 1900, followed by a decline, and re-acceleration in the mid-20th century (Fig. 6). The trends for other Asian regions are similar to that for Oceania but have markedly lower absolute numbers of alien species per time period.

(*b*) *Current status*

Regions in Asia & the Pacific include global hotspots of alien plant species (Dawson *et al.*, 2017), and this holds true for islands in Oceania (Moser *et al.*, 2018; Essl *et al.*, 2019). Examples include New Zealand with 1798 alien plants (Brandt *et al.*, 2021), Tahiti (1346), and Guam (833; Raulerson, 2006). Australian states harbour from 1186 established species in Western Australia to 1584 in New South Wales, corresponding to 12–25% of the total plant diversity in these states (Randall, 2002; Walsh & Stajsic, 2007; Pyšek *et al.*, 2017). Australasia has had the most rapid accumulation of numbers of alien plants with expanding colonisation, and the Pacific islands show the steepest increase of all global regions using this measure (van Kleunen *et al.*, 2015). The most widespread alien species on the Pacific Islands include *Euphorbia hirta* (garden spurge), *Cenchrus echinatus* (southern sandbur), and *Phyllanthus amarus* (Jamaica weed). In Australia and New Zealand, it is *Sonchus oleraceus* (common sowthistle), *Solanum americanum* (American black nightshade), and *Chenopodiastrum murale* (nettle-leaf goosefoot) (Pyšek *et al.*, 2017).

Global hotspots also occur in other Asian regions; in South Asia, India (471 alien plants; Inderjit *et al.*, 2018), the Philippines (628; Pelser, Barcelona & Nickrent, 2011), and Indonesia (503; SEAMEO BIOTROP, 2003) are invasion hotspots. In Northeast Asia, Japan is richest in alien plants (1311) and numbers from China range from 861 to 933 (Hao & Ma, 2023). The most recent inventory based on 236 studies documented the presence of 241 invasive alien

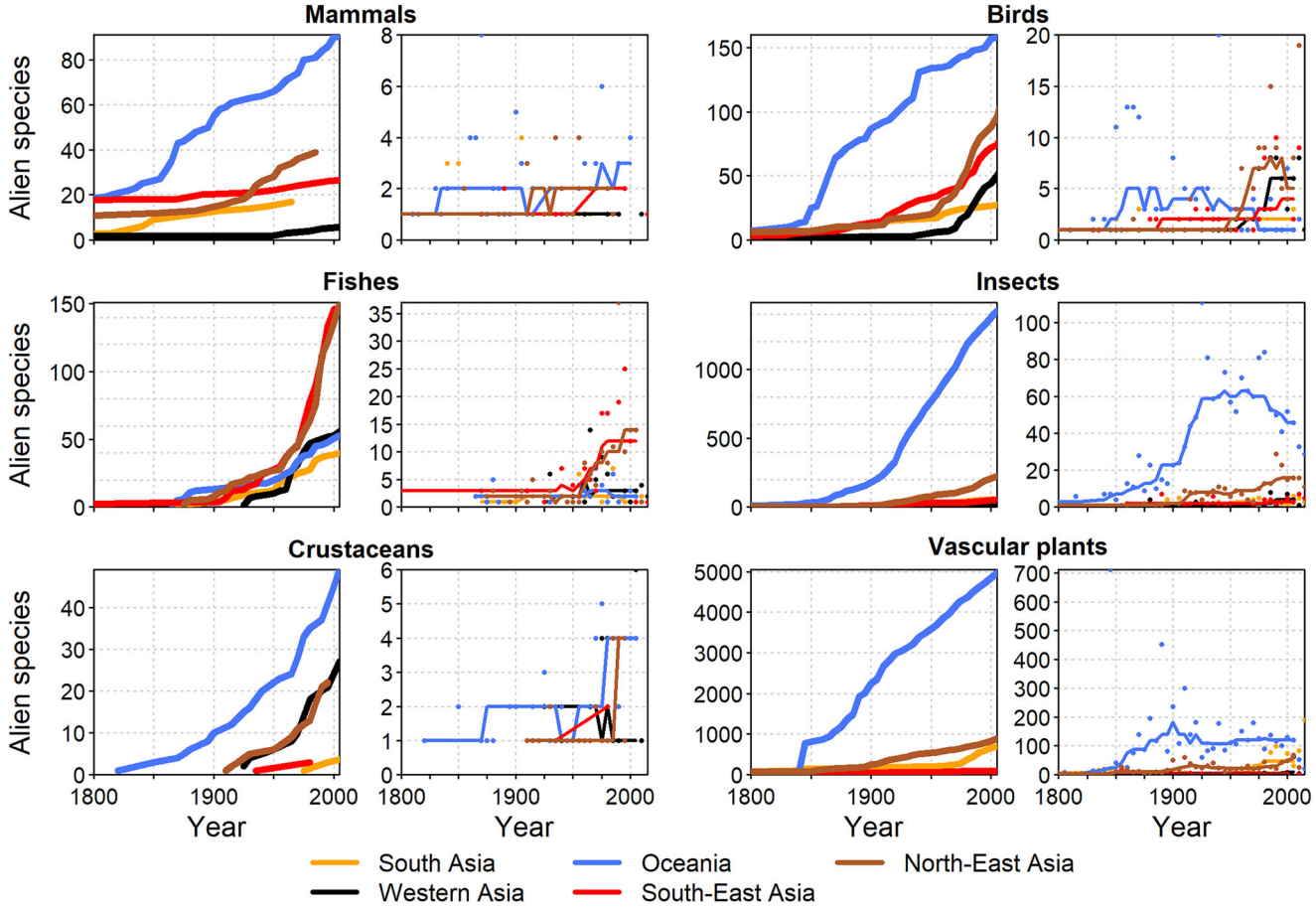

Fig. 6. Trends in numbers of established alien species for Asia & the Pacific. Panels by taxon show cumulative numbers (left panels, thick lines) and number of new alien species per five-year intervals (right panels, thin lines). Numbers shown here underestimate the actual extent of alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians. Note that numbers presented may deviate from those reported in the text due to variation among data sources.

plant species across seven countries of South Asia, with the highest invasive species richness in India (185) followed by Bhutan (53), Sri Lanka (45), Bangladesh (39), Nepal (30), Pakistan (29) and the lowest in Maldives (15) (Gulzar *et al.*, 2024). Western Asia is comparatively species poor in alien plants (Pyšek *et al.*, 2017). The most widespread alien plants in South and Southeast Asia include *Chromolaena odorata* (siam weed), *Lantana camara* (lantana), *Leucaena leucocephala* (leucaena), and *Prosopis juliflora* (mesquite) (Sankaran & Suresh, 2013). The Hawaiian Islands are a global hotspot of plant invasions with 1466 alien plant species, and numbers for individual main islands within the archipelago range from 398 to 963 alien species (Imada, 2019). Alien plants are a serious issue in forests of many Asian Pacific islands, such as Tahiti (Meyer & Florence, 1996), Fiji (Lenz *et al.*, 2022; Forey *et al.*, 2023), Lord Howe Island (Auld & Hutton, 2004), and Carnac Island (Abbott, Marchant & Cranfield, 2000). The most problematic species in urban areas of the islands include *Mikania micrantha* and *Spathodea campanulata* (Lowry *et al.*, 2020).

(5) Animalia

(a) *Historical trends*

Before European colonisation, alien mammals in Southeast Asia were introduced *via* ancient exchanges between the Indonesian Archipelago, Papua New Guinea, and Australia with numerous prehistoric introductions, such as *Phalanger orientalis* (northern common cuscus), *Sus celebensis* (Sulawesi pig), and *Dendrolagus matschiei* (Matschie's tree-kangaroo) (Heinsohn, 2003; Long, 2003; Biancolini *et al.*, 2021). Since 1500, the numbers of alien animal species increased continuously for all taxonomic groups and all subregions of Asia & the Pacific (Fig. 6). The steepest increases were observed in Oceania, particularly during the 19th century for all considered animal groups, except for fishes, mostly because of European colonisation. In other subregions, steep increases were mostly observed after 1950 for insects (Huang, Haack & Zhang, 2011; Yamanaka *et al.*, 2015), gastropods (Barker, 1999; Roll *et al.*, 2009), amphibians and reptiles (Lee *et al.*, 2019), and marine alien species of different groups (Hewitt *et al.*, 2004; Bailey *et al.*, 2020). During the 19th century, acclimatisation societies sought to 'improve' local fauna by introducing many aesthetically pleasing and game species to Australia and New Zealand (Lever, 1992; Simberloff & Rejmánek, 2011; Pipek, Pyšek & Blackburn, 2015; Pipek, Blackburn & Pyšek, 2019). The Asia & the Pacific region has also experienced a growing number of alien bird, reptile, and amphibian introductions, a trend likely to continue in the future (Kraus, 2009; Keppel *et al.*, 2014; Chapple *et al.*, 2016; Lee *et al.*, 2019; Pili *et al.*, 2020; Toomes *et al.*, 2020).

The numbers of alien freshwater species grew slowly in Asia & the Pacific until the 19th century (Fig. 6) after which they increased rapidly (Yuma, Hosoya & Nagata, 1998; Tan *et al.*, 2020; Muñoz-Mas *et al.*, 2023). During the 20th century, aquaculture was the main pathway for freshwater fish species introductions (Xiong *et al.*, 2015; Saba *et al.*, 2020). In addition, mosquitofishes (*Gambusia* spp.) and guppy (*Poecilia reticulata*) were widely introduced for the control of mosquitoes and disease while several other freshwater fish species were introduced for ornamental purposes (Yuma *et al.*, 1998; Tan *et al.*, 2020). The number of ornamental freshwater fish rapidly increased towards the end of the 20th century and the ornamental trade is now the main pathway of introduction (Yuma *et al.*, 1998; Goren & Ortal, 1999; Saba *et al.*, 2020).

(b) *Current status*

Asia & the Pacific is the region with the highest number of alien mammals in the world (130 species) (Biancolini *et al.*, 2021), with numbers ranging from 97 to 163 depending on the data source (Table 6). Areas with high numbers of alien mammals are Japan, the Indonesian archipelago, Australia, New Zealand, and the Pacific islands. For example, *Oryctolagus cuniculus* (European rabbit) is a prominent invasive alien species in Australia (Kirkpatrick, Page & Massam, 2008), and *Trichosurus vulpecula* (brushtail possum) was introduced to New Zealand in 1858 for the domestic fur and meat trade (Gormley *et al.*, 2012; Forsyth *et al.*, 2018). Mammals have been widely introduced on islands in Asia & the Pacific (Russell *et al.*, 2017), with synanthropic species, such as mice, rats, rabbits, pigs, goats, cats, and foxes, causing devastating impacts on insular ecosystems (Russell & Kueffer, 2019). The number of alien bird species in Asia & the Pacific is among the highest within IPBES regions with particularly high numbers recorded for Oceania, followed by Southeast Asia and Northeast Asia (Table 6). More than 100 alien birds are found in tropical Asia, which is likely a consequence of the intensive bird trade in this region (Corlett *et al.*, 2020). Particularly high numbers of alien birds were recorded in Australia, New Zealand, Taiwan, and Japan (Dyer *et al.*, 2017a). Asia & the Pacific harbours two of the best-known examples of alien reptiles and amphibians, namely *Boiga irregularis* (brown tree snake) in Guam and *Rhinella marina* (cane toad) in Australia and other Pacific islands (Lever, 2003; Zug, 2013; Rogers *et al.*, 2017; Engeman, Shiels & Clark, 2018; Shine, 2018). Invertebrates outnumber vertebrate species, and many examples of alien invertebrate introductions are known. Hawaii is a classic example of an archipelago heavily invaded by many species' groups, being among the three regions with most records of alien species in the world (Dawson *et al.*, 2017), including 3000 arthropods (Nishida, 2002). In Guam, but also on Christmas Island, an *Anoplolepis gracilipes* (yellow crazy ant) invasion was assisted by the invasive *Tachardiaephagus tachardiae* (yellow lac scale insect) (O'Dowd, Green & Lake, 2003; Reaser *et al.*, 2007). Other typical examples are gastropod invasions on many Polynesian islands, such as *Lissachatina fulica* (giant African land snail) and *Euglandina rosea* (Tsatsia & Jackson, 2022), with disastrous consequences for the endemic gastropod fauna (Gerlach *et al.*, 2021).

The number of alien freshwater fishes is highest in China (61) (Luo *et al.*, 2019), followed by Singapore (42) (Tan *et al.*, 2020), the Philippines (39) (Casal *et al.*, 2007), and Japan (23) (Yuma *et al.*, 1998). Most of the alien fishes were introduced for aquaculture, while the proportion of introduced ornamental fishes is much lower (Casal *et al.*, 2007; Luo *et al.*, 2019; Muñoz-Mas *et al.*, 2023). The national status of alien freshwater invertebrates was only reported in China and Singapore, including 13 alien invertebrates in China (Chen *et al.*, 2017b) and 14 alien molluscs in Singapore (Ng *et al.*, 2016); these figures include only the most conspicuous invertebrates and distinctly underestimate invertebrate introductions. As with fishes, most known invertebrates were introduced *via* aquaculture and ornamental pathways (Ng *et al.*, 2016; Chen *et al.*, 2017b). On Pacific islands, about 59 freshwater snails, 38 of them cryptogenic, have been introduced (Cowie, 2001). In Pearl Harbour (Hawaii) alone, 191 inland water species of eight phyla but mostly insects, crustaceans, molluscs, and annelids were identified by 1997–1998 (Englund, 2002).

A regional assessment of marine alien species across Asia & the Pacific is lacking, and, as in many other marine regions, the number of actual introductions is sorely underestimated (Carlton & Schwindt, 2024). Large-scale studies report 73 alien species for the Central Indo-Pacific, a region subject to intensive maritime traffic importing marine alien species from around the world for more than 500 years (Carlton & Schwindt, 2024). For the Northwest Pacific, 208 species are reported and 368 for the Northeast Pacific (Lee & Reusser, 2012; Kestrup, Smith & Therriault, 2015). Several marine studies exist for individual countries, such as Japan (42 marine alien species) (Iwasaki, 2006), Republic of Korea (41) (Lutaenko *et al.*, 2013), and Russia (66) (Zvyagintsev *et al.*, 2011). For the South Pacific Ocean, the highest research effort has been around Australia and New Zealand. In Port Phillip Bay (Australia), 100 marine alien species were reported (Hewitt *et al.*, 2004), while 214 alien species were reported for New Zealand (Therriault *et al.*, 2018). The knowledge of marine alien species of the Pacific Island countries and territories is scattered and dispersed in diverse publications. Surveys in Pago Pago Harbour (American Samoa) recognised 17 marine alien species (Coles *et al.*, 2003), 40 alien species were detected from Guam (Paulay *et al.*, 2002), and 11 alien species in Malakal harbour, Palau (Campbell, Hewitt & Miles, 2016). We emphasise that few, if any, of these numbers approach reality.

VIII. EUROPE & CENTRAL ASIA

(1) Bacteria and Protozoa

With 55 species of alien Bacteria (Magliozzi *et al.*, 2022), Europe is the IPBES region with the highest number of species in this group. The main reason for the comparatively high number of species is the availability of a report of alien Bacteria and viruses (Magliozzi *et al.*, 2022), which is unique among IPBES regions. According to this report, the vast majority of alien Bacteria in Europe have been introduced from North America (64%), followed by South America (16%). Highest numbers of alien Bacteria were found in Italy, France, and the Netherlands. However, for a large number of species (56%) the invasion status, and thus the native range, could not be identified. Among prokaryotes, the majority of species are Proteobacteria, such as *Erwinia amylovora* (fire blight), and several species of the genera *Xanthomonas* and *Pseudomonas*. The second largest group is Cyanobacteria including the freshwater species *Cylindrospermopsis raciborskii*, *Sphaerospermopsis aphanizomenoides*, and *Raphidiopsis mediterranea*. For Central Asia, *E. amylovora* has been reported for Armenia (Vanneste, 2008). Eight species of alien protozoans have been reported for Europe & Central Asia with *Bonamia ostreae* being the most widespread species. This species is a pathogen of shellfish and was first reported in 1987 in Ireland (Pederson *et al.*, 2017). Other species are the marine algae *Poropila dubia*, *Haplosporidium armoricanum*, and *Haplosporidium nelsoni*, the latter two being oyster pathogens.

(2) SAR

The number of alien SAR has been rising continuously until recently with a peak in the early 2000s according to the SInAS database. Within the past 20 years, five downy mildew pathogens with the potential to cause significant losses have been introduced into Europe (Thines, 2011; Gilardi *et al.*, 2013; Voglmayr, Montes-Borrego & Landa, 2014; Görg *et al.*, 2017; Thines *et al.*, 2020) with seed or latently infected plants. In total, 373 alien species of SAR have been reported for Europe & Central Asia (Table 7). The majority belong to Ochrophyta (140 species), followed by Myzozoa (87), Foraminifera (70) and Oomycota (59). Alien species widespread throughout the IPBES region include *Aphanomyces astaci* (crayfish plague), *Colpomenia peregrina* (oyster thief), *Prorocentrum cordatum* (dinoflagellate), and *Sargassum muticum* (brown alga). The highest numbers of alien SAR have been reported from France (72 species), followed by Ukraine (61), Turkey (58), and Germany (38) (see also Çinar *et al.*, 2005; Rabitsch & Nehring, 2017). For several regions, comprehensive lists of alien species have been published, which also include SAR; for example, Austria (43 oomycete species; Voglmayr *et al.*, 2023), France (36 oomycete species; Desprez-Loustau *et al.*, 2010), Norway (18 species; Sandvik *et al.*, 2020), Switzerland (36 oomycete species; Beenken & Senn-Irlet, 2016), the UK (13 species; Roy *et al.*, 2012), and the Mediterranean Sea (85 species, Galanidi *et al.*, 2023). The majority of SAR are marine. Europe has a well-documented history of invasions for certain alien pathogenic oomycetes, such as *A. astaci* (crayfish plague; Mrugała *et al.*, 2015), *Phytophthora infestans* that triggered the Irish Great Famine in the 1840s (potato blight; Yoshida *et al.*, 2013), *Phytophthora x alni* (alder dieback; Jung *et al.*, 2018), and *Plasmopara viticola* (grapevine downy mildew), which was introduced in 1878 (Gessler, Pertot & Perazzolli, 2011). One of the few

Table 7. Numbers of established alien species for subregions of Europe & Central Asia. The numbers are extracted from the SInAS database (see Section II) and may deviate from those reported in regional studies. The numbers should be considered as minimum values as the true level of invasion is likely much higher. Empty cells may reflect a lack of research. For mammals, birds, and vascular plants ranges of values indicate variation among databases. Duplicated taxa for the same region and Totals were removed.

	Central and Western Europe	Central Asia	Eastern Europe	Totals
Mammals	64–133	5–23	24–80	72–164
Birds	218–627	4–5	20–24	221–630
Fishes	423	51	119	469
Reptiles	94		6	98
Amphibians	42	2	5	43
Insects	2698	28	213	2747
Arachnids	289	2	6	289
Molluscs	557	4	75	584
Crustaceans	508	11	120	563
Vascular plants	4498–7896	134–361	1950–2400	5146–8519
Algae	210		5	212
Bryophytes	37		1	37
Fungi	594	3	28	609
SAR	332		79	373
Bacteria and protozoans	22		2	23
Totals	10,586–14,462	244–490	2653–3163	11,486–15,360

records of alien SAR from Central Asia is from Georgia with a collection of marine species (Editorial Board of AquaNIS, 2024).

(3) Fungi

In Europe & Central Asia, 609 alien fungi have been reported (Table 7). Nearly all records are from Europe with only a few from Central Asia: five alien fungi in Georgia, two in Kazakhstan, and one in Azerbaijan and Uzbekistan. *Ophiostoma novo-ulmi* (Dutch elm disease) has been reported from all of these countries (Brasier, 1991; Brasier & Kirk, 2001). In addition to the impact of *B. dendrobatidis* on many amphibians, *Batrachochytrium salamandrivorans* causing declines in *Salamandra salamandra* (salamander) populations has been recorded recently in Germany, Belgium, Spain, and the Netherlands and is likely to invade other areas, such as North America (Scheele *et al.*, 2019; Castro Monzon *et al.*, 2022).

Earliest first records of alien fungi date back to a report of the mediterranean *Clathrus ruber* (latticed stinkhorn) in 1752 in Germany (Monteiro *et al.*, 2020) and the North American *Ustilago maydis* (corn smut) in 1760 in France (Kreisel & Scholler, 1994). *Cronartium ribicola* (white pine blister rust) originates from Eastern Asia and was recorded first in the mid-19th century in Eastern Europe from where it spread to other European countries and North America (Richardson *et al.*, 2009). The SInAS database reports a continuous increase in the number of new alien fungi species with a first peak of a mean of seven new alien fungi annually around 1900 and the highest numbers today (10 annually). Using dried reference-collection samples, Gross *et al.* (2021) demonstrated that three species of *Erysiphe* could be linked to the incidence of powdery mildew in oaks, a disease that emerged in Europe at the beginning of the 20th century. One century earlier, in 1845, powdery mildew of grapevine (*Erysiphe necator*) was introduced from North America to England, a story analogous to that of the fungus-like grapevine downy mildew (Gadoury *et al.*, 2012).

The highest numbers of alien fungi have been published for Austria (323; Voglmayr *et al.*, 2023), Switzerland (247; Beenken & Senn-Irlet, 2016), Slovenia (216; de Groot *et al.*, 2020), and France (191; Desprez-Loustau *et al.*, 2010); mostly a result of high research efforts or national assessments. Those studies show steep increases in the number of newly recorded alien fungi particularly since 1900. A similar increase until today was found in an assessment of 79 alien fungi in Norway (Sandvik *et al.*, 2019). For the UK, 157 alien fungi were recorded and the number of new alien fungi did not show a clear trend since 1970 with *ca.* 15–20 new species per five-year interval (Jones & Baker, 2007). The highest numbers of invasive forest pathogenic fungi are reported from the central part of Europe (France, Italy, and Switzerland; Santini *et al.*, 2013); most are native to the Northern Hemisphere, but about one-third are of unknown origin (Desprez-Loustau, 2009). Some of the most widespread are *Hymenoscyphus fraxineus* (ash dieback) and *Ophiostoma novo-ulmi* (Dutch elm disease), which caused severe diebacks in ash and elm, respectively, throughout Europe. The number of alien powdery mildews (Erysiphales) in Europe is rather high (Desprez-Loustau *et al.*, 2010; Beenken & Senn-Irlet, 2016; Voglmayr *et al.*, 2023) and may reflect responses to climate change in a group adapted for long-distance aerial spore dispersal (Heluta *et al.*, 2009).

(4) Plantae

(a) Historical trends

Several studies have reported long-term increasing trends of alien plants for individual countries, such as Estonia

(Ööpik *et al.*, 2008), Albania (Barina *et al.*, 2014), Italy (Celesti-Grapow *et al.*, 2009), Turkey (Çinar *et al.*, 2005), Slovakia (Medvecká *et al.*, 2012), Poland (Tokarska-Guzik, 2005), Czech Republic (Pyšek *et al.*, 2012a), Ukraine (Protopopova & Shevera, 2014), Iceland (Wasowicz, Przedpelska-Wasowicz & Kristinsson, 2013), and Portugal (Almeida & Freitas, 2012). The reported temporal patterns are very similar across regions with a distinct acceleration of new plant records either during the early (e.g. Pyšek *et al.*, 2012a) or late 19th century (e.g. Wasowicz *et al.*, 2013). The first comprehensive study of alien plant invasions across European countries showed a slow increase of new introductions until 1800 and a marked acceleration thereafter (Lambdon *et al.*, 2008). Whereas before 1800 the majority of alien plants were of European origin, this changed during the 19th century with the large majority of alien plants now being of non-European origin (Lambdon *et al.*, 2008). In addition to cumulative numbers, the rate of new alien plant records increased from 1800 until today as well (Fig. 7), reaching around 20 new alien species records annually in Europe (Seebens *et al.*, 2017). Information about alien plant introductions in Central Asia is scarce (Lazkov & Sultanova, 2011) but it seems likely that trends resemble those of neighbouring regions in Europe and other Asian regions, such as Nepal (Shrestha, 2016) or Siberia (Vinogradov & Kupriyanov, 2016), albeit at different levels.

Similarly, numbers of alien bryophytes have increased continuously, starting with the first observed species introduced to Europe, *Lunularia cruciata*, in 1828 (Essl & Lambdon, 2009). First records for alien ferns indicate similar trends although the available data are too scant to reveal robust trends (Jones *et al.*, 2019). The introduction of alien aquatic plants increased after 1950, with the trade in ornamentals being the main pathway, followed by cultivation and contaminants of commodities; the former two exhibited similar rates in different European areas, while contaminants of commodities were mostly recorded in Southern Europe (Nunes *et al.*, 2015). The number of alien aquatic plant species is still relatively low in European freshwaters but sharply increasing and has e.g. doubled in ∼30 years in Germany (Hussner *et al.*, 2010).

(*b*) *Current status*

The most recent and most comprehensive survey reports 4139 alien vascular plants in Europe & Central Asia (van Kleunen *et al.*, 2019). According to this survey, the highest numbers have been recorded in England (1379), Sweden (874), Scotland (861), Wales (835), France (716), and Norway (595) (Pyšek *et al.*, 2017), indicating that the Northern part of the continent, particularly the UK and Scandinavia, is heavily invaded by alien plants (Lambdon *et al.*, 2008). Only a few regions in Eastern Europe harbour comparably high numbers of alien species, such as the European part of Russia (649), Ukraine (626), and Bulgaria (593). In some countries, such as the UK, Sweden, and Norway, alien species make up 32–47% of the total flora (Pyšek *et al.*, 2017). Central Asia is generally less invaded by alien plants, with country floras in this region harbouring 50–70 alien species, corresponding to a 1.9–4.5% contribution to the total plant diversity (Pyšek *et al.*, 2017). In some cases, this paucity reflects environmental conditions that are unfavourable for invasion. In Mongolia, a recent study recorded 154 taxa of alien plants, of which 33 are established and 121 casual; the low number of established plants is attributed to harsh conditions and historic isolation of this country (Vanjil *et al.*, 2024). In Uzbekistan, intensive long-term research yielded 242 alien plant species of which 211 are established, and 36 of these are invasive (Makhkamov *et al.*, 2024). However, generally low alien species numbers in Central Asia can also be due to low research effort. Thirty-five alien species have become established in more than 30 regions of Europe, representing at least half of this continent's territory, the most widespread being *Erigeron canadensis* (Pyšek *et al.*, 2017). Some of the best-studied plant invasions in Europe include the terrestrial herbs *Heracleum mantegazzianum* (giant hogweed) (Pyšek *et al.*, 2017; Shackleton *et al.*, 2020), *Fallopia* sp. div. (knotweed) (Bailey & Conolly, 2000), *Carpobrotus edulis* (Hottentot-fig) (Novoa *et al.*, 2013), *Senecio inaequidens* (narrow-leaf ragwort) (Heger & Boehmer, 2005), the aquatic herbs *Elodea canadensis* (American duckweed), and the trees *Robinia pseudoacacia* (black locust), *Acer negundo* (ash-leaf maple), and *Acacia dealbata* (silver wattle) (Nentwig *et al.*, 2018).

There are 210 alien plants recorded in European freshwaters, mostly originating from North America and Asia (Nunes *et al.*, 2015). *Elodea canadensis* is the most widely distributed alien aquatic plant in Europe, occurring in 41 European countries, followed by *Azolla filiculoides* (water fern) (25), and *Vallisneria spiralis* (tape grass) (22). Some of the established aquatic species are widespread and have increasing negative impacts across Europe, such as *Elodea* spp. (waterweeds), *Hydrocotyle ranunculoides* (floating pennywort), and *Myriophyllum aquaticum* (parrot feather watermilfoil) (Hussner, 2012).

Among alien bryophytes, 32 identified alien species in Europe comprise 21 mosses, 11 liverworts but no hornworts. The countries with the most alien bryophytes are the UK (14 species) and Ireland (six species). Overall, countries and regions with a humid and cool climate are most invaded, whereas countries with drier and warmer climates are poor in alien bryophytes (Essl & Lambdon, 2009). *Campylopus introflexus* (present in 21 countries) and *Orthodontium lineare* (15 countries) are the most widely distributed alien bryophytes in Europe (Essl *et al.*, 2014).

Galanidi *et al.* (2023) list 110 marine alien plants from the Mediterranean Sea. The major putative pathway of introductions to the Northwestern Basin and the Adriatic Sea is shellfish transfer, and to the Eastern and Central Mediterranean, the Suez Canal. Well-known and widespread seaweeds are *Caulerpa taxifolia* (killer alga), *C. cylindracea* (grape caulerpa), *Codium fragile* (dead man's finger), the invasive strain of *Asparagopsis taxiformis*, and *Womersleyella setacea*. *Halophila stipulacea* (broadleaf seagrass), the sole alien seagrass species in

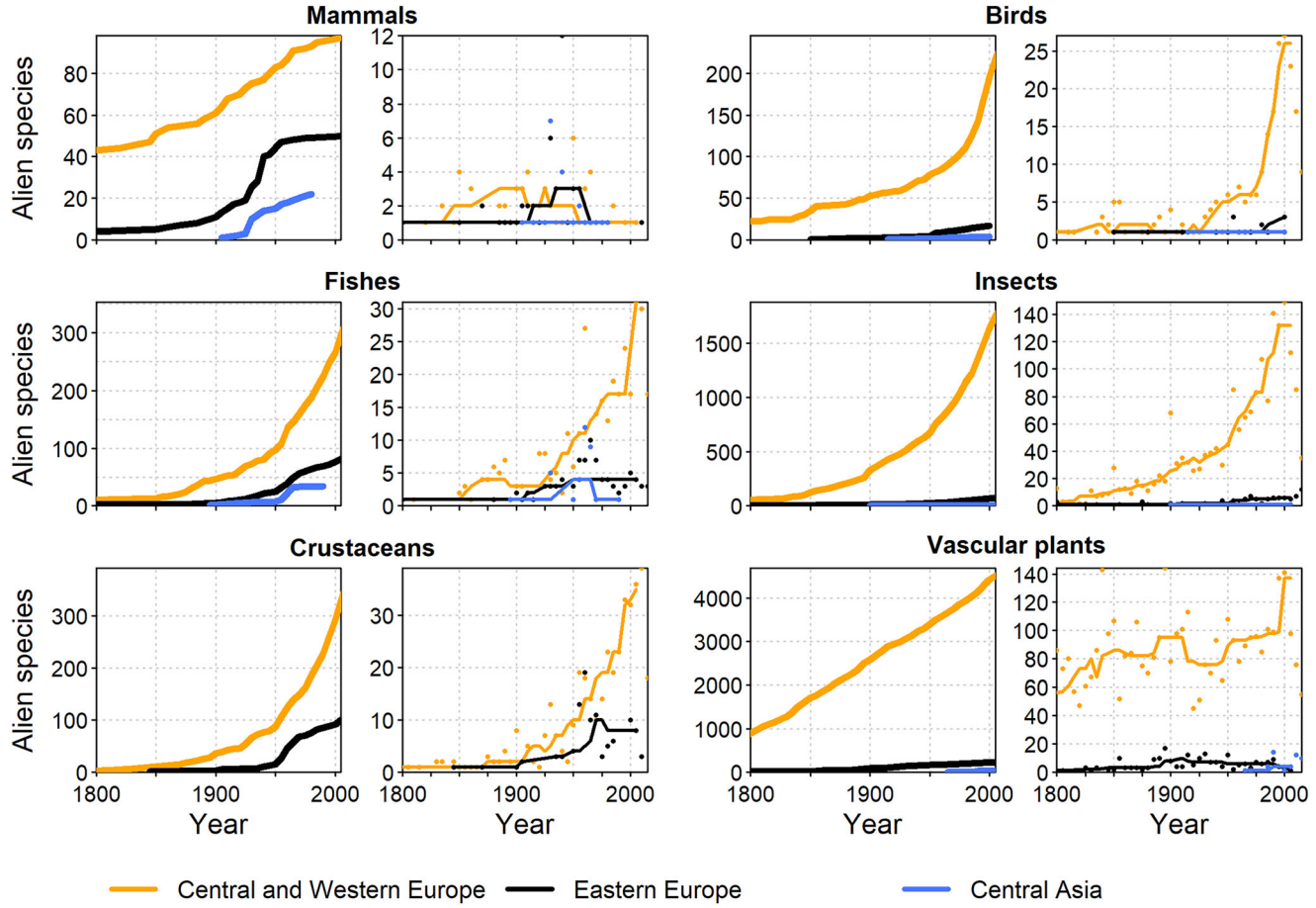

Fig. 7. Trends in numbers of established alien species in Europe & Central Asia. Panels by taxon show cumulative numbers (left panels, thick lines) and number of new alien species per five-year intervals (right panels, thin lines). Numbers shown here underestimate the actual extent of alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians. Note that numbers presented may deviate from those reported in the text due to variation among data sources.

the Mediterranean, was first recorded in 1894, a couple of decades after the opening of the Suez Canal (Fritsch, 1895). It has since spread across the Mediterranean. In the 2000s, it spread to the Caribbean (Winters *et al.*, 2020).

(5) Animalia

(a) *Historical trends*

The number of alien animal species in Europe & Central Asia is increasing across various groups, including vertebrates (Rabitsch & Nehring, 2017), insects (Roques *et al.*, 2016), molluscs (Peltanová *et al.*, 2012), and freshwater animals (Nunes *et al.*, 2015; Muñoz-Mas & García-Berthou, 2020), especially for Central and Western Europe (Fig. 7). The number of alien mammals introduced to European countries accelerated particularly in the late 19th century and continues to increase (Genovesi *et al.*, 2012). The rates of new records of alien species remained low over the last 200 years, but rose sharply in recent decades for birds and invertebrates (Seebens *et al.*, 2017). Amphibians, reptiles, and mammals share a similar pattern: historical events and trade routes around the Mediterranean Basin have resulted in some of the oldest known introductions of vertebrates in the world. The observed increases in alien species numbers will likely continue (Seebens *et al.*, 2017, 2021a), and the pet trade is expected to contribute more species in the near and medium future (Pleguezuelos, 2002; Mateo, Ayres & López-Jurado, 2011).

Introductions of alien freshwater fishes increased after the mid-19th century due to the activities of acclimatisation societies, mainly for angling (Gherardi *et al.*, 2009), and again after World War II due to more intensive trade, openings of major inland canals and waterways, and the intensification of aquaculture (Goren & Ortal, 1999; Gherardi *et al.*, 2009; Nunes *et al.*, 2015). In Central and Northern Europe, interconnected canals and waterways were the main pathways of introduction for aquatic invertebrates, while introductions of vertebrates were mainly by releases and escapes linked to

aquaculture and pet and aquarium trades. A slight decrease in introduction rates was reported for recent decades on the Iberian Peninsula (Muñoz-Mas & García-Berthou, 2020). Three North American crayfish were intentionally introduced following the decimation of native crayfish populations: *Faxonius limosus* (spiny-cheek crayfish) in 1890s, *Pacifastacus leniusculus* (signal crayfish) in 1960s, and *Procambarus clarkii* (red swamp crayfish) in the 1970s. These species are ubiquitous and currently spreading in Central and Eastern Europe (Soto *et al.*, 2023). At least five North American species (genera *Faxonius* and *Procambarus*) have been subsequently documented. The fastest spreading crayfish is *Procambarus virginalis* (marbled crayfish), a parthenogenetic species previously related to *P. fallax*. Its fast growth, high fecundity, frequent spawning, short embryogenesis and environmental plasticity has enabled it to establish self-sustaining populations from Estonia to Israel within two decades of its first population in the wild (Kouba, Petrusek & Kozák, 2014; Aluma *et al.*, 2023; Carneiro, Galil & Lyko, 2023).

Across European Seas, the number of recorded alien species has increased continuously until today (Galil *et al.*, 2014; Zenetos *et al.*, 2022). In the North Sea, the annual introduction rate has more than doubled, from 2.9 species per year in 1950–1999 to 4.3 between 2000 and 2014, and 7 between 2015 and 2022 (ICES, 2022), whereas along the coast of Israel their number has tripled between 1970 (138 alien animal species) and 2020 (432 alien animal species), nearly 6 species per year (Galil *et al.*, 2021).

(*b*) *Current status*

Currently, 85 alien mammals are known to be established in Europe & Central Asia, particularly in Central Western Europe, numerous Mediterranean islands, the British Isles, Italy, Scandinavia, Eastern Europe, and European Russia (Biancolini *et al.*, 2021). *Ondatra zibethicus* (muskrat), *Nyctereutes procyonoides* (raccoon dog), and *Neovison vison* (American mink) are among the most widespread (Genovesi *et al.*, 2012; Biancolini *et al.*, 2021; Tedeschi *et al.*, 2022). Many islands in European Seas have been invaded by large numbers of alien mammals for centuries (Bonesi & Palazon, 2007; Ruffino *et al.*, 2009; Chainho *et al.*, 2015; Capizzi, 2020). Europe has also been a hotspot of alien bird introductions for centuries, with highest numbers recorded in the UK, Spain, and Portugal (Dyer *et al.*, 2017a). Although European-Union-wide import bans on caged birds, established after the bird flu epidemic of 2005, have greatly restricted the bird trade with other continents (Reino *et al.*, 2017), there is still an extensive within-Europe trade of captive-bred birds that can potentially lead to new introductions. Europe hosts several global hotspots of alien amphibians and reptiles: the Balearic Islands, mainland Spain, Italy, France, and the UK (Ficetola *et al.*, 2007; Kark *et al.*, 2009; Kraus, 2009; Mateo *et al.*, 2011; Capinha *et al.*, 2017). Fewer alien reptiles and amphibians have been reported in Central Asian countries than in Europe (Kraus, 2009; Capinha *et al.*, 2017). Numbers of alien insects have steadily increased in Europe but this accumulation lagged behind other regions, such as The Americas prior to 1900 (Figs 5 and 7). Historical patterns of insect species spread with Europe have been influenced by changes in governmental alliances and associated changes in trade (Roques *et al.*, 2016).

There have been 534 alien animal freshwater species recorded in Europe & Central Asia, with the Iberian Peninsula, France, Italy, the UK, and Germany harbouring the highest numbers (Nunes *et al.*, 2015). The most numerous known introduced organisms are fishes, arriving through stocking, aquaculture, or pet and aquarium trades, followed by crustaceans and molluscs, introduced mainly *via* ornamental trade and through canals and waterways (Nunes *et al.*, 2015). Fish, such as *Cyprinus carpio* (common carp), *Sander lucioperca* (pike perch), *Silurus glanis* (European catfish), or Ponto-Caspian gobies, have now established in much of European fresh waters (Leprieur *et al.*, 2008) and threaten native fish faunas with a high level of endemism (Clavero & García-Berthou, 2006). Data from Central Asia are scarce. At least, 31 alien freshwater fishes have been recorded in Uzbekistan (Yuldashov, 2018). Many freshwater and brackish water invertebrates, such as *Dreissena polymorpha* (zebra mussel), *D. bugensis* (quagga mussel), and many amphipods, such as *Dikerogammarus villosus* (killer shrimp), reached Europe from their Ponto-Caspian native range through human-made canals built for transport (Bij de Vaate *et al.*, 2002). Other Asian crustaceans were introduced through rice cultivation, which brought at least 13 ostracods to Mediterranean wetlands (Bisquert-Ribes *et al.*, 2023). The Chinese pond mussel (*Sinanodonta woodiana*) has been introduced through the introduction of fish, which were infected by the parasitic larvae of the mussel (Douda *et al.*, 2025).

The European Union (EU) has encouraged its member states to assess the status of marine alien species as part of the Marine Strategy Framework Directive (MSFD). Yet, there is no scientifically validated current inventory of marine alien animals recorded across European coastal and adjacent waters, and data are currently scattered among national and regional reports and databases. Several studies are available for individual countries, reporting numbers of marine alien animal species off, for example, Finland (27; Outinen *et al.*, 2024), Denmark (55; Jensen *et al.*, 2023), Republic of Ireland (65; Gittenberger *et al.*, 2023a), the Netherlands (133; Gittenberger *et al.*, 2023b), and the Atlantic coast of Spain (89; Png-Gonzalez *et al.*, 2023). The number of marine alien animal species recorded in the Mediterranean Sea (where only 8 of 22 countries are EU member states) is 810 (of a total of 1006 alien species) (Galanidi *et al.*, 2023), of which about 75% have been introduced through the Suez Canal (Galil *et al.*, 2021). Examples of marine invasions are the expansion of *Lagocephalus sceleratus* (silver-cheeked toadfish) throughout the Mediterranean, an avid predator introduced through the Suez Canal (Ulman *et al.*, 2024), the spread of *Neogobius melanostomus* (round goby), a Ponto-Caspian introduction into the Baltic Sea (Kornis, Mercado-Silva & Vander Zanden, 2012), and the introduction of the

comb jellyfish *Mnemiopsis leidyi* (sea walnut) into the Black Sea (Oguz, Fach & Salihoglu, 2008).

IX. ANTARCTICA

Antarctica has been much less affected by alien species than other regions, for several reasons: Antarctica is difficult to access, anthropogenic pressures have been low so far (Bennett, 2015; McGeoch *et al.*, 2015; Galera *et al.*, 2018), and its inhospitable environments, such as low nutrient soils, freezing temperatures, and high ultraviolet (UV) levels, do not favour establishment of alien species. However, climate change and increased human activities through tourism and research are enhancing introductions (Bender, Crosbie & Lynch, 2016; Duffy *et al.*, 2017; Bartlett, Convey & Hayward, 2020; Chwedorzewska, Korczak-Abshire & Znój, 2020). Plants (seeds, fragments, and other propagules) and invertebrates, such as springtails, were introduced on clothing and personal equipment of tourists and national Antarctic programme ship and aircraft personnel, as well as associated with packing materials (Chown *et al.*, 2012; Huiskes *et al.*, 2014), vehicles (Hughes *et al.*, 2010), and fresh food imports (Hughes *et al.*, 2011). In 11 years of surveillance (2006–2017) at the Scott Base in the Ross Sea region of continental Antarctica, 68 invertebrate species (16 of which are known to be invasive elsewhere globally, including in some instances the broader Antarctic region) were intercepted on food (60%), clothing and equipment (11%), aircraft and cargo (11%), and packaging material (11%) (Newman *et al.*, 2018). During 2007–2008, more than 20 alien lichens and fungi were intercepted in Antarctica in packaging, foodstuffs, and timber (Osyczka, 2010; Osyczka *et al.*, 2012). Seeds of eight alien plant species were reported in the topsoil of Fildes Peninsula, King George Island (Antarctica), in areas intensively frequented by humans (Fuentes-Lillo *et al.*, 2017).

Terrestrial alien plants in the Antarctic are predominantly herbs, mostly introduced unintentionally with soils or imported fodder for domestic animals (Frenot *et al.*, 2005; Chwedorzewska *et al.*, 2015). Alien plants have been introduced on several occasions since the 1950s: for example, *Poa pratensis* (smooth meadow-grass) was introduced unintentionally during tree transplantation experiments in the 1950s and eradicated in 2015 (Pertierra *et al.*, 2017). Altogether, 15 alien species are known to occur in Antarctica: one plant, *Poa annua* (annual bluegrass), and 14 invertebrates [seven Collembola, four Arachnida, two Insecta (Diptera), one Annelida], most of which are found in the Antarctic Peninsula region (Hughes, Cowan & Wilmotte, 2015; Baird *et al.*, 2019; Enríquez *et al.*, 2019, Hughes *et al.*, 2020). This could be due to several factors. The Antarctic Peninsula is the area closest to another continent (South America), it is the least climatically extreme region of Antarctica (and has also experienced a rapid rise in temperatures since the 1950s due to climate change) and has the largest concentration of human activity (due to research teams and tourism) resulting in a relatively high propagule pressure (Hughes *et al.*, 2020). On the sub-Antarctic islands, which circle the continent, at least 108 alien plants, 72 terrestrial invertebrates, and 16 vertebrates are reported (Frenot *et al.*, 2005).

Alien vertebrates with established populations are reported only for sub-Antarctic islands. Environmental conditions on the continent of Antarctica itself are too extreme unless the species can live synanthropically: some mammals, such as rats and mice, were unintentionally introduced as early as the 18th century, while others, such as ungulates, cats, rabbits, and salmonids, were intentionally introduced beginning in the early 20th century (Frenot *et al.*, 2005; Lecomte *et al.*, 2013). Alien invertebrates, such as the springtail *Hypogastrura viatica*, were reported from the 1940s onwards in the Antarctic (Hack, 1949; Hughes *et al.*, 2015).

To date, five marine alien invertebrate species have been found (plus one cryptogenic seaweed species); these were free-living specimens with no known established populations (McCarthy *et al.*, 2019; Cárdenas *et al.*, 2020). Marine alien species were likely introduced by vessels (three by hull fouling, one by ballast water), with the first recorded alien species (a bryozoan) dating back to 1960, followed in 1986 by a crab, and in 1996 by a tunicate and a hydroid; the most recent introduction (a mollusc) was recorded in 2019, although it is likely that this species has subsequently disappeared (McCarthy *et al.*, 2019; Cárdenas *et al.*, 2020). There is no evidence that any of these species are established in Antarctica (McCarthy *et al.*, 2019).

The number of alien species is expected to increase in the future due to climate change and increasing human pressure, but reported numbers are also expected to be higher due to the greater research effort, as noted by the growing number of relevant publications (Hughes & Pertierra, 2016; Duffy *et al.*, 2017; Ricciardi *et al.*, 2017; Chan *et al.*, 2019; Chwedorzewska *et al.*, 2020). A recent horizon scan for future potentially invasive alien species in the Antarctic Peninsula underlined the main threat posed by marine invertebrates that can be unintentionally transported in ballast waters and on ship hulls (McCarthy *et al.*, 2019; Hughes *et al.*, 2020). The threat could be even greater considering the cruise ship volume from the Northern Hemisphere to Antarctica that may increase the probability of introduction.

X. FUTURE TRENDS OF BIOLOGICAL INVASIONS

Many studies have been conducted to explore the potential future developments of the distribution and accumulation of alien species at various geographic scales. Across eight continental regions, alien species numbers for seven major taxonomic groups are projected to increase on average by 36% until 2050 under a business-as-usual scenario (Seebens *et al.*, 2021a). Taxon-specific studies at global or regional scales about future invasion potential have been conducted

for different individual species or taxonomic groups, such as ants and termites (Chen, 2008; Buczkowski & Bertelsmeier, 2017), beetles (Berzitis *et al.*, 2014; Wang *et al.*, 2017), flies (Hill *et al.*, 2016; Ryan *et al.*, 2019), other insects (Hill, Gallardo & Terblanche, 2017; Lu *et al.*, 2020), amphibians (Ihlow *et al.*, 2016; Forti *et al.*, 2017), fish (Liu *et al.*, 2019; Dong *et al.*, 2020), and mammals (Louppe *et al.*, 2019, 2020; Biancolini *et al.*, 2024), mostly projecting an increase in range sizes. Species distribution models for 100 alien species with severe impacts (as assessed by the IUCN) found a decreased potential for future global distribution of mammals, birds, fishes, reptiles, and amphibians, but an increase in distributions of aquatic and terrestrial invertebrates due to region-specific projected changes in climate (Bellard *et al.*, 2013).

Species-specific studies about future distributions of alien microorganisms are available only for a few species and the majority deal with just one species or multiple species from one genus (e.g. *Phytophthora*; Scott *et al.*, 2019). In general, invasion potentials are projected to be higher than currently observed, both in terms of numbers of alien fungi present (Bebber *et al.*, 2019; Barwell *et al.*, 2021) and of occupied range (Kriticos *et al.*, 2013; Feldmeier *et al.*, 2016). For crop pests including herbivorous arthropods, pathogenic microbes and viruses, numbers within regions are projected to be higher than observed levels (Bebber *et al.*, 2019). Hotspots of pest invasion are in Central America, Europe, East Asia, and Australia (Bebber, 2015). Global plant pathogen studies project an increase in potentially suitable areas, especially towards higher latitudes (Burgess *et al.*, 2017; Avila *et al.*, 2019). Crop pests are projected to shift poleward under climate change and increased human activities (Fisher *et al.*, 2012; Bebber, Ramotowski & Gurr, 2013) and under currently observed trends, the main crop-producing countries will be saturated with crop pathogens by 2050 (Bebber *et al.*, 2014).

Future hotspots for alien plant invasions have been identified in Europe, South America, North America, Southwest China, and New Zealand as well as the coast of West Africa and the Southern coast of Asia (Wan, Wang & Yu, 2016), while potential hotspots for cacti emerge in the Mediterranean, tropical savanna regions, and xeric shrubland biomes (Masocha & Dube, 2018). Most projections of future distributions of alien plant species identified expanding ranges (Adhikari, Tiwari & Barik, 2015; Wan *et al.*, 2016; Dullinger *et al.*, 2017), although for some species ranges are projected to shrink (Bellard *et al.*, 2013). Studies for the USA and Europe suggest that most current invasion hotspots will remain spatially stable, but potential alien species numbers will increase by 64–102% (Allen & Bradley, 2016). For Europe, increases of alien plant numbers were projected for northern parts, while southern parts may experience declining numbers (Chytrý *et al.*, 2012). South American countries, such as Brazil, Mexico, and Argentina, are expected to face comparatively strong increases in numbers of alien plant species based on global trade dynamics and climate change (Seebens *et al.*, 2015), which may invert the current status of North America as more invaded by plants than South America (Pyšek *et al.*, 2019).

Studies of alien animals often found projected expansions of current distributions. For example, for birds *Corvus splendens* (house crow) and *Acridotheres tristis* (common myna), the current distributions indicate a large potential to spread to new areas (Nyári, Ryall & Peterson, 2006; Magory Cohen *et al.*, 2019). Similarly, mammals, such as *Sus scrofa* (feral pig), *Urva auropunctata* (small Indian mongoose), and *Procyon lotor* (raccoon), often have a large potential for further spread worldwide (Lewis *et al.*, 2017; Louppe *et al.*, 2019, 2020; Biancolini *et al.*, 2024). For insects, several studies investigated the invasion potential of agricultural pest species (Kroschel *et al.*, 2013; Kriticos *et al.*, 2017; Marchioro & Krechemer, 2018), with the *Spodoptera frugiperda* (fall armyworm) (Early *et al.*, 2018) and *Drosophila suzukii* (spotted wing drosophila) being prominent examples (dos Santos *et al.*, 2017), and all studies found a high risk of invasion beyond the current realised distribution. The ranges of many problematic invertebrate invaders other than insects have also been projected to expand, such as the harmful freshwater bivalves *Dreissena* (zebra and quagga mussels), *Limnoperna* (golden mussel), and *Corbicula* (basket clams) (Gama *et al.*, 2016; Petsch *et al.*, 2021). In the marine realm, a study of 19 ascidian species found a large invasion potential especially at higher latitudes (Lins *et al.*, 2018). Projections of planktonic and benthic species, as well as algae, suggest that under climate change scenarios the probability of establishment of alien species will increase at higher latitude (Seebens *et al.*, 2016; Goldsmit *et al.*, 2020).

In summary, the suite of studies available for projections of future dynamics of alien species suggests that overall ranges of alien species are expected to increase in most cases although with large variation due to a continuous introduction of new individuals and an expansion of ranges. In addition, ranges are expected to shift poleward as a consequence of global warming (Walther *et al.*, 2009). However, projections of future dynamics of alien and invasive alien species are severely limited by (*i*) data availability of past and current distributions of species, (*ii*) limits in understanding of causal relationships between species occurrences, environmental changes, drivers of biological invasions, and the roles of dispersal, biotic interactions, and impacts caused by invasive alien species, (*iii*) lack of models to project future dynamics of biological invasions robustly, and (*iv*) the lack of scenarios covering a range of plausible future dynamics of drivers, which would allow exploring future trends under different scenarios. While models and scenarios can still be developed further, closing data gaps, particularly of historic distributions, is very difficult and even impossible in many cases.

XI. WAYS FORWARD TO IMPROVE ASSESSMENTS ON BIOLOGICAL INVASIONS

Although we aimed to provide a balanced global overview for both regions and taxonomic coverage of species, we acknowledge that a complete global coverage across all

regions and taxa remains elusive due to many data and knowledge gaps. The true extent of biological invasions is vastly underestimated, as large numbers of species are probably not yet identified as established in many regions. No checklist is likely to be complete, but particularly large gaps in data exist for most African countries and parts of Asia; for invertebrates, fungi, SAR, and Bacteria; and for freshwater and marine species compared to terrestrial species.

To close the information gaps, we call for funding agencies, administrations, and scientists to collaborate to address the following key challenges (Fig. 8).

(1) *Checklists of alien species are lacking for many taxonomic groups and regions*. Checklists (i.e. species lists for individual regions) of alien species are missing for many taxonomic groups, particularly invertebrates, fungi, SAR, and prokaryotes, and for many countries in Africa and Asia. Developing such checklists is essential to enable more comprehensive and robust assessments of biological invasion trends.

(2) *Existing checklists of alien species are often incomplete and outdated*. We found substantial differences in alien species occurrences among neighbouring countries and across taxonomic groups. Such variations may arise from varying survey efforts and accessibility of data of alien species rather than actual occurrences. Because the spread of alien species is highly dynamic, maintaining up-to-date occurrence lists requires substantial investment in regular monitoring, taxonomic expertise, and continuous maintenance of databases and standards.

(3) *Available alien species lists lack standardisation*. Studies and reports often use different terms, definitions, concepts, taxonomies, data collection, and sampling methods making comparisons across regions and taxa challenging, particularly for distinguishing invasion status (i.e. introduced, established, and invasive). Such distinctions are often not specified, or if they are, definitions are often lacking (Wilson *et al.*, 2020). Comparisons and assessments of biological invasions need international standards in monitoring and reporting (Latombe *et al.*, 2017; Packer *et al.*, 2017; Meyerson *et al.*, 2022).

(4) *Data are often difficult to access or are inaccessible*. Information about alien species occurrences is often stored in formats that are inaccessible or challenging to access, such as appendices of articles or tables in pdf documents (Crall *et al.*, 2006). Integration of standardised data into open databases or data portals, such as GBIF or the Ocean Biodiversity Information System (OBIS), would enable researchers and stakeholders to access information in a standardised way and to conduct tailored biodiversity assessments. Recording and storing data should follow standard and published protocols to make science, decision-making, and the assessment of biodiversity comprehensive, transparent, interoperable, and reproducible, which ultimately increases trust in results and decisions (e.g. De Pooter *et al.*, 2017; Groom *et al.*, 2017; Roy *et al.*, 2018; Haider *et al.*, 2022).

(5) *Coarse spatial resolutions of occurrences impede assessments of distribution and spread*. Although checklists provide the basis for analysing status and trends of alien species, their spatial resolution is too coarse to enable a robust assessment of distributions and spread of alien species. This is particularly problematic for large countries, but introduces challenges for monitoring species even within smaller countries. Further, checklists are often restricted to administrative units, such as countries, although information at biogeographic (e.g. biomes, islands) or ecological (e.g. habitat types) levels would allow improved assessments. Accurate assessments of biological invasions across spatial scales require data at finer spatial resolutions that are ideally georeferenced. Only very few countries, such as the UK or Czech Republic, have updated information on alien species occurrences in the form of raster mapping (Preston, Pearman & Dines, 2002; Pyšek *et al.*, 2022).

(6) *Addressing the challenge of biological invasions requires international collaboration*. Greater international collaboration is

Fig. 8. Six recommendations to improve the assessment of the status of the distribution of alien species. GBIF, Global Biodiversity Information Facility; OBIS, Ocean Biodiversity Information System.

needed to build more robust global networks for monitoring, data sharing, and technology transfer (Packer *et al.*, 2017; Nuñez *et al.*, 2021; Kuebbing *et al.*, 2022; Meyerson *et al.*, 2022; Soubeyrand *et al.*, 2024). While several research networks, database repositories, intergovernmental and international organisations, and international agreements related to biological invasions do exist (reviewed in Meyerson *et al.*, 2022), additional coordination and collaboration are needed, particularly because individual countries often lack the capacities to respond appropriately to biological invasions (Early *et al.*, 2016; Pyšek *et al.*, 2020). Engaging in discussions based on a genuine interchange that recognises and incorporates differences in knowledge, values, perspectives, and interests across political boundaries is critical (Courchamp *et al.*, 2017) to increase understanding of biological invasions and support data acquisition.

Thoroughly assessing the trends and status of biodiversity requires deep knowledge about nature and the ecosystems supporting biodiversity. Although information about nature is accumulating at an unprecedented pace, major knowledge gaps persist, particularly for inconspicuous organisms, such as invertebrates, fungi, SAR, and Bacteria, and less-accessible systems, such as marine ecosystems and inland waters, and in geographic areas such as Central Africa, Central Asia, Antarctica, and several remote islands. Our current knowledge of species interactions with their environment is inadequate to understand comprehensively how species respond to environmental changes in order to build sufficient models to anticipate future biodiversity change under different scenarios of human development and climate change. Reducing these knowledge gaps is therefore key to improve policies that can safeguard nature and move societies towards sustainability. New technologies ranging from satellite products, automated sampling, citizen science and environmental DNA (eDNA) will help in gathering information and reducing gaps. Still, knowledge gaps will persist and must be considered explicitly when assessing status and trends of biological invasions.

XII. CONCLUSIONS

(1) Increasing amounts of data and new databases on various facets of biological invasions have become available recently. However, drawing robust conclusions from data also requires the assessment of data and knowledge biases and gaps by experts. To evaluate changes over time, such assessments and updates must be done regularly; this is essential for informing stakeholders and policymakers, and for guiding targeted management efforts.
(2) Every region on Earth has experienced introductions of alien species. We have reports of introductions and establishments of alien species even from the most remote and inhospitable places, often in surprisingly large quantities.
(3) The reported distribution of alien species worldwide is highly uneven. Many reports are from economically wealthy countries and far fewer are from countries of the Global South. It remains unclear how much collated distribution patterns reflect sampling effort rather than the 'true' distribution of alien species.
(4) Numbers of alien species are increasing for all taxonomic groups and regions, and this trend is likely to continue.
(5) Available information about numbers and distributions of alien species is often very incomplete. As a result, numbers and distributions shown in this review represent (sometimes severe) under-estimates. Although we can draw robust conclusions about the general trends of biological invasions for many regions and taxonomic groups, much more effort and data are needed to facilitate more thorough assessments of the status and trends for all taxonomic groups and regions.
(6) We provide six recommendations to improve the situation of assessing status and trends of alien species. These cover priorities relating to data collation (including developing and applying standards), free and FAIR data provisioning, and concerted efforts across borders, among others.

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