



Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management

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Abstract Our ability to predict invasions has been hindered by the seemingly idiosyncratic context-dependency of individual invasions. However, we argue that robust and useful generalisations in invasion science can be made by considering “invasion syndromes” which we define as “a combination of pathways, alien species traits, and characteristics of

the recipient ecosystem which collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions”. We describe this approach and outline examples that highlight its utility, including: cacti with clonal fragmentation in arid ecosystems; small aquatic organisms introduced through ballast water in harbours; large ranid frogs with frequent secondary transfers; piscivorous freshwater fishes in connected aquatic ecosystems; plant invasions in high-elevation areas; tall-statured grasses; and tree-

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feeding insects in forests with suitable hosts. We propose a systematic method for identifying and delimiting invasion syndromes. We argue that invasion syndromes can account for the context-dependency of biological invasions while incorporating insights from comparative studies. Adopting this approach will help to structure thinking, identify transferrable risk assessment and management lessons, and highlight similarities among events that were previously considered disparate invasion phenomena.

Keywords Biological invasions · Context dependency · Invasion science · Invasive species

Introduction

A major challenge in invasion science is to identify general patterns that help us to predict, prevent and manage biological invasions. To this end, recent research has focused on identifying pathways by which alien taxa are likely to be introduced and disseminated (Reichard and White 2001; Hulme 2009; Essl et al. 2015; Pergl et al. 2017; Saul et al. 2017), alien taxa most likely to become invasive and cause impact (Hayes and Barry 2008; Tingley et al. 2010; van Kleunen et al. 2010; Pyšek et al. 2012b; Hawkins

et al. 2015; Kumschick et al. 2015; Bacher et al. 2018), and environments that are particularly susceptible to invasion and impacts from alien taxa (Chytrý et al. 2008a, b; Catford et al. 2012; Guo et al. 2015). Some of the more robust and broadly applicable invasion patterns (Pyšek and Richardson 2006) include: the probability that invasion increases with propagule pressure (Cassey et al. 2018); alien taxa with large native ranges are more likely to become invasive and cause impact than those with smaller ranges (Rejmánek and Richardson 1996; Goodwin et al. 1999; Pyšek et al. 2009; Shah et al. 2011); and isolated oceanic islands are more susceptible to the establishment of alien taxa than continental regions (van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017; Delavaux et al. 2019). There are, however, many exceptions to such generalizations (Kueffer et al. 2013). The probability of an invasion can be insensitive to propagule pressures across a wide range of values (e.g. if invasions are simply not possible due to incompatible environmental conditions, or if an invasion is likely to result from the introduction of a single propagule; Bacon et al. 2014; Duncan et al. 2014). Similarly, while the positive relationship between native range size and the likelihood of an alien species becoming established and/or causing an undesirable impact has been demonstrated for some aquatic (Bates et al. 2013), bird (Duncan et al. 2001), mammal (Forsyth

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et al. 2004) and plant (Pyšek et al. 2009; Hui et al. 2011; Moodley et al. 2013; Potgieter et al. 2014; Moodley et al. 2016; Novoa et al. 2016b) species, such correlations are not always clear-cut (Jeschke and Strayer 2006; Swart et al. 2018). New formulations and fine-tuning of generalizations are thus needed (Jeschke et al. 2012; Kueffer et al. 2013).

Two main approaches have been proposed to deal with context-dependencies in ecology. Some authors suggest focusing research efforts on finding relatively simple general patterns at large scales (i.e. large numbers of species, large spatial scales, or over long time periods) (Lawton 1999; Hui et al. 2013; Prins and Gordon 2014). However, such general patterns informed by ‘big’ data have many exceptions and are often heuristic—useful but with limited predictive value. For example, they are not particularly helpful when deciding whether a specific alien species of potential commercial value can be imported or whether it poses an unacceptable risk (Keller and Kumschick 2017). Others have argued against seeking generalizations and instead propose focusing on small scales to collate and catalogue comprehensive case studies containing more rigorous evidence (Crowley 1987; Sun et al. 2013; Simberloff 2014). The second approach helps us understand and manage particular invasions. However, studying each ongoing invasion separately is incredibly costly (Dawson et al. 2017). It is also unclear how insights gained from the increasing numbers of case studies can be distilled to provide general lessons for management.

In response to this challenge, Kueffer et al. (2013) proposed that invasion scientists should focus on

identifying “typical recurrent associations of species biology and invasion dynamics with particular invasion contexts such as an invasion stage, invaded habitat and/or socioeconomic context” (p. 616), which they termed “invasion syndromes” (see Box 1 for a list of definitions). The premise of “invasion syndromes” is that no single combination of factors is applicable to all invasions and determines which management options are appropriate for all alien taxa in the same way, but that it is still possible to find useful general patterns (Perkins and Nowak 2013) that characterize groups of invasion events. The key challenge is to determine the shared context under which generalizations are possible, robust, and useful (Kueffer 2012).

The concept of “invasion syndromes” is often confused with the traditional concept of “model systems”, defined by Kueffer et al. (2013) as “in-depth research of particular invasions of particular species or in a particular site” (p. 616). Model systems are, however, groups of taxa/ecosystems that contain many species/sites, have a long history of introduction/invasion, contain many species at different stages of the continuum and/or a large literature exist on their invasion, allowing for in-depth studies (e.g. Moodley et al. 2013; Richardson et al. 2011). The results from model system research may therefore allow us to identify recurrent patterns of species-ecosystem (pathways) interactions, i.e. ‘invasion syndromes’.

A revised definition

Here we revise the definition of an invasion syndrome as “a combination of pathways, alien species traits, and characteristics of the recipient ecosystem which collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions” (Fig. 1). Our definition builds on Kueffer et al. (2013), as well as some more recent studies (McGeoch et al. 2016; Wilson et al. 2018; Latombe et al. 2019a), in several key respects. To improve our understanding of biological invasions and how to best manage them, the context of any invasion event must explicitly consider human actions or pathways, the traits of the introduced taxa (which determine their invasiveness), and the characteristics of the recipient ecosystems (which determine their invasibility), as well as any

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Box 1 Glossary

Alien species traits A combination of attributes that defines alien species in terms of how they interact with the abiotic environment and with other alien and native species

Case study An in-depth analysis of a specific invasion event and its related contextual conditions, invasion outcomes, and response options

Characteristics of the recipient ecosystem A combination of abiotic and biotic features that defines the ecosystems where invasion events might occur

Context The characteristics that form the setting for an invasion event, including the pathways of introduction, the alien species traits, and the characteristics of the recipient ecosystem

Impact The environmental and socioeconomic changes that alien species cause in the recipient ecosystems. These impacts can be desirable or undesirable depending on people's values.

Invasion dynamics A description of the dynamics from introduction to invasion (e.g. a long lag phase, rapid long-distance dispersal, and more generally the path to commonness). It can include both population-level properties like extent, local abundance, and dispersal patterns, and community-level properties like biotic interactions

Invasion event The context and details of a particular alien taxon being introduced to a particular recipient environment and the resulting invasion dynamics and impacts

Invasion syndrome "A combination of pathways, alien species traits, and characteristics of the recipient ecosystem which collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions". This means an invasion syndrome should be formed of generalisations that are as broad as possible, but which are still robust and useful. Note: this is a development of the definition proposed by Kueffer et al. (2013) "typical recurrent associations of species biology and invasion dynamics with particular invasion contexts such as an invasion stage, invaded habitat and/or socioeconomic context"

Invasion outcomes The consequences of an invasion event in terms of invasion dynamics and impacts

Response options The set of actions that can be used to manage the outcomes of invasion events or to prevent them from happening in the first place

Pathways A combination of processes and opportunities that result in the human-mediated movement of alien taxa from one area to another

interactions between these factors (Wilson et al. 2018). We also specify the *outcomes* (i.e. invasion dynamics and impacts) of invasion events in the definition, with the intention that the invasion syndrome approach is explicitly designed to improve management efficacy.

Pathways

Pathways are defined as "a combination of processes and opportunities resulting in the movement of propagules from one area to another" (Richardson et al. 2011, p. 412). The different pathways by which alien taxa are intentionally or unintentionally introduced to areas outside their native range and/or spread within their introduced range (Hulme et al. 2008) can influence the dynamics of their invasion or impacts (Lambdon and Hulme 2006; Westphal et al. 2008; Wilson et al. 2009; Kueffer 2017; Pergl et al. 2017). For example, since the number of individuals moved and the frequency of these movements depend on the

characteristics of the pathway used, pathways are intrinsically linked to colonization and propagule pressure, which in turn influence invasion outcomes (Lockwood et al. 2009, 2013). Some species might also lack the opportunity to invade because no pathway currently exists to move them beyond their native range. Therefore, assessing particular pathways of introduction and spread is crucial for enhancing prevention and, more generally, for guiding policies and management responses to invasions (Padilla and Williams 2004; Hulme 2009; Kikillus et al. 2012; Essl et al. 2015).

Pathways can be characterized in general terms (e.g. "disseminated as ornamental plants"), or more specifically by identifying vectors involved in the introduction of particular alien taxa from specific donor regions (Hulme 2009; Novoa et al. 2017). Whatever the level of pathway specificity, the goal should be to provide insights of direct relevance for management and policy. For example, identifying the stakeholder groups associated with particular

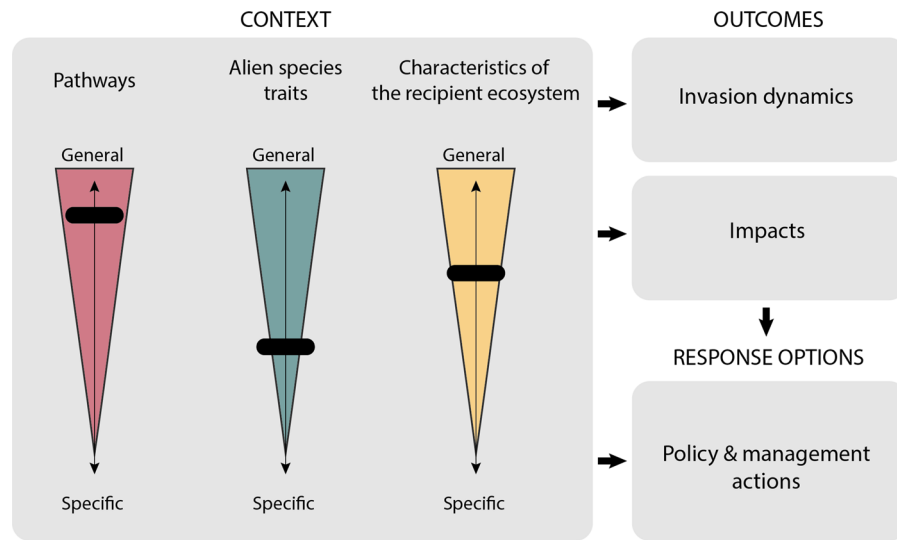


Fig. 1 An invasion syndrome is defined as a combination of pathways, alien species traits, and characteristics of the recipient ecosystem which collectively result in predictable dynamics and impacts, and that can be managed effectively using specific policy and management actions. For it to be coherent, the shared characteristics (pathways, alien species traits, and characteristics of the recipient ecosystem) must result in predictable outcomes (regarding invasion dynamics and impacts) which in turn can be best managed using similar management or policy responses. This means an invasion syndrome should be created from generalizations that are as broad as possible, but which are still robust and useful. The invasion context is displayed here on three vertical axes (i.e.

vertical black bars) that range from general (at the top) to specific (at the bottom). For example, the alien species traits axis could vary (top/general to bottom/specific) from all aquatic species, to aquatic species within a specific genus, to congeneric freshwater species within a specific body size range. The positions along the axes (i.e. black boxes) are adjusted so that all invasion events within the selected context result in similar outcomes and response options. A change in any one of the axes, or a change in the outcomes or response options that are to be encompassed by the invasion syndrome, will likely affect all other aspects of the framework, which means that circumscribing a syndrome is an iterative process

pathways can provide valuable data about the characteristics of each pathway (e.g. the areas where the species are moved to, and the identity and number of species moved), and promote responsible behaviour (Cole et al. 2019).

The Convention on Biological Diversity (CBD) recently adopted a hierarchical system of classifying introduction pathways in particular (Hulme et al. 2008; CBD 2014). This is being applied in the implementation of the European Union Regulation 1143/2014 on invasive alien species and is being used in South Africa for its national-level reporting on biological invasions (van Wilgen and Wilson 2018). While these are important and increasingly used classification schemes, it is often also important to explicitly consider key characteristics of the introduction pathways, for example, the frequency of introduction, the vectors involved, and the likelihood of co-introduction of different alien species (Wilson et al. 2009).

Alien species traits

Species traits are attributes that relate to how species interact with the abiotic environment and with other species (Díaz and Cabido 2001). Possessing certain traits conveys advantages for alien species [e.g. alien plants with longer flowering durations tend to be more likely pollinated (Cadotte et al. 2006), and therefore more invasive]. Research on how traits differ among species has been a topic of particular interest in invasion science because it is thought that identifying and comparing species traits associated with invasion dynamics and impact can improve the prediction and management of invasions. Such research has sought to link species traits with invasion outcomes (Pyšek and Richardson 2007; Pyšek et al. 2009; Capellini et al. 2015; Mahoney et al. 2015; Gallien and Carboni 2017), impacts (Nentwig et al. 2010; Pyšek et al. 2012b; Elleouet et al. 2014; Novoa et al. 2016b; Measey et al. 2016), and policy and management

actions (Murray et al. 2011; Novoa et al. 2015a). Within the invasion syndrome approach, a wide variety of alien species traits (from life-history traits to behavioural traits or ecological preferences; see Supplementary information for examples) can be selected to adjust the context.

Characteristics of the recipient ecosystem

The biotic and abiotic characteristics of the recipient ecosystem, including its anthropogenic modifications (Kueffer 2017), influence alien species' invasion dynamics and impact (Hood and Naiman 2000; Denslow 2003; Riley et al. 2005; Johnson et al. 2008; Catford et al. 2009; Vermonden et al. 2010; Pyšek et al. 2012b, 2017). A wide range of characteristics of the recipient ecosystem can be important: from broad classifications such as biome types (Campbell 1996), ecoregions (Olson and Dinerstein 2002; Abell et al. 2008) or habitats (Chytrý et al. 2008a, b; Latombe et al. 2019b), to more specific abiotic (e.g. altitude, precipitation or nutrient availability; Chytrý et al. 2008a, b), biotic (e.g. native biodiversity or abundance of mutualists or natural enemies; Le Roux et al. 2017; Latombe et al. 2018; Hui and Richardson 2019) or socioeconomic characteristics and processes (e.g. national wealth or human population density; Pyšek et al. 2010). Biotic and abiotic matches between the donor and the recipient ecosystems can also influence the outcomes of invasions (Thuiller et al. 2005; Gallien et al. 2015; Hui et al. 2016), their impact (Ricciardi and Atkinson 2004), and management (Sun et al. 2017).

Outcomes

To be considered as an invasion syndrome, the invasion events defined by the context (i.e. the pathways, alien species traits, and characteristics of the recipient ecosystem) must result in similar outcomes, i.e. they must share similar invasion dynamics or cause similar impacts. In other words, the outcomes of an invasion event defined by the context need to be predictable. Invasion dynamics refer both to the dynamics from introduction to invasion [e.g. a long lag phase, rapid long-distance dispersal, and more generally the path to commonness (McGeoch and Latombe 2016)]; to general properties like extent, local abundance, dispersal patterns; and potentially, biotic

interactions (Hui and Richardson 2017). Impacts refer to a wide range of both positive and negative environmental and socioeconomic changes that invasive alien species can cause in the social-ecological systems to which they are introduced (Shackleton et al. 2007; Binimelis et al. 2008; Kull et al. 2011; Vilà et al. 2011; Pyšek et al. 2012b; Gallardo et al. 2016; Gallien et al. 2017; Zengeya et al. 2017). For example, depending on the context, invasive alien species can cause changes in the biodiversity or the ecosystem properties of the invaded areas (Pyšek et al. 2012a; Blackburn et al. 2014), or affect human well-being (Vilà and Hulme 2017; Bacher et al. 2018, Shackleton et al. 2019). These impacts result, in part, from the invasion dynamics themselves (e.g. extent, abundance, dispersal, and biotic interactions).

Response options

The context and outcomes associated with a particular syndrome will affect the set of suitable response options for managing invasions. For an invasion syndrome to be of practical value, there have to be some general rules as to which management responses are effective to deal with invasion events included in the syndrome. This might include steps taken to prevent invasive alien species from entering a new area; if introduced, efforts to remove species before they become widely established; and if species are widely established, and it is no longer possible to remove them, actions to limit negative impacts while retaining any benefits (van Wilgen et al. 2011; Shackleton et al. 2017; Novoa et al. 2019).

Examples of invasion syndromes

Invasion syndromes occur across a broad range of taxonomic groups and environments (see Fig. 2 for a schematic summary), and in the following section we discuss seven examples to highlight this diversity.

A. Cacti with clonal fragmentation in arid ecosystems

The Cactaceae family contains 1919 species of succulent plants (Novoa et al. 2015b), almost all of which are endemic to the Americas (Novoa et al. 2016a). Fifty-seven cactus species are currently listed

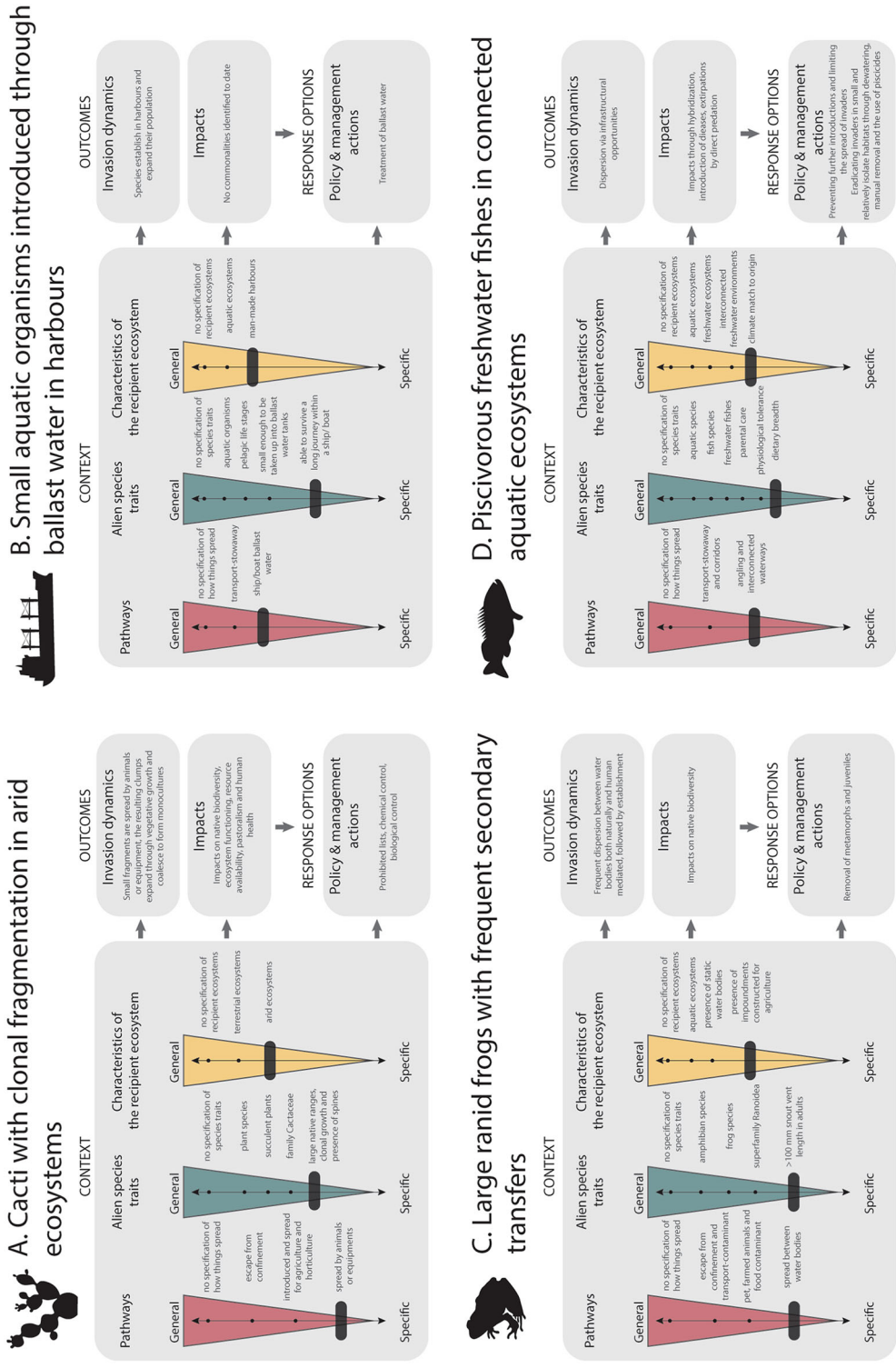


Fig. 2 Examples of seven invasion syndromes proposed in this paper. See text for explanation.

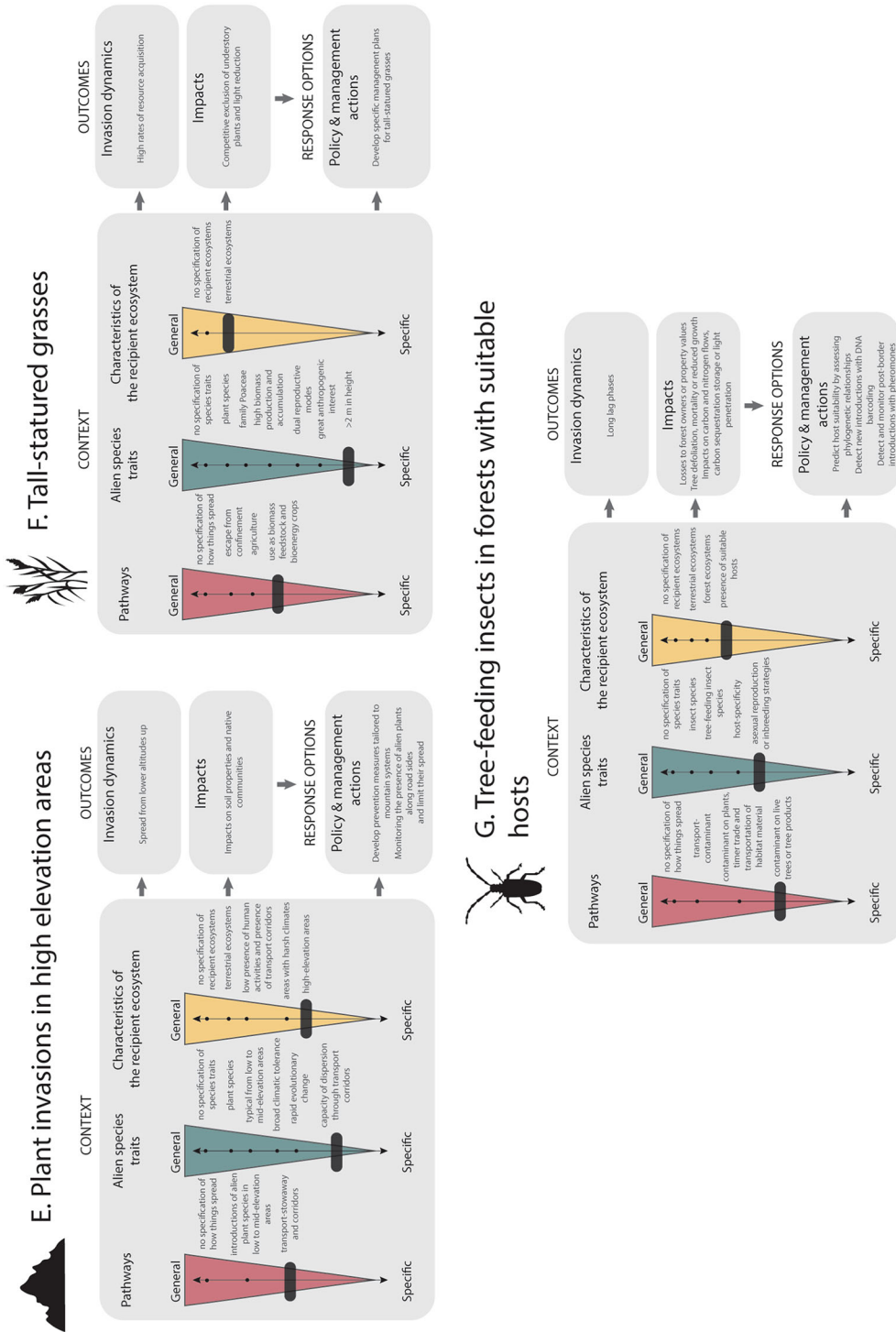


Fig. 2 continued

as invasive around the world (Novoa et al. 2015b). While all cacti have thick, fleshy and swollen stems and/or leaves, and are adapted to dry environments [and so primarily invade arid **recipient ecosystems** (Anderson 2001)], invasive cacti share several **species traits** that include large native range size, spread by clonal fragmentation, and spines (Novoa et al. 2016b). They were introduced and spread along similar **pathways**—historically a few taxa were used for food, fodder, as barrier plants, or for cochineal production; and more recently a wide range of species have been introduced and spread for horticulture (Novoa et al. 2016a). Once introduced, they often have similar **invasion dynamics** and **impacts**. Due to the presence of spines and fragments, invasive cacti can attach and disperse via animals, clothes or equipment. The resulting small clumps expand rapidly through vegetative growth, and coalesce to form monocultures, resulting in impenetrable thickets with negative impacts on biodiversity, ecosystem functioning, resource availability, pastoralism, and human health (Novoa et al. 2016b). Moreover, similar **management** actions are highly effective in controlling invasions of different cactus species (Novoa et al. 2019). Classical biocontrol agents have been used to manage 28 invasive cactus species, achieving complete control in many situations (i.e. no other management interventions are required to reduce impacts to an acceptable level; Zimmermann et al. 2009). The cacti syndrome is potentially extendable for all succulent plants that reproduce vegetatively, have large native ranges and spines, such as *Agave* species (Badano and Pugnaire 2004).

B. Small aquatic organisms introduced through ballast water in harbors

Ship ballast water is a specific introduction sub-**pathway** as per the CBD's scheme, categorized under the broader transport-stowaway pathway category. This pathway explicitly selects for particular **species traits**, i.e. aquatic organisms with pelagic life stages that are small enough to be taken up into ballast water tanks, and that can survive the journey to a new destination (Briski et al. 2014). Survival during transport often correlates with high levels of phenotypic plasticity. The **recipient ecosystems** are inevitably boat harbours and can be marine, estuarine or freshwater. As such, the **invasion dynamics** initially

have some similarities, whereby entire pelagic communities are taken up in one or more locations and transferred to a new location. Alien species establish in these artificial habitats and expand from these points of entry. Thus far, there is not enough information on the common **impacts** of these invasion events. Various **response options** have been proposed but managing invasions reactively has been found to be mostly infeasible in marine systems. Therefore, the focus has been on preventing introductions through monitoring and pathway management (Ojaveer et al. 2015). Although the Ballast Water Convention came into force in 2017 with the aim of minimizing the biosecurity risk associated with ballast water, it is yet to be fully implemented. Ultimately, it is envisaged that vessels will carry an international ballast water management certificate, demonstrating compliance with ballast management standards, including the use of on-board ballast water treatment units.

C. Large ranid frogs with frequent secondary transfers

Ranoidea is a superfamily of frogs that contain seventeen different families. Ten ranid species within the genera *Lithobates* and *Hoplobatrachus* have been recorded as invasive in many climatic zones (including arid regions). These invaders share the same **pathways** of introduction—intentional introductions for consumption and the pet trade (Tingley et al. 2010), or as contaminants in aquaculture (Mohanty and Measey 2019). Once introduced, they often disperse through natural spread between lentic water bodies, although intentional human-mediated transfers often also occur. In terms of **species traits** they tend to have large body sizes (> 100 mm snout-vent length). They are environmentally constrained to breeding in static water bodies, and so **recipient ecosystems** with aquatic impoundments, e.g. agricultural impoundments, can be a prerequisite for an invasion. Invasive large ranid frogs **impact** native biodiversity by preying on invertebrates and small vertebrates, serving as reservoirs of diseases, and competing with other anurans during the larval stage (Measey et al. 2016). Removal of metamorphs and juveniles was identified to be the best **management** intervention (Govindarajulu et al. 2005).

D. Piscivorous freshwater fishes in connected aquatic ecosystems

Fishes are among the most widely introduced alien vertebrates and their invasions are a global problem because of their importance in fisheries, aquaculture, recreational fishing and the global pet trade (Cucherousset and Olden 2011; Dawson et al. 2017). Piscivorous freshwater fishes (e.g. rainbow trout *Onchorhynchus mykiss*, largemouth bass *Micropterus salmoides*), are mainly introduced through intentional **pathways** (e.g. for enhancing fisheries) and are mostly released outside of captivity, with high propagule pressure, to provide opportunities for recreational fishing (Cucherousset and Olden 2011). Establishment depends on the interaction between the **recipient ecosystem** and **species traits**, including reproductive strategy and physiological tolerance (Marchetti et al. 2004). They primarily invade connected aquatic **ecosystems** (Marchetti et al. 2004; Ruesink 2005) and inter-catchment movement is dependent on human activity resulting in direct releases, escape or dispersal via infrastructural opportunities, e.g. inter-basin water transfers (Ellender and Weyl 2014).

The **impacts** of piscivorous freshwater alien fish invasions often include hybridization with native species, introduction of disease, and extirpations of native taxa by direct predation (Cucherousset and Olden 2011). Fishes are extremely difficult to eradicate once established. Methods such as dewatering, manual removal and the use of piscicides are only practical in small and relatively isolated habitats (Britton et al. 2011). Moreover, management of established piscivorous freshwater fishes can be contentious because of conflicting values of stakeholders (Zengeya et al. 2017). For this reason, the **management** of invasive fishes focusses on preventing further introductions and limiting their spread. To guide this process, considerable research has focussed on developing the widely applied Fish Invasiveness Screening Kit (FISK) which evaluates invasion risk (Copp 2013). Retrospective assessments of the FISK have found the tool relatively robust in predicting successful invaders (Vilizzi et al. 2019).

E. Plant invasions in high elevation areas

Most human-mediated introductions of alien plants are to low- or mid-elevation areas (Alexander et al.

2011; McDougall et al. 2011). As a result, invasive alien plants are rarely mountain specialists, and high elevation areas are generally less invaded than other ecosystems (Chytrý et al. 2008b, 2009; Pauchard et al. 2009). Most invasive plant species in high elevation areas share the same **pathways of introduction**, since they are species that were initially introduced to low or mid-elevation areas and were then able to spread to higher elevations along roads or other transport corridors, either through their own dispersal or aided by human disturbance, construction, or livestock movements. They also share the **species trait** of a broad climatic tolerance, which allows them to establish in high elevation **recipient ecosystems** (Leger et al. 2009; Monty and Mahy 2009; Alexander et al. 2011; Haider et al. 2011; McDougall et al. 2011; Gallien et al. 2016). The **outcomes** of such invasions are typified by the spread from lower to higher altitudes, with impacts on soil properties and native communities along the way (Alexander et al. 2016). Therefore, when planning the **management** of plant invasions in high elevations at regional scales, the major goal should be to monitor the presence of alien plants along roadsides and limit their spread (Pauchard and Alaback 2004). This syndrome of “plant invasions in high elevation areas” might be extended to other areas with harsh climates, low propagule pressure and low human populations, such as polar ecosystems.

It is important to note that those species that are specialists in high elevation areas might be intentionally introduced directly to other high elevations (instead of low- or mid-elevations) outside their native range in the future, e.g. through the intensification of agriculture, as ornamental or forestry plants, for the restoration of ski runs, or for managed relocation (McDougall et al. 2011). If this happens and some of the intentionally introduced species become invasive, then the syndrome of “plant invasions in high elevation areas” will become outdated.

F. Tall-statured grasses

Tall-statured grasses include grasses that reach heights of at least 2 m (~8.6% of grasses; 929 species scattered among 21 tribes in seven subfamilies; Canavan et al. 2019). Tall-statured grasses share similar **pathways of introduction** outside their native range (e.g. for use as biomass feedstock and for bioenergy crops). Moreover, typical **species traits** that

confer tall-statured grasses their invasion success include high biomass production and accumulation, dual reproductive modes, and a generally great anthropogenic interest (Canavan et al. 2017, 2019). Although they can invade different **ecosystems** (e.g. grasslands, wetlands and forests), invasions by tall-statured grasses often have similar **outcomes** (e.g. high rates of resource acquisition, competitive exclusion of understory plants, and light reduction) related to their production of biomass. It remains to be assessed whether this group of grasses can be addressed with similar policies or **management** actions. However, since the traits of invasive tall-statured grasses are very specific, targeted risk assessments should probably be developed. It seems likely that the tall-statured grasses syndrome can be extended to include some other tall species within the order Poales, such as species from the Juncaceae or Cyperaceae families, but this is still to be explicitly tested. Additionally, Canavan et al. (2019) found that species in the subfamily Bambusoideae (woody bamboos; tribes Arundinarieae and Bambuseae) have lower rates of naturalization compared to other tall-statured grasses, seem to invade predominately forest ecosystems post-disturbance, and species within the group typically receive lower risk scores in risk assessments, suggesting that bamboos might be a distinct invasion syndrome.

G. Tree-feeding insects in forests with suitable hosts

Tree-feeding insects are prominent as invasive species. For example, 455 and 400 non-native tree-feeding species are recorded in the USA (Aukema et al. 2010) and Europe (Roques et al. 2016) respectively. They are mainly introduced through unintentional **pathways**, associated with live plant imports, machinery, roundwood, sawn timber, sea containers, ships or wood packaging materials (Roques 2010). Once introduced, their secondary spread is generally facilitated by anthropogenic dispersal, such as the movement of wood (e.g. wood for campfires or home heating) or attached to live ornamental trees (Brocknerhoff and Liebhold 2017). Tree-feeding insect invasions share similar **species traits**. Asexual reproduction or inbreeding strategies help to avoid mate-finding failure (Liebhold et al. 2016), and most

tree-feeding insects are host-specific, i.e. they only feed on their natural hosts or closely related trees. Therefore, introduced species are only able to establish when their **recipient ecosystems** present suitable hosts (Brocknerhoff and Liebhold 2017), and phylogeographic patterns can help to predict host suitability (Gilbert et al. 2012), i.e. the most likely donors of invasive tree-feeding insects are from related biogeographic regions. Once established, they often have similar **invasion dynamics**. For example, they often exhibit long lag phases between establishment and impact (Roques et al. 2016). These can be due to an initial low habitat suitability, or to the need to reach high densities before their presence and impacts are detected.

Tree-feeding insect invasions are among the greatest threats to forests worldwide (Liebhold et al. 1995), causing highly visible **impacts**, such as severe defoliation, mortality or reduced growth (Morin and Liebhold 2016). These impacts can, in turn, facilitate non-host tree species, causing changes in tree compositions or indirect effects on other species in the food web. They can also affect other characteristics of the invaded forests, such as carbon and nitrogen flows, carbon sequestration and storage or light penetration. These impacts pose an existential threat to forestry in some areas (Wingfield et al. 2015; Brocknerhoff and Liebhold 2017). Finally, by killing street trees and those in gardens, tree-feeding insects can affect both property values and people's sense of place (Shackleton et al. 2019).

The exchanges of tree-feeding insect species among world regions is increasing, leading to an increasing number of established non-native tree-feeding insect species. For example, in the USA, on average, two new species are detected each year (Aukema et al. 2010). Several specific tools are available to assist with **managing** such invasions. For example, phylogenetic relationships can help to predict host suitability (Gilbert et al. 2012), i.e. are most likely to come from regions that are biogeographically and climatically similar to the introduced regions. DNA barcoding can help detect immature stages, such as eggs and larvae, at the ports of entry (Ball and Armstrong 2006), and pheromones can help in detecting and monitoring post-border (Myers and Hosking 2002, Suckling et al. 2005).

A method to identify further invasion syndromes

To facilitate the identification of additional invasion syndromes, we propose a systematic method for their circumscription and confirmation (Latombe et al. 2019a), based on the premise that an invasion syndrome should be formed of generalizations that are as broad as possible, but which are still robust and useful (Fig. 3). Often the starting point is to identify invasion events with similar contexts, i.e. pathways, species traits, and characteristics of the recipient ecosystem. However identifying similar outcomes and responses might also be a useful starting point. If the invasion events classified into a putative syndrome vary in the context, outcomes or appropriate responses, then the syndrome needs to be adjusted until it encompasses the invasion events. Putative invasion syndromes should be made progressively more general (i.e. by including more invasion events), and if the context, outcomes, and responses still fit the expanded set of invasion events, then the more general invasion syndrome should be preferred. In other words, the more specific the invasion syndrome, the less useful it is.

The invasion syndrome approach thus helps to determine under which situations it is meaningful to generalize, and so make predictions about biological invasions—this is crucial if management lessons are to be shared. We argue that jointly considering groups of invasion events presenting similar management requirements is the only practical way of dealing with the growing numbers of alien species (OEPP/EPPO 2008; van Wilgen et al. 2011). The invasion syndrome approach can facilitate the transfer of lessons between invasion events; for example, transferring insights from Australian *Acacia* spp. (van Wilgen et al. 2011), *Pinus* spp. (Nuñez et al. 2017) and *Prosopis* spp. (Shackleton et al. 2017) between regions of introduction. Moreover, grouping invasion events according to their context and outcomes can identify not only common management goals but also shared stakeholders, thereby potentially simplifying decision-making processes (Novoa et al. 2016a, 2018). We believe that the approach outlined here will provide new insights into the drivers of invasion dynamics; help establish management priorities; and identify more accurate, efficient and transferable management responses. Applying invasion syndromes paves the way for easier sharing of information among

stakeholder groups to reveal and identify solutions for new or extant invasions. Incorporating invasion syndromes into decision-making may also help to link practitioners and managers working on different taxa or in regions or ecosystems that, perhaps unknowingly, are actually dealing with similar problems.

Testing the approach

The concept of invasion syndromes remains to be tested empirically. Although data on the characteristics that define the context for an invasion syndrome are becoming more accessible, challenges remain. Information on pathways of introduction and secondary spread is not always available, in particular on their quantitative aspects such as when, how often, or how many individuals are introduced or dispersed. On the other hand, data on species traits are becoming more accessible due to the development of trait databases that encompass a large number of taxa (Supplementary information). For example, the global TraitBank database contains data on more than 330 different traits for 1.7 million species (Parr et al. 2016). However, data quality remains an issue, especially: if the methodology used to measure the traits is not indicated; if traits are not comparable because they are measured differently or in different contexts; if it is unclear whether traits were measured in the native or the alien range; or if trait databases ignore geographic variations in trait values (Yesson et al. 2007; Robertson 2008; Moravcová et al. 2010). Moreover, trait databases often have data for a limited number of species or have many missing values. Such data gaps make it difficult to define a syndrome for a large group of species or invasion events.

Information on the outcomes of invasion events is also becoming increasingly available for a large number of taxa (Zenetos et al. 2005; van Kleunen et al. 2015; Pyšek et al. 2017). For example, the recently released Global Naturalized Flora (GloNAF) database contains information on the distribution of more than 13,000 naturalized alien species in more than 1000 regions of the world (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). The Global Register of Introduced and Invasive Species (GRIIS), supported by the Secretariat of the Convention on Biological Diversity, currently provides checklists of naturalized and invasive species for 20 countries, and aims to soon

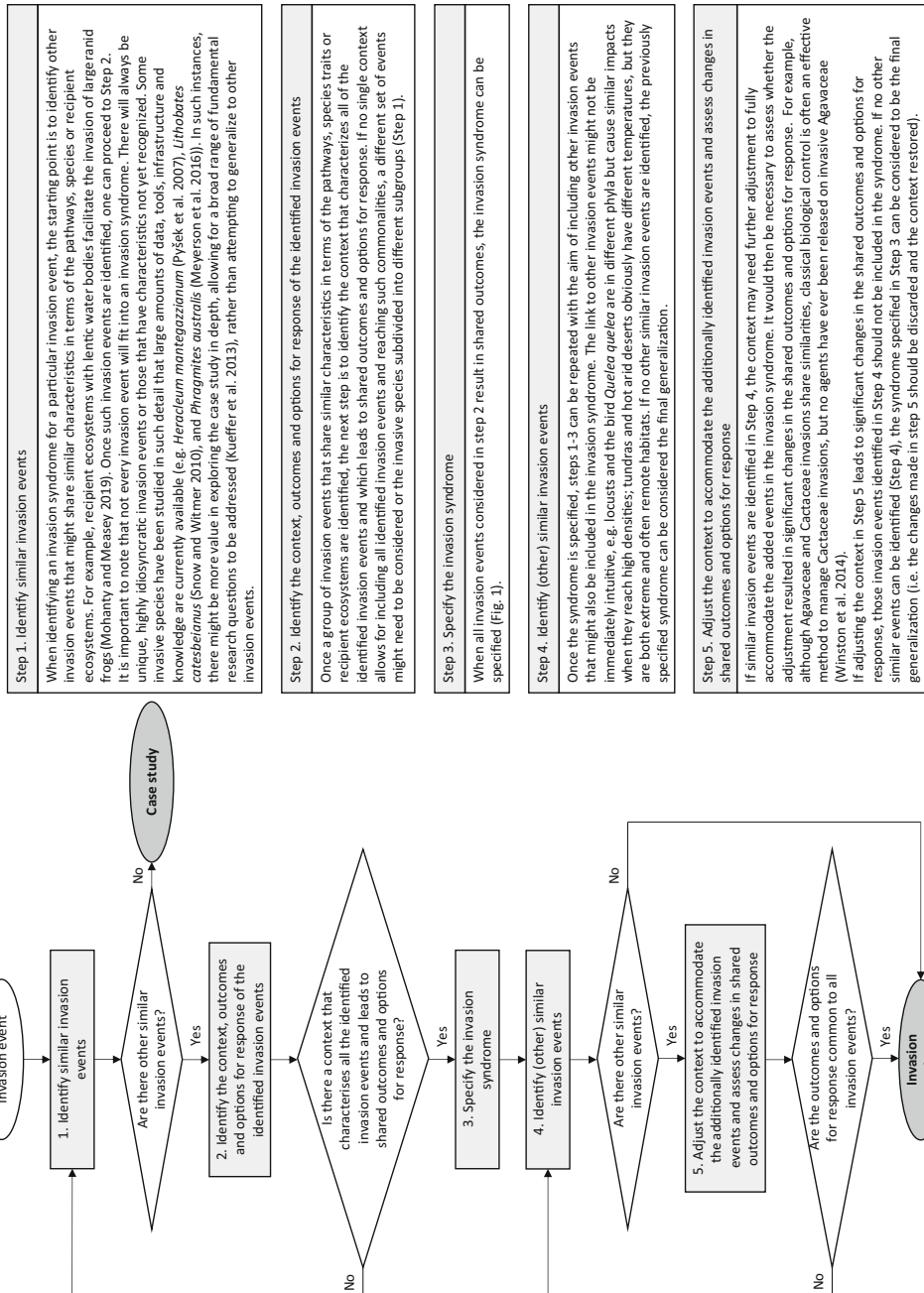


Fig. 3 Schematic diagram and description of the five steps proposed for identifying invasion syndromes

provide checklists for most countries globally (Pagad et al. 2018). This is, however, a very coarse measure (i.e. naturalized vs. invasive) at relatively large scales (i.e. country level) and only represents a “snapshot in time” since many species are still progressing along the introduction—naturalization—invasion continuum (Pyšek et al. 2012a). GRIIS also conflates the concepts of spread and impact when defining a species at a site as invasive (whereas in reality and practice spread and impact are mediated by different factors). A coordinated monitoring and reporting scheme with standard metrics is clearly needed at the global level (Latombe et al. 2017). More precisely defined categorizations (e.g. the 11 categories proposed by Blackburn et al. 2011 to identify the invasion stage of any invasion event) or population dynamics metrics (Leung et al. 2012), at finer scales, are preferable for characterizing invasion syndromes.

A number of analytical approaches could be used for quantitatively identifying invasion syndromes. As one example, machine learning techniques (see Kelleher et al. 2015 for a detailed review) are possibly the most powerful approaches for identifying invasion syndromes (even with the current limitations). Unsupervised clustering techniques (e.g. hierarchical clustering, k-means clustering, etc.) could be applied to data describing the **context, outcomes and response options** of invasions (Fig. 1). While this approach ignores the links between the three facets of an invasion syndrome, as shown in Fig. 1, such links could be specified via numerous regressions between multiple response variables (i.e. **outcomes and response options**) and multiple predictor variables (**context**) and a clustering method applied to these regressions (Qin and Self 2006). Alternatively, supervised classification techniques could be used (e.g. Random Forest, Support Vector Machines, and Artificial Neural Networks). Data representing the **context, outcomes and response options** would be collected for a training set of invasion events, which researchers would have already assigned to a predefined invasion syndrome (e.g. cacti with clonal fragmentation in arid ecosystems). Then, a test dataset for a collection of invasion events not yet assigned to any invasion syndrome (e.g. succulents with clonal fragmentation in arid ecosystems) would be fed into the model to determine their possible affiliation to this invasion syndrome. Machine learning techniques are already widely used in invasion science; for example

to predict the invasion stage of alien plants using trait and biogeographical data (Chen et al. 2015), to predict eradication success (Xiao et al. 2018), and to identify the source of ballast water using bacterial species composition (Gerhard and Gunsch 2019).

Conclusion

We believe the invasion syndrome approach is a dynamic, composite, and repeatable way of accounting for context-dependencies within invasion science. Its application will facilitate a more mechanistic and predictive understanding of biological invasions, thereby offering better guidelines for management. We suggest that developing and refining invasion syndromes should be a key activity of the “global networks for invasion science” proposed by Packer et al. (2017).

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workshop, refined the initial idea, commented on the manuscript and contributed to the final version.

Compliance with ethical standards

Conflict of interest All authors declare no competing interests.

Data availability All data generated or analysed during this study are included in this article (and its Supplementary Information files).

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Supplementary information. Examples of databases containing data on diverse alien species traits

Name of the Database	Trait data	Organism	Area	Traits	Number of taxa	Link	Reference
Amniote life-history database	Life history	Birds, mammals, and reptiles	Global	29	21 322	http://www.esapubs.org/archive/ecol/E096/269/	1
AmphiBIO	Ecology, morphology and reproduction features	Amphibians	Global	17	6 500	https://doi.org/10.6084/m9.figshare.4644424	2
AnAge	Ageing and longevity	Animals	Global	3275	4244	http://genomics.senescence.info/species/	3
BIOTIC	Biological	Benthic species	Global	>40	590	https://www.marlin.ac.uk/biotic/	4
Carabids.org	Hind wing development, trophic level and hunting abilities	Carabids	Global	3	10 000	http://carabids.org/	5
CLO-PLA3	Clonal growth and vegetative regeneration	Plants	Central Europe	29	2 909	http://clopla.butbn.cas.cz/	6
Coral Trait Database	Life history, phylogenetic and biogeographic	Corals	Global	158	1548	https://coraltraits.org/	7
Database of lotic invertebrate traits	Ecology, morphology, behaviour, and physiology	Invertebrates	North America	62	ca. 2200	-	8
D ³ Database	Dispersal diaspore	Plants	Global	33	5000	www.seed-dispersal.info	9
Ecological traits of New Zealand Flora	Ecological	Plants	New Zealand	50-55	-	http://ecotraits.landcareresearch.co.nz/	-
FishBase	Taxonomy, biology, trophic ecology, life history and uses	Fishes	Global	11	33 700	http://www.fishbase.org/search.php/	10

FishTraits Database	Trophic ecology, life history, habitat associations and tolerances	Freshwater fishes	United States	>100	809	http://www.fishtraits.info/	11
FRED 1.0	Fine-Root Ecology	Plants	Global	>300	1213	http://roots.ornl.gov/	12
freshwaterecology.info	Autecological characteristics, ecological preferences and biological	Freshwater fish, macroinvertebrates, macrophytes, diatoms and phytoplankton	Europe	106	21 167	http://www.freshwaterecology.info/	13
Global Biotraits Database	Thermal responses of physiological and ecological	General	Global	220	1508	http://biotraits.ucla.edu/	14
Life-history trait database of European reptile species	Life history	Reptiles	Europe and neighbouring Asian and African countries	ca. 25	122	-	15
Marine Species Traits	Biological, ecological, distribution and species' importance to society	Marine species	Global	10	372 388	http://www.marinespecies.org/traits/	16
PanTheria	Life history traits	Mammals	Global	30	5000	http://esapubs.org/archive/ecol/e090/184/	17
Phytotraits	Functional traits such as N ₂ fixation or buoyancy	Phytoplankton	Global	19	2549	https://www.riinaklais.com/phytotraits/	-
Polytraits	Morphological, behavioural, reproductive and larval	Polychaetes	Global	47	> 1000	http://polytraits.lifewatchgreece.eu/	18

TraitBank	General	General	Global	>330	1.7 million	http://eol.org/traitbank/	19
Trait database for marine copepods	Functional traits related to life missions, feeding, growth and reproduction	Marine pelagic copepods	Global	14	ca. 10 800	-	20
Traits	Habitat, life history, mobility, morphology and ecological	Freshwater macroinvertebrates	North America	74	3857	https://www.epa.gov/risk/freshwater-biological-traits-database-traits/	21
TRY	General	Plants	Global	1 800	148 000	https://www.try-db.org/	22
UConn	Ornamental attributes, appropriate use, and identification	Woody landscape plants	North America	29	557	http://hort.uconn.edu/	23

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