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The Role of Eco-Evolutionary Experience in Biological Invasions: Implications for Theory, Management, and Conservation

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Summary

Biological invasions are a significant component of global change and represent a major challenge for biodiversity conservation. A comprehensive understanding of the reasons for invasion success and failure is crucial for our ability to predict and manage invasions effectively. Up to now, this remains difficult, and in view of the growing number of individual hypotheses and concepts, as well as increasingly dispersed empirical data, there is a need for synthesis. The main objective of this thesis was thus to contribute to these synthesizing efforts by consolidating empirical data from different sources, and by finding conceptual ways to interrelate existing invasion hypotheses focusing on the role of species' evolutionary legacy.

Diverging definitions may be regarded as an obstacle for research synthesis. However, the present study argues that recurring debates about a single 'correct' definition of invasive species and biological invasions should be put aside. Invasion researchers have different, but equally valuable perspectives on invasions (e.g. historical-biogeographic, nature conservation, and ecological and evolutionary perspectives). A uniform usage of terms is probably not feasible, but a stronger awareness of the concepts underlying the terms used in interrelated research fields would enhance communication and still promote progress in invasion research. For synthesis, definitions and assumptions have to be explicit but not necessarily identical. Acknowledging different perspectives on invasions is also important for management, which often has to take into account widely diverging interests of several stakeholders (e.g. conservationists, policy-makers, and entrepreneurs) in order to be effective and sustainable.

The success or failure of an invasion is possibly influenced by the way in which the organism reaches a new region. Empirical data about such introduction pathways is currently scattered across many databases which use differing terminology to describe the same pathways. Thus, this study harmonized and consolidated information on introduction pathways from two major invasion databases (GISD and DAISIE), successfully applying a recently developed standard pathway categorization scheme. The relative importance of broad introduction pathways (release, escape, contaminant, stowaway, corridor) was assessed for major taxonomic groups (plants, vertebrates, invertebrates, algae, fungi, other) and for all environments (terrestrial, freshwater, marine). The analysis covered more than 8,300 species and showed striking differences among taxonomic groups, whereas differences among environments were much less pronounced. Further, high-impact invaders, in contrast to other alien species, were frequently introduced both intentionally *and* unintentionally. These findings are highly useful for prioritization in management of invasive alien species.

An important reason for invasion success or failure may also lie in the presence or absence of particular combinations of invasion traits in introduced species. Thus, from several online sources and databases, a dataset was compiled that comprised information on 13 invasion traits for 201 invasive species from seven taxonomic groups (animals, green plants, fungi, heterokonts, bacteria, red algae, alveolates). A cluster analysis and the comparison of trait frequencies revealed that even though a connection between taxonomic affiliation and differences in invasion mechanisms could not be neglected, also invasive species from different taxonomic groups often share similar combinations of invasion traits. Overall, the findings suggested that there are no universal invasion traits that could explain the invasion success of all invaders, but that invaders are successful for different reasons represented by different combinations of invasion traits across taxonomic groups (‘invader types’).

Finding patterns in empirical data can yield important first clues about how to react in certain invasion scenarios, but they do not provide mechanistic explanations of the actual processes that drive success or failure of invasions, which would allow more reliable predictions. Accordingly, a conceptual framework was developed in this thesis that emphasizes the species’ evolutionary legacy and its role in shaping novel biotic interactions. It consists of five hypothetical scenarios (covering all major types of ecological interaction) about the influence of so-called ‘eco-evolutionary experience’ in resident native and invading non-native species on invasion success. It was shown that several major ecological invasion hypotheses can be integrated into this framework by uncovering their shared implicit reference to the concept of eco-evolutionary experience. As a first step towards a better mechanistic understanding and the application of the experience concept in management contexts, an assessment routine was drafted using a food web-based example, and two indices were developed for the actual quantification of experience.

The applicability of the experience concept for management of invasive and other novel organisms was further increased by investigating the implications of different combinations of high and low degrees of experience in interacting resident and non-resident species. This resulted in the definition of four broad risk categories for estimating the probability of successful establishment and impact of novel species: two categories covering the extremes, high and low risk, and two other categories representing intermediate levels of risk. Risk categories of particular interest for conservation and management are likely to be those that comprise interactions with true ‘novel species’, i.e. non-resident species that are unfamiliar to their resident interaction partners. The thesis also addressed how the effects of novelty may change over time:

ultimately, a decrease in these effects is expected over time, but potentially severe impacts may have been caused in the resident community meanwhile. To mechanistically address the influence of eco-evolutionary experience on novel species interactions, explicit and testable expectations were formulated in regard to differences and temporal dynamics in parameters of the predation cycle when highly experienced non-resident predators or prey, instead of their resident comparator species, interact with inexperienced resident species. Simulations of predator functional responses based on these expectations showed that non-resident species may have specific density-dependent advantages in such high-risk scenarios that add to conservationists' concerns: novel predators may pose a threat of particular relevance to inexperienced and endangered (i.e. rare) resident prey species, while novel prey facing inexperienced resident predators seem to enjoy particularly pronounced advantages (compared to resident prey) during their low-density establishment phase.

Overall, this thesis revealed important insights into the causes of variation in invasion success by combining empirical and theoretical approaches. Particularly in regard to the conceptual considerations, the next important step is to test and validate the formulated expectations on the basis of empirical data. Ultimately, the considerations presented in this thesis shall be helpful not only for research on biological invasions but for the understanding and management of novel interactions in general. This is critical in view of the growing and accelerating alterations of ecosystems worldwide in the ongoing Anthropocene.

Zusammenfassung

Biologische Invasionen sind eine wesentliche Komponente des globalen Wandels und eine große Herausforderung für den Schutz der Biodiversität. Ein umfassendes Verständnis der Gründe für Erfolg und Misserfolg von Invasionen ist entscheidend, um Invasionen vorherzusagen und effektiv zu managen. Bis jetzt ist dies schwierig, und angesichts der steigenden Anzahl an Einzelhypothesen und Konzepten, sowie zunehmend zerstreuten empirischen Daten, ist die Zusammenführung bisheriger Erkenntnisse dringend nötig. Das Hauptziel dieser Dissertation war daher, zu diesen integrativen Bemühungen beizutragen, indem empirische Daten aus unterschiedlichen Quellen zusammengeführt werden und konzeptionelle Ansätze zur Verbindung wichtiger Invasionshypothesen gefunden werden, die ein besonderes Augenmerk auf die Rolle der evolutionären Vorgeschichte der Arten richten.

Voneinander abweichende Definitionen können als Hindernis für die Zusammenführung von Forschungsergebnissen gesehen werden. Dennoch empfiehlt die vorliegende Studie, dass die regelmäßig wiederkehrenden Debatten über eine einzige, „richtige“ Definition von invasiven Arten und biologischen Invasionen überwunden werden sollten. Invasionsforscher haben unterschiedliche, doch gleichwertige Perspektiven auf Invasionen (z.B. historisch-biogeographische, naturschützerische, ökologische und evolutionäre Perspektiven). Ein einheitlicher Gebrauch von Begriffen ist daher wahrscheinlich nicht zu erreichen, jedoch würde ein erhöhtes Bewusstsein über die unterschiedlichen Konzepte, die den Begriffen in aneinandergrenzenden Forschungsbereichen zugrunde liegen, deren Kommunikation verbessern und Fortschritte in der Invasionsforschung zeitigen. Zur Zusammenführung von Erkenntnissen müssen Definitionen und Annahmen also zwar ausdrücklich formuliert, aber nicht unbedingt auch identisch sein. Die Berücksichtigung unterschiedlicher Perspektiven auf Invasionen ist zudem wichtig für ein wirkungsvolles und nachhaltiges Invasionsmanagement, da hier häufig weit auseinanderliegende Interessen beteiligter Gesellschaftsgruppen (z.B. Naturschützer, Politiker und Unternehmer) miteinander in Einklang gebracht werden müssen.

Invasionserfolg oder -misserfolg wird möglicherweise dadurch beeinflusst, auf welchem Weg der Organismus die neue Region erreicht. Empirische Daten über solche Einbringungspfade finden sich über viele Datenbanken verstreut, die zudem unterschiedliche Begriffe für gleiche Pfade verwenden. Daher wurden in dieser Studie Daten über Einbringungspfade aus zwei großen Invasionsdatenbanken (GISD und DAISIE) harmonisiert und zusammengeführt, wobei ein erst kürzlich entwickeltes Standard-Kategorisierungsschema für Einbringungspfade erfolgreich angewendet werden konnte. Ausgewertet wurde die relative Bedeutung von weitgefassten Pfadkategorien (Freisetzung, Entkommen, Kontaminierung, blinder Passagier, Korridore) für große taxonomische Gruppierungen (Pflanzen, Wirbeltiere, Wirbellose, Algen, Pilze, Andere) und für alle Habitate (terrestrisch, Süßwasser, marin). Die Analyse beinhaltete mehr als 8300 Arten und zeigte auffällige Unterschiede zwischen den taxonomischen Gruppen, während Unterschiede zwischen den Habitaten deutlich weniger ausgeprägt waren. Es zeigte sich auch, dass invasive Arten mit besonders negativen Auswirkungen häufig absichtlich *und* unabsichtlich eingeführt wurden. Diese Ergebnisse sind von hohem Wert für die Verbesserung der Priorisierung von Managementmaßnahmen bezüglich invasiver Arten.

Ein weiterer wichtiger Grund für Erfolg oder Misserfolg von Invasionen kann im Auftreten bestimmter Kombinationen von Invasionsmerkmalen der eingebrachten Arten liegen. Daher wurde mit Daten aus mehreren Online-Informationsquellen und Datenbanken ein Datensatz zu 13 Invasionsmerkmalen für 201 invasive Arten aus sieben taxonomischen Gruppen zusammengestellt (Tiere, Pflanzen, Pilze, Heterokonten, Bakterien, Rotalgen. Alveolaten). Eine Clusteranalyse und der direkte Vergleich von Merkmalshäufigkeiten zeigten, dass ähnliche Kombinationen von Invasionsmerkmalen häufig bei Arten aus sehr verschiedenen taxonomischen Gruppen auftreten, doch auch ein Zusammenhang zwischen taxonomischer Zugehörigkeit und Unterschieden in Invasionsmechanismen konnte nicht völlig ausgeschlossen werden. Insgesamt legen die Ergebnisse nahe, dass die Erklärung für Invasionserfolg eher nicht in bestimmten, universellen Invasionsmerkmalen liegt, die alle invasiven Arten aufweisen, sondern dass es verschiedene Kombinationen von Invasionsmerkmalen („Invasorentypen“) sein könnten, die den Erfolg von Invasionen bestimmen.

Die Identifizierung von Mustern in empirischen Daten kann wichtige erste Hinweise liefern, wie in bestimmten Invasionsszenarien reagiert werden kann. Jedoch ergibt sich hieraus noch kein mechanistisches Verständnis der Prozesse, die für den Invasionserfolg oder -misserfolg verantwortlich sind. Dies würde zuverlässigere Vorhersagen ermöglichen. Mit diesem Ziel wurde hier ein konzeptionelles Rahmenwerk entwickelt, das insbesondere die evolutionäre Vorgeschichte der beteiligten Arten und ihre Bedeutung für neuartige biotische Interaktionen berücksichtigt. Es besteht aus fünf hypothetischen Szenarien (für alle Grundtypen ökologischer Interaktionen) zur Bedeutung sogenannter „evolutionsökologischer Erfahrung“ in residenten und nicht-residenten Arten für den Invasionserfolg. Mehrere wichtige Invasionshypothesen konnten aufgrund ihres impliziten Bezugs zum Konzept der evolutionsökologischen Erfahrung in dieses Rahmenwerk integriert werden. Als ein erster Schritt in Richtung eines tieferen mechanistischen Verständnisses und der Anwendbarkeit des Erfahrungskonzepts im Managementkontext wurde eine Auswertungsroutine am Beispiel eines Nahrungsnetzes entwickelt sowie zwei Indices für die eigentliche Quantifizierung der Erfahrung.

Zur weiteren Steigerung der Anwendbarkeit des Erfahrungskonzepts im Management von invasiven oder sonstigen neuartigen Organismen wurden die Folgen unterschiedlicher Kombinationen von ausgeprägter und geringer Erfahrung in den interagierenden residenten und nicht-residenten Arten untersucht. Dies führte zur Aufstellung vier weitgefasster Risikokategorien zur Abschätzung der Wahrscheinlichkeit einer erfolgreichen Etablierung und negativen Auswirkungen durch neuartige Arten: zwei Kategorien an den Extremen, hohes und niedriges Risiko, sowie zwei weitere Kategorien mit mittlerem Risiko. Von besonderem Interesse für Naturschutz und Management dürften die Risikokategorien sein, welche die Interaktionen mit eigentlich „neuartigen Arten“ abdecken, d.h. mit nicht-residenten Arten, mit denen die residenten Interaktionspartner keine Erfahrung haben. Die Dissertation beschäftigte sich auch mit zeitlichen Veränderungen in den Auswirkungen der Neuartigkeit: letztlich wird zwar eine Verringerung dieser Auswirkungen im Laufe der Zeit erwartet, jedoch können währenddessen bereits gravierende negative Auswirkungen in den einheimischen Lebensgemeinschaften entstanden sein. Um auch mechanistisch den Einfluss der evolutionsökologischen Erfahrung auf neuartige biotische Interaktionen zu betrachten, wurden überprüfbare Erwartungen formuliert, wie sich Parameter aus dem Prädationszyklus unterscheiden (und über die Zeit entwickeln), wenn sehr erfahrene, nicht-residente Räuber oder Beute anstelle ihrer einheimischen Pendants mit unerfahrenen residenten Arten interagieren. Basierend auf diesen Erwartungen ergab die Simulation von funktionellen Reaktionen, dass die nicht-residenten Arten in solchen „hochriskanten“ Räuber-Beute-Interaktionen von dichteabhängigen Vorteilen profitieren könnten, die aus Sicht des Naturschutzes Grund zu weiterer Besorgnis geben: neuartige Räuber könnten eine besonders große Gefährdung gerade für unerfahrene und bedrohte (d.h. seltene) einheimische Beutearten darstellen, während neuartige Beute Vorteile insbesondere während der Etablierungsphase mit geringen Populationsdichten genießen könnte (im Vergleich zur einheimischen Beute).

Insgesamt konnte die Dissertation durch die Kombination empirischer und theoretischer Ansätze wichtige Einblicke in die Ursachen der Variation von Invasionserfolg zutage fördern. Insbesondere bezüglich der theoretischen Überlegungen steht als nächster Schritt die Überprüfung und Validierung der formulierten Erwartungen mit empirischen Daten an. Die hier gewonnenen Erkenntnisse sollen letztendlich nicht nur der Invasionsforschung von Nutzen sein, sondern allgemein dem Verständnis und Management von neuartigen Interaktionen. Dies ist von zentraler Bedeutung angesichts der weltweit zunehmenden und sich beschleunigenden Veränderungen von Ökosystemen im Anthropozän.

General introduction

Background: Biological invasions and ecological novelty

Since Charles Elton's (1958) influential publication *The Ecology of Invasions by Animals and Plants*, awareness has grown, that biological invasions are a significant component of global change and represent a major challenge for biodiversity conservation (Vitousek et al. 1997; Mooney & Hobbs 2000; Sax & Gaines 2003; Millennium Ecosystem Assessment 2005; Simberloff 2005). Species are being transported around the globe at an unprecedented rate (Elton 1958; Vermeij 1991; Butchart et al. 2010; Lockwood et al. 2013), and they may alter existing ecosystems significantly and cause substantial socio-economic damage (Mack et al. 2000; Pimentel et al. 2005; Perrings et al. 2010; Wardle et al. 2011; Simberloff et al. 2013). This is increasingly accounted for on high political levels, as exemplified in particular by Article 8(h) of the Convention on Biological Diversity (CBD 1992) and subsequent decisions by conferences of the CBD parties (see e.g. CBD 2002; Aichi Biodiversity Target 9, CBD 2010), as well as by regional strategies on invasive alien species (for Europe see e.g. Genovesi & Shine 2004; Target 5 of the EU Biodiversity Strategy, EU 2011; EU 2014).

However, views and judgements about biological invasions are not unanimous. Perhaps due to the fact that invasion ecology is still a relatively young research area (compared to established fields such as zoology, botany, biogeography, or genetics), there is still much discussion in this regard. One main topic of debate concerns what invasions actually are and what may be special about them. Part of this discussions focuses on the very foundations of the field, debating about the actual usefulness of invasion ecology as a separate area of scientific research. On the one hand, some authors argue that there is no relevant difference between invasive alien species (IAS) and colonizing native species, and that the assumption of a 'native/non-native dichotomy' is fundamentally flawed or at least hampers advances in our understanding of the relevant underlying mechanisms and processes (Davis & Thompson 2000; Davis et al. 2001, 2011; Warren 2007; Davis 2009; Valéry et al. 2009, 2013). On the other hand, many researchers see considerable support for the notion that there are relevant differences and that invasions do comprise processes and mechanisms that set them apart from other processes (e.g. succession or colonization of neighbouring areas), thus deserving to be studied with special emphasis (Richardson et al. 2000, 2008; Heger 2004, pp. 5–13; Pyšek et al. 2004; Strauss et al. 2006a; Wilson et al. 2009a; Richardson & Ricciardi 2013; Blondel et al. 2014; Simberloff & Vitule

2014). As will be shown below, findings in this thesis largely corroborate the latter opinion (see in particular Chapters 4 and 5).

Furthermore, invasion research increasingly develops into a transdisciplinary research field linking science and biodiversity management (Kueffer & Hirsch Hadorn 2008; Richardson 2011), with contributions from a diversity of academic and also non-academic fields. They all have different conceptions of what characterizes biological invasions, which leads to persistent discussions about a ‘correct’ definition of invasions and invasive species (e.g. Davis & Thompson 2000; Richardson et al. 2000, 2011; Valéry et al. 2008). However, as will be argued in more detail in Chapter 1, attempts to define biological invasions as one phenomenon that exists *per se*, i.e. independent of the observer, are probably fruitless. Rather, the ways of addressing and defining biological invasions probably depend on the observer’s perspective on the issue. Which perspective researchers adopt, depends in turn on their professional (and ideological) background, personal interests and probably also on the biological system they work with.

In this thesis, I adopt an eco-evolutionary perspective on invasions (see Chapters 1, 4, 5). A central assumption of this perspective is that ecological interactions are significantly influenced by the evolutionary legacy of the interacting species, and this of course also applies to new ecological interactions that arise due to invasions. Specific definitions I use are given in the different chapters if necessary since foci slightly change between them. Generally speaking, in most parts of the thesis the focus lies not so much on the distinction between ‘threatening’ invasive species and ‘merely’ introduced ones (Chapters 1, 2), but rather on the broader distinction between native and non-native species (Chapter 4), or termed more neutrally between resident and non-resident species, or even less geographically framed between ‘familiar’, ‘new’ and ‘novel’ species (Chapter 5).

On a side note, not only the exact definitions of terms but also an appropriate terminology *per se*, i.e. the adequate choice of words, is a matter of discussions. For instance, there is a large variety of terms to denominate species that arrive or emerge in an area: ‘alien’, ‘exotic’, ‘introduced’, ‘invasive’, ‘non-indigenous’, ‘non-resident’ etc. It has been pointed out that unreflecting use of metaphors with strong connotations outside the actual area of study (e.g. phrases like ‘the battle against alien species’ or ‘aliens causing an invasional meltdown’) may be ill-advised (Colautti & MacIsaac 2004; Larson 2005, 2008; Gurevitch 2006; Larson et al. 2013; Kueffer & Larson 2014). Even though catchy terms can be helpful to quickly raise attention to the problem at hand, they may also be counterproductive in so much as they are prone to oversimplify a complex topic and cause the impression that there is only one correct perspective and only one ideal way in which to react. Furthermore, such terms unnecessarily encourage those who, based on the metaphors chosen and drawing parallels to sociological phenomena, suspect general xenophobic tendencies to actually drive the discourse instead of objective and evidence-based science (Simberloff 2003; Warren 2007; Davis et al. 2011; Simberloff 2011).

A second main topic of debate concerns what effects invasions actually have and how we should respond to them. While detrimental impacts are documented for a growing number of invasions (e.g. Mooney & Hobbs 2000; Millennium Ecosystem Assessment 2005; Simberloff 2005; Wilson et al. 2009a; Simberloff et al. 2013), there are also voices that relativize or question the magnitude and pervasiveness often ascribed to these impacts (e.g. Brown & Sax 2004; Gurevitch & Padilla 2004; Sagoff 2005; Davis et al. 2011; see Richardson & Ricciardi 2013 for a short review of opposing positions). In most current approaches of responding to invasions, precautionary conservationist considerations certainly play a predominant role, aiming to prevent introductions of non-native species, reduce their trading, restrict their admissibility to certain areas, and mitigate their detrimental effects (Ruiz & Carlton 2003; Clout & Williams 2009; Simberloff 2009, 2011; Perrings et al. 2010; Simberloff et al. 2013). However, concomitant to the realization that global change and accelerating worldwide trade and traffic render absolute prevention of biological invasions unrealistic if not unfeasible, also new ways of dealing with this issue are explored (e.g. Hobbs et al. 2006, 2009, 2013; Davis et al. 2011; Kueffer & Kaiser-Bunbury 2014). Besides purely ecological and environmental reasoning, socio-economic aspects as well as insights from social sciences and even arts and humanities (e.g. about perceived social values) gain more influence in the discussion about how to respond to biological invasions (Keller et al. 2009; Pejchar & Mooney 2010; Essl et al. 2011; Kueffer et al. 2011; Liu et al. 2011; Kueffer 2013; Larson et al. 2013; Frawley & McCalman 2014).

This includes possible beneficial, i.e. desirable, effects of invasions, which are increasingly brought into consideration (e.g. Walther et al. 2009; Carroll 2011; Schlaepfer et al. 2011; Thomas 2013). Beyond the intended positive effects of intentionally introduced organisms (e.g. for ornamental purposes, fauna improvement, or biological control of pest species), beneficial effects of both intentionally and unintentionally introduced species may even be crucial for supporting efforts to conserve ecological processes in ecosystems affected by human activities (Schlaepfer et al. 2011). For instance, introduced species may provide habitat or resources for other (native) species (e.g. Graves & Shapiro 2003; Sogge et al. 2008), they may take up ecosystem services that were formerly provided by now extinct resident species (e.g. Cox 1983; see also Griffith & Harris 2010 on the potential of taxon substitution), or they may be able to fulfil such services under future climatic conditions that are unsuitable for resident species (Williams 1997). Still, an effect that is deemed positive by one stakeholder might be considered detrimental by another due to diverging ecological, economic and social value judgements. It is thus critical and topic of current debate how impacts should be defined and how they and the stakeholder's interests can be weighted in ways that are transparent and retraceable for the stakeholders and the general public (see e.g. Liu et al. 2011; Kumschick et al. 2012; Blackburn et al. 2014; Jeschke et al. 2014).

Speaking more generally, biological invasions are increasingly placed into the broader context of 'ecological novelty' (see also Chapter 5), i.e. ongoing environmental change in the Anthropocene (Crutzen & Stoermer 2000; Crutzen 2002), where "not change *per se*, but rather the magnitude, rapidity, unfamiliarity and uncertainties of these changes – the novelty – […] challenge traditional science and human-nature relationships" (Kueffer 2014; see also Steffen et al. 2011, 2015). Research on ecological novelty has recently strongly intensified, focusing on novel ecosystems (Hobbs et al. 2009, 2013), novel communities and species interactions (Williams & Jackson 2007; Lurgi et al. 2012; Pearse & Altermatt 2013; Bezemer et al. 2014; Carthey & Banks 2014) and novel organisms (Jeschke et al. 2013). Importantly, the latter comprise not only invasive species but also GMOs, synthetic organisms, resurrected species or emerging pathogens, and findings that we can establish for one of these groups (as intended in this thesis for invasive species) will further our understanding for the other groups as well and contribute to related fields of research (e.g. about climate change or restoration ecology).

Objective: Synthesize fragmented knowledge for a better understanding of variation in invasion success

Outcomes of species introductions can range from complete failure, over successful establishment without significant impacts, to establishment of such high success that introduced species may be considered pests. A comprehensive understanding in regard to this variation in invasion success is crucial for our ability to predict and manage invasions more effectively. It will help the development of effective tools to prevent, remediate or mitigate negative impacts, while also identifying potential benefits for society.

Efforts have greatly intensified in the last decades to widen our knowledge about the underlying mechanisms that determine the success or failure of biological invasions, considering the invasiveness of the introduced species, the invasibility of the receptive ecosystem, combinations of both, and differentiating the invasion process in time (e.g. Drake et al. 1989; Mooney & Hobbs 2000; Lockwood & McKinney 2001; Heger & Trepl 2003; Ruiz & Carlton 2003; Inderjit et al. 2005; Mooney et al. 2005; Cadotte et al. 2006; Nentwig 2007; Keller et al. 2011; Richardson et al. 2011; Simberloff & Rejmánek 2011; Lockwood et al. 2013). Ecological studies represent the main part of these efforts, putting forward a variety of hypotheses regarding specific processes, e.g. the hypotheses of enemy release (Maron & Vilá 2001; Keane & Crawley 2002), novel weapons (Callaway & Aschehoug 2000), biotic resistance (Elton 1958; Levine & D'Antonio 1999) and invasional meltdown (Simberloff & Von Holle 1999). Aspects of evolutionary ecology are also being considered increasingly (e.g. Sax & Brown 2000; Sakai et al. 2001; Hänfling & Kollmann 2002; Lee 2002; Cox 2004; Heger 2004; Sax et al. 2005, 2007; Cox & Lima 2006; Facon et al. 2006; Kondoh 2006; Mitchell et al. 2006; Strayer et al. 2006; Hufbauer & Torchin 2007; Novak 2007; Carlsson et al. 2009; Orians & Ward 2010; Sih et al. 2010; Thuiller et al. 2010). Furthermore, large amounts of data are being accumulated in a variety of databases on invasive species, e.g. IUCN/ISSG's Global Invasive Species Database GISD, the European DAISIE and NOBANIS databases, as well as many other specialized databases (see Chapter 2).

However, despite considerable progress, the explanation, prediction, and management of biological invasions remain difficult (Davis 2009; Richardson 2011; Heger et al. 2013). In view of the growing amount of hypotheses, concepts and dispersed empirical data on invasions it seems that we are beginning to 'drown in information while starving for knowledge', as put in the famous quote by John Naisbitt (1982). Thus, there is a need for consolidation and synthesis. Accordingly, efforts are being increased to validate and interrelate existing hypotheses and concepts (e.g. Hufbauer & Torchin 2007; Catford et al. 2009; Gurevitch et al. 2011; Blackburn et al. 2011; Jeschke et al. 2012a), and to make better use of data on introduced species from different sources of information (e.g. EASIN; Katsanevakis et al. 2012).

This thesis aims at contributing to these synthesizing efforts, which shall help to gain a better understanding of variation in invasion success, and improve our means for prediction, prevention and management. Both empirical ('data-mining'; Chapters 2, 3) and theoretical approaches (Chapters 4, 5) are employed to this end.

Empirical approach: Taxonomic patterns in data on successful invasions

As a first, phenomenological step towards a better understanding of variation in invasion success, it is helpful to identify parameters and circumstances that are commonly associated with successful invasions (and may thus differentiate the latter from unsuccessful invasions). Aside from detailed experiments and observations, this may also be done by searching for broad patterns in the rapidly growing sets of empirical data about invasions. For instance, particular groups of successful invasive species may share similar (frequency) patterns in the ways in which they arrive in a new region, so-called introduction pathways. The suitability of a pathway is certainly related to the general ecological, physiological, morphological and behavioural traits of the respective species. But successful invaders may also share traits that are particularly advantageous to overcome obstacles in the invasion process, so-called invasion traits which determine a species' invasiveness. Therefore, it is interesting to investigate if patterns in pathways and species traits can be identified and whether they align with taxonomic relationships between the respective species, or if other factors less related to taxonomy have to be taken into account (Chapters 2, 3). Such alternative factors could be, for instance, that success may be significantly influenced by the environmental characteristics of the receptive area, i.e. by the area's invasibility, or that there are 'invader types' that share certain combinations of invasion traits irrespective of their taxonomic affiliation (Chapter 3).

Of course, determining possible correlations between invasion success and the taxonomic affiliation of an introduced species or environmental characteristics of an invaded area (provided such patterns can be identified) will not suffice to reliably predict the outcome of highly complex invasion processes. For this purpose, also a mechanistic understanding will be needed (see section on theoretical approach below and Chapters 4 and 5). However, it can provide valuable clues as to what may be important species traits or environmental conditions for an invasion to be successful and, importantly, it can also indicate *vice versa* what traits or conditions may be disadvantageous. While only on a very general level, this would promote effective management and prevention of invasions by enabling us to adapt actions and legislative regulation, e.g. depending on which taxonomic group is expected to be involved in an invasion event or which environment is expected to be affected. To this end, Chapter 2 focuses on the first phase of the invasion process, i.e. 'transport', investigating the relative importance of different pathways for successfully introduced species from different taxonomic groups and environments, and Chapter 3 considers advantageous trait combinations that may be relevant in different invasion phases.

Theoretical approach: Integrative conceptualization by taking an eco-evolutionary perspective on invasions

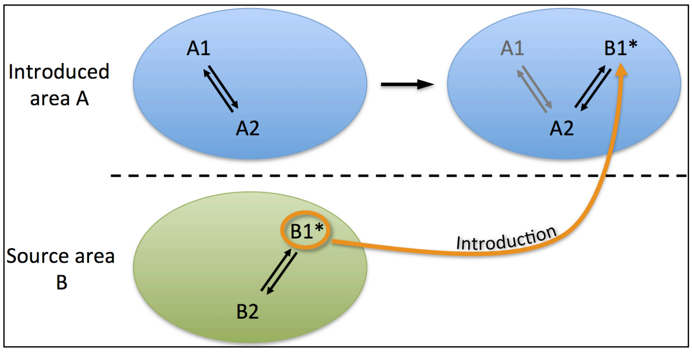
Finding patterns in empirical data as those described above can yield important clues about how to react in certain invasion scenarios, but they do not provide mechanistic explanations of the actual processes that drive success or failure of invasions. And even though there is, as already mentioned, a growing number of individual hypotheses and concepts about invasion mechanisms, a solid integrative understanding that would allow reliable predictions is still lacking.

Therefore, the main part of this thesis focuses on conceptual considerations (Chapters 1, 4, 5), wherein I suggest that adopting an eco-evolutionary perspective on invasions is a promising approach to achieve a broader conceptual synthesis in invasion ecology. This perspective focuses on the role of the species' evolutionary legacy for the outcome of newly arising ecological interactions (see e.g. Cox & Lima 2006; Kondoh 2006; Mitchell et al. 2006; Sih et al. 2010; Thuiller et al. 2010). Chapters 4 and 5 elaborate on a conceptual framework for studying variation in invasion success (due to differences in species' evolutionary legacy) across all major types of ecological interaction and interrelating several major invasion hypotheses based on the concept of 'eco-evolutionary experience'. This concept emphasizes (1) that during evolution, species adapt to biotic interactions in their native environment and thereby accumulate eco-evolutionary experience in dealing with these interactions; and (2) this heritable experience may be applicable in new ecological contexts, as for example when species are introduced to non-native environments and thus interact with species with which they have not evolved.

The degree to which (resident *and* non-resident) species can apply their experience depends on the ecological similarity between previous interaction settings and those in the new context, and significantly influences the species' proficiency to persist *vis-à-vis* new interaction partners (Cox & Lima 2006). Ecological similarity of species is often assumed to be positively correlated with the taxonomic or phylogenetic relatedness between them (e.g. Agrawal & Kotanen 2003; Cavender-Bares et al. 2004; Ricciardi & Atkinson 2004; Strauss et al. 2006b; Diez et al. 2008; Procheş et al. 2008). However, similarity – be it in respect to morphological, behavioural, or ecological traits – is different from relatedness (Losos 2008; Thuiller et al. 2010). This becomes most evident in cases of convergent evolution where relatively unrelated species show a high degree of similarity (see e.g. Futuyma 2005). Thus, taxonomic classification and phylogenetic relatedness of species are not entirely reliable indicators for ecological similarity and for the similarity of biotic interactions of these species before and after an invasion event. Correspondingly, Chapter 4 presents a routine for assessing ecological similarity and eco-evolutionary experience without reference to taxonomic affiliation or phylogenetic relatedness of species.

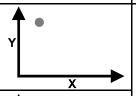
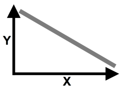
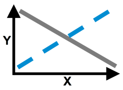
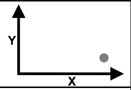
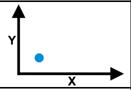
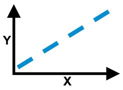
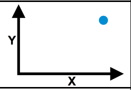
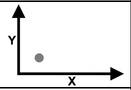
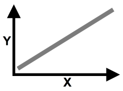
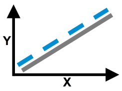
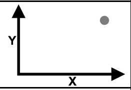
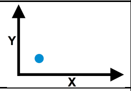
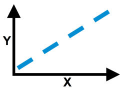
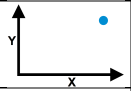
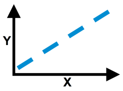
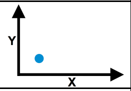
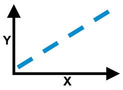
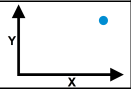
The experience concept assumes that higher ecological similarity of interactions entails higher levels of applicable eco-evolutionary experience (and *vice versa*). Depending on which of the involved interaction partners we are looking at (the resident or non-resident species), and also which type of ecological interaction is affected, this implies a reduced or an increased probability of invasion success. Box I lists expected effects of low and high degrees of applicable experience in resident and non-resident species on the probability of invasion success for different types of ecological interaction. This represents the basis for developing preliminary hypotheses about the general relationships between experience and probability of invasion success (see last two columns in Box I), which are used and described in Chapter 4. All further details of rationales, implications and advantages of an eco-evolutionary perspective on invasions and of the concept of eco-evolutionary experience are described in Chapters 1, 4 and 5.

Box I – Preliminary hypotheses about the effect of low and high degrees of applicable experience in resident and non-resident species on the success probability of species B1* being introduced into target area A, considering different types of ecological interaction (cf. Chapter 4). The degree of applicable experience depends on the ecological similarity between previous and new interaction partners (see inset): e.g. the ability of resident species A2 to cope with the invasion depends on the similarity between the original interaction partner A1 and introduced species B1*; for B1*, the similarity between new interaction partner A2 and former interaction partner B2 is decisive.



Axes in all graphs:

Y = probability of invasion success;
X = degree of applicable eco-evolutionary experience

Type of interaction A2 ⇆ B1*	Compared interaction partners of A2 or B1* (see inset)	Ecological similarity between compared species	Resulting applicable experience in A2 or B1*	Expected effect on probability of invasion success of B1*	Prelimin. general hypothesis	Combined prelimin. hypotheses
Predation (+/-) or Competition (-/-)	A1 *vs.* B1*	low	low in resident A2	⊕ 		
		high	high in resident A2	⊖ 		
	A2 *vs.* B2	low	low in non-resid. B1*	⊖ 		
		high	high in non-resid. B1*	⊕ 		
Mutualism (+/+)	A1 *vs.* B1*	low	low in resident A2	⊖ 		
		high	high in resident A2	⊕ 		
	A2 *vs.* B2	low	low in non-resid. B1*	⊖ 		
		high	high in non-resid. B1*	⊕ 		
Commensalism (+/0; non-resid. commensalist)	A1 *vs.* B1*	low	n/a (resid. host A2 is unaffected)	– –	– –	
		high	n/a (resid. host A2 is unaffected)	– –		
	A2 *vs.* B2	low	low in non-resid. B1*	⊖ 		
		high	high in non-resid. B1*	⊕ 		

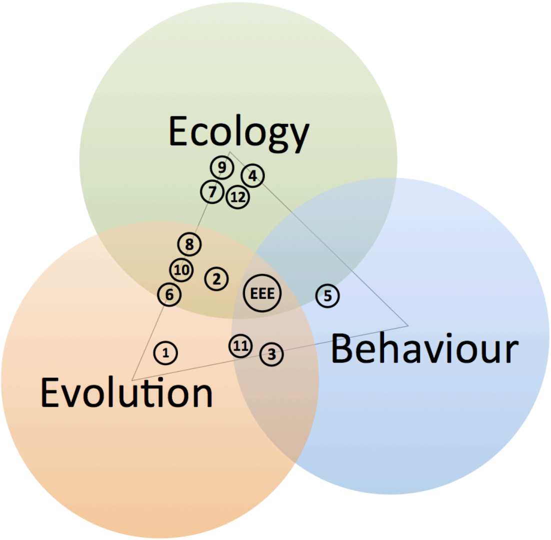
With regard to the concept's name 'eco-evolutionary experience' itself, 'experience' implies that the challenges (and opportunities) of new interactions are looked at from the organism's perspective. The qualifying term 'eco-evolutionary' emphasizes that the concept refers to species traits that have *evolved*, mostly in times prior to the invasion event, and that are relevant for the new *ecological* interaction arising in present times (e.g. predation, competition, mutualism or commensalism). Contemporary evolutionary adaptations in a species (including epigenetic changes) in response to its involvement in a new interaction can – after the time span necessary for these changes – add to the experience that the species may have already had. Thus, an important characteristic of eco-evolutionary experience is its heritability. Learning of abilities during an individual's lifetime is *not* considered a direct component of eco-evolutionary experience since only rarely learned abilities are passed on from one generation to the next (but see e.g. cultural transmission). Learning may only indirectly figure as a possible component of experience when it is the expression of evolutionarily acquired phenotypic plasticity that may have constituted an adaptive advantage in the species' past, e.g. in response to frequently changing living conditions.

Clearly, the concept of eco-evolutionary experience has connections to other terms used in the context of invasion ecology. This includes, for instance, 'ecological naïveté' (Diamond & Case 1986; Salo et al. 2007), 'contact experience' (Cox & Lima 2006; Kondoh 2006), 'functional distinctiveness' (Strayer et al. 2006), 'adaptation', 'preadaptation', and 'exaptation' (Gould & Vrba 1982; Futuyma 2005; Sol 2007) (for more related terms see Box II). All these terms differ slightly in their respective focus, e.g. in regard to their affiliation with ecological, evolutionary and behavioural reasoning (see figure in Box II). For instance, adaptation and preadaptation are terms deeply rooted in (and, strictly speaking, confined to) considerations of evolutionary biology, naïveté has a strong behavioural connotation, and ecological similarity tackles the issue at hand from a purely ecological viewpoint. However, in essence, all of them boil down to the underlying principle that lies at the core of this thesis: the degree of naïveté, novelty, adaptedness, distinctiveness or similarity etc. in newly formed interactions (and with that the effect on the outcome of these interactions) is determined by – what I propose to call – eco-evolutionary experience that the involved species have with their new interaction counterparts.

In summary, the concept of eco-evolutionary experience is not presented in this thesis as a completely novel theory, but as an integrative conceptual tool that interrelates terms, concepts and hypotheses from different fields of research (for details see Chapter 4) and provides a framework to enhance our mechanistic understanding of variation in invasion success.

Box II – Terms related to the concept of eco-evolutionary experience (abbreviated here as 'EEE'). Note that this is not an exhaustive list. The placement of the terms in relation to each other within the Venn matrix depends in part on subjective perceptions, i.e. other constellations are conceivable. Also, other research areas may be additionally considered.

Related term	Exemplary references
1 adaptation/ preadaptation/ exaptation	Gould & Vrba 1982; Futuyma 2005; Sol 2007
2 biological/ecological foreignness	Heger & Trepl 2003; Heger 2004
3 contact experience	Cox & Lima 2006; Kondoh 2006
4 ecological fitting	Janzen 1985; Agosta 2006
5 ecological naïveté	Diamond & Case 1986; Salo et al. 2007
6 ecological novelty	Strauss et al. 2006b
7 ecological similarity	Davies et al. 2011
8 evolutionary novelty	Verhoeven et al. 2009
9 functional distinctiveness	Strayer et al. 2006
10 phylogenetic distinctiveness	Ricciardi & Atkinson 2004; Ricciardi et al. 2013
11 predator archetypes	Cox & Lima 2006
12 unlike invaders	Alpert 2006



Outline

Chapter 1 *What biological invasions 'are' is a matter of perspective* deals with the general question in invasion ecology why it is so difficult for researchers of different areas, managers, and policy makers to find an unanimous definition of biological invasions. The chapter discusses how different perspectives and research motivations – one of them the eco-evolutionary perspective – lead to specific opinions about what the peculiarity of invasions is, which in turn determine the respective invasion definition. Suggestions are put forward concerning the consequences of such different approaches to define invasions, whether finding one universal definition of invasions and stipulating a uniform usage of terms is possible (or even desirable), and what this means for discussing findings in invasion ecology among researchers of different fields of expertise in an efficient and meaningful way.

Chapter 2 *Turning information into knowledge: Linking major databases to analyse and prioritise introduction pathways of alien species* assesses the relative importance of different introduction pathways (release, escape, contaminant, stowaway, corridor) for major taxonomic groups (plants, vertebrates, invertebrates, algae, fungi, other) and across all environments (terrestrial, freshwater, marine) by collating information from two major databases on invasive alien species: the Global Invasive Species Database GISD, expanded for this study with data from the related Invasive Alien Species Pathway Management Resource (IASPMR), and the DAISIE European Invasive Alien Species Gateway. A focus is put on the comparison between unintentional and intentional pathways, and between pathways of species listed among the '100 of the Worst', i.e. high-impact species, and all other non-native species registered in these databases. Implications for the prevention of introductions and particularly for prioritization of pathways in management and surveillance are discussed.

Chapter 3 *Species from different taxonomic groups show similar invasion traits* comprises a cluster analysis of a global dataset compiled from online sources and databases, e.g. including GISD, DAISIE, the IUCN Red List, and NOBANIS. The dataset comprises 201 invasive species from seven major taxonomic groups (animals, green plants, fungi, heterokonts, bacteria, red algae, alveolates) and 13 invasion traits that are applicable across taxa. Given that all invasive species go through the same stages of the invasion process (transport, escape, establishment, spread), it is investigated to what extent similarity in invasion traits in successful invasive species is related to taxonomic affiliation (i.e. close relatedness between species), or if such similarity can also be found regularly in invasive species taxonomically distant from each other.

Chapter 4 *The role of eco-evolutionary experience in invasion success* develops the concept of so-called 'eco-evolutionary experience' to account for the evolutionary legacy's role in invasion success. An integrative conceptual framework is presented consisting of hypothetical scenarios about the influence of eco-evolutionary experience in both resident and non-resident species on invasion success considering different types of ecological interaction. The chapter describes how several major ecological invasion hypotheses can be interrelated within this framework by uncovering their shared implicit reference to the experience concept. Furthermore, a routine including two mathematical indices for the quantification of eco-evolutionary experience is presented, using a food-web based example.

Chapter 5 *Eco-evolutionary experience in novel species interactions* investigates the implications of different combinations of high and low degrees of experience in interacting resident and non-resident species, defines risk categories for estimating the probability of successful establishment and impact of novel species, and discusses how the effects of novelty change over time. To mechanistically address the influence of eco-evolutionary experience on novel species interactions, novel predator-prey interactions are then put into focus, formulating explicit expectations regarding differences and temporal dynamics in parameters of the predation cycle when highly experienced novel predators or prey, instead of their resident comparator species, interact with resident species. The chapter specifies which advantages non-resident species may have in such scenarios, illustrating the density-dependence of these advantages by simulating predator functional responses and comparing these model simulations between novel species and their resident comparators. The relevance of these considerations also for ecologists interested in genetically modified organisms (GMOs), synthetic organisms, resurrected species, emerging pathogens, and range-expanding species is highlighted and implications for conservation are discussed in this context.

Chapter 1

What biological invasions ‘are’ is a matter of perspective

The content of this chapter was published as:
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Abstract

Invasion research today integrates active fields like biogeography, nature conservation, ecology, and evolutionary biology, and each of these fields contributes its own conceptual and terminological background. In this essay we advance the view that this is the reason why discussions on terminology keep flaring up time and time again. Our basic argument is that biological invasions cannot be perceived and defined independent of the specific research motivation. There are different, but equally valuable perspectives on biological invasions, each entailing a specific opinion about what the peculiarity of invasions is. We argue that a uniform usage of terms is not feasible, and even not desirable for invasion research, and suggest that the existing plurality of terms and concepts should be taken as an incentive to discuss the implications of different definitions. A stronger awareness and acknowledgement of the concepts underlying the terms used in interrelated research fields will enhance communication and promote progress in invasion research towards integrative, problem-oriented transdisciplinarity.

Keywords: alien, invasive, definitions, terminology, terms and concepts

Introduction

An ever increasing number of articles, journals and books bearing 'invasion' in their titles (e.g., Davis 2009; Lockwood et al. 2007; Simberloff & Rejmánek 2011) document that invasion research is an extremely active research area, integrating a diversity of fields such as biogeography, ecology, evolutionary biology, biosecurity, conservation practice and applied management. A major challenge in this transdisciplinary undertaking, which has to combine scientific with applied knowledge, is the large variety of technical terms such as 'alien', 'exotic', 'non-native', and 'invasive' and the even more variable meanings that scientists, politicians, conservationists and managers attach to each of these terms. Heated discussions keep flaring up time and again, sometimes even raising fundamental criticism concerning the concept of invasive species (Davis & Thompson 2002; Thompson & Davis 2011a,b).

There have been many attempts to achieve a more standardized usage of terminology and to induce a consensus; prominent examples are the contributions of Richardson et al. (2000) or the 'neutral framework' of Colautti and MacIsaac (2004). In a recent compilation, Richardson, Pyšek and Carlton (2011) once again seek to generate a “*uniform, broadly accepted and acceptable set of terms and concepts for invasion science*” (p. 410). Despite such attempts, the debate on what biological invasions are and how we should define alien and invasive species remains unresolved (Colautti & Richardson 2009; Larson 2005, 2007; Liebold 2006; Valéry et al. 2008, 2009; Wilson et al. 2009a,b).

In the recently published Encyclopedia of biological invasions (Simberloff & Rejmánek 2011), a novel approach is taken. Instead of one unifying definition for invasive species, the authors give two complementary concepts: "*Invasive species 1. A naturalized species that produces reproductive offspring, often in very large numbers, and that spreads over large areas. This definition is usually used by ecologists. 2. A nonindigenous species that spreads rapidly, causing environmental or economic damage. This definition (equivalent to "non native pest species") is often used by managers, particularly in the United States.*" (p. 727). This entry accounts for the fact that there are at least two different views on what invasive species are. In giving two definitions, the authors apparently call for acceptance of both of these views. We regard this as remarkable progress for communication about biological invasions, and we would like to follow up on this perspective and expand it even further.

In this article we elaborate on the view that different fields of research and action generate different perspectives on invasions, naturally leading to differences in concepts and definitions. A uniform usage of terms connected to biological invasions thus will not be achieved despite all efforts, and – importantly – we argue that this is not even a desirable aim.

What an 'invasion' is depends on the observer

Many of the definitions proposed so far are based on the assumption that there is the one phenomenon 'biological invasion' that exists *per se*, i.e. independently of the observer. Advocates of this view assume that biological invasions only have to be scrutinized closely enough in order to be able to identify a universally characterizing essence of the phenomenon. For instance, Valéry et al. (2008) explicitly aim at deducing such a single, in their view 'real' definition of 'biological invasion'. Other authors follow this rationale more implicitly, maybe even unknowingly (e.g. Colautti & MacIsaac 2004; Davis & Thompson 2000; Wilson et al. 2009a). However, this approach is highly problematic. The view that objects are knowable in their essence is characteristic of the time before the rise of empiricism and transcendentalism. Indeed, Valéry et al. (2008) invoke Aristotle. But in current philosophy of science, there are nearly no representatives of this view. According to influential philosophers like David Hume and Immanuel Kant, the 'thing-in-itself' is not knowable. Our mind structures the experiences we make; we can never be passive observers (e.g. Kant 1788).

To get along with and even benefit from the diversity of definitions, instead of searching for the one definition, it would be much more helpful to consciously acknowledge that there are in fact different perceptions of what is peculiar about biological invasions. Advocates of contrasting concepts tend to blame each other for using a 'wrong' definition of invasions (e.g. Colautti & MacIsaac 2004, p. 137; Thompson & Davis 2011b, p. 319). But in fact they are referring to different phenomena when talking about biological invasions, and there is no objective criterion that would allow declaring one of them as the 'right', 'real' or 'true' one.

It seems somewhat paradoxical: some kind of definition is needed before defining something. In order to contrive a specific definition of biological invasions, it is necessary in the first place to have an idea which kind of phenomena count as 'invasion' and which do not. Only based on this it is possible to determine those criteria that are useful for a definition that precisely describes the phenomenon according to the conception of the defining person. Which conception precedes the eventual definition clearly depends on the background of the respective person. Even scientists belonging to closely related research fields (e.g. evolutionary biology and ecology) do not necessarily have the same conceptions, and thus may not consider the same criteria as decisive for a definition. Clearly, this is one of the toughest challenges for invasion research and management.

Definitions reflect perspectives

Invasion research today is not a purely ecological sub-discipline, but evolves more and more towards a transdisciplinary, problem-oriented research field that interlinks science and biodiversity management (Kueffer & Hirsch Hadorn 2008; Richardson 2011). Thus, a diversity of complementary scientific and also non-academic fields contribute to invasion research. They all have their own conception of biological invasion, which – often implicitly or even unknowingly – leads to different approaches. It has been stated before that different views on biological invasion exist (e.g. DiCastri 1990), and Kueffer and Hirsch Hadorn (2008) point out that "*[t]he different meanings of the terms [in invasion research] reflect the dynamics of the research field*" (p. 14). Different definitions of alien and invasive species and related terms thus are based on contrasting but equally valuable research interests; these lead to contradicting opinions about what is important in invasions, which in turn influences the choice of defining criteria. To illustrate this line of argument, we describe in the following a selection of such contrasting perspectives. We think that the often – but in our view unnecessarily – lamented variety of definitions of biological invasions is caused by these and other complementary views on biological invasions. Which perspective researchers adopt depends on their professional (and ideological) background as well as on the systems they work with.

Historic-biogeographical perspective

Many authors writing about biological invasions refer to Charles Elton's book published in 1958, which is commonly regarded as the foundation of invasion research (Richardson & Pyšek 2007). The great appreciation devoted to this book suggests that its content strongly influences which phenomena are classified as biological invasions and which are not. Having a closer look at the processes Elton described, it becomes clear that he focused on a specific unique, historic incident with high biogeographical relevance, namely the breakdown of barriers to dispersal. This breakdown began abruptly around the year 1500 due to the development of worldwide trade, traffic and travel, and is ongoing ever since (for a detailed historical treatment see Crosby 1986). As a consequence, ecologically suitable but formerly inaccessible habitats have now come within reach. This is of considerable historic-biogeographical relevance. Its impact on the distribution of species on Earth is beyond comparison, as similar events only happen within an interval of hundreds of millions of years (cp. the closing of the Isthmus of Panama). This might be the reason why for a large number of invasion biologists the overcoming of a dispersal barrier is essential for defining invasions: for them, the phenomenon is closely connected to such novel biogeographical settings (e.g. Pyšek 1995; Pyšek et al. 2004).

The perspective of nature conservation

From a nature conservation perspective, all processes that have the potential to threaten ‘naturalness’ (Machado 2004) are of importance. Current range expansions of species can be relevant in this respect on two levels. First, most alien species have been transported with ships, airplanes etc. to areas outside their native ranges. From the perspective of nature conservation, this socio-culturally induced dispersal, no matter whether it happened deliberately or unintentionally, differs fundamentally from a ‘natural’ transportation, e.g. by strong currents or wind, especially regarding range and frequency. This is why ‘introduction by man’ is used as defining criterion in many definitions of alien species (e.g. IUCN 2011). From a nature conservation point of view, the difference between alien (defined as species transported by human means) and native species is highly relevant.

Secondly, alien species have the potential to threaten native species and ecosystems (e.g. Walsh et al. 2012). From the nature conservation point of view it is reasonable, thus, to distinguish between species that have a negative impact on ‘natural’ systems (often times termed invasive species) and those that do not (non-invasive aliens; e.g. CBD 2002). Negative impact is viewed as an essential component of invasiveness here. A major point for discussion remains, however, how ‘impact’ can be measured on a scientific basis (e.g. Zaiko et al. 2011).

Ecological and evolutionary perspectives

There are several possible perspectives on biological invasions within ecology. For example, they can be studied in reference to the general process of species’ spread and impact (e.g. Davis & Thompson 2000; Davis 2009), or in reference to changes in dominance relationships (Valéry et al. 2008). If one of these particular two perspectives is taken, the difference between native and alien species becomes less important. There are native species that show the same patterns of regional spread, impact or dominance as some of the dominant alien invaders, and from a purely ecological point of view it can be reasonable to regard both groups of species as invasive (Davis 2009). But invasions may also be studied with a focus on the fact that species spread into areas where they have never occurred before (e.g. Colautti & MacIsaac 2004; Sih et al. 2010), i.e. from an eco-evolutionary perspective. Its basic assumption is that ecological interactions are significantly influenced by the evolutionary legacy of interacting species. It is assumed that due to evolution in a specific biotic and abiotic environment, species accumulate what might be called 'eco-evolutionary experience' in dealing with the conditions and interactions they face in their native environment. Regarding biological invasions, this perspective suggests that the phenomena of spread will show significant differences, depending on whether the area a species reaches is ecologically similar or dissimilar to the region where it has evolved (Mitchell et al. 2006).

In practice, invasion research perspectives are rarely adopted in such a strict way as implied by the categorization above. They are often intermingled with each other and with other ideas. To illustrate this, we list some current definitions in Table 1.1 and state our interpretation concerning which invasion perspectives they are actually connected to. The intermixture of perspectives within one definition is not necessarily a problem as long as it is clearly stated. However, it may become a problem if such a definition does not fit a study's intention by implicitly carrying along suppositions that are not in line with the rest of the work. In many publications on biological invasions, definitions are used that stem from the perspective of nature conservation highlighting the negative impact of an invasive species (e.g. Lockwood et al. 2007, p. 8). The purpose of this clearly is to emphasize the relevance of the research for nature conservation. But caution is warranted if ecological studies that have a basic rather than an applied focus base their research on definitions that include societal normative decisions, as for instance the decision about which kinds of impact are regarded as negative (see Daehler 2001a). The definition used influences the choice of the study system, probably also the choice of methods, and it may even influence the interpretation of results. In the extreme case, this leads to a corroboration of prejudices instead of rigorous tests of hypotheses. Ecological studies with a basic as opposed to an applied focus should therefore avoid using definitions that are based on criteria stemming from the conservation perspective. For basic ecological research, the recently proposed unified framework for biological invasions (Blackburn et al. 2011) offers an excellent setting for clear communication about the meaning of terms attached to spreading species. If an eco-evolutionary perspective is chosen, we propose a definition based on criteria stemming from the ecological and eco-evolutionary perspectives only (see Table 1.1).

Table 1.1 – Selection of current definitions of alien and invasive species. The right-hand column presents our interpretation concerning which research perspectives are involved. B, biogeography; C, nature conservation; Ec, ecology; Ev, evolution.

Ref.	Definition	Perspective
IUCN 2011	"Invasive alien species are animals, plants or other organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species."	C
Davis & Thompson 2000	"Clearly, an invader is not just any newcomer, but one that has a large impact on the new environment."	C
	"'alien species' refers to a species (…) introduced outside its natural past or present distribution (…)."	C
Richardson et al. 2000	"Alien plants: plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activity"	B or C
	"Invasive plants: Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distance from parent plants (...), and thus have the potential to spread over a considerable area"	Ec
CBD 2002	"'introduction' refers to the movement by human agency, indirect or direct, of an alien species outside of its natural range (past or present)."	B or C
	"invasive alien species: an alien species whose introduction and/or spread threatens biological diversity"	C
Valéry et al. 2008	"A biological invasion consists of a species' acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population."	Ec
Wilson et al. 2009a	"Introduced (or alien) species: A species that has shown extra-range dispersal owing directly or indirectly to human activity"	B or C
	"Invasive species: An introduced species that has sustained self-reproducing populations and can produce reproductive offspring at considerable distances from parent plants"	Ec
Our suggestion	Alien species: Any species that occurs at a location beyond its area of origin; the occurrence of the species in the new area must have been prevented in the past by a dispersal barrier, not by unsuitable conditions. It does not matter whether the passing of the major geographical barrier was aided by humans or not.	B or Ev
	Invasive species are species spreading in the new area, i.e. they are colonizing sites beyond the area of the founder population(s).	Ec

Conclusion

To conclude, we advocate a plurality of approaches and definitions in invasion research. It could be argued that science has to strive for objectivity, or at least inter-subjectivity. But we (and others, e.g. Hodges 2008; Kueffer & Hirsch Hadorn 2008) believe that inter-subjectivity can be achieved even if different meanings are attached to one term. Different perspectives on invasions exist. This is a fact that will not change in the near future and probably not even in the long term. We believe that awareness of the existence of different perspectives is necessary but also sufficient to allow good communication, and that a conscious decision about the research aim and an explicit choice of a definition serving this specific aim is a perfect basis for major progress. It leads to the disclosure of implicit assumptions which otherwise could influence the choice of methods and the data interpretation in a subliminal, therefore questionable way. Exposing these hidden assumptions makes them accessible to scientific verification. Overall, this will improve integration within invasion research, since integrative research in our opinion does not necessarily rely on speaking the exact same language – clear communication and open-mindedness is the key.

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Chapter 2

Turning information into knowledge: Linking major databases to analyse and prioritise introduction pathways of alien species

This chapter will be submitted as:

Saul W-C, Roy HE, Booy O, Carnevali L, Chen H-J, Genovesi P, Harrower CA, Pagad S, Pergl J, Jeschke JM. Turning information into knowledge: linking major databases to analyse and prioritise introduction pathways of alien species.

Abstract

To reduce impacts of invasive alien species, we need to know how they arrive in new regions. However, information on such introduction pathways is currently scattered across many databases which use differing terminology to describe the same pathways. Using a recently developed standard pathway categorization scheme and collating pathway information from two major databases (GISD/IASPMR and DAISIE), we assessed broad introduction pathways (release, escape, contaminant, stowaway, corridor) for major taxonomic groups (plants, vertebrates, invertebrates, algae, fungi, other) and across all environments (terrestrial, freshwater, marine). Our analysis covers more than 8,300 species and shows striking differences among taxonomic groups, whereas differences among environments are much less pronounced. Further, high-impact invaders, in contrast to other alien species, are frequently introduced both intentionally *and* unintentionally. Based on our results, we discuss implications for the prevention of introductions and particularly for prioritization of pathways in management and surveillance.

Keywords: comparative analysis, DAISIE, GISD, IASPMR, management, non-native species, prioritization

Introduction

Alien species, i.e. organisms introduced by man into places outside their natural range of distribution, are being introduced into new regions at unprecedented rates worldwide. Some of these become invasive, i.e. established, spreading and posing a major biodiversity threat for local ecosystems (Millennium Ecosystem Assessment 2005; Hulme 2009). The Guiding Principles of the Convention on Biological Diversity (CBD) advocate a three-tiered approach to avoid future biodiversity losses due to invasions: (i) prevention, (ii) eradication and (iii) control, with prevention of the arrival of invasive alien species (IAS) being the most desirable strategy (CBD 2002; Leung et al. 2002). A prerequisite for effective prevention is a detailed knowledge about the ways in which alien species are transported from their native range to new regions (‘introduction pathways’). For example, many plants have been introduced to gardens but escape confinement and are therefore considered to have arrived through the ornamental pathway (Mack 2003). Given that alien species can be introduced via a large variety of pathways (Box 2.1), it is essential to identify these and to create a framework for decision-makers to determine which pathways should be prioritized and how they can be addressed through legislation and management (Mack 2003; Hulme et al. 2008). Indeed a number of policies are emerging for which this information is critical to underpin implementation. For instance, a new EU regulation on IAS came into force in January 2015, requiring member states to prioritize pathways of invasion (Beninde et al. 2015; EU 2014), and the Aichi Biodiversity Target 9 states that “by 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated and measures are in place to manage pathways to prevent their introduction and establishment” (www.cbd.int/sp/targets/).

A major challenge to achieving this goal is the way in which pathway information is scattered across various databases that utilize disparate terminology and categorization for documenting pathways of arrival (e.g. Gatto et al. 2013). Moreover, the databases often have a limited coverage, for example focusing only on specific taxonomic groups (e.g. EPPO, www.eppo.int/INVASIVE_PLANTS/ias_plants.htm), environments (e.g. FAO Database on Introductions of Aquatic Species DIAS, www.fao.org/fishery/dias/) or particular regions (e.g. NOBANIS for northern Europe, www.nobanis.org). Fewer databases cover different environments and taxa as well as larger spatial scales, e.g. the Global Invasive Species Database GISD (www.issg.org/database/welcome) and the DAISIE European Invasive Alien Species Gateway (www.europe-aliens.org). The situation is beginning to resemble that aptly framed by John Naisbitt (1982): “We are drowning in information but starved for knowledge.” Linking databases by harmonizing and consolidating their pathway information is critical to turn accumulating and dispersed data into knowledge. This will allow us to analyse larger datasets and facilitate comparative analyses between different taxonomic groups, environments, and spatial scales to underpin understanding and inform research and policy (Gatto et al. 2013; see also the European Alien Species Information Network EASIN, Katsanevakis et al. 2012).

Our study focuses on two major international alien species databases already mentioned above: (i) GISD, expanded for this study with data from the related Invasive Alien Species Pathway Management Resource (IASPMR), and (ii) DAISIE. We harmonized the pathway information between these databases testing the application of a standard pathway categorization scheme developed by the Global Invasive Alien Species Information Partnership (GIASIPartnership), an initiative of the Convention on Biological Diversity (CBD 2014). Then we analysed the consolidated data, identifying and comparing patterns in the relative proportions of introduction pathways for different taxonomic groups and environments.

Methods

Standard pathway categorization scheme

Harmonizing pathway information between different databases (here GISD/IASPMR and DAISIE) requires that existing pathway classifications within each database are mapped to a shared categorization scheme. Such standard pathway categorization scheme has been developed recently by the GIASIPartnership (reported in CBD 2014) based on a framework proposed by Hulme et al. (2008). The standard scheme comprises the pathway categories ‘Release in nature’, ‘Escape from confinement’, ‘Transport – Contaminant’, ‘Transport – Stowaway’, ‘Corridor’, and ‘Unaided’ (for definitions see Appendix Table A2.1). ‘Release’ and ‘Escape’ are considered pathways of intentional introduction, while the remaining categories are considered pathways of unintentional introduction. Box 2.1 describes in detail the scheme and challenges in the mapping process.

Box 2.1 – Mapping pathways to the standard pathway categorization scheme

The terminology used to classify the arrival pathways of alien species has historically varied between alien species databases (Essl et al., submitted). The classification system proposed by Hulme et al. (2008) has been further developed by the GIASIPartnership initiative of the Convention on Biological Diversity (CBD 2014) and tested using two major alien species databases (DAISIE and GISD). The process of mapping existing pathway classifications within DAISIE and GISD to the CBD classification provided useful insights into potential issues regarding standardization of pathway information and associated terminology. Here we present a schematic representation of the mapping process between these existing classifications and the CBD classification.

The DAISIE classification includes a multi-level hierarchical approach which has been simplified to six broad categories (Intentional release, Escapes, Unintentional release, Hybrid, Other, and Unknown) comprising 22 sub-categories of pathway descriptions. The GISD classification includes 34 categories with no overarching broad categorization. The DAISIE subcategories and the GISD categories were mapped onto the CBD classification comprising six broad categories (Release in nature, Escape, Transport – Contaminant, Transport – Stowaway, Corridor, and Unaided) and 44 subcategories (for definitions see Appendix Table A2.1). For DAISE where possible, the subcategories were mapped onto the equivalent CBD categories, which was achievable for 79% of the pathway information within the database. Mapping the remaining 21% of pathway information is involving assessment on a species-by-species basis. In contrast, the GISD mapping process was completed on a species-by-species basis.

The schematic representation illustrates the mapping process. The thick solid lines indicate comparable classifications with the majority of pathway information from DAISIE or GISD mapping to the CBD classification. The dotted lines indicate a less direct link between the existing classifications and the CBD classification, for example the subcategory ‘Vessels’ within DAISIE is split between six subcategories within the CBD broad category ‘Transport – Stowaway’.

The CBD classification provides an opportunity for a standardized approach to pathway classification. The mapping process was relatively straightforward for the majority of the pathway information that mapped directly onto the CBD classification. However, a minority of subcategories presented difficulties. The DAISIE classification included a subcategory ‘Leisure’ within the broad category ‘Intentional release’, which did not appear to have a direct link within the CBD classification, but assessment at the species-level indicated that ‘Leisure’ spanned two broad categories within the CBD classification: ‘Release’ and ‘Escape’. In some cases, the pathway information for alien species which were arriving on or within other host alien species was attributed to the host alien species. So, for example, within DAISIE a number of pest insects arriving on ornamental plants were attributed to the subcategory ‘Ornamental’ but in the CBD classification the appropriate subcategories applicable to these species is either ‘Contaminant on plants’ or ‘Parasites on plants’ within the broad category ’Transport – Contaminant’. Three broad categories (Hybrid, Other, and Unknown) within DAISIE were not represented in the CBD classification. Hybrid was not considered a valid pathway but represents a consequence of invasion by some species. Pathway information attributed as ‘Other’ or ‘Unknown’ required further investigation to map on the CBD classification.

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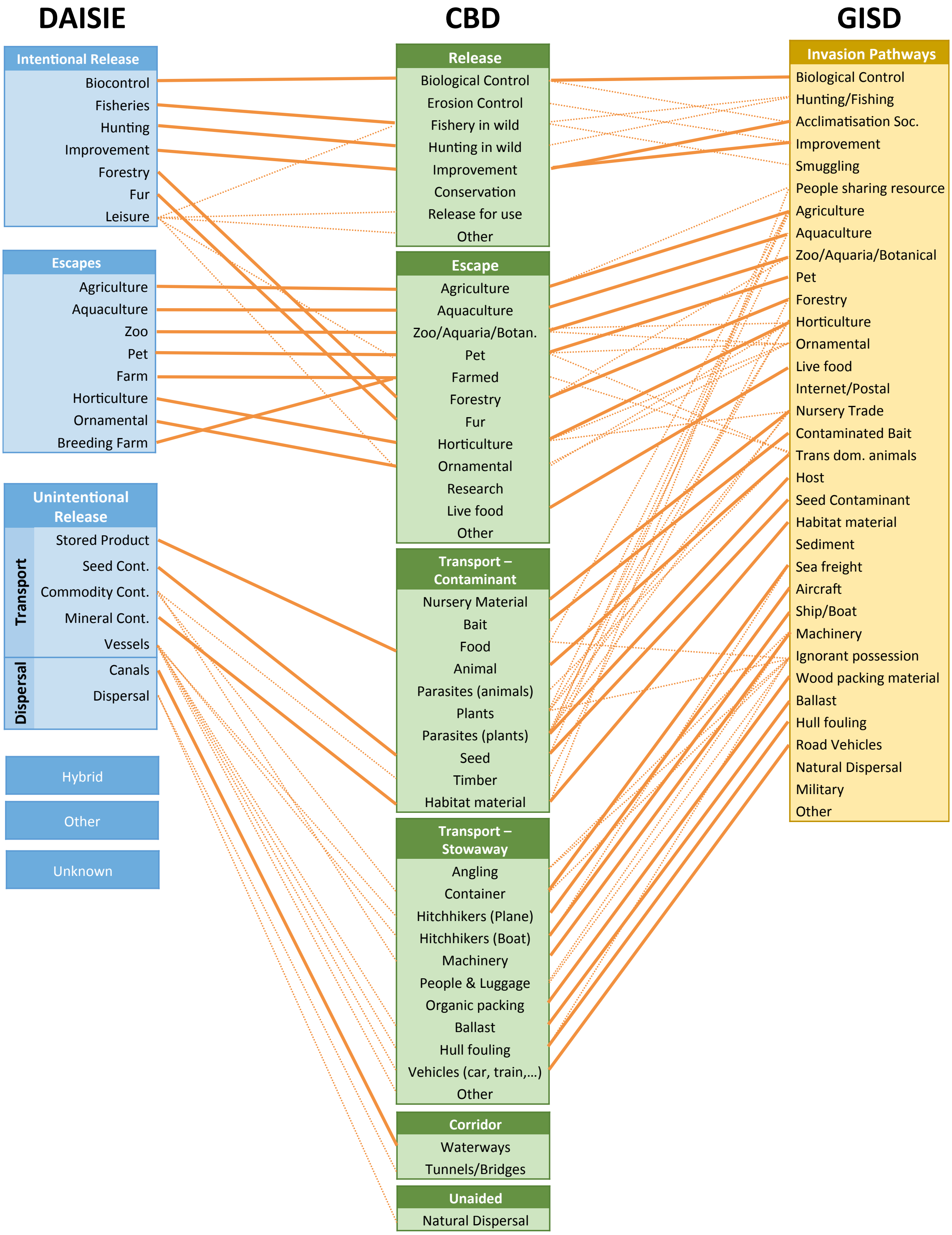
– Box 2.1 continued –



Future recommendations include the need for detailed documentation on the CBD classification and this is ongoing alongside the development of IASPMR as the GISD pathway tool. Provision of detailed pathway information in addition to the classification for each species would facilitate the mapping process. It will also be necessary to develop further subdivisions of the CBD subcategories to enable prioritization of pathways at country or regional levels.

Datasets

a) General data handling

The following original information was extracted from both databases: species name, organism type (mammal, shrub, bacterium etc.), environment (terrestrial, freshwater, marine, or combinations of these), introduction vector and pathway according to the classification of the respective database, and whether the species is named on a '100 of the Worst IAS' list featured by both databases independently from each other. Species names were screened for errors and synonyms, and were standardized according to accepted nomenclature. Entries below species rank (e.g. subspecies or varieties) were considered only at species level. Entries with ambiguous species names (e.g. '*Tilapia* spp.') were excluded unless they were the only record of a particular introduction pathway for the respective genus. Within each dataset, duplicates (i.e. entries concerning the same species and stating the same introduction pathway) were removed, as well as entries with missing pathway information or concerning hybrid species.

All remaining entries were assigned one of six major taxonomic groups: plants, vertebrates, invertebrates, algae, fungi, other (comprising mainly micro-organisms: bacteria, oomycetes, prions, protists, and viruses). Environment categories were standardized to terrestrial, freshwater, marine, and multiple, the latter being assigned when species inhabit more than one type of environment. If missing in the original data, information on the environment was completed using scientific literature and online resources (e.g. the IUCN Red List database). Introduction pathways were standardized according to the standard categorization scheme (see above and Box 2.1). In a final step, semi-systematic plausibility checks were performed, double-checking e.g. for implausible combinations of data entries or for inconsistencies regarding the environment (e.g. entries concerning the same species but stating different environments). Corrections were made where necessary.

b) GISD/IASPMR dataset

The pathway information in GISD has recently been included in the Invasive Alien Species Pathway Management Resource (IASPMR, www.acronym.co.nz:8086), a database that is being developed and implemented by ISSG within the framework of the GIASIPartnership. Original data were retrieved from IASPMR (including GISD data) in February 2014. The pathway categories in the GISD/IASPMR data comply with the standard categorization scheme, since they were already mapped in the course of the development of the scheme. The only exception is that IASPMR lacks the category 'Unaided' but has a non-standard category 'Other'. The 10 records in the latter category were excluded from our analyses. Data for six species listed in GISD as 'worst IAS' (*Cinara cupressi*, *Eleutherodactylus coqui*, *Euglandina rosea*, *Pinus pinaster*, *Prosopis glandulosa*, *Trichosurus vulpecula*) and for two other species (*Cenchrus polystachios*, *Herpestes javanicus*) were missing in IASPMR, thus we completed the information using the scientific literature and online databases.

The analysed GISD/IASPMR dataset contained pathway information for a total of 2,414 species (493 plants, 1,664 vertebrates, 215 invertebrates, 12 algae, 9 fungi, and 21 other), including 99 worst IAS (*Anopheles quadrimaculatus* was excluded since reasons for its classification as one of the worst IAS are unclear). 24 species within this dataset based on entries with ambiguous species names (see section on general data handling). For four of these, it was not possible to specify the environment category, hence they were excluded from the respective analysis (see below). For a detailed numerical description of the dataset, see Appendix Table A2.2.

c) DAISIE dataset

Original data were retrieved from DAISIE in May 2014. Most of the DAISIE categories were mapped to the standard categorization scheme prior to our study (Essl et al., submitted). However, for unmapped DAISIE categories containing many species, we carried out additional mappings for the purposes of this analysis in order to include these species: (1) Species in the DAISIE category ‘Commodity contaminant’ were assigned to the category ‘Transport – Contaminant’, and species in the DAISIE category ‘Transport’ were assigned to ‘Contaminant’ or ‘Stowaway’, depending on the species in question. For the analyses (of both the DAISIE dataset and the combined dataset, see below), all of these species ended up in the combined transport category ‘Contaminant & Stowaway'. Such pooling was necessary since by the time of the analyses a differentiation between the two transport categories was not possible with sufficient certainty for a significant number of species within the DAISIE dataset (please note that for the GISD/IASPMR dataset the transport pathways are shown separately; see Appendix Fig. A2.1). (2) Species in the DAISIE category 'Unintentional release' were assigned to 'Escape'. By inspecting numerous randomly sampled individual species, we double-checked whether these additional mappings are reasonable. Entries in the few remaining unmapped DAISIE categories were excluded from analysis.

The analysed DAISIE dataset contained pathway information for a total of 6,370 species (3,636 plants, 377 vertebrates, 2,040 invertebrates, 167 algae, 77 fungi, 73 other), including 99 species listed in DAISIE as worst IAS (*Spartina anglica* was excluded as its pathway categorization was uncertain). 13 species within this dataset based on entries with ambiguous species names (see ‘General data handling’). For a detailed numerical description of the dataset, see Appendix Table A2.2.

d) Combined dataset

For combined analyses, the GISD/IASPMR and DAISIE datasets were collated into one table. Only 460 species were shared by the two datasets, and so the combined dataset included 8,324 species (3,950 plants, 1,823 vertebrates, 2,203 invertebrates, 174 algae, 85 fungi, 89 other). If records for species present in both datasets deviated in organism type or environment, we referred to the scientific literature and online databases to check the entry and corrected it as required; these corrections were also made in the GISD/IASPMR and DAISIE datasets. Subsequently, duplicate entries were removed. For a detailed numerical description of the dataset, see Appendix Table A2.2.

Analyses and statistics

We counted the number of species per introduction pathway category, based on which we calculated the relative proportions of the pathway categories within each taxonomic group and environment. For instance, 3,242 of the 3,950 plant species in the combined dataset have been introduced by 'Escape from confinement', i.e. approximately 82%. Relative proportions were also calculated for grouped intentional and unintentional pathways. For all proportions, we calculated 95% Wilson confidence intervals, which have distinctive advantages over ordinary confidence intervals (Newcombe 1998, Newcombe & Altman 2000, Brown et al. 2001, 2002). The analyses were carried out separately for the individual datasets of GISD/IASPMR and DAISIE as well as for the combined dataset. We also compared the subsets of 'Worst IAS' and 'Other IAS' for the individual datasets (not for the combined dataset) in order to identify differences between invasive species of particular concern and all other invasive species.

Results and Discussion

Analysis of introduction pathways in taxonomic groups and environments

The analyses for all 8,324 species in the combined dataset (Fig. 2.1) as well as those for the GISD/IASPMR (Appendix Fig. A2.1) and DAISIE (Appendix Fig. A2.2) datasets revealed that for plants and vertebrates, introduction via the intentional pathways 'Escape' and (to a lesser extent) 'Release' is dominant, while for invertebrates, algae, fungi and micro-organisms, the unintentional pathways prevail (particularly, the transport pathways 'Contaminant' and 'Stowaway'). The relatively high proportions of 'Release' for plants and vertebrates reflect the importance of these organisms in human activities such as e.g. 'improving' local flora and fauna for aesthetic reasons, establishing game animals in the wild, aquaculture, or pasture improvement (Nentwig 2007). However, 'Escape' is a significantly more frequent pathway for these organisms, following their (originally confined) introduction, e.g. for ornamental purposes, agriculture, pet trade, or live food trade. This finding highlights the need for continued efforts to increase containment effectiveness and awareness in people. Also for invertebrates, the pathways ‘Release’ and ‘Escape’ are of importance, as exemplified by biocontrol agents that are intentionally released into the wild and that may escape the intended area of release (e.g. the ladybird *Harmonia axyridis*; Roy & Wajnberg 2008).

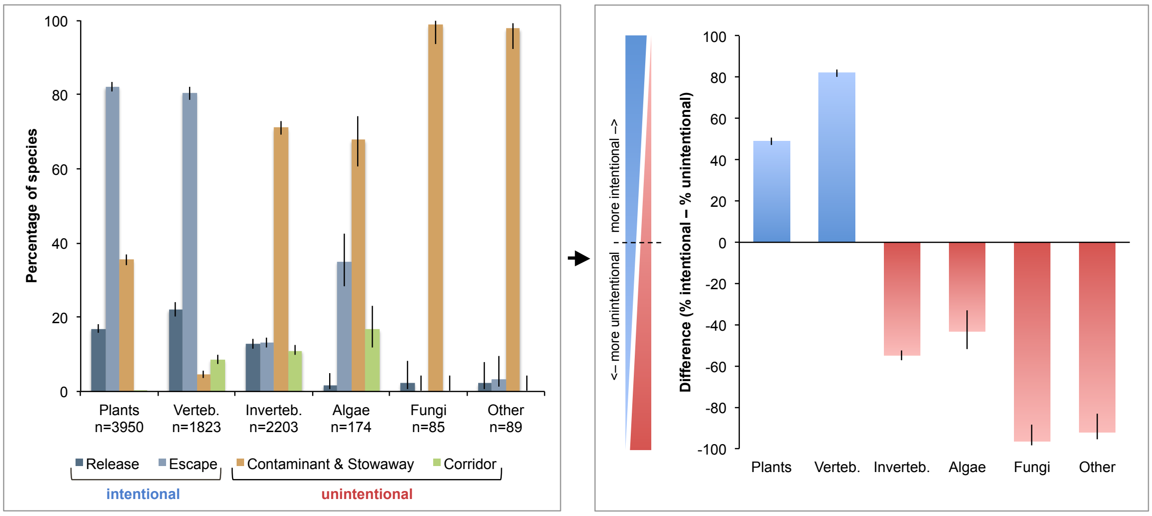
Regarding the transport pathways ‘Contaminant’ and ‘Stowaway’ (pooled as ‘Contaminant & Stowaway’ in DAISIE and the combined dataset), it is not surprising to find these most highly represented in invertebrates, algae, fungi, and micro-organisms due to their ubiquity and inconspicuousness. For instance, pathogens and parasites are often introduced as contaminants with their hosts (Kenis et al. 2007), and many marine invertebrates with ballast water or as ship fouling (Katsanevakis et al. 2013). Also, a considerable proportion of plants is unintentionally introduced, e.g. as seed contaminants in crop seeds or as stowaways in soil attached to machinery and vehicles (Mack 2003). The ‘Corridor’ pathway is of importance for algae, invertebrates and vertebrates, and is primarily associated with aquatic environments (Fig. 2.1b; see also Hulme et al. 2008). This emphasizes the role of transbiogeographical canals that connect river catchments, waterways, basins and seas; it possibly underestimates the importance of terrestrial corridors such as tunnels and land bridges. The ‘Unaided’ pathway fell out of the analyses since IASPMR lacked this category (in GISD, no species were reported for this pathway), and in DAISIE no analogous category had yet been mapped to it.

Remarkably, pathway proportions differ much more distinctly among taxonomic groups (Fig. 2.1a) than among environments (Fig. 2.1b). In other words, we found very similar patterns of pathway proportions across most environments: high for ‘Escape’, intermediate for ‘Release’ and ‘Contaminant & Stowaway’, and low for ‘Corridor’. The marine environment deviates to some extent from this pattern, showing higher proportions of unintentional pathways, probably due to the high importance of marine corridors for international trade (e.g. the Suez canal; Katsanevakis et al. 2013). The unequal distribution of intentional and unintentional pathways between the different taxonomic groups and the more uniform distribution in favour of intentional pathways throughout the different environments is clearly illustrated by the right-hand side graphs in Figs. 2.1a,b. This general pattern can also be found for the individual GISD/IASPMR and DAISIE datasets (Appendix Figs. A2.1, A2.2).

'Worst IAS' vs. *'Other IAS'*

Comparing the sub-samples 'Worst IAS' and 'Other IAS' of the GISD/IASPMR dataset, we also found significant differences (Figs. 2.2a,b). In the 'Other IAS' sub-sample (left-hand graphs of Figs. 2.2a,b), proportions of intentional and unintentional pathways again differ more distinctly among taxonomic groups than among environments, and do so even more clearly than in the results for the combined dataset described above. An underlying reason could be that intentional introduction strongly prevails over unintentional introduction in plants and vertebrates (Fig. 2.2a); due to the high overrepresentation of these taxonomic groups in all environments in the sub-sample, this pattern is replicated across all environments (Fig. 2.2b). In the 'Worst IAS' sub-sample (right-hand graphs of Figs. 2.2a,b), proportions not only differ among taxonomic groups, but also show variation among environments. This is probably due to the fact that in the 'Worst IAS' sub-sample, plants and vertebrates are not nearly as overrepresented as in the 'Other IAS' sub-sample. Interestingly, in the 'Other IAS' sub-sample, the proportion of species being introduced via both intentional *and* unintentional pathways is comparatively low for all taxonomic groups; by contrast, the 'Worst IAS' sub-sample shows significantly increased proportions of species that are introduced both intentionally and unintentionally. For the DAISIE dataset, very similar patterns were found (Appendix Fig. A2.3), hence it seems that high-impact IAS generally tend to be introduced more often via both intentional and unintentional pathways than other IAS.

a) Taxonomic groups



b) Environments

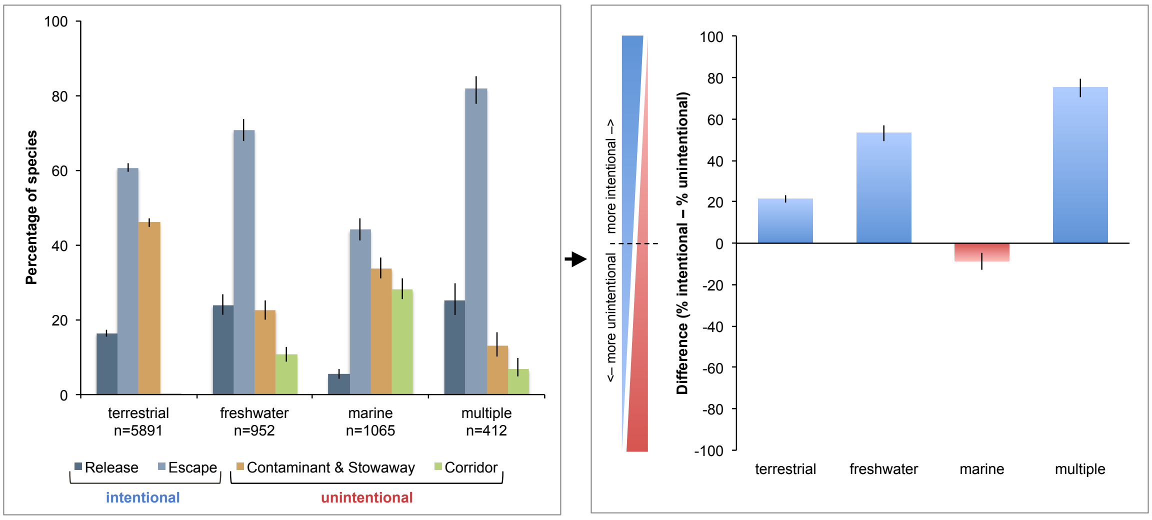
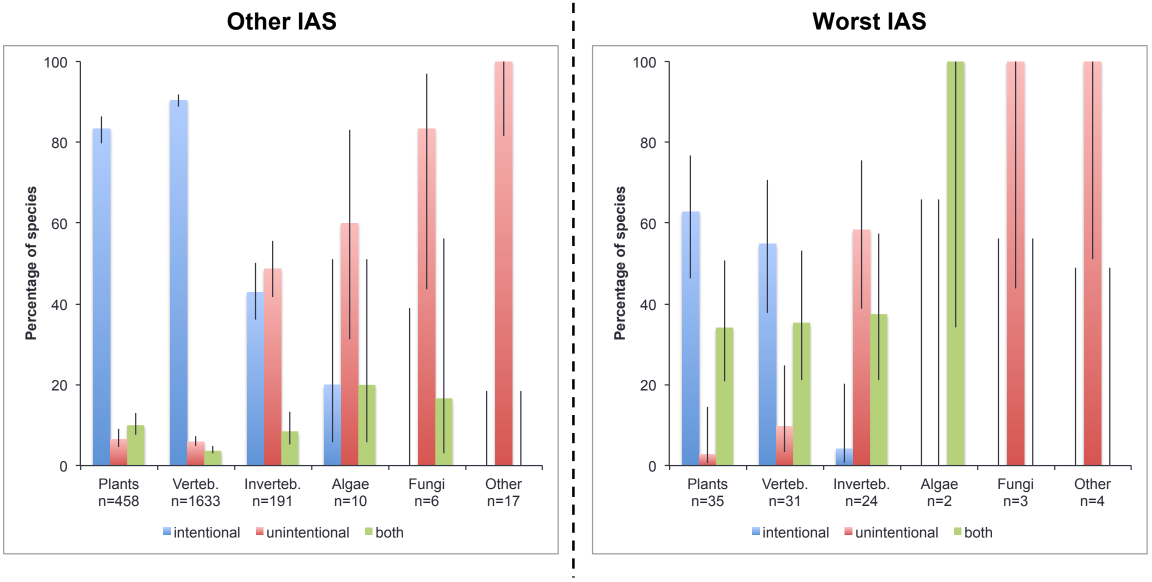


Figure 2.1 – Introduction pathways in the combined dataset (GISD/IASPMR & DAISIE). Pathways were analysed according to (a) taxonomic groups (8,324 species) and (b) environments (8,320 species). Left-hand side graphs show individual proportions of pathways (the sum of proportions is larger than 100% in all taxonomic groups and habitats since species can be introduced via more than one pathway). Right-hand side graphs show the difference in accumulated proportions of intentional and unintentional pathways (excluding species that fall into both categories). Error bars indicate 95% Wilson confidence intervals.

a) Taxonomic groups



b) Environments

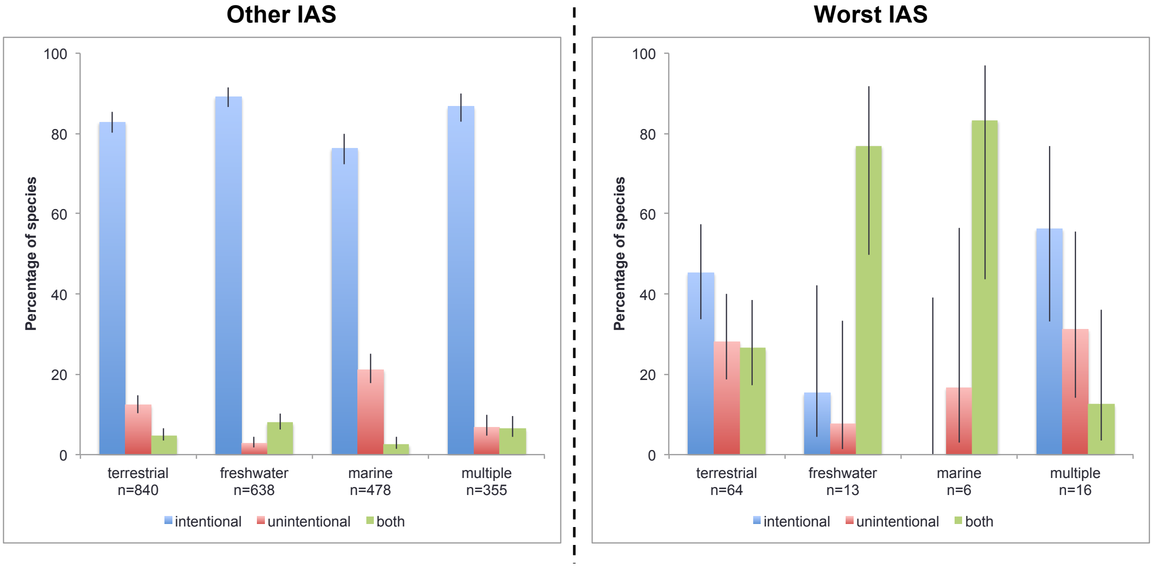


Figure 2.2 – Introduction pathways in regard to their intentionality for ‘Other IAS’ (left-hand side) *vs.* ‘Worst IAS’ (right-hand side) in the GISD/IASPMR dataset. Pathways were analysed according to (a) taxonomic groups (Other IAS: 2,315 species; Worst IAS: 99 species) and (b) environments (Other IAS: 2,311 species; Worst IAS: 99 species). Error bars indicate 95% Wilson confidence intervals.

Conclusions

Our study provides an overview of pathway information contained in two major IAS databases in order to support prioritization in IAS management. Analysing the combined dataset and the individual datasets of GISD/IASPMR (global) and DAISIE (European), we found that plants and vertebrates are mostly introduced via intentional introduction pathways, whereas unintentional pathways are of greater importance for invertebrates, algae, fungi, and micro-organisms. These patterns are largely consistent with previous research by Hulme et al. (2008), but are based in this study on much more comprehensive and updated data.

Differences in pathway proportions are more pronounced among taxonomic groups than among environments. Thus, since each taxonomic group has a characteristic pathway profile, reducing the risk of introduction of IAS from different taxonomic groups will probably also require different legislative regulation and management. Discriminating between pathways of intentional and unintentional introduction provides an immediate idea about adequate management priorities for different taxonomic groups: for preventing the introduction of species from taxonomic groups that arrive mainly via intentional pathways, i.e. in particular plant and vertebrate species, prevention focused on the species level is probably reasonably effective. However, for species that are unintentionally introduced, i.e. mainly invertebrates, algae, fungi, and micro-organisms, strategies are necessary that target entire pathways.

Looking at the species that are present in the GISD/IASPMR dataset but not in the DAISIE dataset may serve as early warning in that it enhances our ability to predict how those species may eventually arrive in Europe in the future, allowing us to take adequate preventive action. Therein, shifts in the importance of pathways over time, e.g. from intentional introductions in former times (e.g. by acclimatization societies) towards more unintentional introductions nowadays as a by-product of increasing trade and transport, will have to be considered (Hulme et al. 2008; Wilson et al. 2009).

Another intriguing insight from this study is that high-impact invaders are frequently introduced both intentionally *and* unintentionally. This is discouraging for preventive IAS management and conservation policy, as it indicates that even if a species of particular concern can be identified and its introduction banned (e.g. by way of impact scoring and blacklisting approaches; see e.g. Kumschick et al. 2012; Blackburn et al. 2014), considerable risk remains that the species will nonetheless enter the region by one of the pathways of unintentional introduction. Thus, high-impact IAS clearly need all our attention in devising effective measures for entry prevention covering all pathways (including extensive surveillance and monitoring), not only because of their severe impacts but also because they seem particularly prone to be introduced.

Importantly, identifying the most relevant pathways of introduction is only the first step. It needs to be followed by the development of adequate responses in legislation and management for the key pathways. The impacts of these policies need to be monitored. Combining findings on the most relevant pathways with knowledge about the most harmful invasive species seems promising in this regard and may enhance prioritization of prevention and management actions.

Acknowledgements

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Chapter 3

Species from different taxonomic groups show similar invasion traits

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Abstract

Invasion ecology tends to treat taxonomic groups separately. However, given that all invasive species go through the same stages of the invasion process (transport, escape, establishment, spread), it is likely that – across taxa – comparable traits help to successfully complete this process ("invasion traits"). Perhaps not all invasive species have the same invasion traits, but different combinations of invasion traits can be found among invaders, corresponding to different possibilities to become a successful invader. These combinations of invasion traits might be linked to taxonomic affiliation, but this is not necessarily the case. We created a global dataset with 201 invasive species from seven major taxonomic groups (animals, green plants, fungi, heterokonts, bacteria, red algae, alveolates) and 13 invasion traits that are applicable across all taxa. The dataset was analysed with cluster analysis to search for similarities in combinations of invasion traits. Three of the five clusters, comprising 60% of all species, contain several major taxonomic groups. While some invasion trait frequencies were significantly related to taxonomic affiliation, the results show that invasive species from different taxonomic groups often share similar combinations of invasion traits. A post-hoc analysis suggests that combinations of traits characterizing successful invaders can be associated with invasion stages across taxa. Our findings suggest that there are no universal invasion traits which could explain the invasion success of all invaders, but that invaders are successful for different reasons which are represented by different combinations of invasion traits across taxonomic groups.

Keywords: alien species, cluster analysis, cross-taxonomic study, taxonomic bias, invasion mechanisms

Introduction

Invasion ecology, as many other biological disciplines, is split into taxonomically delineated sub-disciplines among which there is limited transfer of knowledge. Some important hypotheses, e.g. enemy release or biotic resistance, are mainly investigated for plants but rarely for animals (Jeschke et al. 2012b). *Vice versa*, the hypothesis that islands are more susceptible to invaders than continents has been mainly studied for vertebrates (Jeschke et al. 2012b). A commonly presented argument in favour of this taxonomic split is that different invasion mechanisms might be relevant for different taxonomic groups (e.g. Blackburn et al. 2009).

Although taxonomic differences certainly are important, there is a challenge to this argument: species of all taxonomic groups have to overcome the same difficulties during the invasion process – they have to be transported to an exotic range where they have to be released or escape; they have to establish a self-sustaining population in the wild; and finally, they have to overcome difficulties with spread (Williamson 1996; Kolar & Lodge 2001; Heger & Trepl 2003; Theoharides & Dukes 2007; Blackburn et al. 2011). It is therefore conceivable that invasive species share traits that help overcome such difficulties in transport, escape, establishment and spread, independently of which taxonomic group they belong to.

Cross-taxonomic studies in invasion ecology are rare, however some studies provided evidence that invasion mechanisms across different taxa are similar. In particular, Pyšek et al. (2010) found that, concerning habitat affinity, alien insects are more similar to alien plants than to alien vertebrates. Newsome & Noble (1986) analysed traits distinguishing bird and plant invaders in Australia. They found analogies between invasive bird and plant species, particularly in regards to their ability to inhabit anthropogenic sites, as well as the longevity of individuals. Hayes & Barry (2008), based on Kolar & Lodge (2001), found three variables that promote establishment success across taxonomic groups: climate/habitat match, invasion success elsewhere and propagule pressure. Other authors came to the conclusion that propagule pressure is the only trait promoting invasion success across taxonomic groups (reviewed in Lockwood et al. 2007; Blackburn et al. 2009).

In addition to such cross-taxonomic similarities in single variables or traits, species may also show similarities across taxa in sets of several traits relevant for invasion success. For this study, we test the following hypothesis: Species of different taxonomic groups show similar combinations of invasion traits (i.e. traits that facilitate the invasion process). The alternative hypothesis, which we expect to be rejected, is that similar combinations of invasion traits are congruent with taxonomic groups. We assessed these hypotheses by compiling information on traits known to increase the probability that a species becomes invasive ("invasion traits"). The respective trait values were generalized in order to be applicable across varying taxa and were compiled for 201 invasive species derived from seven major taxonomic groups. For each invasion trait, we compared the frequency of trait expressions among taxonomic groups and to the results of published studies. According to our hypothesis, we expected no strong differences among taxonomic groups. Next, we applied cluster analysis to search for similarities among species with respect to invasion traits (for similar approaches focused on plants, see Newsome & Noble 1986; Thuiller et al. 2006). If taxonomic groups do not differ fundamentally concerning invasion traits, species of each taxonomic group should be dispersed across clusters.

Methods

Dataset

Our dataset includes 201 invasive species (species established and spreading in an area beyond their native range). Aiming for a broad generalization of our findings, we chose species from a wide range of taxonomic groups, trophic levels, life forms, habitats, geographic origins and invaded ranges. For each species, we collected data on 13 invasion traits (Table 3.1) in the scientific literature, databases and online sources (Appendix Table A3.1). Although unequal availability of these data precluded reaching a balanced number of species throughout all taxa, ecological traits, origins and target regions, we chose this approach to initiate novel (at least preliminary) insights from cross-taxonomic research, which we believe are essential for progressing in our understanding of species' invasiveness.

Invasion traits

The 13 traits included in the study were selected based on a checklist of factors influencing biological invasions (the INVASS model of invasion steps and stages, Heger 2004; see also Heger & Trepl 2003). They cover the complete invasion process and have been shown to enhance invasion success (Table 3.1). We described them in a generalized, taxon-independent way, so that each trait is applicable to species of any taxonomic group (e.g. "one individual can form a population" instead of "vegetative reproduction").

The resulting data set consists of binary values ("yes" or "no" for each trait and each species). We chose this method of qualitative assessment because for most traits it is not possible to compare quantitative values in a meaningful way among taxonomic groups (e.g. the number of offspring). Nonetheless, three of the invasion traits have a strong association with taxonomic affiliation: “spread as active mobile organism” can never be found in plants, fungi and red algae (39% of all species in our data set), whereas “transportation as diaspore” and “seed bank” (in the broad sense of any organism’s dormant life stages able to survive a period of unfavourable conditions) can never be found in vertebrates (71% of all animals, and 38% of all species in our dataset). This, of course, has implications for the interpretation of results and will be discussed below. In addition to species characteristics, we included information on human actions (e.g. deliberate transport), as they have a strong impact on invasion processes (Kowarik 2003; Lockwood et al. 2007; Blackburn et al. 2009).

Taxonomic groups

We determined the taxonomic group of each species using the Tree of Life web project (Maddison & Schulz 2010). The 201 analysed species belong to seven superordinate taxonomic groups (Appendix Table A3.1): 108 animals (Metazoa, 54%), 70 green plants (all organisms commonly known as green algae and land plants, including mosses and ferns as well as seed plants, 35%), six fungi (3%), six heterokonts (brown algae, diatoms, and relatives; 3%), five bacteria (Eubacteria, 2%), three red algae (Rhodophyta, 1%) and three alveolates (dinoflagellates and relatives; 1%). The large percentage of animals and green plants in our dataset reflects the high proportion of these groups among studied invasive species (Pyšek et al. 2008). Despite the large size of these groups, we decided not to split animals and plants into smaller taxonomic units, as a further split would not have been possible in all other superordinate groups. Our criterion was to have larger taxonomic distances among than within taxonomic groups, and an unbalanced split of the groups would have obscured these distances. When interpreting our results we kept in mind that analysed numbers of species differ among taxonomic groups.

Statistical analyses

Descriptive statistics consisted of the assessment and comparison of the proportion of invasion traits of the taxonomic groups (incl. 95% confidence intervals). In order to group the species in our dataset according to their invasion traits we applied agglomerative hierarchical cluster analysis, using average linkage between groups as grouping criterion and simple matching for the similarity index (SPSS Statistics 22). The optimum number of clusters was determined based on the largest distance between the clusters in the distance matrix. We ignored the distance that separated all species with completely matching traits from the rest of the species. Clustering was rerun for the three best cluster solutions.

To assess if taxonomy reflects the statistical clusters, we produced a contingency table relating the two groupings (clusters and taxonomic groups) to each other. As a measure of contingency, we calculated Cramér's V (Conover 1999). A Cramér's V of 1 shows a perfect fit of rows and columns in the contingency table; values larger than 0.3 are interpreted as a relevant association and values larger than 0.6 as a strong relationship.

Table 3.1 – Description of invasion traits used to characterise each species. Traits have been chosen based on Heger (2004). References indicating significance of the traits for invasion success are given in the rightmost column. Cases are indicated where the wording in the cited references differs from our formulation. In our dataset, trait values can be either "yes" or "no".

	Invasion trait	**Description**	**Reference**
Transport	Intentional transport	Is or was the transport of the species into the new area predominantly intentional?	Hulme et al. 2008
	In IUCN Red List	Is the species classified as "near threatened" or worse in the IUCN Red List of Threatened Species (IUCN 2013)? [†]	Lavoie et al. 2013: narrow-ranging species are less likely to be dispersed via propagule transportation vectors
	Transport as diaspore	Is the species often transported as diaspore or another easily transportable life stage?	Foy et al. 1983
	Seed bank	Does the species form seed banks, or has it other life stages able to survive a period of unfavourable conditions?	Martínez-Ghersa & Ghersa 2006; Figueroa et al. 2004
Escape	Intentional release	Is the escape and naturalisation of the species in most cases intentional?	Hulme et al. 2008
	Release adult	Are mainly organisms released that are in their reproductive life stage?	This trait has rarely been studied but is likely to positively relate to invasion success.
Establishment	Phenotypic plasticity	Does the species show pronounced morphological or physiological plasticity?	Rejmánek 2011
	One individual can form a population	May one individual suffice to build up a population, e.g. because of vegetative reproduction, parthenogenesis or else?	Kolar and Lodge 2001: vegetative reproduction; Burns et al. 2011: autogamy; Statzner et al. 2008: ovoviviparity
	More than one reproductive phase per year	Is there more than one clutch, phase of flowering, spawning etc. per year?	Kolar & Lodge 2001: broods per season
	Fecundity above average	Does the species produce more offspring than ecologically similar, related species?	Rejmánek 2011
	Offspring in first year	Is an individual able to produce offspring in its first year of life?	Rejmánek 2011: minimum generation time
Spread	Intentional spread	Is or was the spread of the species in the new area predominantly intentional?	Kowarik 2003
	Spread as active mobile organism	Does the species spread as an active mobile organism?	Kolar & Lodge (2001): migrating

[†] We used the IUCN Red List status as a proxy for rarity and thus for the probability of being transported accidentally (red-listed species are less likely to be accidentally transported than other species).

Results

Are frequencies of the investigated invasion traits similar across taxonomic groups?

To assess whether invasive species belonging to different taxonomic groups show similar frequencies in traits relevant for invasion success, we compared the relative frequencies of each invasion trait. In the following, we order the results of this analysis according to the invasion stage to which the respective traits are related.

Transport – For 59% of the species in our dataset, transportation to new regions is typically intentional (Fig. 3.1; Appendix Table A3.2). Especially green plants and animals are deliberately transported (77% and 58% respectively) and these form the majority of species in the dataset. The species of the remaining five taxonomic groups in our dataset are predominantly (67% of red algae and 83% of heterokonts) or exclusively (bacteria, fungi and alveolates) transported accidentally. Three per cent of the species in the dataset (only plants and animals) are included in the IUCN Red List, which means they have an especially low chance of getting transported accidentally. Thirty-six per cent of all species are transported as diaspores, and include species of green plants, fungi, alveolates, heterokonts and – to a small degree – animals (mainly aquatic species, e.g., *Neogobius melanostomus* and *Dreissena polymorpha*). Thirty-three per cent of the species in our dataset produce a seed bank or other dormant life stages; this trait is found in every taxonomic group (Fig. 3.1; Appendix Table A3.2). Fifty species (25% of all species included in our analysis, among them 37 plants, six animals, three heterokonts, two alveolates, one red algae and one fungus) share both traits, i.e. they are transported as diaspores and produce dormant life stages.

Escape – A relatively high proportion of the examined species (36%) are released intentionally, again mainly plants and animals. All species with intentional release have also been intentionally transported. Sixty-five per cent of all investigated species are in a reproductive stage when released. Concerning green plants, however, this is only true for about 31% of the species (among them mainly trees and aquatic species).

Establishment – Twenty-eight per cent of the analysed species are known to show pronounced morphological or physiological phenotypic plasticity; these are plants, red algae and animals. Fifty-two per cent of all species in the dataset are able to build up a population from a single individual (e.g. because females can reproduce asexually or store sperm cells, or due to layering). The only taxonomic group with less than 50% of species showing this ability is animals. Fifty-six per cent of the investigated species are able to reproduce more often than once a year. Only plants and animals include species lacking this ability. The number of offspring is higher than that of related taxa for 38% of the species, and more than 60% of the species in our dataset are able to produce offspring already in their first year of life. Green plants and animals are in our dataset the only groups that include species lacking this ability.

Spread – Dispersion within the exotic range was actively promoted by humans for only 9% of the species in our dataset (mainly plants used for landscaping, e.g. *Spartina alterniflora* and fish, e.g. *Lates niloticus*); 51% of the included species are able to spread actively.

To validate the recorded trait frequencies, we compared our results with other studies. Cross-taxonomic data compilations were available in the literature for three of our invasion traits. For "intentional transport" and "intentional release", these studies reported similar frequencies as in our dataset (Table 3.2). In regards to "seed bank", the frequencies reported in Bennett (2001) and Statzner et al. (2008) suggest that our approach might have overestimated the number of species able to build up a seed bank. An alternative explanation would be that our study differs from Bennett (2001) and Statzner et al. (2008) in how "seed bank" is defined.

Comparing our recorded frequencies among taxonomic groups, significant differences in trait frequencies can be found (e.g. for "transport as diaspore", "release adult"; cf. 95% CIs in Fig. 3.1). For other invasion traits, though, differences are less pronounced ("in IUCN Red List", "intentional release", "offspring in the first year", "intentional spread"). The two taxonomic groups with the largest sample sizes, plants and animals, differ significantly in the frequencies of several invasion traits (e.g. "phenotypic plasticity", "can one individual form a population"). Other invasion traits, however, are similarly frequent in all seven taxonomic groups (e.g. "intentional release", "more than one reproductive phase per year", "intentional spread").

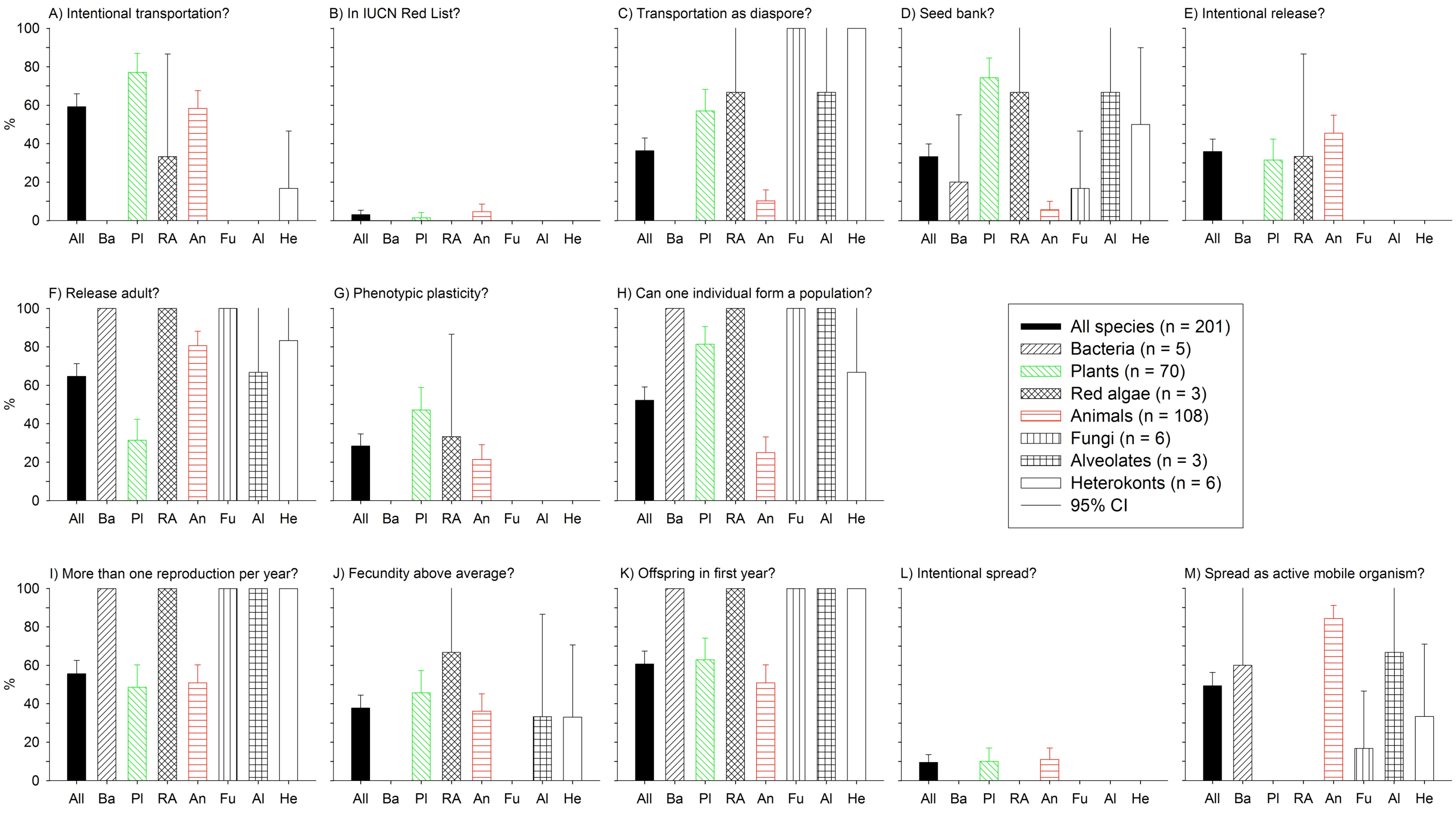

Figure 3.1 – Relative frequencies of invasion traits. Frequencies (± 95% CI) are given for all species in our dataset and for each of the seven taxonomic groups separately. Exact values are provided in Appendix Table A3.2.

Table 3.2 – Relative frequencies of invasion traits according to our dataset and compared to literature data. Frequencies (%) are given for the invasion traits "intentional transport", "seed bank", and "intentional release"; dots mark empty fields.

Invasion trait	All taxa		Plants		Animals		Fungi	
	Our data	Literature	Our data	Literature	Our data	Literature	Our data	Literature
Intentional transport	59	61[1]	77	69[1]	58	59[1]	0	0[2]
	.	52[2]	.	89[2]	.	43[2]	.	.
	.	.	.	68[3]	.	54[5]	.	.
	.	.	.	>50[4]	.	.	.	.
Seed bank	33	.	74	0.2[6]	6	0[7]	17	.
Intentional release	36	37[1]	31	12[1]	45	48[1]	0	.
	.	.	.	1[3]	.	.	.	.

[1] Hulme et al. (2008)
[2] Keller et al. (2009): nonindigenous freshwater species in Great Britain
[3] Lambdon et al. (2008): naturalised alien plant species in Europe
[4] Mack & Erneberg (2002): naturalised plant species in the United States
[5] Lockwood et al. (2007): re-analysis of data given on p. 33
[6] Bennett (2001): invasive plant species in the Great Lakes National Parks
[7] Statzner et al. (2008): invertebrates in Europe

Taxonomic composition of clusters: Are clusters classifying the species according to invasion traits congruent with taxonomic groups?

Cluster analysis, using all 13 invasion traits and all 201 species, indicates that assigning species to two, three or five clusters are the three best clustering solutions. All three cluster solutions are based on the same branching pattern. Fig. 3.2 shows the main furcations of the underlying dendrogram, with cluster solutions differing in the number of furcations included: Only one furcation is needed to reach the 2-cluster solution; for the 3-cluster solution, Cluster 1 of the two clusters identified in the 2-cluster solution is further split into two; and for the 5-cluster solution, Clusters 1 and 2 of the 3-cluster solution are each split into two (Fig. 3.2).

In the 5-cluster solution, Cluster 1 (n = 46) includes species from all seven taxonomic groups (Fig. 3.2): all red algae and alveolates can be found here, plus 40% of all bacteria, 83% of all fungi and 67% of all heterokonts (Appendix Table A3.3). Twenty-six per cent of all green plants and 10% of all animals are included as well. The 41 species contained in Cluster 2 are animals, bacteria, fungi and heterokonts. Thirty-two per cent of all animals are classified into this cluster, additionally three of the five bacteria, one of the six fungi and one of the six heterokonts. Cluster 3 (n = 39) is dominated by green plants: it contains 51% of all plant species in our data set. Additionally, two animal species (*Daphnia lumholtzi* and *Rapana venosa*) and a heterokont (*Undaria pinnatifida*) can be found in this cluster. The 64 species of Cluster 4 are mainly animals

(59 animal species, representing 55% of all animal species included in this study), complemented by five plant species (*Cupressus macrocarpa*, *Pinus nigra*, *P. strobus*, *Pseudotsuga menziesii* and *Lysichiton americanus*). Cluster 5 is the smallest group (n =11) and contains only green plants.

The analysis of the respective contingency table (Appendix Table A3.3) revealed that there is a weak association between the five clusters and the taxonomic groups (Cramér's V = 0.478, $p <$ 0.001; Table 3.3). The association between the three clusters in the 3-cluster solution and the taxonomic groups is stronger (Table 3.3). Here, one cluster contains a mixture of all taxonomic groups, a second cluster is dominated by animals and a third contains only plants (Fig. 3.2; Appendix Table A3.4). The two clusters in the 2-cluster solution show the strongest association with the taxonomic groups (Table 3.3). Sixty-eight per cent of the 96 species in cluster 1 are plants and 90% of the 105 species in cluster 2 are animals (Fig. 3.2; Appendix Table A3.5).

Table 3.3 – Association of the three best cluster solutions with taxonomic groups and potential invader types. Strength of association is given as Cramér's V. Higher values indicate stronger association; a Cramér's V of 1 would indicate a perfect fit of rows and columns in the respective contingency table and thus congruence of the two classifications.

	5-cluster solution	**3-cluster solution**	**2-cluster solution**
Taxa	0.478 (p < 0.0001)	0.576 (p < 0.0001)	0.789 (p < 0.0001)
Potential invader types	0.584 (p < 0.0001)	0.598 (p < 0.0001)	0.743 (p < 0.0001)

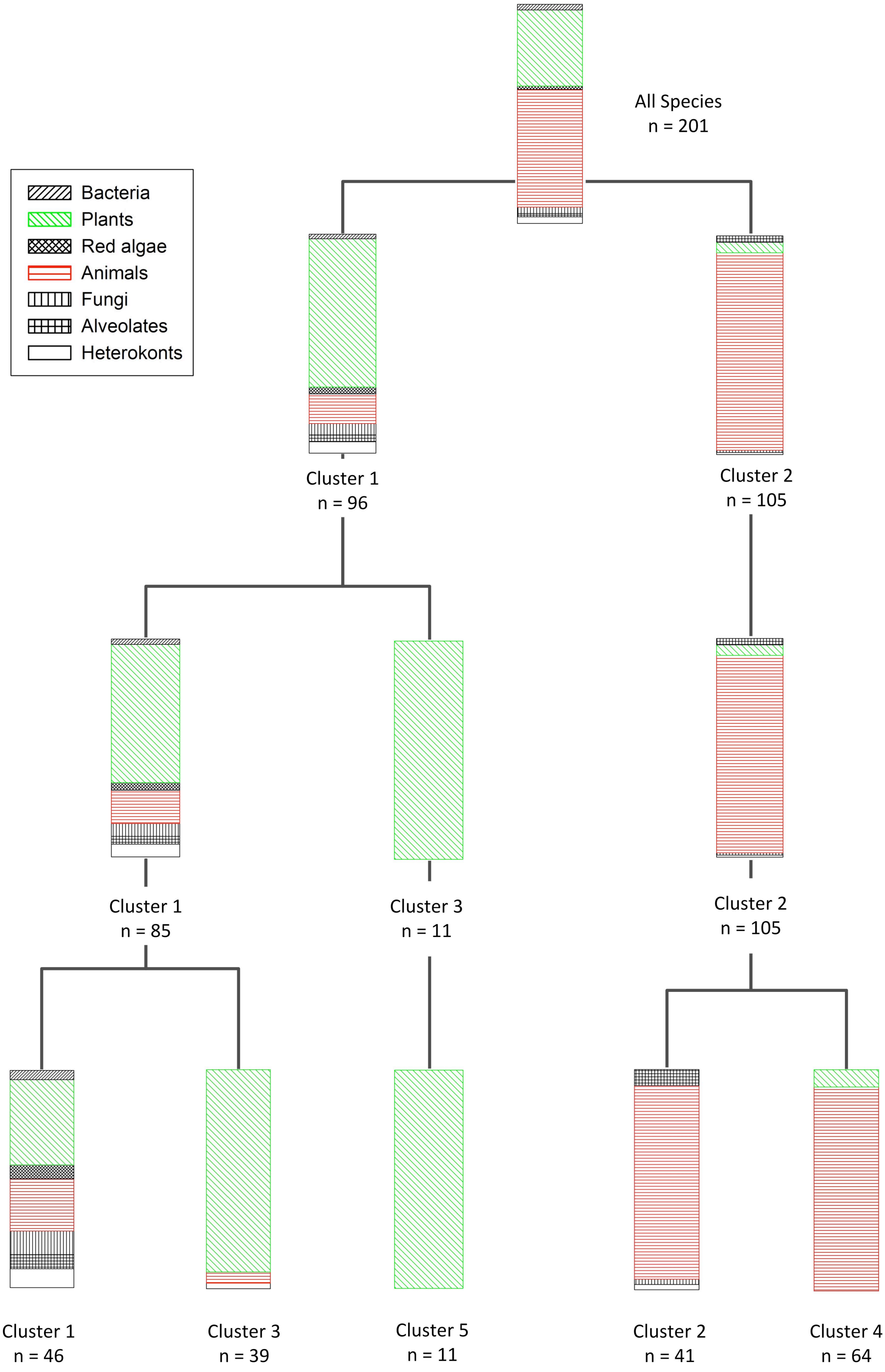

Figure 3.2 – Results of cluster analyses depicted as a schematic dendrogram. 201 invasive species have been clustered according to similarity in invasion traits. For the three best cluster solutions, size and taxonomic composition of statistical clusters are shown: 2-cluster solution in the second row, 3-cluster solution in the third row, and 5-cluster solution in the fourth row. Exact values are provided in Appendix Tables A3.3–A3.5.

Discussion

Species from different taxonomic groups show similar combinations of invasion traits

We hypothesized that species of different taxonomic groups show similar combinations of invasion traits. This would be confirmed if clusters of species with similar invasion traits contain species of different taxonomic groups. All in all, our results support this notion. In the 5-cluster solution, Cluster 1 contains species from all seven taxa, and the three clusters with species of three or more taxonomic groups (Clusters 1, 2 and 3) contain 60% of all species. All taxonomic groups with a sample size of more than three species in our dataset can be found in more than one cluster. The two largest groups (green plants and animals) are both dispersed across four out of five clusters. These results suggest that species in fact show similar combinations of invasion traits across taxonomic groups. Interestingly, the composition of clusters is also heterogeneous on a smaller taxonomic scale: the 36 animals in Cluster 2, for example, include one starfish, 3 molluscs, 15 arthropods and 17 vertebrates (one lamprey, three fish, 3 amphibians, 3 reptiles, 4 birds and 3 mammals). The 36 green plants in Cluster 3 are comprised of one moss, three ferns, two conifers and 30 angiosperms. Angiosperms are scattered over 4 out of the 5 clusters. Nevertheless, three clusters (2, 3 and 4) are strongly dominated by one taxonomic group, and one cluster (Cluster 5 with 11 species in total) contains exclusively species from one taxonomic group (green plants). In the 3-cluster solution, two clusters are dominated by one taxonomic group, whereas one cluster contains a mix of all seven taxa. In the 2-cluster solution, one cluster is dominated by plants and the other by animals, but still, all taxa represented by more than three species in our dataset are present in both clusters.

Figure 3.1 shows that some invasion traits can be found frequently across different taxa, but a connection between taxonomic affiliation and differences in invasion mechanisms cannot be neglected. For example, ecological differences between animals and plants are mirrored by significant differences in invasion-trait frequencies. On the one hand, thus, there seem to be differences among taxonomic groups in what drives biological invasions, while on the other hand, cluster analysis indicates the existence of important taxon-independent drivers of invasions. Our results call for more cross-taxonomic analyses of invasion traits to disentangle these two categories of drivers. Research on invasion traits has often focused on traits that are only relevant for the focal taxonomic group, e.g. seed weight for plants (Pyšek et al. 2009) or brain mass for animals (Jeschke & Strayer 2006). It would be desirable for future data compilations to also integrate data on traits relevant for multiple taxonomic groups.

Statistical clusters are not congruent with taxonomic groups: Do trait combinations reflect certain invader types?

Hierarchical cluster analysis grouped together species with similar combinations of invasion traits, and our analyses show that the resulting clusters are similar to, but not congruent with taxonomic groups. Each cluster is characterized by a complex combination of invasion traits (Appendix Table A3.1). In the following, our approach to the interpretation of the clusters is to specify *post-hoc* hypothetical invader types characterised by a defined combination of traits, and to analyse how good these hypothetical invader types match the clusters.

It has previously been shown for a number of taxonomic groups that during different steps of the invasion process, different species characteristics can be useful (Kolar & Lodge 2001; Cassey et al. 2004; Jeschke & Strayer 2006; Dehnen-Schmutz et al. 2007; Dawson et al. 2009; but see Ribeiro et al. 2008). It is also well known that the promoting influence of humans on species invasions has to be considered (e.g., Hulme 2009). Thus, species having traits helpful during every single step of the invasion process, and which in addition may even be promoted by humans, are supposedly very successful invasive species. Nevertheless, invasion success can also be achieved with only a subset of these helpful traits: for instance, if due to the contingencies inherent to invasion processes particular traits are not necessary to advance in the invasion process, a species can be successful without these traits (Heger & Trepl 2003). We suggest that invasion processes differ with regards to which of the invasion steps (transport, escape, establishment and spread) is the most challenging one from the viewpoint of the species, also depending on the introduction pathway and the ecosystem where it is introduced. Accordingly, we suggest that invasive species can be classified into invader types, each having traits especially suitable to overcome one of the invasion steps.

In a preliminary attempt to further explore this idea, we conceived five hypothetical invader types *post hoc* (Table 3.4), four of them characterized by a combination of traits that help species to advance during specific invasion stages (transport, escape, establishment and spread), and one characterized by human promotion. Species in our dataset were assigned to one of the invader types when they matched the relevant trait combinations more than 50%. This method was applied to 142 species, although 59 species could not be assigned to a specific invader type because they either did not match any of the types (18 species) or qualified equally for multiple types (41 species). Twenty-five species were assigned to the invader type “drifters”, 23 to the type “fugitives”, 30 to “establishers”, 40 to “spreaders” and 24 to the invader type “promoted”.

Table 3.4 – Characterisation of five hypothetical invader types, using contrasting combinations of invasion traits. Invader types 1–4 include traits that help species to advance during the four stages of the invasion process; invader type 5 includes traits that indicate promotion by humans. For a more detailed description of the invasion traits, see Table 1. Dots mark empty fields.

	Transport				Release		Establishment					Spread	
	Intentional transport	In IUCN Red List	Transport as diaspore	Seed bank	Intentional release	Release adult	Phenotypic plasticity	One individual can form a population	More than one reproductive phase per year	Fecundity above average	Offspring in first year	Intentional spread	Spread as active mobile organism
1 Drifters	No	No	Yes	Yes	.	.	.	.	.	.	.	.	.
2 Fugitives	.	.	.	.	No	Yes	.	.	.	.	.	.	.
3 Establishers	.	.	.	.	.	.	Yes	Yes	Yes	Yes	Yes	.	.
4 Spreaders	.	.	.	.	.	.	.	.	.	.	.	No	Yes
5 Promoted	Yes	.	.	.	Yes	.	.	.	.	.	.	Yes	.

Figure 3.3 shows the frequencies of the hypothetical invader types for each cluster. Except for the "establishers", each invader type has its main occurrence (≥ 60%) in just one cluster (Appendix Table A3.6). Calculating the match between statistical clusters and the preliminary hypothetical invader types using Cramér's V, we observed a better match between clusters and invader types than between clusters and taxonomic groups for the 5- and the 3-cluster solution (Table 3.3). Note that this comparison is conservative, as the category "no assignment" was included as one of the hypothetical invader types. The significant association of the clusters with the hypothetical invader types indicates that the latter reflect some of those similarities of invasion traits among species that lead to their clustering. The trait combinations we found to cluster together are not exactly those trait combinations we suggested to be especially useful during specific invasion stages, or the promotion of the species through human actions (i.e. Cramér's V for the comparison of clusters and hypothetical invader types is not 1). But as indicated by the high values of Cramér's V, the hypothetical invader types explain the clusters at least as good as the taxonomic groups do. This indicates that distantly related invasive species do not only share invasion traits, but that moreover, these shared invasion traits are linked to specific properties of the invasion process.

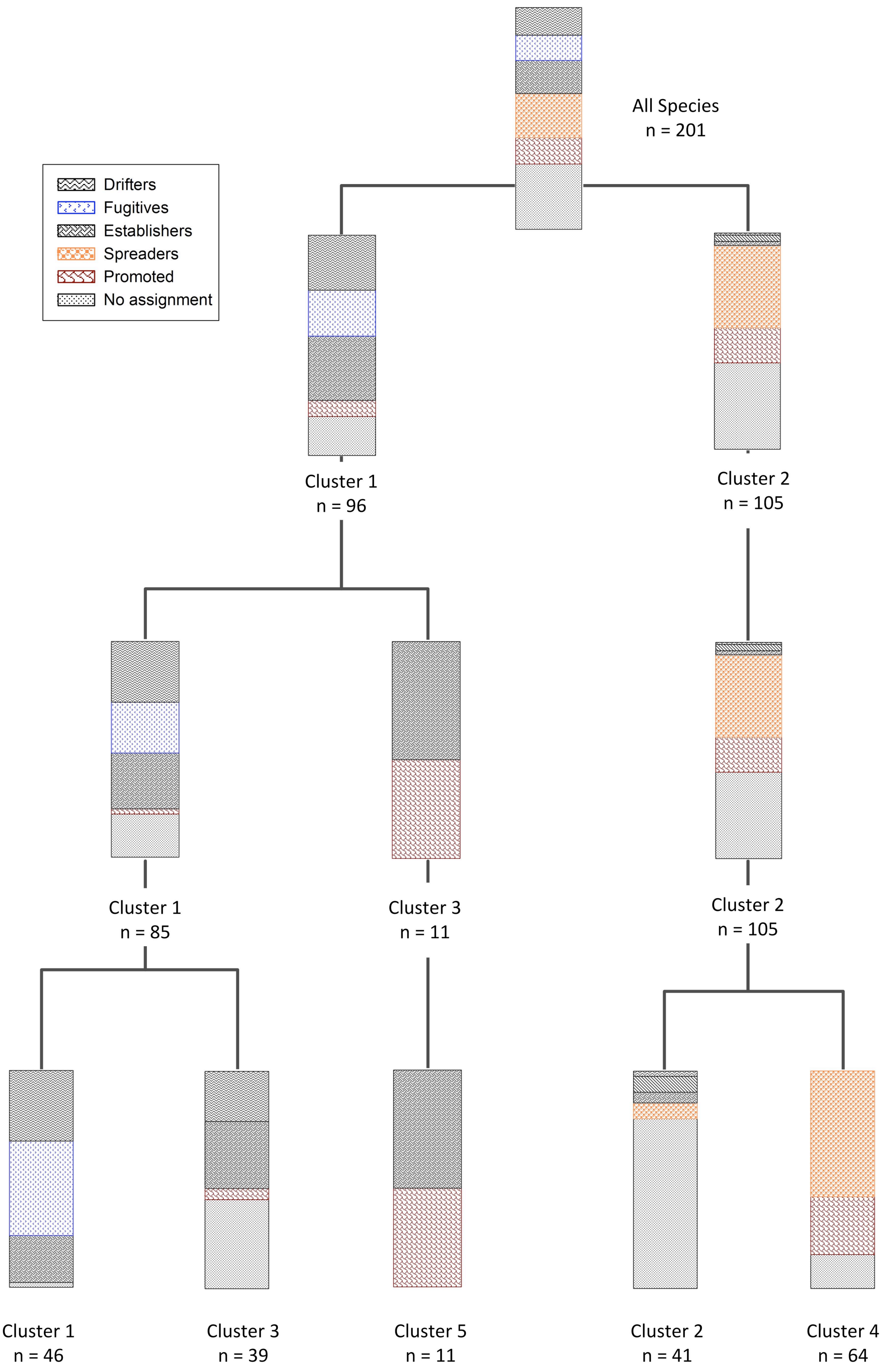

Figure 3.3 – Contributions of hypothetical invader types to clusters. For each cluster given in Fig. 2 the per cent frequencies of species corresponding to one of five hypothetical invader types is shown: 2-cluster solution in the second row, 3-cluster solution in the third row, and 5-cluster solution in the fourth row. Exact values are provided in Appendix Table A3.6–A3.8.

Conclusion

Our analysis of 13 “invasion traits” in 201 invasive species indicates that the same mechanisms might drive biological invasions across taxa. However, this study only represents a first step as (i) our dataset comprises only a small (and taxonomically unbalanced) subset of invasive species, (ii) we did not include a comparison with non-invasive species, and (iii) we assessed the “invasion traits” qualitatively rather than quantitatively. Nevertheless, this study delivers some important insights. Our results suggest the existence of recurring combinations of invasion traits (invader types), which reflect different possibilities to become a successful invader. A promising line of future research could be to identify syndromes of invasion situations that can be overcome by such specific combinations of invasion traits, independently of taxonomic affiliation. Such research focusing on combinations of invasion traits appears to have more potential than continuing the rather fruitless search for single invasion traits to explain the invasion success of all invaders.

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Chapter 4

The role of eco-evolutionary experience in invasion success

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Abstract

Invasion ecology has made considerable progress in identifying specific mechanisms that potentially determine success and failure of biological invasions. Increasingly, efforts are being made to interrelate or even synthesize the growing number of hypotheses in order to gain a more comprehensive and integrative understanding of invasions. We argue that adopting an eco-evolutionary perspective on invasions is a promising approach to achieve such integration. It emphasizes the evolutionary antecedents of invasions, i.e. the species' evolutionary legacy and its role in shaping novel biotic interactions that arise due to invasions. We present a conceptual framework consisting of five hypothetical scenarios about the influence of so-called 'eco-evolutionary experience' in resident native and invading non-native species on invasion success, depending on the type of ecological interaction (predation, competition, mutualism, and commensalism). We show that several major ecological invasion hypotheses, including 'enemy release', 'EICA', 'novel weapons', 'naïve prey', 'new associations', 'missed mutualisms' and 'Darwin's naturalization hypothesis' can be integrated into this framework by uncovering their shared implicit reference to the concept of eco-evolutionary experience. We draft a routine for the assessment of eco-evolutionary experience in native and non-native species using a food web-based example and propose two indices (xp_{Focal} index and $xp_{Residents}$ index) for the actual quantification of eco-evolutionary experience. Our study emphasizes the explanatory potential of an eco-evolutionary perspective on biological invasions.

Keywords: alien species, ecological novelty, ecological similarity, introduced species, invasibility, invasiveness, naïveté, non-indigenous species

Making the case for an eco-evolutionary perspective on biological invasions

A large number of hypotheses about the mechanisms that determine the success or failure of biological invasions have been proposed (reviews in Inderjit et al. 2005; Hufbauer & Torchin 2007; Catford et al. 2009; Jeschke et al. 2012a). However, most of these hypotheses are restricted to specific processes (e.g. enemy release hypothesis, Keane & Crawley 2002, or novel weapons hypothesis, Callaway & Aschehoug 2000) and do not explain variation in invasion success on a more inclusive level. Thus, despite considerable progress in invasion ecology, the search for a more comprehensive and integrative understanding of biological invasions is still on-going (Davis 2009; Richardson 2011; Heger et al. 2013). Accordingly, increasing efforts are being made to interconnect or even synthesize the growing number of hypotheses and concepts (e.g. Catford et al. 2009; Blackburn et al. 2011; Gurevitch et al. 2011).

With this conceptual paper we aim at contributing to this important development. We suggest that adopting an eco-evolutionary perspective on invasions is a promising approach to achieve a broader conceptual synthesis in invasion ecology (cf. Chapter 1). Scientific awareness of evolutionary aspects in biological invasions has increased in the last decade (Sax & Brown 2000; Sakai et al. 2001; Hänfling & Kollmann 2002; Lee 2002; Sax et al. 2005, 2007; Facon et al. 2006; Kondoh 2006; Hufbauer & Torchin 2007). But the focus of most studies in this field lies particularly on the evolutionary *consequences* of invasions, i.e. the evolutionary response of species to invasions (see e.g. Cox 2004; Strayer et al. 2006; Carlsson et al. 2009; Orians & Ward 2010). Our focus, on the contrary, lies on elucidating the role that evolutionary *antecedents* may play for invasion success (see e.g. Cox & Lima 2006; Kondoh 2006; Mitchell et al. 2006; Sih et al. 2010; Thuiller et al. 2010). It is a general presumption in ecology that biotic interactions are influenced by the evolutionary legacy of the interacting species (Pianka 2000). During invasions, species reach areas where they are not native and interact with species that they have not evolved with (Heger & Trepl 2003; Cox 2004). Such settings lead to 'novelty' in biotic interactions in invaded areas, which may likely be decisive for the success or failure of invasions. In the following, we show on theoretical grounds that adopting an eco-evolutionary perspective on invasions (i) offers the possibility to consider the roles that both native *and* non-native species play in invasion success or failure, i.e. species invasiveness *and* community invasibility; (ii) allows an integrative and at the same time differentiated treatment of invasions that affect different types of ecological interaction (competition, predation, mutualism, commensalism); and (iii) has the potential to link so far apparently disconnected major invasion hypotheses in one common framework.

A framework for explaining variation in invasion success based on the concept of eco-evolutionary experience

During evolution, species adapt to biotic interactions in their native environment. They thereby accumulate what we propose to term ‘eco-evolutionary experience’ in dealing with these interactions. We hypothesize that this inherited experience – possibly complemented by experience acquired during an individual’s lifetime (e.g. predators getting better at capturing prey during successive encounters) – ultimately determines the species’ proficiency to survive and prosper within new ecological contexts, as for example when invasions take place. For an introduced species, the biotic community in its exotic range may differ fundamentally from the one in its native environment. Biotic interactions that evolutionarily shaped the introduced species in its native environment may become interrupted (Mitchell et al. 2006). At the same time, the resident organisms in the exotic range are confronted with a species they have never met before. For instance, native prey species may not be familiar with the hunting strategy of a non-native predator, and at the same time the latter may be unprepared for having to compete for prey with other (resident) predators. Thus, as a consequence of biological invasions, biotic interactions arise that may be novel to both introduced and native species. Both sides then depend on their inherited eco-evolutionary experience to react appropriately to the new situation. Plasticity (e.g. in behaviour or morphology) resulting from adaptation to unstable environmental conditions in previous times may play an important role here (Nussey et al. 2005; Richards et al. 2006; Sol et al. 2008, Engel et al. 2011). The degree of eco-evolutionary experience available on either side may thus also be interpreted in terms of the introduced species’ invasiveness and the native community’s invasibility, respectively.

Figure 4.1 illustrates a conceptual framework to explain variation in invasion success based on the concept of eco-evolutionary experience. The framework consists of five hypothetical scenarios, corresponding to five major types of ecological interaction: the introduced species acting as prey (Fig. 4.1A), predator (including herbivores, parasites, and parasitoids; Fig. 4.1B), competitor (Fig. 4.1C), mutualist (Fig. 4.1D) or commensal (Fig. 4.1E). The graphs presented in each scenario are speculative, their exact shape still to be substantiated with empirical data in future studies. However, the scenarios formulate our generalized hypotheses about the relationship between the eco-evolutionary experience in the interacting introduced and native species on the one hand and the relative probability of the respective invasion to succeed on the other: For predator-prey and competitive interactions, the probability of a successful invasion is likely to be higher with a low degree of applicable eco-evolutionary experience in the native species and a high degree in the non-native species (Fig. 4.1A, B, C). Widely known examples where these circumstances likely apply include the invasion of purple loosestrife (*Lythrum* *salicaria*) in North America where it lacks herbivorous enemies that feed on it in its native range (Blossey & Nötzold 1995, Fig. 4.1A), mammalian invasions on oceanic islands causing the extinction of naïve local avifauna (Blackburn et al. 2004, Fig. 4.1B), and introduced diffuse knapweed (*Centaurea diffusa*) having allelopathic effects on competing resident native grass species in North America (Callaway & Aschehoug 2000, Fig. 4.1C). In mutualistic interactions, a high degree of experience in both the non-native and the native mutualist is likely to be advantageous for invasion success (Fig. 4.1D). This may be the case e.g. for yellow crazy ants (*Anoplolepis gracilipes*) associating with honeydew-producing hemipteran insects on Christmas Island (O'Dowd et al. 2003; see also Styrsky & Eubanks 2007). In commensal interactions, eco-evolutionary experience may only have an influence on invasion success if the non-native species is the benefiting commensal (Fig. 4.1E). In such cases, a higher non-native experience for taking advantage of the native host should be favourable, while the experience level of native hosts is irrelevant, since *per definitionem* the host is not affected by the commensal. This may be the case e.g. for human affiliates like house sparrows (*Passer domesticus*) that successfully invade new areas by being able to reach high population densities in human settlements (cf. Jeschke & Strayer 2006). In the case of a native commensal (not shown in Fig. 4.1), experience on neither side should have an effect on invasion success, because the non-native host remains unaffected, and the facilitation of the native commensal does not necessarily bear on invasion success.

Notably, several major invasion hypotheses can be integrated into this framework. From an eco-evolutionary viewpoint, it becomes apparent that they actually share an implicit reference to the role of evolutionary legacy in invasion success. This includes such often-cited hypotheses as 'enemy release' (Keane & Crawley 2002), 'evolution of increased competitive ability' (EICA; Blossey & Nötzold 1995), 'novel weapons' (Callaway & Aschehoug 2000) and 'Darwin's naturalization hypothesis' (Daehler 2001b; Procheş et al. 2008; Thuiller et al. 2010). Further examples are the hypotheses of 'new associations' (Hokkanen & Pimentel 1989; Mitchell et al. 2006), 'naïve prey' (Cox & Lima 2006), 'missed mutualisms' (Alpert 2006), 'mutualist facilitation' (Richardson et al. 2000), and 'human commensals and imperialism' (Jeschke & Strayer 2006). Most of the invasion examples given in the previous paragraph directly apply to one of these hypotheses. Appendix Panel A4.1 provides examples of how the central reasoning of the hypotheses can be related to the concept of eco-evolutionary experience, which is visualized correspondingly in Fig. 4.1 by shaded ovals. Despite this implicit relatedness, they are usually considered separately, sometimes even as mutually exclusive. Only few studies consider potential interrelations between the hypotheses (but see Inderjit et al. 2005; Hufbauer & Torchin 2007; Sih et al. 2010; Gurevitch et al. 2011).

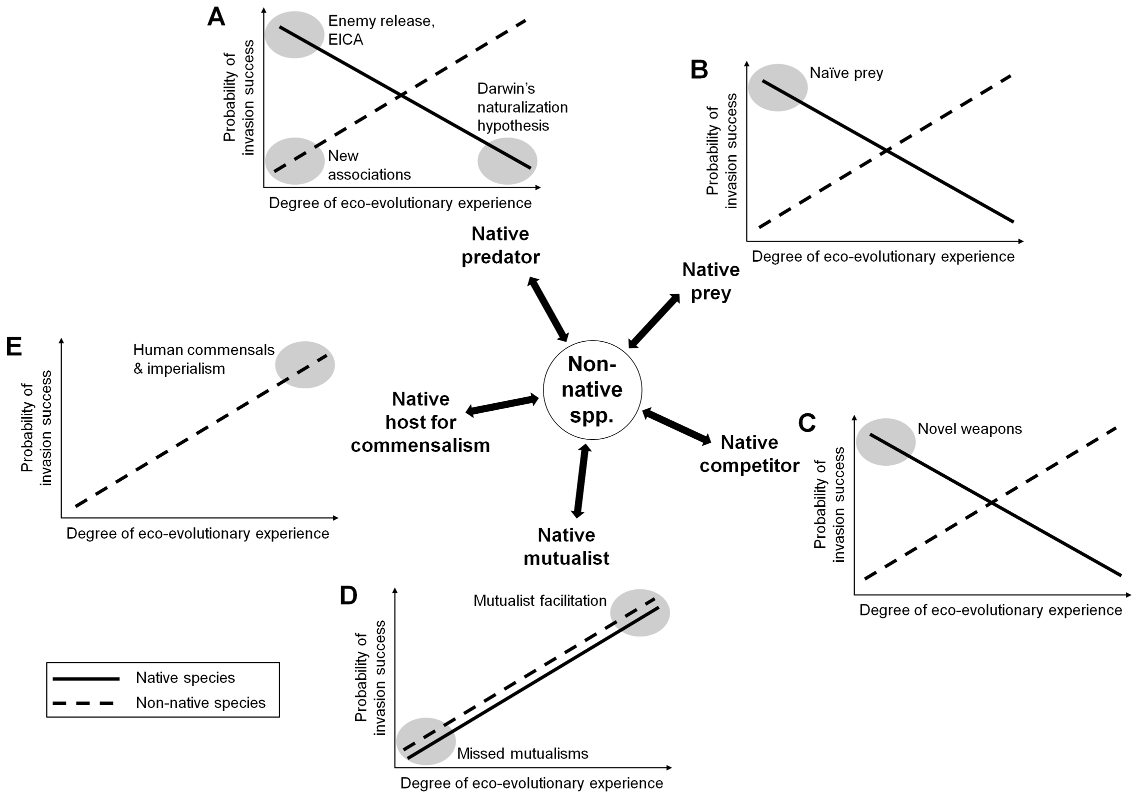

Figure 4.1 – Framework of five hypothetical scenarios about the influence of eco-evolutionary experience in the non-native (dashed line) and native species (solid line) on the relative probability of invasion success, according to the type of ecological interaction (A/B: predator–prey, C: competition, D: mutualism, E: commensalism). In general, lower native experience (except in mutualistic interactions) and higher non-native experience is likely to be advantageous for invasion success. Shaded ovals exemplarily indicate parts of the framework covered by major hypotheses in invasion ecology that implicitly share a reference to the importance of evolutionary legacy for invasion success (see main text and Appendix Panel A4.1 for details and references).

By adopting an explicit eco-evolutionary perspective, the framework provides a basis for interrelating the hypotheses (as defined in Appendix Panel A4.1) and conclusions based on them, but it also highlights their shortcomings: the hypotheses of enemy release, EICA, Darwin's naturalization hypothesis, naïve prey and novel weapons consider the degree of experience only on the native species' side (Appendix Panel A4.1: *a*, *b*, *d*, *e*, *f*), while new associations, missed mutualisms, and the human commensals and imperialism hypothesis focus on the non-natives' experience (Appendix Panel A4.1: *c*, *g, i*). Only the mutualist facilitation hypothesis at least implicitly considers both sides (Appendix Panel A4.1: *h*). Thus, these invasion hypotheses emphasize either the invasibility of native communities or the invasiveness of non-native species and neglect that the outcome of an invasion is probably influenced by the degree of applicable eco-evolutionary experience on both interacting sides (cf. Sih et al. 2010). The framework presented here provides a basis for considering both sides simultaneously in order to achieve a more comprehensive understanding of variation in invasion success.

Quantifying eco-evolutionary experience: a food web-based example

Clearly, in connection with the framework presented here, practicable approaches to actually quantify eco-evolutionary experience are needed. Such approaches can build on the general assumption that more of the eco-evolutionary experience in species (native or introduced) will be applicable to a new interaction setting if that setting is ecologically similar to previous interactions. In other words, the degree of ecological similarity between new and previous interaction settings may be taken as a proxy for the degree of applicable eco-evolutionary experience in native and non-native species.

Ecological similarity of species is often assumed to be positively correlated with the taxonomic or phylogenetic relatedness between them (e.g. Agrawal & Kotanen 2003; Ricciardi & Atkinson 2004; Cavender-Bares et al. 2004; Strauss et al. 2006; Diez et al. 2008; Procheş et al. 2008). Although convenient, this approach has important limitations. In particular, similarity – be it in respect to morphological, behavioural, or ecological traits – does not necessarily correlate with relatedness (Losos 2008; Thuiller et al. 2010). This becomes most evident in cases of convergent evolution where relatively unrelated species show a high degree of similarity (see e.g. Futuyma 2005). Thus, taxonomic classification and phylogenetic relatedness of species are unreliable indicators for their ecological similarity and therefore also for the similarity of biotic interactions of these species before and after an invasion event.

Our approach for quantifying eco-evolutionary experience of introduced and native species assesses the ecological similarity of the ecological *interaction settings* these species are part of before and after the invasion. Such comparisons can be done for any ecological network, e.g. plant-pollinator networks, seed-dispersal interactions, host–parasite systems or food webs. We here present an example for a quantification routine based on food webs (summarized in Appendix Panel A4.2), which covers predator-prey, competitive, and indirect mutualistic interactions (e.g. a predator and a primary producer indirectly benefitting from each other as the predator feeds on the herbivore that consumes the primary producer). We compare the food webs of the original 'source' area and a new 'target' area of the introduced species (hereafter called the 'focal species') regarding the occurrence and occupancy (in terms of number of species) of ecological guilds. Note that the term 'guild' as we use it here is not restricted to referring exclusively to "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). We use a broader definition, where guilds can also be, for instance, groups of species that share the same predators or anti-predator strategies. The exact definition should be chosen based on the particular context of a study. Other ecological groupings (e.g. functional groups or types) can be used instead of guilds as well (for more details on ecological groupings, see e.g. Hawkins & MacMahon 1989; Wilson 1999; Blondel 2003; Blaum et al. 2011).

Eco-evolutionary experience of the introduced focal species

In order to assess the experience of the focal species after its introduction to a target area, we compare the interactions in the food webs of these two areas from the perspective of the focal species (steps 1 to 4 in Appendix Panel A4.2). Both food webs will be composed of different trophic levels, each of which may contain species of different ecological guilds. For simplicity, we restrict our analysis to direct interactions and single-step indirect interactions (i.e. including one intermediate species as for example in exploitative competition) of the focal species with resident species (step 1 in Appendix Panel A4.2). These interactions can be assumed to have the most immediate consequences for the invasion success of the focal species. Separately for each type of interaction (i.e. the focal species acting as prey, predator, competitor or indirect mutualist), and for both the source and target area, the respective interaction partners are classified into their ecological guilds and the members of each guild are counted (steps 2 and 3 in Appendix Panel A4.2). In this way, we obtain datasets for each type of interaction, with species numbers per guild in both the source and target area (see exemplary Table A in Appendix Panel A4.2).

To actually calculate the eco-evolutionary experience of the focal species (step 4 in Appendix Panel A4.2), we need an index of similarity. The Bray-Curtis similarity index (*sbc*) is often used in ecological studies when comparing the species composition of different samples, e.g. community samples:

$$sbc_{jk} = 1 - \frac{\sum_{i=1}^{n} \left| N_{ij} - N_{ik} \right|}{\sum_{i=1}^{n} \left(N_{ij} + N_{ik} \right)} \quad , \qquad \text{(Eq. 1)}$$

where n is the total number of species considered, and N_{ij} and N_{ik} represent the number of individuals of species i in the samples j and k, respectively. Absolute abundance differences in all species are summed up in the numerator and standardized by the total number of individuals in all species from both samples in the denominator. However, while this index provides some grasp on the absolute difference between the samples, it does not consider the direction of change in numbers. But this is important from an eco-evolutionary perspective in the invasion context: for the focal species, it is decisive whether it encounters more or fewer interaction partners from particular guilds in the target area than in the source area. We thus adapted the Bray-Curtis index to account for this specific need. The new index is an index of experience rather than just similarity. We thus call it 'xp_{Focal} index':

$$xp_{Focal} = 1 - \frac{\sum_{i=1}^{n} \max(0; N_{iT} - N_{iS})}{\sum_{i=1}^{n} \left(N_{iT} + N_{iS}\right)} \quad , \qquad \text{(Eq. 2)}$$

where n is the total number of guilds considered, and N_{iS} and N_{iT} represent the number of species in guild i in the source (S) and target (T) area, respectively, that interact with the focal species. Values of xp_{Focal} range between 0 (no applicable experience in the target area) to 1 (maximum applicable experience). By considering not only the presence or absence of guilds but also how numbers of species occupying these guilds differ between source and target area, the xp_{Focal} index accounts for trait differences on the guild level as well as species level. In contrast to the Bray-Curtis index, however, the xp_{Focal} index only considers those differences in the number of guild members where $N_{iS}<N_{iT}$ by introducing the 'max' term in the numerator. From the perspective of the focal species, these are the relevant differences between the source and target area, because a larger number of interaction partners of a guild in the target area compared to the source area implies a reduced (or even absent) eco-evolutionary experience of the focal species in the new interaction setting.

This is obvious in cases where the focal species meets interaction partners of a guild in the target area that was entirely absent in the source area (i.e. when $N_{iS}=0$ and $N_{iT}>0$), being then unable to count on applicable eco-evolutionary experience for these new interactions. But reduced experience is also expected when the focal species interacts with species even of a familiar guild if they occur in larger numbers in the target area as compared to the source area ($N_{iS}<N_{iT}$). This is reasonable to assume because also species of the same guild differ from each other. Although these differences are relatively small (otherwise the species would be classified into different guilds), they can still be relevant for the focal species. Thus, the more interacting species exist in the target area in comparison to the source area (i.e. the larger N_{iT} is in relation to N_{iS}), the higher is the probability that the focal species will have to respond to unknown ecological traits, and the lower is its experience in the target area. By contrast, the probability of having to respond to unfamiliar ecological traits of species of a particular guild is low when the focal species has already interacted with a larger number of species from that guild in the source area than in the

target area. Our model makes the simplifying assumption of a threshold where the focal species has the maximum eco-evolutionary experience with the new interaction setting ($xp_{Focal}=1$) when it has interacted with at least as many species in each guild in the source area as it encounters in the target area (i.e. if $N_{iS} \geq N_{iT}$). In future studies, alternative formulations without such a threshold may be explored.

To a certain degree, the xp_{Focal} index allows reduced experience with members of a particular guild to be compensated by experience in the same type of interaction with species of other guilds. For instance, in predator–prey interactions the focal species may not be familiar with predators of a particular guild in the target area, but may also not be entirely naïve because of having evolved in its source area in the presence of predators at least from other guilds. However, under the assumptions of the xp_{Focal} index, such 'unspecific' experience with a type of interaction (in this example 'predation') will not completely offset missing experience with a particular guild.

Eco-evolutionary experience of the resident species community

In order to assess the experience of the resident species community facing a new introduced species, we first determine the focal species' guilds for each type of interaction, i.e. when it may act either as a predator, prey, competitor or indirect mutualist. We then count the number of resident species that are already present in these specific guilds in the target area (see step 5 and exemplary Table B in Appendix Panel A4.2). Finally, by calculating the following '$xp_{Residents}$ index' separately for each type of interaction (step 6 in Appendix Panel A4.2), we can assess, in a first approximation, how much experience native species have with the focal species:

$$xp_{Residents} = 1 - \frac{1}{N_{i^*T} + 1} \quad , \qquad \text{(Eq. 3)}$$

where N_{i^*T} is the number of resident species in the same guild (i^*) as the focal species in the respective type of interaction. The fraction in this index provides an estimate how ecologically 'novel' the focal species is for the resident community. The maximum novelty of the focal species (i.e. the least experience in resident species) can be expected if no resident species are present in the focal species' guild before the invasion event. The novelty of the focal species gradually decreases with an increasing number of resident species that are in the same guild as the focal species. Subtracting the fraction from 1, we obtain the eco-evolutionary experience of the resident species community ($xp_{Residents}$), with values ranging again between 0 (no applicable experience of resident species with the focal species) to 1 (maximum applicable experience).

Having thus calculated both the eco-evolutionary experience of the focal species (xp_{Focal}) and the experience of the resident species community ($xp_{Residents}$) for different types of interaction, we can return to the framework in Fig. 4.1 and estimate the probability of the invasion to succeed.

Discussion

In the previous sections, we introduced a framework that – by adopting an eco-evolutionary perspective – integrates so far unrelated approaches for explaining biological invasions, and we drafted a routine to quantify eco-evolutionary experience, which is the key variable in this framework. It has to be emphasized again that the framework is of conceptual nature. For instance, the assumed relationship between eco-evolutionary experience and invasion success has to be substantiated with empirical data beyond the hypothetical graphs presented in Fig. 4.1. Furthermore, the quantification routine makes several simplifying assumptions that have to be kept in mind for an appropriate interpretation:

- Species are adapted to virtually all of their biotic interactions in the source area, which constitutes the inherited eco-evolutionary experience that may matter in ecologically similar communities in the target area. In reality, species are not necessarily adapted to all interactions, e.g. due to weak selection pressure, evolutionary trade-offs, or gene flow. Furthermore, we assume there is no significant intraspecific variation in species traits, e.g. among different populations of the same species.

- Adaptation has no costs. Consider, for example, two focal species that face a single predator species of guild R3 from the example in Appendix Panel A4.2 in their respective target areas. For both of them, we would calculate $xp_{Focal}=1$ if during their evolution in the source area they adapted to at least one predator species of the guild R3. The same xp value would be computed even if one of the focal species had adapted to additional predator species. In reality, such ‘over-adaptation’ would probably have generated costs, which could imply disadvantages when compared to the other focal species, but in our model it does not translate into a lower probability of invasion success.

- All interactions are assumed to be equal in strength and frequency. For instance, no distinction is made between generalists and specialists, or whether the focal species interacts in the target area with exactly the same species as in the source area or just with a member of the same guild.

- There is no amplifying effect within interaction types: an interaction partner is counted only once in each type of interaction, even if it maintains more than one ‘connection’ with the focal species within that interaction type (e.g. when competing with the focal species for several prey species).

- As mentioned above, only a subset of all interactions in the studied food webs is included in the analysis, i.e. direct and single-step indirect interactions, and the number of interacting partners in each guild depends on the particular guild definition chosen.

On a side note, we focused in this paper on novel *biotic* interactions that may influence invasion success in order to demonstrate the usefulness of an eco-evolutionary perspective in invasion research. This is not to argue, of course, against the substantial effect that other factors may have on invasion success as well. The significant influence of abiotic conditions has been indicated, for instance, by studies on the effect of climate change (Hellmann et al. 2008; Walther et al. 2009; Engel et al. 2011). Also, Mitchell et al. (2006, p. 734) correctly pointed out that biotic interactions may be influenced “not only directly through the gain and loss of enemies, mutualists and competitors, but also indirectly by putting interactions with the same species in a different environmental context“. Furthermore, among many other factors, the roles of propagule pressure or of intrinsic factors such as (lack of) genetic variability and reproductive systems have to be considered in this context. We believe that the indices proposed here (xp_{Focal} and $xp_{Residents}$) constitute an important first step towards an efficient quantitative estimate of the influence of species’ evolutionary legacy on the success of biological invasions. A particular strength of this approach lies in its high flexibility: it allows considering not only food webs but also other ecological networks; different kinds of ecological groupings (ecological guilds, functional groups etc.) can be used; and it is applicable to all living organisms across taxonomic boundaries (e.g. plants and animals alike). From an applied perspective, the further development of the framework and quantification routine to include less simplifying assumptions is certainly highly desirable and a stimulating research perspective. An important next step is to actually test the usefulness of our framework and the quantification routine for empirical case studies. Also, it should be investigated how the various *xp* values computed for the different types of interaction can best be integrated to provide an *overall* estimate of invasion probability. This could, for instance, be done by reducing complexity (and potential inconsistencies) considering only the most important type(s) of interaction in the respective case study, or it could comprise the development of a single, combined *xp* value.

Conclusion

An integrative and comprehensive conceptual treatment of conclusions derived from findings in both ecological *and* evolutionary research is still hard to find in invasion ecology. However, as we have outlined above, such an eco-evolutionary perspective would not merely add parenthetical historical information but would increase our potential to uncover invasion patterns. Our framework provides the means for interrelating seemingly isolated ecological invasion hypotheses by identifying implicit eco-evolutionary assumptions (Fig. 4.1; Appendix Panel A4.1). The framework thus helps to synthesize the conclusions drawn from these hypotheses, providing a stronger basis for a more general understanding of invasion mechanisms and reasons for variation in invasion success. It ties in with the idea of a ‘hierarchy of hypotheses’ (Jeschke et al. 2012a; Heger et al. 2013), where overarching conceptual ideas in invasion ecology (e.g. the concept of eco-evolutionary experience) branch into more precise and testable hypotheses at lower levels (e.g. enemy release, EICA, novel weapons etc.). Such a hierarchy helps to systematically organize the specific predictions of the large number of individual hypotheses and the evidence accumulated for or against them (Jeschke et al. 2012a). This in turn allows evaluating the more general predictions represented by the complete branch of an overarching idea and to identify more fundamental patterns in biological invasions.

The framework generates new, although still very general conceptions on how invasion success depends on eco-evolutionary experience and emphasizes the importance of considering both interacting sides simultaneously: native and non-native species. It also takes into account that non-native species may take up different ecological roles in the exotic range and allows differentiated conclusions for the major types of ecological interactions that may be affected by the invasion.

We believe that the conceptual insights that can be derived from our framework and the quantification routine can be of significant help to guide future research. Ultimately, this research may lead to effective management measures to prevent the introduction of species that seem particularly ‘risky’ for a specific target area, or to adopt appropriate mitigation or restoration measures.

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Chapter 5

Eco-evolutionary experience in novel species interactions

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Abstract

A better understanding of how ecological novelty influences interactions in new combinations of species is key for predicting interaction outcomes, and can help focus conservation and management efforts on preventing the introduction of novel organisms or species (including invasive species, GMOs, synthetic organisms, resurrected species and emerging pathogens) that seem particularly ‘risky’ for resident species. Here, we consider the implications of different degrees of eco-evolutionary experience of interacting resident and non-resident species, define four qualitative risk categories for estimating the probability of successful establishment and impact of novel species and discuss how the effects of novelty change over time. Focusing then on novel predator–prey interactions, we argue that novelty entails density-dependent advantages for non-resident species, with their largest effects often being at low prey densities. This is illustrated by a comparison of predator functional responses and prey predation risk curves between novel species and ecologically similar resident species, and raises important issues for the conservation of endangered resident prey species.

Keywords: alien species, Anthropocene, ecological novelty, ecological similarity, introduced species, invasibility, invasiveness, management, naïveté, steady-state satiation equation

Introduction

Research on ecological novelty resulting from human action (Kueffer 2014) has strongly intensified recently, focusing on novel organisms (Jeschke et al. 2013), novel species interactions and communities (Williams & Jackson 2007; Lurgi et al. 2012; Pearse & Altermatt 2013; Bezemer et al. 2014; Carthey & Banks 2014) and novel ecosystems (Hobbs et al. 2009, 2013). A better understanding of how ecological novelty (and naïveté) influences interactions in new combinations of species is key for predicting interaction outcomes and finding appropriate measures of prevention and mitigation of negative consequences. Researchers are now asking how similarities and differences in species assemblages (compared between the area of origin of an invasive species and its target area) and varying degrees of functional similarity of resident and non-resident species may affect invasion success (e.g. Facon et al. 2006; Mitchell et al. 2006; Hufbauer & Torchin 2007; Sih et al. 2010). For example, phylogenetic patterns, consumptive and non-consumptive effects, abiotic conditions and behavioural aspects (e.g. prey use of general *vs.* specific cues) have been considered, which may result in novelty advantages or disadvantages (Procheş et al. 2008; Sih et al. 2010; Thuiller et al. 2010; Carthey & Banks 2014). Most existing studies focus on a particular type of ecological interaction, e.g. plant–herbivore (Verhoeven et al. 2009; Harvey et al. 2010; Forister & Wilson 2013; Pearse et al. 2013; Bezemer et al. 2014; Desurmont et al. 2014), predator–prey (Cox & Lima 2006; Kondoh 2006; Sih et al. 2010; Carthey & Banks 2014), plant–pathogen (Parker & Gilbert 2004) or competitive interactions (Procheş et al. 2008). Only few studies examine implications for several interaction types at the same time (Mitchell et al. 2006; Thuiller et al. 2010).

In Chapter 4, we focused on the evolutionary legacy of species and developed a framework for studying variation in invasion success across all major interaction types and interrelating several major invasion hypotheses based on the concept of ‘eco-evolutionary experience’. This concept emphasises that (1) during evolution, species adapt to biotic interactions in their native environment and thereby accumulate eco-evolutionary experience in dealing with these interactions; and (2) this heritable experience may be applicable in new ecological contexts, as for example when species are introduced to non-native environments. Experience is defined here broadly as familiarity not only with particular species but rather with archetypes of interaction partners. An archetype refers to a set of species that occupy a similar ecological niche and show similar morphological and behavioural traits when interacting with other species (see Cox & Lima 2006). Experience can thus also be derived from ‘ecological fitting’ (Agosta 2006) or exaptations (Gould & Vrba 1982). The degree to which a species can actually apply its experience in new ecological contexts depends on the ecological similarity between previous interactions and those in the new contexts, and significantly influences a species' proficiency to persist *vis-à-vis* the new interaction partners (Cox & Lima 2006). The framework formulates general hypotheses about the relationship between eco-evolutionary experience (in both resident and non-resident species; see Box 5.1 regarding terminology) and the relative probability of invasion success. Scenarios therein differentiate between major types of ecological interactions in which the non-resident species may be involved: predation, competition, mutualism and commensalism. For example, in predator–prey or competitive interactions, we expect that the probability of a successful invasion is likely to be high with a low degree of applicable experience in the resident species and a high degree in the non-resident species (Fig. 5.1). Such circumstances may likely apply, for instance, to the invasion of purple loosestrife (*Lythrum salicaria*) in North America where it lacks herbivorous enemies (Blossey & Nötzold 1995), and of diffuse knapweed (*Centaurea diffusa*) having allelopathic effects on competing resident native grass species in North America (Callaway & Aschehoug 2000).

The experience concept can be applied to biological invasions as well as all other interactions that involve non-resident species. This includes genetically modified organisms (GMOs), synthetic organisms, resurrected species, emerging pathogens and range-expanding species (Jeschke et al. 2013; Seddon et al. 2014). The importance of at least some of these species will probably increase in the future when utilisation on a regular basis, e.g. for economic reasons, comes into reach and impacts have to be assessed or mitigated (e.g. Forabosco et al. 2013; Ledford 2013; Oke et al. 2013; Sundström et al. 2014).

This study aims to expand the applied value of the experience concept in relation to conservation and management efforts in communities with novel species interactions (see Box 5.1), i.e. novel species communities. To this end, we define risk categories of establishment and impact based on the degree of experience in resident and non-resident species, examine the temporal dynamics of the experience's influence on the outcome of novel species interactions and strive to deepen our mechanistic understanding of this influence by focusing on predator–prey interactions, particularly predator functional responses.

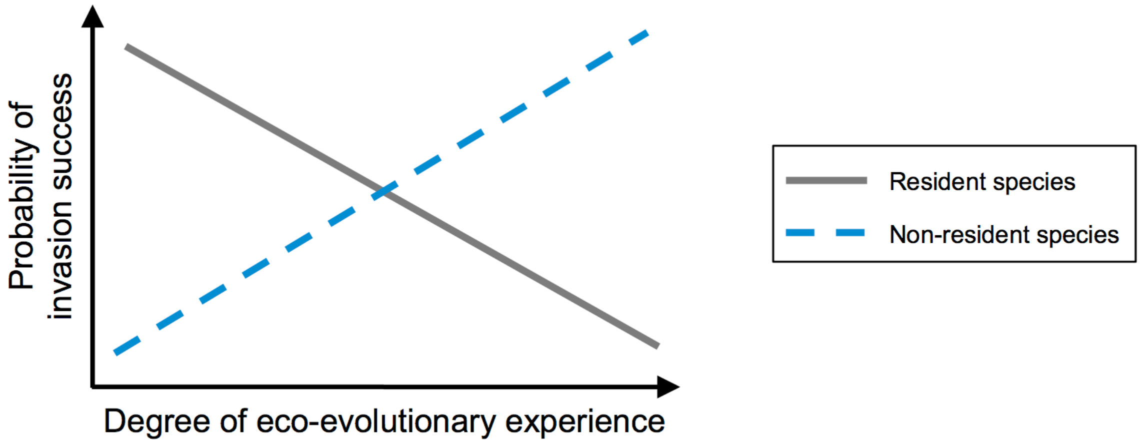


Figure 5.1 – Hypothetical scenario about the influence of eco-evolutionary experience in the resident (solid line) and non-resident species (dashed line) on the relative probability of invasion success in predator–prey and competitive interactions. It is expected that, in general, lower resident experience and higher non-resident experience increases invasion success (cf. Chapter 4).

Risk categorisation of the effects of eco-evolutionary experience

The framework for studying variation in invasion success in relation to eco-evolutionary experience, combined with an approach to actually quantify experience (see Chapter 4), can help focus management efforts on preventing the introduction of species that seem particularly ‘risky’ for the resident biotic community in a specific target area. Novelty in species interactions can stem from the incoming non-resident species (i.e. resident species have low experience with the non-resident species), from the resident species (i.e. the non-resident species is inexperienced with resident species) or from both (i.e. both resident and non-resident species have low experience with each other). Differentiating between these origins of novelty allows us to estimate the risk that the arrival of a particular species may pose for the resident biotic community. Here, we refer to risk primarily in terms of probability of establishment. However, we assume that a higher probability of establishment on average also entails a higher risk of impact. Following the key questions proposed by Jeschke et al. (2014), we define impact as a deleterious (unidirectional) change – with no restriction to particular spatio-temporal scales or organisational levels – that is ecologically or socio-economically significant. Considering the possible combinations of high and low degrees of experience in resident and non-resident species with each other, we can identify four general risk categories regarding establishment probability and impact (Fig. 5.2): two categories cover the extremes, high and low risk, and the two other categories represent intermediate levels of risk.

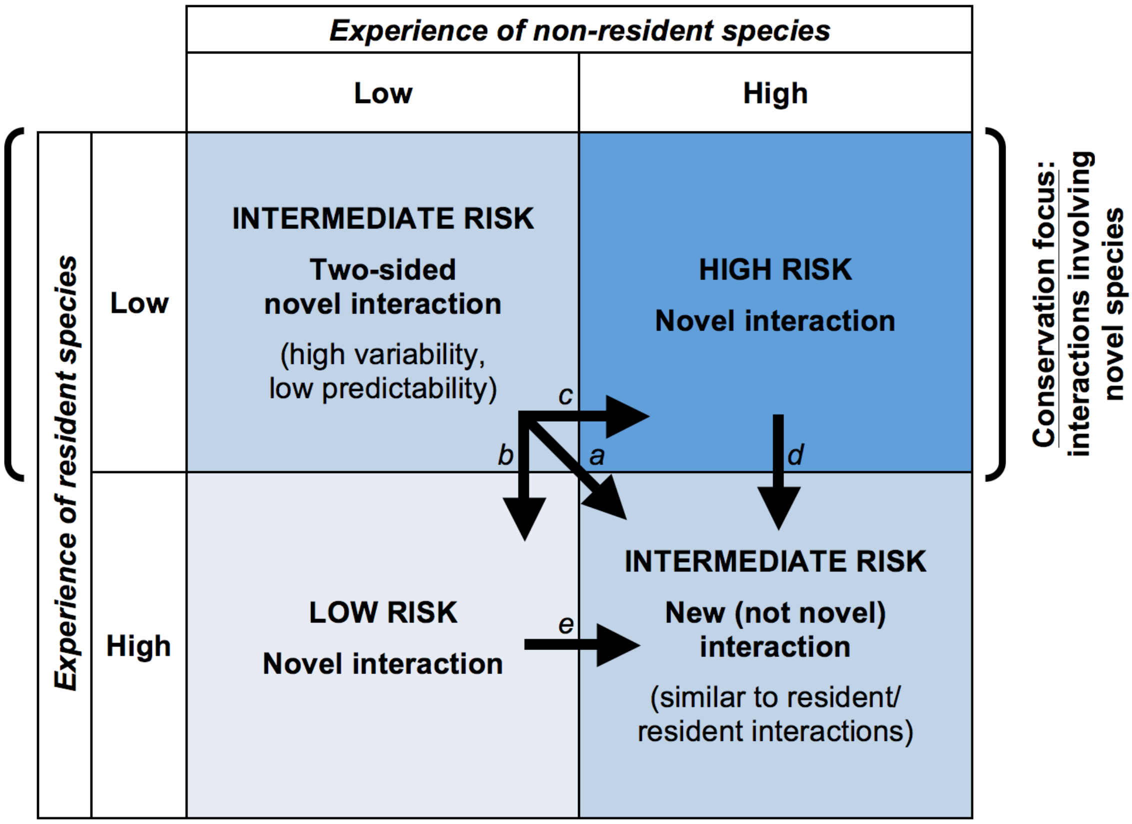


Figure 5.2 – Risk categories of invasion success based on the combination of low and high degrees of eco-evolutionary experience in resident and non-resident species. Arrows *a*–*e* indicate expected transitions between risk categories, with non-resident species expected to become familiar with and to the resident community over time (temporal dynamics). Risk categories of particular interest for conservation and management (two upper cells) are likely to be those that comprise interactions with true 'novel species', i.e. non-resident species that are unfamiliar to their resident interaction partners (see definitions in Box 5.1). For a brief discussion of the proposed differentiation between 'novel' and 'new' interactions, see also Box 5.1.

The highest risk can be expected when the experience of resident species is low and the experience of the non-resident species is high (dark blue area in Fig. 5.2). Such would be the case when a non-resident predator occupies an ecological niche or represents a predator archetype that is novel to resident prey species. For instance, consider the introduction of the Brown tree snake (*Boiga irregularis*) to Guam or of mammalian predators to New Zealand. We know today that these introductions had devastating consequences for native bird and other prey species that had evolved in the absence of such enemies: on Guam, the Brown tree snake is held responsible for the extirpation of almost all native forest birds (9 of 11 species) and two lizard species, and was possibly also involved in the demise of native bat species (Fritts & Rodda 1998); in New Zealand, introduced mammalian predators have decreased the numbers of many species of native birds, reptiles and invertebrates, some to the point of extinction (Blackwell 2005; Atkinson 2006). Classifying these interaction settings as 'high risk' seems straightforward, but we need to make sure that such classifications are not just done *a posteriori*, i.e. based on the impacts that we know now, otherwise it could be a circular argument. For *a priori* classifications, it is useful to think in terms of archetypes that are involved in the interactions. Going back to our example, let us imagine we are in historical New Zealand before mammalian predators were introduced, particularly cats, rats and foxes. These species represent an archetype of highly mobile, ground-foraging and mid-sized predators – an archetype that was not present in New Zealand before. Evidence suggests that the flightlessness of birds in New Zealand and on other islands is, at least partly, due to the previous absence of such a predator archetype (e.g. Ewing 2009). How about the experience of the non-resident predators with flightless birds such as kiwi (*Apteryx* spp.) or kakapo (*Strigops habrotilus*)? Although bird species are typically not flightless where cats, rats and foxes are native, it seems reasonable to assume that from the predators' perspective, flightless birds are quite similar to other ground-dwelling prey species with which these predators are already familiar. Also, predators of bird species that can fly should have no problem capturing nestlings or injured adult birds that cannot fly. In fact, most predators probably have experience with a whole range of intraspecific variation in morphological and behavioural phenotypes among individuals of their accustomed prey. Such differences between prey individuals can occur with regard to handicaps (e.g. an injured bird unable to fly *vs.* a healthy bird that can fly), ontogenetic status (e.g. flightless nestling *vs.* flying adult bird, sedentary larva *vs.* mobile adult individual), pronounced phenotypic plasticity (e.g. spined *vs.* unspined morphs in *Daphnia* waterfleas and other species, Tollrian & Harvell 1999), sexual dimorphism (e.g. in size or the presence of antlers), etc. As a result, predators are somewhat flexible in their foraging behaviour and can broaden the spectrum of affected prey in the context of novel interactions, as can be assumed in the New Zealand example. Hence, this example does seem to apply to the high-risk category from an *a priori* perspective. Analogous considerations can be done for the three other risk categories (Fig. 5.2).

The lowest risk for the resident community may be expected when the resident species are highly experienced and can thus exert biotic resistance, while the non-resident species' experience is low (grey area in Fig. 5.2). Such a scenario is invoked, e.g. by the hypotheses of new associations (Hokkanen & Pimentel 1989) and increased susceptibility (Colautti et al. 2004), which assume that non-resident prey are selectively attacked in their new ranges because they are not adapted to deter the resident consumers (cf. Parker & Hay 2005). In a similar vein, Forister & Wilson (2013) predict that resident herbivores will 'generalise' their host spectrum to include a non-resident host plant if the latter is similar to resident host plants in ecological factors that affect herbivore population dynamics (e.g. regarding specific phytochemicals or traits that provide protection against the herbivore's own enemies). This is again an example of species being familiar with an archetype of interaction partners, rather than with certain interacting species in particular.

Probably quite variable levels of risk that are hard to predict, and which may be considered to have an intermediate risk level overall, arise in the third category when both resident and non-resident species lack experience (two-sided novel interactions), which can be the case for missed mutualisms (Alpert 2006). As Richardson et al. (2000) pointed out, "for many ectomycorrhizal plants, notably for *Pinus* spp. in the southern hemisphere, the lack of symbionts was a major barrier to establishment and invasion before the build-up of inoculum through human activity".

Finally, both resident and non-resident species have a high degree of experience in the fourth scenario. This scenario may be considered to be of intermediate risk as well and probably resembles 'resident/resident' interactions: both sides are familiar with their interaction partner due to previous similar interactions (see Box 5.2 for a brief discussion of how the experience approach reveals insights for the recent controversy on differences between native and non-native species). For example, unlike many other Australian predators of introduced cane toads (*Rhinella marina*), the resident keelback snake (*Tropidonophis mairii*) is unaffected by the toad's poison, presumably due to its ancestral Asian origins and thus evolutionary history of exposure to Asian bufonids (Llewelyn et al. 2011).

Note that assigned risk categories can differ for a particular non-resident species between the types of ecological interaction in which it takes part. For instance, when interacting as prey with resident predators, the non-resident species may maintain a 'new interaction' that is similar to the respective resident/resident interaction. But in its role as predator (or herbivore or parasite), the same non-resident species may be classified as 'high risk'. Comparing the assigned risk categories can indicate which interaction type will probably be most impacted by the advent of a particular non-resident species. An overall estimate of the risk of establishment and impact across interaction types could be approximated by assessing the relative importance of each interaction type in the affected target community and weighting the assigned risk categories accordingly. A cautionary approach for management decisions would be to take the highest risk category (cf. Blackburn et al. 2014).

Box 5.1 – Terminology in the context of 'novel species interactions'

To facilitate unambiguous communication in research on ecological novelty, we offer some thoughts about the terminology of this increasingly important field. For the sake of simplicity, we refer to interactions between species even though biotic interactions occur between individual organisms.

Throughout this study, we use the terms 'resident' and 'non-resident' for describing the difference in origin between interaction partners. We define **resident species** as species with an ongoing evolutionary legacy in the study area that is long enough for them being fully familiar with and to the other species in the ecological network (e.g. Carthey & Banks 2012). **Non-resident species**, by contrast, have no recent evolutionary history in the focal ecological network and are not fully familiar with and to the species in this network (still, they may have eco-evolutionary experience that is applicable in the new interaction context; see main text). In our view, this terminology (resident/non-resident) has some advantages in the context of ecological novelty as compared to frequently used alternatives such as native/alien or indigenous/non-indigenous: (i) it is less strongly associated with invasion ecology but applies equally well to other potentially novel species interactions, e.g. involving genetically modified or synthetic organisms, emerging pathogens or range-expanding species (subsumed under the term 'novel organisms' in Jeschke et al. 2013), and (ii) it appropriately denominates also those species that did not originate in the target area (and are thus not native or indigenous) but have become familiar with and to the target community since their arrival, so as to be considered a resident interaction partner in interactions with subsequently arriving species.

Furthermore, we advocate to differentiate between the terms 'novel' and 'new'. Both have been used in the past (sometimes interchangeably) to denote an allochthonous origin of a species in a particular area, or to characterise a species as unfamiliar to an interaction partner regarding some of its ecological traits. With respect to species interactions, we suggest to use the term 'novel' only for settings in which unfamiliarity with ecological traits plays a significant role: a **novel species interaction** would thus involve species combinations in which at least one species has little or no experience with relevant ecological traits of its interaction counterpart (applying to three of four risk categories in Fig. 5.2). When referring more broadly to all kinds of combinations of newly interacting species, without particular regard to differences in experience and including cases with high experience in all involved species, we propose to use the general denomination **new species interaction** (applying to all four categories in Fig. 5.2). Novel species interactions thus constitute a subset of new species interactions. With respect to the interacting species themselves, we suggest that **novel species** are only those that have unfamiliar ecological traits *and* are non-resident in the study area. This excludes resident species unfamiliar to their non-resident interaction partners, since calling them 'novel' appears counterintuitive. They might best be described as unfamiliar resident species. **New species** are, again more broadly, all species in new interactions (including those that are familiar to their interaction partners) regardless of their resident or non-resident status.

We use the terms 'experienced' or 'inexperienced', 'new' or 'novel', or 'resident' or 'non-resident', being aware that they describe only the extremes of what may actually be envisioned more appropriately as continua of differences between species. Future research may bring up descriptions that can consider a finer-scaled array of levels of experience and novelty in new species interactions.

Box 5.2 – Eco-evolutionary experience and the native/non-native debate

The fourth risk scenario presented in Fig. 5.2 (‘New (not novel) interaction’) represents an interaction situation that – within the experience context – comes closest to the controversially debated perspective in invasion ecology that there might be “no distinction between native colonisers and introduced invaders” (Davis et al. 2011; see also Davis et al. 2001; Valéry et al. 2013). In that view, the successful establishment and spread of ‘introduced invaders’ (‘non-resident species’ in our terminology) is determined by exactly the same ecological processes as in ‘native colonisers’ (‘resident species’ in our terminology), rather than by conditions resulting specifically from the foreign origin (e.g. ecological novelty). Indeed, highly experienced non-resident species that are themselves highly familiar to their resident interaction partners do not constitute much of a difference in comparison to a native colonising species: the latter entails the same setting of high reciprocal experience *because* of being native (resident), and thus being by definition highly experienced with, and highly familiar to, its resident interaction partner(s). That is the reason why we label this risk category as ‘similar to resident/resident interactions’. By contrast, non-resident species actually may have low degrees of experience with their resident interaction partners (and *vice versa*). Importantly, this leads to different risk expectations than when only resident colonising species are involved (Fig. 5.2). Thus, the explicit consideration of the evolutionary legacy of species, as in terms of eco-evolutionary experience, brings to light that there actually *is* a difference between ‘native colonisers’ and ‘introduced invaders’, which can be of importance for determining the outcome of novel species interactions (see also Strauss et al. 2006; Salo et al. 2007; Heger et al. 2013; Paolucci et al. 2013; Richardson & Ricciardi 2013).

Temporal dynamics of eco-evolutionary experience and novelty

Let us now consider how eco-evolutionary experience changes over time and how this relates to the risk categories. The basic question here is: How long does a novel species actually stay ‘novel’ in a particular interaction setting? Since research on long-term effects of invasions is still in its infancy (Strayer et al. 2006), detailed answers concerning the temporal dynamics of eco-evolutionary experience are yet to be found. As a general pattern, however, novel species will gradually become familiar with and to their interaction partner(s) over time (Cox 2004; Strauss et al. 2006; Verhoeven et al. 2009; Carthey & Banks 2012; Pearse et al. 2013). Arrows in Fig. 5.2 (labelled *a*–*e*) indicate the expected transitions between risk categories for a given interaction of resident and non-resident species: the arrows point from low to high experience for at least one interaction partner, the other species’ experience increasing at a similar rate (resulting in arrow *a*) or with some delay (arrows *b*, *c*, *d*, *e*). Thus, we expect an inherent overall trend of novelty to decrease over time and of novel interactions to develop in the direction of the intermediate risk category comprising new interactions, i.e. ‘similar to resident/resident interactions’.

How long transitions between risk categories take, and whether both sides gain experience at similar rates depends on the species traits that are relevant in the respective type of ecological interaction. Some traits may be readily adjustable to a novel interaction setting and allow a relatively rapid reduction in novelty, particularly through phenotypic plasticity (which may include a high capacity of rapid learning; Webb et al. 2008). Other traits may require evolutionary adaptation over at least some generations to reduce novelty, e.g. evolution of resistance against toxins (see Cox 2004 for examples of evolutionary responses of non-resident to resident species and *vice versa*). In summary, novelty may decrease over shorter ecological or longer evolutionary time spans (Cox 2004; Carroll et al. 2005; Strauss et al. 2006; Carlsson et al. 2009). The length of this time span should be of importance for the novel species' impact in the target area. The slower resident species are gaining experience to successfully interact with non-resident species, the higher is the potential of the latter to have significant impacts on the target community. For example, it may have caused in the meantime substantial changes in the trophic structure of the species community (Roemer et al. 2002), significant alterations of abiotic conditions (e.g. fire regimes; D'Antonio & Vitousek 1992) or resident species may have been extirpated (e.g. Wiles et al. 2003; Varnham 2010). Waiting for the transition of novel interaction settings to become similar to resident/resident interactions is thus not an acceptable response for dealing with novel species from a conservationist perspective.

Also, in a given community there is typically not only one non-resident species, but multiple species arrive simultaneously or in close succession (Carrasco et al. 2010). Thus, the community never reaches the equilibrium scenario where all interactions would be similar to resident/resident interactions. The community will also be affected by other environmental factors such as climate change or habitat fragmentation that alter the experience of resident species with their resident interaction partners, and which may compromise their potential to successfully handle interactions with non-resident species (e.g. Norbury et al. 2013).

Novel predator–prey interactions in high-risk scenarios

To gain a better mechanistic understanding of the postulated influence of eco-evolutionary experience on the outcome of novel species interactions, and of the temporal dynamics, we now focus on the example of novel predator–prey interactions in high-risk scenarios (analogous considerations can be made for plant–herbivore and host–parasite interactions).

General expectations regarding experience-related effects on the predation cycle

As predator–prey interactions have been studied over centuries, we can draw from a wealth of empirical data and theoretical knowledge about them (e.g. Stephens & Krebs 1986; Begon et al. 2006; and references therein). One useful concept is the predation cycle, which consists of consecutive stages that predators and prey pass during their interaction: search, encounter, detection, attack and consumption (Fig. 5.3). The cycle is regulated by parameters such as the probability of predator–prey encounters and prey detection, or attack efficiency. These are, in turn, affected by species traits such as activity period, camouflage or attack behaviour, among many others, which either accelerate (predator offences) or decelerate or interrupt (prey defences) the cycle (see Jeschke 2006; Jeschke et al. 2008). Importantly, non-resident species may differ from trophically analogous resident species (comparator species, see also EFSA (European Food Safety Authority) 2013) in these traits, causing differences between resident/resident and resident/non-resident interactions (Haddaway et al. 2012; Dick et al. 2013; Alexander et al. 2014). Since in a high-risk scenario, on which we focus in this section, the (non-resident) novel species and its resident comparator are assumed to be equally well experienced, such differences between resident/resident and resident/non-resident interactions stem from the low experience in the resident species with the novel species.

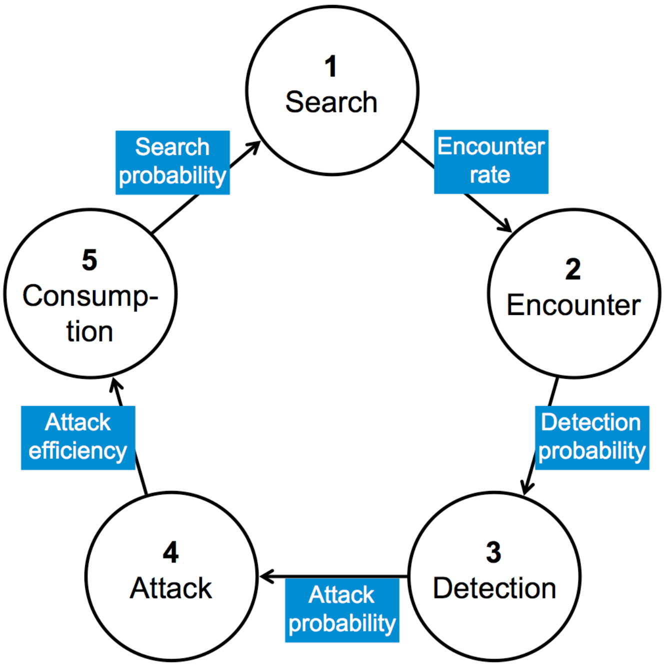


Figure 5.3 – The predation cycle, consisting of five stages (circles) that are reached one after the other depending on predator–prey encounter rate, predator detection probability, etc. (blue boxes). These parameters are influenced by predator offences and prey defences which promote or interfere, respectively, progressing through the cycle (modified from Jeschke et al. 2008).

We propose that in high-risk scenarios, novel species can have advantages relative to their resident comparators in one or more stages of the predation cycle (see Appendix Table A5.1 for detailed rationales and supporting references). Highly experienced, novel predators (Appendix

Table A5.1A) – as compared to resident comparators – may have a higher searching activity (e.g. due to reduced digestion times), encounter and detect resident prey with greater probability (e.g. due to ineffective avoidance or camouflage strategies of the prey) and/or attack prey more often and more effectively (e.g. due to failing predator recognition or ineffective escape behaviour). In the alternative high-risk scenario where a highly experienced, novel prey interacts with low-experienced resident predators (Appendix Table A5.1B), the latter may exhibit lower performance in one or more stages of the predation cycle when preying on the novel prey as compared to resident prey: these resident predators may have a lower searching activity (e.g. due to longer digestion times), lower encounter rate and detection probability (e.g. due to ineffective foraging strategies or search images) and/or reduced attack probability and attack efficiency (e.g. due to dietary wariness or unsuitable attack behaviour).

Regarding the temporal dynamics (see 'expected development' in Appendix Table A5.1), even though novel predators and prey will probably become familiar to the resident community over evolutionary time (see previous section), we expect that they may stay novel for their resident interaction partners at least over ecological time spans for some stages of the predation cycle (see Appendix Table A5.1 for detailed rationales and supporting references): novel predators could retain higher searching effort, detection probability and attack efficiency until resident prey are able to evolutionarily adapt to the novel predator, i.e. develop prey defences that are effective at these stages (Appendix Table A5.1A), or go extinct. Novel prey, on the other hand, may experience lower searching effort and lower attack efficiency from resident predators until the latter develop offences that are effective at these stages (Appendix Table A5.1B).

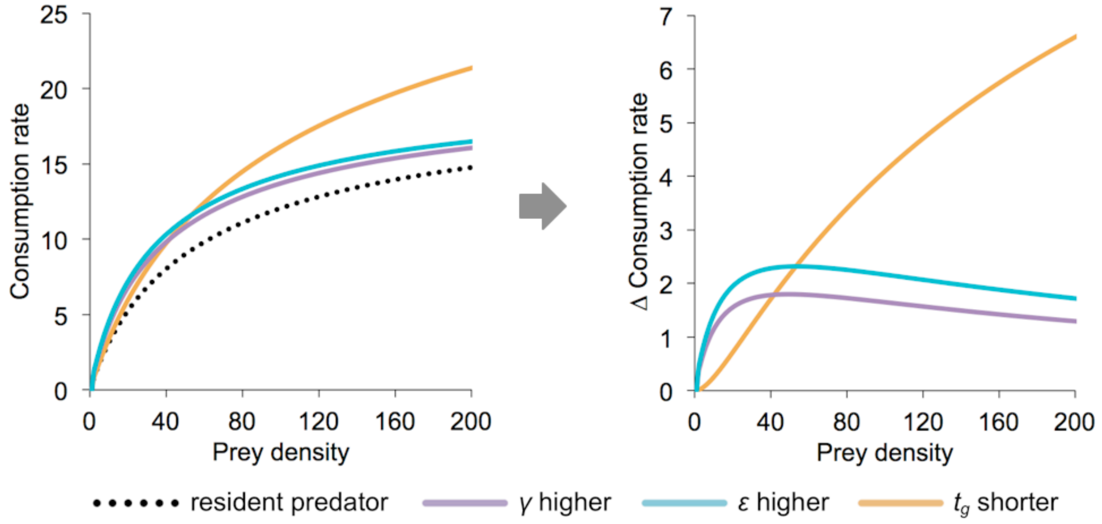
Density dependence of experience-related effects in high-risk scenarios

The above-mentioned advantages of novel predators and prey are density-dependent, most of them (with the exception of the advantages related to predator searching effort, see below) having their largest effect at low prey densities and small effects at high prey densities (cf. Jeschke et al. 2002, 2008; Jeschke 2006). For example, the novel predator's higher probability of detecting prey is highly advantageous if prey is rare but less advantageous if prey is abundant, as predator consumption rate is typically not limited by detection probability at high prey densities but by the time the predator needs to digest prey (Jeschke et al. 2002).

The density dependence of experience-related effects becomes particularly apparent when looking at predator functional responses, i.e. the relationship between per-capita consumption rate and prey density (Holling 1959). Functional responses have recently been recognised as a promising tool for estimating the impact of non-resident species on target communities (Dick et al. 2013, 2014). They are ideal means for a mechanistic understanding of food-web changes following the arrival of non-resident species since they can precisely quantify the density-dependent strength of an interaction in a food web. A large body of both theoretical and empirical work on functional responses is available in the literature (reviewed in Jeschke et al. 2002, 2004). Mechanistic models, in contrast to phenomenological models, are characterised by using parameters that can all be directly measured and biologically interpreted, so that these models can be used, for example, to calculate the effects of changing predator or prey characteristics on predation rate.

Using the mechanistic steady-state satiation (SSS) equation (Jeschke et al. 2002), let us now look at (potential) differences between functional responses of resident/resident predator–prey interactions and of interactions involving a novel prey or predator species (Fig. 5.4). The SSS equation refers to the five stages of the predation cycle as shown in Fig. 5.3. We modified the values for three exemplary parameters (gut retention time t_g, detection probability γ and attack efficiency ε) according to our expectations for high-risk scenarios (as described above and in Appendix Table A5.1; see Appendix Table A5.2 for expectations regarding additional parameters that are considered in the SSS equation). The resulting functional responses shown in Fig. 5.4 describe the situation at the onset of the novel interactions, i.e. without considering temporal dynamics. The simulation results suggest that functional responses of predator–prey interactions involving novel species in a high-risk scenario distinctly differ from those of the respective resident/resident interaction settings. Novel predators (Fig. 5.4A) have a higher consumption rate at any given prey density, but the advantage of detecting prey with higher probability and attacking it more efficiently than resident predators, i.e. the actual effect of low experience in resident prey, is particularly pronounced at low to intermediate prey densities (see ΔConsumption rate); by contrast, shorter gut retention times affecting the predator's searching effort provide an advantage for novel compared to resident predators that is increasing with prey density. In Fig. 5.4B, we take the perspective of novel and resident prey facing resident predators by comparing their predation risk (number of individuals consumed per total number of prey individuals for that species). Clearly, predation risk is lower for novel prey at any given prey density, but this advantage sharply decreases with prey density if it is due to reduced detection probability or attack efficiency (see ΔPredation risk); by contrast, if the novel prey is harder to digest than the resident prey, the advantage of the novel prey first increases and then decreases with prey density. It should be noted that the SSS equation, which we used for the simulations, only models type II functional responses. Although these have been empirically observed most frequently (Jeschke et al. 2004), other types of functional responses (especially type I, III, and dome-shaped responses) are highly important as well and should be considered in the future.

(A) Novel predators



(B) Novel prey

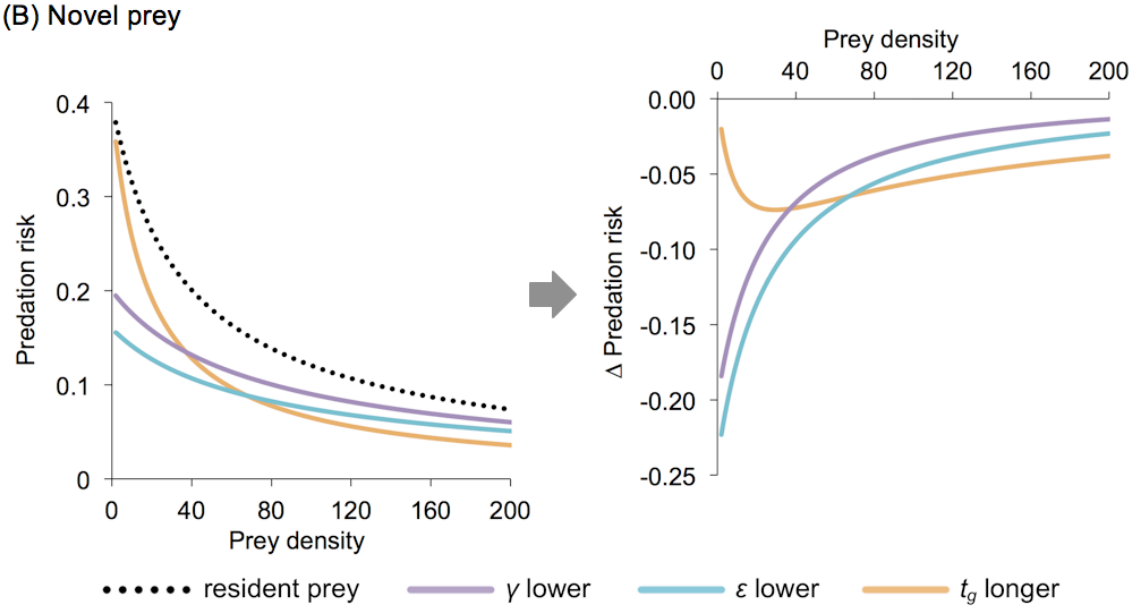


Figure 5.4 – Density-dependent effects of high eco-evolutionary experience in novel predators and prey on consumption rate and predation risk. The parameters detection probability γ, attack efficiency ε, and gut retention time t_g were modified according to the expectations for novel species described in the main text and in Appendix Tables A5.1 and A5.2. (A) Comparison of functional responses between resident and novel predators. ΔConsumption rate is the consumption rate of the novel predator minus that of the resident predator. (B) Comparison of predation risk between resident and novel prey. ΔPredation risk is the predation risk for novel prey minus that for resident prey. Model inputs (SSS equation): resident predator or prey with β=2, γ=0.5, δ=0.8, ε=0.5, t_{att}=0.005, t_{eat}=0.01, t_g=0.1, g=2; (a) novel predators with either higher γ (0.75), higher ε (0.8), or shorter t_g (0.05), otherwise as for resident predator; (b) novel prey with either lower γ (0.25), lower ε (0.2), or longer t_g (0.25), otherwise as for resident prey.

In summary, differences between highly experienced novel species and their resident comparators are particularly pronounced at low to intermediate prey densities. In the context of conservation of native biodiversity, this implies that novel predators are not merely one additional predator in the target area. Instead, they may constitute a threat of particular relevance to inexperienced endangered resident prey species. On the other hand, novel prey may benefit from an extra protection as compared to resident prey against resident predators in their initial and most vulnerable phase of population growth directly after arrival, by which the chances of successful establishment in the target area increase. Ultimately, higher consumption rates and lower predation risks for experienced novel predator and prey species, respectively, allow them to reach higher abundances than their resident comparators (cf. numerical response of predators). In fact, extreme abundances have been observed in invasive species, and invader abundance is regarded as one major determinant of invader impact besides per-capita effect and area of invaded range (Parker et al. 1999; Thiele et al. 2010). Furthermore, their higher consumption rates and lower predation risks also imply that novel species, relative to their resident comparators (for equal abundances), exert a stronger selection pressure on their resident interaction partners. This potentially amplifies the changes in the resident community that may already result from the mere inclusion of additional interaction partners into the ecological network of the target area.

Conclusion

This study aims to promote a deeper and more mechanistic understanding of the influence of eco-evolutionary experience on the outcome of novel species interactions. It increases the applied value of the experience concept (Chapter 4) by defining risk categories that will help prioritise conservation and management measures related to novel organisms. Furthermore, we formulated testable expectations about how prior experience in both resident and non-resident organisms may influence the outcome of novel interactions. This includes expected changes in novelty over time. Expectations were detailed in particular for novel predator–prey interactions within high-risk scenarios (see Appendix Tables A5.1 and A5.2), and these were integrated with mechanistic functional response models and simulations. Mechanistic insights were achieved as to when and how long novelty effects may be particularly strong. We explicitly propose our expectations and the underlying rationales (Appendix Tables A5.1 and A5.2) as hypotheses. Although these hypotheses are based on ecological and evolutionary reasoning supported by published empirical and theoretical findings (see references in Appendix Tables A5.1 and A5.2), alternative effects of the differences in experience with novel species and their resident comparator species are conceivable. In any case, the formulation of testable hypotheses is the necessary first step to advance our understanding in the area of novel interactions. The next important step is thus to test and validate our expectations on the basis of empirical data, which can feed back into the refinement of models.

Acknowledgements

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General discussion

As argued in the introduction, there is a need for consolidation and synthesis in invasion ecology. The main objective of this thesis was therefore to interrelate hypotheses and to consolidate dispersed data regarding invasions in order to enhance our understanding of variation in invasion success and improve invasion management. An array of methodical approaches was used, with phenomenological descriptions and statistical analyses of large amounts of empirical data (Chapters 2, 3) complementing the extensive development of theoretical rationales and an integrative conceptual framework, including mathematical modelling and simulation for mechanistic insights (Chapters 1, 4, 5). Considered together, the different aspects investigated in the chapters of this thesis contribute to a more comprehensive picture of potential factors influencing success or failure of invasions with implications for theory, management and conservation as detailed below.

Implications for theory

Chapter 1 – Different perspectives on biological invasions

The first chapter started with a general, theoretical contemplation of the ways how biological invasions and the processes that drive their success or failure can be approached. Considering in this chapter reasons for the ongoing discussions about how to define invasive species and biological invasions (and thus also about what constitutes a ‘successful’ invasion) led to the identification of differing but equally valuable research perspectives on invasions. We argued that this needs not impede research progress and good communication among researchers of different fields, provided that there is a general awareness of these different perspectives and that definitions (and the underlying research foci) are clearly stated. Clear communication that exposes otherwise hidden assumptions makes them accessible to scientific verification and prevents their subliminal (i.e. unnoticed) influence on the choice of methods or even data interpretation. From this point of view, one single definition of invasions is neither possible nor essential for scientific progress in invasion ecology. Rather, viewed on a larger scale, each perspective contributes different pieces of a mosaic that will, when put together, reveal a more comprehensive picture of invasions.

Chapter 2 – Challenges of data consolidation

This chapter illustrated important challenges when combining data from different databases. This is critical when the goal is to transform accumulating and dispersed data into knowledge, for researchers, managers, and policy-makers. To be able to combine data, standard categories have to be defined. Developing a meaningful and representative standard pathway categorization scheme is a major challenge *per se*, since invasive alien species arrive in new regions via extremely diverse pathways. This diversity has to be broken down into broader categories that are applicable to organisms of all taxonomic groups. Applying then the standard categorization to different databases has to be accompanied by repeated double-checks regarding its consistency for all included data across taxa. Categories of different databases that may at first sight seem analogous or comparable among different databases may actually deviate in how they map to the standard categorization due to subtle differences in the premises of assigning organisms to them. This can lead to systematic errors and result in patterns that mislead data interpretation. Thus, although consolidation of data is a highly valuable tool for describing patterns in invasions by allowing us to analyse larger datasets and facilitate comparative analyses, it also requires special care and meticulousness in its execution.

Chapter 3 – Insights from cross-taxonomic approaches

According to the findings in this chapter, there seem to be various possibilities for invaders to be successful, rather than universal invasion traits explaining the invasion success of all invaders. Such possibilities may be reflected by different combinations of invasion traits that were recurrently found in the analysed dataset. This dataset was explicitly designed to comprise information from a wide range of taxonomic groups instead of focussing on species of one group. Only in doing so it was possible to learn that similar combinations of invasion traits can be found in successful invaders from very different taxonomic groups, which can be interpreted as an indication for a high importance of these combinations for invasions to be successful. Invasion processes differ with regards to which of the invasion steps (transport, escape, establishment, or spread) is the most challenging one from the viewpoint of the species, and this also depends on the introduction pathway and the ecosystem where it is introduced. Accordingly, it was proposed that invasive species can be classified into taxon-independent ‘invader types’ (drifters, fugitives, establishers, spreaders, and invaders promoted by humans), each of which represents a kind of specialization with traits especially suitable to overcome one of the invasion steps. Remarkably, the idea of considering invader types was a direct consequence of a cross-taxonomic approach. More research into this topic with larger and taxonomically more balanced datasets is needed to assess the usefulness of the concept of invader types in general and to confirm, reject or modify the invader types postulated in Chapter 3.

In any case, the contrasting findings of Chapters 2 and 3 (taxonomic patterns in introduction pathways *vs.* taxon-independent combinations of invasion traits) underscore that although taxonomic affiliation seems important for invasion success, comprehensive explanations for variation in invasion success cannot be based on it exclusively. Thus, cross-taxonomic approaches should be considered more often in invasion theory as a complement to the more usual focus on single taxonomic groups. This will elucidate in which cases the taxonomic status of species involved in an introduction may be a useful indicator for invasion success (including consequences for management decisions), but also when and how such patterns may be overruled by factors not captured by taxonomy.

Chapter 4 – Synthesis by adopting an eco-evolutionary perspective on invasions

To strengthen the theoretical foundation for synthesis in invasion ecology, I adopted an explicit eco-evolutionary perspective on invasions in Chapters 4 and 5. In agreement with the above-described need for taxon-independent approaches, the concept of eco-evolutionary experience avoids using the taxonomic or phylogenetic relatedness of species in the source and target area as a proxy for their ecological similarity. Instead, the described routine and indices demonstrated an approach to assess ecological similarity and quantify eco-evolutionary experience comparing functional roles and resulting biotic interactions of the involved species in their ecological communities before and after an introduction takes place. This was explicitly done for both non-native *and* native species, acknowledging the need to jointly consider aspects of species invasiveness and community invasibility, and demonstrating that this is actually possible within a coherent conceptual framework. This framework has the potential to systematically guide empirical experiments by interrelating the growing number of individual findings in regard to major ecological invasion hypotheses (see Appendix Panel A4.1). The experience concept therefore ties in with the idea of a 'hierarchy of hypotheses' (Jeschke et al. 2012a, Heger et al. 2013), which helps to systematically organize the specific predictions of the large number of individual hypotheses and the evidence accumulated for or against them (Jeschke et al. 2012a). This in turn allows evaluating the more general predictions represented by the complete branch of an overarching idea and to identify more fundamental patterns in biological invasions.

Chapter 5 – Origins of novelty, its temporal dynamics, and generalization to novel organisms

This chapter further elaborated on the rationales developed in the previous chapter. Again, the use of jointly considering experience in both resident and non-resident species was emphasized for invasion theory (and management, see next section), in this case by differentiating between alternative 'origins of novelty' in new interactions (resident, non-resident or shared), which lead to different risk levels of establishment and impact. Long-term research was encouraged by addressing probable changes in the effect of novelty with time elapsing, and mechanistic insights were gained by contemplating potential effects on predator-prey interactions. More generally, the concept of eco-evolutionary experience was put into a broader context of novel organisms beyond invasive species, i.e. including new interactions arising due to the appearance of GMOs, synthetic organisms, resurrected species, or emerging pathogens in an area. This included suggestions on how to use terms such as 'new' and 'novel', or 'resident' and 'non-resident' in this context since they are less closely associated only with invasion ecology but apply equally well to other new (and potentially novel) species interactions. Most importantly, however, Chapters 4 and 5 formulated explicit and testable hypotheses based on theoretical reasoning about how prior experience in both resident and non-resident organisms with each other may influence the outcome of novel interactions and how this influence may change over time. Even though alternative effects of the differences in experience with novel species and their resident comparator species may be conceivable, the formulation of testable hypotheses is the necessary first step to advance our understanding in the area of novel interactions.

Implications for management and conservation

Chapter 1 – Sustainable management through consideration of different interest groups

Discussions about definitions and perspectives as described in Chapter 1 are not solely an issue of the theoretical realm of invasion ecology but can also have important repercussions in applied invasion management. Prevention and management can only be effective when interests of all societal groups, i.e. their different perspectives on invasive species, are considered. This includes making compromises that may at first sight seem hard to accept, in particular when very contrasting interests like the conservationists' precautionary principle and economists' opportunity costs have to be balanced against each other. Ultimately, however, sustainable management can only be achieved this way, i.e. a management that is effective because it does not change every few years with political shifts and one that can be maintained for long time spans (if necessary) because it is backed by a society's majority.

Chapter 2 – Management prioritization through taxonomic patterns in introduction pathways

Based on a comprehensive and up-to-date overview of pathway information that consolidated data of two major databases, this chapter revealed insightful patterns that support prioritization in preventive management of invasive alien species. Plants and vertebrates are mostly introduced via the intentional pathways of escape and release, whereas the unintentional pathways of corridor and transport as contaminant or stowaway are of greater importance for invertebrates, algae, fungi, and micro-organisms. For species that are known to be intentionally introduced, the introduction of harmful invasive alien species can be effectively prevented on a species level; for species that are unintentionally introduced, strategies are necessary that target entire pathways (e.g. ballast water treatments). Furthermore, high-impact invaders ('Worst IAS') are frequently introduced both intentionally and unintentionally, posing significant challenges for effectively managing this invader group of particular conservation concern.

Chapter 3 – Taxon-independent combinations (= patterns) in invasion traits

This chapter provided arguments in favour of increasing our efforts to pursue taxon-independent approaches in invasion research and management. The analysis of consolidated data for 201 successfully invasive species revealed that several statistical clusters of similar combinations of invasion traits included species of distant taxa. Patterns in such trait combinations may reflect a tendency of species to either have traits favourable for one specific stage of the invasion process, or to be specifically promoted by humans. The results show that invasive species differ in how they can become invasive, similarities and differences apparently being independent of the species' taxonomic affiliations. Thus, for reaching higher effectiveness management could possibly benefit from developing ideas how best to target certain invader types rather than focusing on specific taxonomic groups. As mentioned above, more research is needed in regard to potential invader types.

Chapter 4 – Assessment of ecological similarity and eco-evolutionary experience

Although at this stage clearly of conceptual nature, the proposed routine and indices presented in Chapter 4 constitute an important first step towards an efficient quantitative estimate of the influence of species' evolutionary legacy on the success of biological invasions. A particular advantage of applying this approach in invasion management lies in its high flexibility: it allows considering not only food webs but also other ecological networks (e.g. plant-pollinator networks, seed-dispersal interactions, host-parasite systems); different kinds of ecological groupings can be used (ecological guilds, functional groups etc.); and it is applicable to all living organisms across taxonomic boundaries (e.g. plants and animals alike).

Chapter 5 – Risk categories, temporal dynamics, and density dependence of novelty effects

This chapter contributed to an increased applicability of the experience concept and to adequate prioritization in invasion management by defining risk categories for estimating the probability of successful establishment and impact of novel organisms on the resident community. These categories can help us initiating appropriate management measures in time. Ecological novelty of organisms (and its effects on biotic interactions) probably changes over time, which indicates the need for monitoring new interactions and a management that adapts to changes in interactions. Importantly, even though novel interaction settings may become similar to resident/resident interactions over time, routinely waiting for the completion of this transition is not an acceptable response for dealing with novel species from a conservationist perspective due to the impacts exerted in the meantime. Furthermore, comparisons particularly addressing novel predator-prey interactions highlighted the density-dependence of experience-related effects in high-risk scenarios and added to conservationists' concerns: novel predators may pose a threat of particular relevance to inexperienced and endangered (i.e. rare) resident prey species, while novel prey facing inexperienced resident predators seem to enjoy particularly pronounced advantages (compared to resident prey) during their low-density establishment phase.

Conclusion and outlook

Even though there will probably never be 'enough' data in the sense that more data would not bring any additional insight, invasion ecology has reached a point where combining already existing empirical data (Chapters 2, 3) and interrelating large numbers of individual invasion hypotheses (Chapters 4, 5) seems promising for identifying foundational principles and mechanisms that are broader than those attributed to specific invasion cases only. More effort is needed to synthesize the continuously growing amount of information into actual knowledge. Besides the advantages of such synthesis for progress in scientific understanding, it is also necessary for being able to adequately involve non-scientific stakeholders (e.g. politicians, entrepreneurs and the general public). Their support and contribution is essential to successfully prevent and mitigate negative consequences of novel organisms, and initiate developments into directions that are beneficial for both human society and nature.

Theory is an important component in this endeavour as it provides a structure along which to align and interrelate individual observations and rationales, i.e. "theory makes ecology evolve"

(Kolasa 2011). Having thus developed in this thesis an experienced-based conceptual framework, a categorization for risk of establishment and impact, and explicit hypotheses regarding the expected effects of eco-evolutionary experience on the outcome of new interactions, the next important step is now to test and validate our expectations (and the simplifying assumptions made) on the basis of empirical data. This could be done, for instance, by first using case studies in the scientific literature where different levels of eco-evolutionary experience can be identified and where the outcomes of both resident/resident and resident/non-resident interactions are known. This can feed back into the refinement of models and provide a sound basis for the design of suitable experiments (e.g. laboratory feeding experiments). In the long run, the produced theoretical and empirical findings can be integrated into increasingly comprehensive models (i.e. food webs and full ecological networks) and exploited also for long-term mesocosms and field experiments. Ultimately, the considerations presented in this thesis shall be helpful not only for research on biological invasions but for the understanding and management of novel interactions in general. This is critical in view of the growing and accelerating alterations of ecosystems worldwide in the ongoing Anthropocene.

Publications and author contributions

The following publications derive from this thesis, for each of which the author contributions are also outlined:

Chapter 1

Heger T, **Saul W-C**, Trepl L (2013) What biological invasions 'are' is a matter of perspective. *Journal for Nature Conservation* 21: 93–96. doi: 10.1016/j.jnc.2012.11.002

Author contributions: LT contributed the basic idea for this manuscript and worked out the philosophic basis. TH did the literature analysis, provided many of the ideas, structured the arguments, and led the writing. I was involved in framing the rationale regarding the eco-evolutionary perspective, and especially in conceiving the concept of eco-evolutionary experience together with TH. I significantly contributed to restructuring and expanding the content of the manuscript and to sharpening the focus in revising the manuscript.

Chapter 2

Saul W-C, Roy HE, Booy O, Carnevali L, Chen H-J, Genovesi P, Harrower CA, Pagad S, Pergl J, Jeschke JM (to be submitted) Turning information into knowledge: linking major databases to analyse and prioritise introduction pathways of alien species.

Author contributions: The general idea for this manuscript was conceived by JMJ, HJC, PG, HER, and myself. This manuscript is based on previous work in the Master's thesis of HJC (supervised by JMJ), and on the development of a standard categorization scheme, including the mapping of categories from DAISIE (HER, CAH, OB) and GISD (PG, SP, LC). Raw data of DAISIE were provided by HER, CAH, OB, and JP; raw data of GISD/IASPMR as well as definitions of the CBD pathway categories were provided by SP, LC, and PG. I conducted all data handling (data integration and harmonization, error screening, plausibility checks etc.) and analyses after discussions with JMJ, HER, JP, and PG. I drafted the manuscript, and all authors revised it.

Chapter 3

Heger T, Haider S, **Saul W-C**, Jeschke JM (2015) Species from different taxonomic groups show similar invasion traits. *Immediate Science Ecology* 3: 1–13. doi: 10.7332/ise2015.3.1.dsc

Author contributions: All authors jointly conceived the idea for the manuscript and designed the statistical analyses. TH conducted the statistical analyses as well as led the writing and revision of the manuscript. As all authors, I researched in scientific literature and online sources the data for a species subset of the complete dataset, including subsequent data revisions and updates. I contributed to the interpretation of the results and made significant suggestions to focusing and re-structuring the content of the manuscript in revising the manuscript.

Chapter 4

Saul W-C, Jeschke JM, Heger T (2013) The role of eco-evolutionary experience in invasion success. *NeoBiota* 17: 57–74. doi: 10.3897/neobiota.17.5208

Author contributions: Together with TH, I developed the rationale and details of the concept of eco-evolutionary experience and the corresponding framework. I structured the conceptual ideas and related them to existing work by conducting a comprehensive literature research. JMJ and I jointly developed the routine and indices for the quantification of eco-evolutionary experience. I drafted the manuscript and led subsequent revisions with significant input from TH and JMJ.

Chapter 5

Saul W-C, Jeschke JM (2015) Eco-evolutionary experience in novel species interactions. *Ecology Letters* 18: 236–245. doi: 10.1111/ele.12408

Author contributions: JMJ and I jointly developed the general idea of the study based on the previously developed experience concept. I worked out the conceptual details, structured the ideas, carried out the functional response simulations, conducted extensive literature research (including for the appendices), and drafted the manuscript. JMJ gave substantial and continuous input to all study parts. Both authors revised the manuscript.

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Appendix

Table A2.1 – Pathway categories in the standard pathway categorization scheme developed by the GIASIPartnership initiative of the Convention on Biological Diversity (CBD).

Main category	Sub-category	Description and examples
RELEASE IN NATURE Refers to the intentional introduction of live alien organisms for the purpose of human use in the natural environment. Examples include releases for biological control, erosion control (and dune stabilization), fishing or hunting in the wild, landscape "improvement", and introduction of threatened organisms for conservation purposes.	Biological control	Biological control agents are species that have been introduced to areas outside their natural range to predate pests that are damaging agricultural crops. This is largely in response to a novel pest species affecting the productivity of a crop where there are no native predators available to control the population of the pest. An example is the cane toad (*Rhinella marina*), which was introduced to Australia to control beetles that were damaging cane crops - the toad population exploded, has become a pest in its own right and has negatively affected native herpetofauna.
	Erosion control / dune stabilization (windbreaks, hedges…)	Plant species with specific, useful attributes such as deep and spreading root systems may be introduced to stabilize mobile or fragile landscapes or increase the resilience of otherwise malleable features such as shingle banks and steep hillsides from alteration and destruction by natural processes (e.g. wave action or flooding). European marram grass (*Ammophila arenaria*) was introduced to California to stabilize dunes, it spread along the entire western coastline of North America and has caused the destruction of native dune systems.
	Fisheries in the wild (including game fishing)	Fishing including game fishing is an important economic activity for many countries; many fish species have been taken from their natural range and introduced into a new watercourse or waterbody to create alternative or novel opportunities for commercial fishing activities, or to provide a more productive source of food for local populations. For example, common carp (*Cyprinus carpio*) have been introduced to a large number of countries to stock fisheries.
	Hunting	In many countries species have been introduced by humans outside of their natural range to provide a source of sport. The species that are predominantly hunted for sport are either large herbivores or large predators; the impacts from the introductions of species with specific food-source requirements can severely alter the natural structure of the habitats and native species of the area to which these sport species are introduced into. Wild boar (*Sus scrofa*) and red fox (*Vulpes vulpes*) have been introduced into countries outside their natural range for the purposes of hunting for sport; feral populations of both species cause significant damage to the ecosystems of the countries into which they have been introduced due to their habits of foraging and predation, respectively.
	Landscape/flora/fauna improvement	With the rise of interest in horticulture, in particular during the intensive period of 19th century global exploration, a large number of plant species were collected and moved from their natural ranges initially as curiosities, but later on to provide a source of novel garden plants. Similarly with new species of animal, an interest developed as to whether novel species could increase the productivity of, or diversify a landscape otherwise perceived as impoverished. Humankind's efforts to improve landscapes and species diversity have lead to a large number of species being moved from their natural range into new areas around the planet. As one example, Japanese knotweed (*Fallopia japonica*) was introduced into gardens around the world during the 19th Century as a landscaping plant due its fast growing nature; however, it soon escaped the confines of gardens and has since spread prolifically creating monospecific stands.

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	Introduction for conservation purpose or wildlife management	Reintroduction programs for conservation purposes return species to areas where they were once locally native but have gone extinct through hunting or habitat destruction by humans. An example would be the return of the North American beaver (*Castor canadensis*) to stretches of watercourse from which it had been previously trapped during the colonial expansion of North America.
	Release in nature for use (other than above, e.g. fur, transport, medical use)	Throughout history, plant and animal species that have been a source of food, or supported agricultural techniques have been taken from their natural ranges and introduced into new regions to provide a dietary supplement for the local human population. This has occurred both in areas where either traditional food sources were not present in newly colonized areas and were subsequently introduced, or where human groups expanding their territories have discovered new species, returned home and introduced these species as a new food source. An example is the European rabbit (*Oryctolagus cuniculus*), which was introduced in limited numbers to one farm in Australia and is now a nationwide pest species.
	Other intentional release	**Bioremediation** is the process whereby a species with a particular capability is introduced into a damaged or polluted habitat, or is introduced to improve the conditions that are present in some way. The aim of the introduction is to alter the conditions at the site to one of less pollution, or more amenable to utilization by humans for development or agriculture. Earthworms (*Lumbricus terrestris*) were introduced outside their native range to alter the productivity of soil for agriculture but then spread outside the initial area of introduction and affected nutrient cycling across many habitats. Similar to bioremediation, **waste management** can incorporate processes whereby species are introduced by humans into damaged or polluted habitat to improve the conditions that are present. The aim of the introduction is to alter the waste product of human activity to less unpleasant organic material that is either safer to handle or to a product that might have commercial value. Earthworms (*Lumbricus rubellus*) were introduced outside their native range to assist in the breakdown of waste products.
ESCAPE FROM CONFINEMENT Refers to the movement of (potentially) invasive alien species from confinement (e.g., in zoos; aquaria; botanic gardens; agriculture; horticulture; aquaculture and mariculture facilities; scientific research or breeding programs; or from keeping as pets) into the natural environment. Through this pathway the organisms were initially purposefully imported or otherwise transported to the confined conditions, but then escaped from such confinement, unintentionally.	Agriculture (including biofuel stocks)	Productive agricultural species and species that provide locally in demand foodstuffs are frequently planted or farmed outside their native range. Whilst introduced into a relatively confined agricultural environment, wind-dispersal of seed or individual migration (for example) from this initial point of introduction has seen a large number of species enter new environments around the world. The African honey bee (*Apis mellifera scutellata*) was introduced to the Americas to bolster failing populations of European honey bee, after which this more aggressive species spread successfully.
	Aquaculture / mariculture	Similar to escape from agricultural confinement, predominantly from fisheries - species that are suitable as a commercial crop and that will provide opportunities for creating a new source of nutrition are introduced into an area in fish farms; a number of individuals escape the confines of the farm and populate the local watercourses or waterbodies with potentially negative impacts on the natural systems. The movement of fish for commercial operations can also transport diseases and other aquatic organisms between areas and introduce new species unintentionally. For instance, signal crayfish (*Pacifastacus leniusculus*) was introduced from North America into Britain to create a commercial crayfish farming industry and then escaped into natural watercourses, introducing with it crayfish plague (*Aphanomyces astaci*).

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This may include accidental or irresponsible release of live organisms from confinement, including cases such as the disposal of live food into the environment or the use of live baits in an unconfined water system.	Botanical garden / zoo / aquaria (excluding domestic aquaria)	Botanical gardens, zoos and aquaria have provided the opportunity to educate about the diversity and value of global fauna and flora; the importation of colourful or agriculturally significant species for display and study has enhanced research within the scientific community and the understanding of global diversity for members of the public. Plants and animals do not always remain successfully contained and accidental releases have frequently occurred introducing new species from the zoo or botanical garden into the surrounding natural areas. For example, the mangrove palm (*Nypa fruticans*) has been accidentally introduced through planting in botanical gardens (and subsequent spread by floating seeds) from its native Asia-Pacific range to West Africa, the Caribbean and Central America.
	Pet / aquarium / terrarium species (including live food for such species)	A large number of exotic species have been moved around the planet outside their native ranges to supply the pet trade. A variety of both terrestrial and aquatic species are bred extensively to feed demand for both traditional and novel or fashionable species. Many pets are taken on as juveniles by people who do not have the capacity to look after a mature adult of that species and as a result many species are released into the wild rather than being kept and looked after. Whilst there are many species that cannot adapt and survive in their new environment there are many species that not only have survived individually, but have found others of the species, bred and established locally. Ferrets (*Mustela furo*), iguanas (*Iguana iguana*), pythons (e.g. *Python molurus*), the list is extensive and globally release of exotic pets is a significant cause of the introduction and creation of new pest species.
	Farmed animals (including animals left under limited control)	Occasionally animals will be introduced into a new part of the world either as working animals or to provide a food source in an area otherwise supporting limited provisions. These animals will be left semi-wild and will quickly expand their range into this new habitat and will only occasionally be taken by humans living and working in the area. Overall the effect can be that the species adapts and establishes successfully, the population size then not significantly affected by an occasional local cull. For example, camels (*Camelus dromedarius*) were introduced into the outback of Australia to provide transport for settlers traversing the vast expanses of the newly colonized continent and are now successfully established there.
	Forestry (including afforestation or reforestation)	Commercial timber operations are a significant worldwide contributor to the spread of invasive tree species; tree species that have specific, required properties and that will produce a valuable crop are planted globally outside their natural range to provide for commercial forestry operations. The conifers are the predominant group of trees that are utilized for these operations and are capable of effective wind dispersal and can readily establish outside the controlled area of forestry plantation. The Monterey pine (*Pinus radiata*) is native to California yet is used globally in forestry operations; in New Zealand, in particular, this species has spread extensively outside areas of forestry operations.
	Fur farms	Desirable animal products, such as fur, lead to the development of farming of animals for specific products for the fashion industry. Animals escaped the confines of these farming operations in a variety of ways, including release by animal rights activists, and lead to the introduction of animal species in areas outside their natural range. The American mink (*Neovison vison*) was farmed for its fur in the UK and successive escapes from mink farms introduced this species to many watercourses.

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	Horticulture	The breeding of new crop and garden varieties of plant species by horticultural organizations across the world has lead to localized introductions of species outside their natural range. Seed dispersal or escape from these locations by plant species developing extensive rooting systems has lead to the spread of non-native plant species from these points of introduction into surrounding natural areas. Asparagus fern (*Asparagus densiflorus*) has been introduced to a number of countries from its native South Africa for horticultural purposes and has spread from gardens into natural areas.
	Ornamental purpose other than horticulture	Species that are colourful, have a dramatic structure, or are bred in their native ranges for ornamental value have been moved around the world to improve or enhance municipal areas or private parks and gardens. Both mallard (*Anas platyrhynchos*) and starling (*Sturnus vulgaris*) have been introduced to countries outside their natural range to provide a colourful and noisy addition to the local fauna. The foraging habits and breeding success of these species have resulted in the successful invasion of their new territory.
	Research and ex-situ breeding (in facilities)	Research laboratories will use animals for a variety of purposes from studying behaviour to vivisection and testing products designed for humans. Historically these laboratories have not always been able to contain their animals and a number have escaped; occasionally, and similar to the fur farms, animal rights activists have released animals from laboratories into the wild. These animals, if conditions are suitable for establishment, can develop a local population outside their natural range and become pest species. Rhesus monkeys (*Macaca mulatta*), outside their native range of Central and Southern Asia, have formed colonies in parts of the US where they were imported for use in laboratories.
	Live food and live bait	Transportation of live, non-native food species to an area can lead to their escape and establishment with severe consequences for native species. This has been the case with the American Bullfrog (*Lithobates catesbeianus*), which has been introduced worldwide to over 40 countries. Fishing baits are a diverse source of introduced and invasive species outside their natural range; sport fishing requires a range of suitable baits. By transporting baits between countries, many species have been introduced unintentionally into new areas and have established there. For example, the rusty crayfish (*Orconectes rusticus*) was introduced into several States in the USA through the importation of bait.
	Other escape from confinement	Plant species that have specific uses in their natural range, e.g. creating boundaries between properties or stock-proofing between grazing areas, have been imported into new locations by colonizing human groups to introduce their useful properties. These plants, outside their natural range, are not always subject to the same natural controls that maintained a balanced population and can establish locally and expand across significant areas. Gorse (*Ulex europaeus*) and bamboo (e.g. *Phyllostachys nigra*) are two structural plant species that have been introduced into new areas by humans for their useful properties and have escaped the confines of their introduced location and become serious pests.
TRANSPORT – CONTAMINANT Refers to the unintentional movement of live organisms as contaminants of a commodity that is intentionally transferred through international trade, development assistance, or emergency relief. This includes pests and diseases of food, seeds, timber and other	Contaminant nursery material	Plant nurseries will import a large number of plant species from different locations around the world. Transporting the plant specimens will ensure the movement of not only the plants themselves, but also the soil around their roots which can support a diverse fauna, a variety of fungi and potentially other plant propagules. The transport of plants and their associated species through countries outside the natural range of all the species within the transporter can potentially disperse species into areas where they can establish. Snails (e.g. *Achatina fulica*) and even lizards (e.g. *Anolis wattsi*) have been distributed by the transport of nursery material from the Old World to the New World and from the Caribbean to South America - the pathways are extensive.

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products of agriculture, forestry, and fisheries as well as contaminants of other products.	Contaminated bait	Fishing baits are a diverse source of introduced and invasive species outside their natural range; sport fishing requires a range of suitable baits and the transport of these bait species can include a variety of other fauna. By transporting baits between countries, many species have been introduced unintentionally into new areas and have become established there.
	Food contaminant (including of live food)	Global trade and food production has ensured the transportation of large numbers of fruit and vegetable species from producing countries to the rest of the world. Species have been introduced into countries to provide a cheaper crop than in their native country. This has both spread crop species to new areas where some have become invasive, and the crop itself has, when being transported to the vendor, moved pest novel pest species associated with the crop. Fruit flies (*Ceratitis capitata*), algae (*Codium fragile*), snails (*Batillaria attramentaria*) etc. have all been transported from their natural range and into new locations, both to and from producing countries, where they have established and become damaging pest species.
	Contaminant on animals (excluding parasites and species transported by host and vector)	The transportation of animals also means the movement of soil material in their hooves/feet, which may also support viable propagules or seeds of plants and perhaps invertebrates that, if capable of establishing at the destination, may prove to be a pest. Seed will also be transported in the coats of many animals with longer hair and similarly has the potential to transfer a species from one location to another. Tree species of *Prosopis* are frequently spread passively by animal movements.
	Parasites on animals (including species transported by host and vector)	Species, whether being transported legitimately or not, will carry other species associated with their natural habit. Many species live in a state of symbiosis with other organisms, some parasites are fatal and transportation of an animal carrying a disease that could spread to other similar species at the destination is a serious risk. Whilst quarantine for travelling animals will prevent some transference from occurring, not all parasites will be prevented from moving with animals. Parasites of current significance globally include beak and feather disease (BFDV) and chytridiomycosis (*Batrachochytrium dendrobatidis*), the latter a fungus that affects a large number of amphibian species worldwide, threatening many of them with extinction.
	Contaminant on plants (excluding parasites and species transported by host and vector)	The transfer of plants from one location to another for commercial crop production or horticulture can result in viable propagules of another species also being transferred. This can occur either with a foreign species' seed being attached to the plant itself, and seed or viable material being lodged in the root bowl or in associated soils. An example of species travelling as a contaminant on another plant species is Asian melastome (*Melastoma candidum*), which has spread prolifically from its native range in south-east Asia across the Pacific to Hawaii and the US.
	Parasites on plants (including species transported by host and vector)	The movement of plant species creates a risk to plant communities at the destination due to the potential of the presence of parasites on and within the tissues of the plant matter that is being moved. Viruses, fungi and mites are a few of the microscopic and potentially undetectable organisms that might be unintentionally introduced by the transport of plants across regions and borders. A significant group of plant pathogens are the blights – for instance, chestnut blight (*Cryphonectria parasitica*).

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	Seed contaminant	The global trade in agricultural seed to provide new or more productive species to new locations considered either impoverished or less productive has created a pathway for the unintentional spread of other species whose seed is harvested or later contaminates the main product. When the seed is planted at the destination location the seed that is introduced is not 100% pure and may contain a variety of other species which may also germinate and potentially establish in the new location. The giant sensitive tree (*Mimosa pigra*) and yellow star-thistle (*Centaurea solstitialis*) have been translocated from the Neotropics and the Mediterranean respectively to Australia, South-east Asia and California.
	Timber trade	Commercial timber operations, particularly in this case, for export has transported untreated wood between countries and otherwise unconnected regions of the planet. Similar to organic packing, the timber can support a number of species that would be living on or in the tree from which the timber was sourced. Some species will survive the timber processing and transport, or are drawn to the timber prior to departure of this product. A number of invertebrate species (e.g. the citrus long-horned beetle, *Anoplophora chinensis*) have been unintentionally transported outside their native range in this manner, creating a new source of pest species in the destination country.
	Transportation of habitat material (soil, vegetation, wood…)	Where the transportation of vegetation matter, soil or other plant products has occurred on a large, commercial scale; or, where vegetation and soil has been passively transported between locations on machinery or other items, a large number of organisms can piggyback these materials and will also be moved between locations. Seed, larvae and juvenile animals have all been transported in this manner from their naturally occurring range to new locations where some have been able to establish. The list of examples is extensive, including plants, invertebrates, fungi that have been spread regionally and globally.
TRANSPORT – STOWAWAY Refers to the moving of live organisms attached to transporting vessels and associated equipment and media. The physical means of transport-stowaway include various conveyances, ballast water and sediments, biofouling of ships, boats, offshore oil and gas platforms and other water vessels, dredging, angling or fishing equipment, civil aviation, sea and air containers. Stowaways of any other vehicles and equipment for human activities, in military activities, emergency relief, aid and response, international development assistance, waste dispersal, recreational boating, tourism (e.g., tourists and their luggage) are also included here.	Angling / fishing equipment	Fishing equipment, particularly that which is immersed for any period of time, can support a diversity of invertebrate and plant life. If this equipment is not cleaned between usage at different locations, then there is ample potential for the spread of species between watercourses, catchments and habitats. Crayfish pots, boats, buoys are all examples of equipment that are regularly submersed and will rapidly develop local flora and fauna associated with their interface with the aquatic environment. Rigid hornwort (*Ceratophyllum demersum*) has been spread significant distances into new catchments and countries by fishing equipment.
	Container / bulk	Moving any items in bulk form, particularly organic matter of any form, between countries has the potential to spread organisms. This is a particular concern where bulk containers are not screened for animals or plant matter, where the items being transhipped are not treated or processed. There is high potential for species to be transported as unintentional stowaways; furthermore large seaports, airports and rail freight yards are unnatural habitats covering large areas and support a novel range of habitats that can provide a suitable environment for these stowaways to establish.
	Hitchhikers in or on airplane	Where pressurized aircraft cabins and holds are not screened or treated, it is possible for mammals and invertebrates to enter these areas prior to a flight, survive the journey and be released on arrival at the destination. Whilst this may not always happen in adequate numbers for the species to establish in the new location, for some species the main vector for transference has been an aircraft. The house mouse (*Mus musculus*) and yellow crazy ant (*Anoplolepis gracilipes*) have been spread from their natural range by becoming accidental stowaways on aircraft, and enough journeys have been made with these species on board such that new populations have been established in different locations by air passage.

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Hitchhikers on ship/boat (excluding ballast water and hull fouling)	Shipping is a relatively simple method of transference. Ships docked at one location are subjected to a large transferal of freight and passengers all of which may directly bring aboard species that are capable of surviving a voyage and have the potential to survive at any destination along the shipping route. Ships are capable of transferring species within their ballast, through freight contents, local populations of rodents present on board (e.g. *Rattus rattus*), and through passengers introducing species on board in purchases, or with seeds, larvae, fungal spores etc. on their possessions.
Machinery / equipment	Commercial machinery used at a number of sites across a country, or between countries, can spread species between locations. Agricultural machinery, if not cleaned properly can have soil which may have plant seeds, fungal mycorhizza, invertebrate eggs or larvae; construction machinery could similarly support soils, mammals and birds have been known to nest in machinery and could be accidentally moved from region to region when the machinery is moved between projects. This mechanism is particularly pertinent for plant species, for example the propagules of aquatic plant species (e.g. water hyacinth, *Eichhornia crassipes*) can easily be transferred large distances into new catchments by moving machinery.
Organic packing material, in particular wood packaging	Global transportation of goods and products for foreign markets requires a large volume of packing material. Wooden packing cases where the timber has not been treated have been commonly used and can support a number of species that would be living on or in the tree from which the timber and packing material was sourced. Some species can survive the timber processing and transport, or are drawn to the organic materials of the packing prior to departure of that packing from its source country. Bark beetles (e.g. the European bark beetle, *Orthotomicus erosus*) and the Asian long-horned beetle (*Anoplophora glabripennis)* have been spread extensively around the world through this vector.
People and their luggage / equipment (in particular tourism)	When travelling abroad, people frequently travel with items that comfort them, are familiar, or have properties that are useful (e.g. medicinal). Frequently these will be animal or plant by-products, organic material, seeds etc. All of these items are either themselves a potential invasive pest threat, or will themselves be carrying species that could similarly become a threat. Argentine ants (*Linepithema humile*) are an example, arriving in New Zealand with air passengers.
Ship/boat ballast water	To stabilize ships that carry freight, water is pumped into tanks within the hull of ships to balance a continually changing freight manifest. Water can be taken on in large quantities in one harbour and then discharged in the next, this may be a few kilometres away, or in a new country several thousand kilometres away. When the water is taken on board to increase the ballast present, there are few controls on what is taken on board in the water; in this way, species are spread around the planet and this vector has been the cause of the spread of a large number of pest species. Mediterranean mussels (*Mytilus galloprovincialis*) and zebra mussels (*Dreissena polymorpha*) have been spread extensively between ports in this manner.
Ship/boat hull fouling	Ships have many different methods of transporting species great distances, a simple vector is for those species that, although themselves being static, they establish a small colony on a ship's hull and develop during a voyage and are spread merely by their normal processes of reproduction being on a mobile substrate. This vector provides for the spread of many mollusks, fanworm, algae and aquatic plant species. Depending on the methods of anti-fouling, when a ship is taken into dry dock and has its hull cleaned species that are removed, if not carefully disposed of, can establish locally when the dock is re-flooded.

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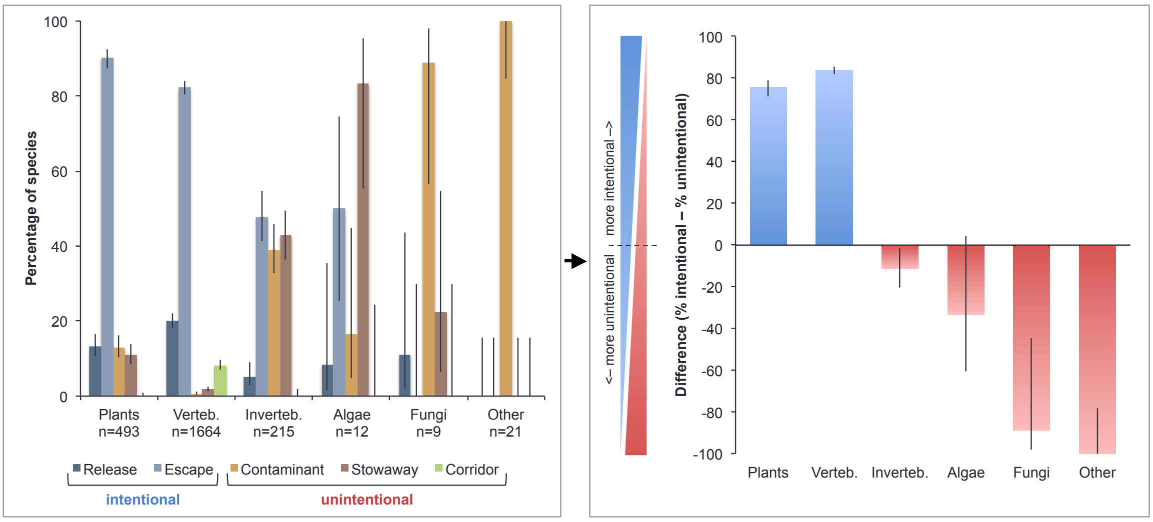
	Vehicles (car, train, …)	Simple, local spread of species can occur involuntarily when species or reproductive organs of species become trapped in cars or trains or other vehicles and are released at the destination. Passengers in a train might eat a fruit or vegetable and throw the remains out of the window inadvertently causing the establishment of a species not naturally present at that location. For instance, Oxford ragwort (*Senecio squalidus*) was spread along the rail network of the UK from Oxford, where it had established in the botanical garden, by seeds being drawn along the tracks.
	Other means of transport	Any form of transportation that interacts with habitats at either end of its journey or continuously passes through a range of habitats and ecosystems has the potential to passively collect and deposit propagules, seeds, animals, fungi etc. and to cause their spread. This does not necessarily have to be a plane or a ship; a person walking through a field, over a mountain pass and through a second field will transfer organisms from the first to the second location. A good example of a species that utilizes any human vector is the Singapore ant (*Monomorium destructor*), a serious pest species that is spread by human trade.
CORRIDOR Refers to movement of alien organisms into a new region following the construction of transport infrastructures in whose absence spread would not have been possible.	Interconnected waterways/basins/seas, tunnels and land bridges	Such transbiogeographical corridors include international canals (connecting river catchments and seas) as well as transboundary tunnels linking mountain valleys or oceanic islands.
UNAIDED Refers to the secondary natural dispersal of invasive alien species that have been introduced by means of any of the above pathways.	Natural dispersal across borders of invasive alien species that have been introduced through any of the other pathways	While the secondary dispersal is unaided, it can only take place because of a previous human intervention. Information on the mechanisms of secondary spread of invasive alien species, after their introduction, are relevant to define the best response measures.

Table A2.2 – Detailed numerical description of the datasets GISD/IASPMR, DAISIE, and combined. Values are numbers of species in the respective dataset.

	GISD/IASPMR						**DAISIE**						**Combined dataset**					
	terrestrial	freshwater	marine	multip.	unassigned*	dataset total	terrestrial	freshwater	marine	multip.	unassigned*	dataset total	terrestrial	freshwater	marine	multip.	unassigned*	dataset total
Plants	275	129	2	85	2	493	3563	40	1	32	0	3636	3713	137	2	96	2	3950
Verteb.	532	441	433	256	2	1664	128	110	70	69	0	377	620	480	447	274	2	1823
Inverteb.	75	79	40	21	0	215	1387	207	427	19	0	2040	1442	276	453	32	0	2203
Algae	0	1	9	2	0	12	0	29	136	2	0	167	0	30	142	2	0	174
Fungi	8	0	0	1	0	9	69	7	1	0	0	77	76	7	1	1	0	85
Other	14	1	0	6	0	21	29	22	20	2	0	73	40	22	20	7	0	89
Total	**904**	**651**	**484**	**371**	**4**	**2414**	**5176**	**415**	**655**	**124**	**0**	**6370**	**5891**	**952**	**1065**	**412**	**4**	**8324**

*These species could not be considered in the environment-focused analysis due to ambiguous species names by which it was not possible to assign a particular environment to the respective records.

a) Taxonomic groups



b) Environments

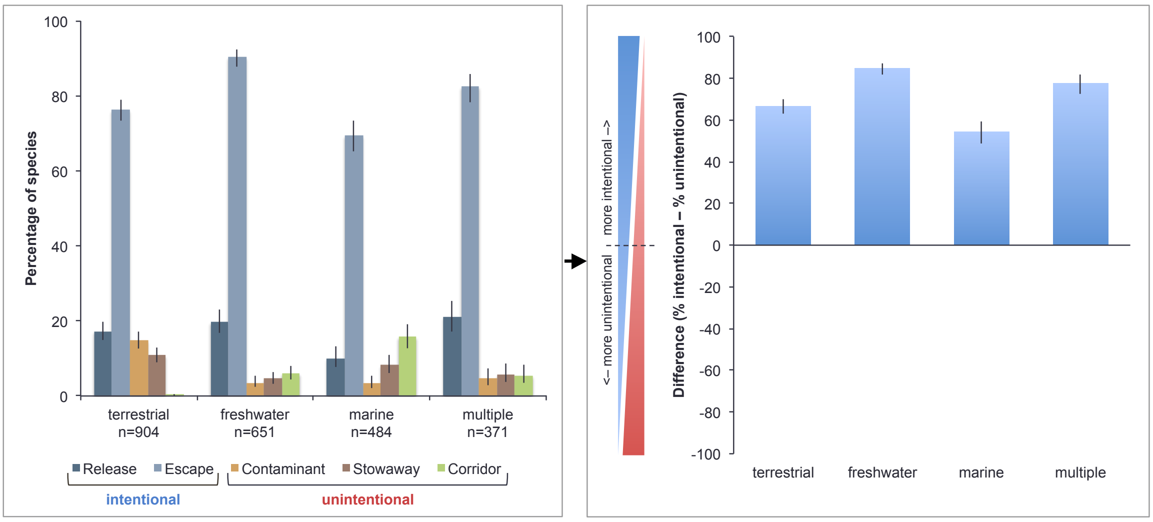
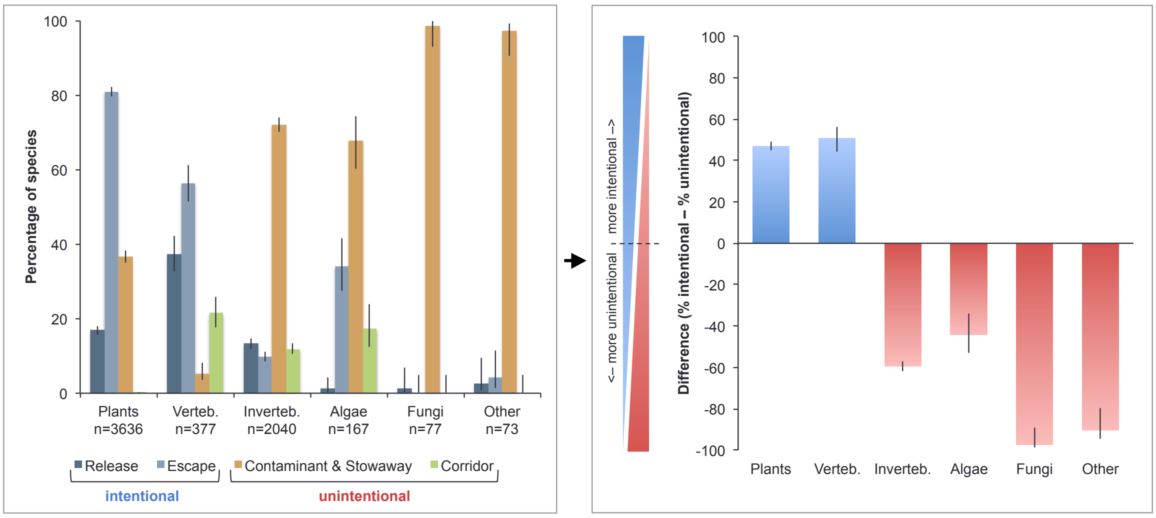


Figure A2.1 – Introduction pathways in the GISD/IASPMR dataset. Pathways were analyzed according to (a) taxonomic groups (2,414 species) and (b) environments (2,410 species). Left-hand side graphs show individual proportions of pathways (the sum of proportions is larger than 100% in all taxonomic groups and habitats since species can be introduced via more than one pathway). Right-hand side graphs show the difference in accumulated proportions of intentional and unintentional pathways (excluding species that fall in both categories). Error bars indicate 95% Wilson confidence intervals.

a) Taxonomic groups



b) Environments

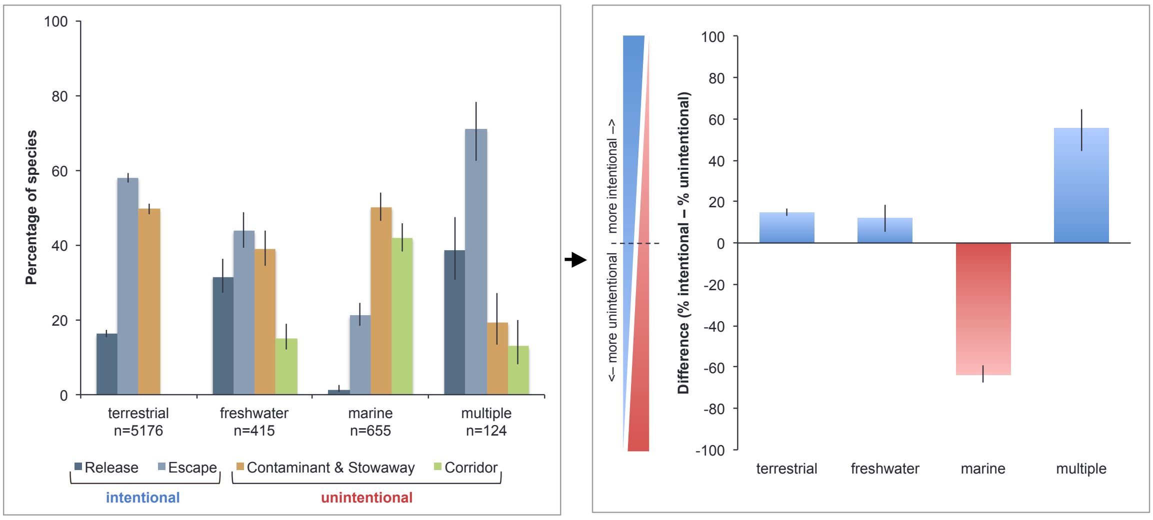
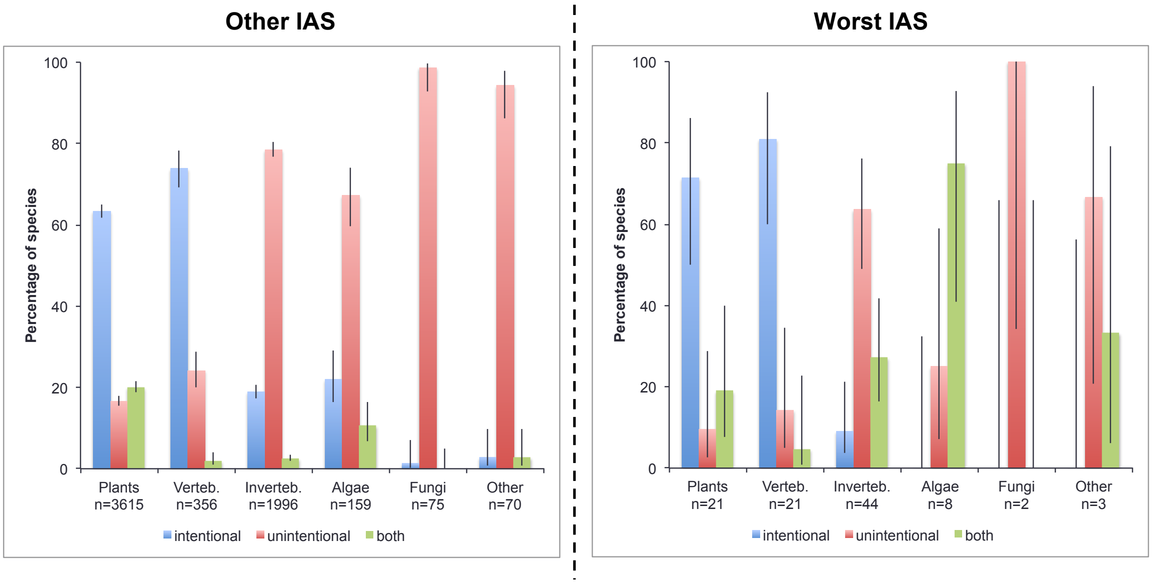


Figure A2.2 – Introduction pathways in the DAISIE dataset. Pathways of 6,370 species were analyzed according to (a) taxonomic groups and (b) environments. Left-hand side graphs show individual proportions of pathways (the sum of proportions is larger than 100% in all taxonomic groups and habitats since species can be introduced via more than one pathway). Right-hand side graphs show the difference in accumulated proportions of intentional and unintentional pathways (excluding species that fall in both categories). Error bars indicate 95% Wilson confidence intervals.

a) Taxonomic groups



b) Environments

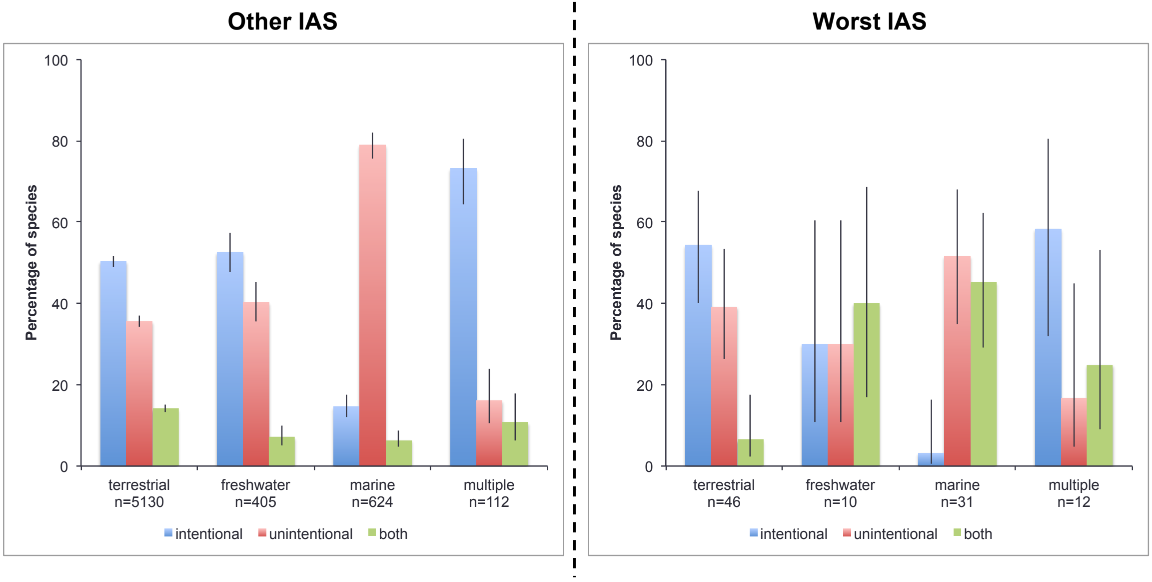


Figure A2.3 – Introduction pathways in regard to their intentionality for 'Other IAS' (left-hand side) *vs.* 'Worst IAS' (right-hand side) in the DAISIE dataset. Pathways were analyzed according to (a) taxonomic groups and (b) environments (Other IAS: 6,271 species; Worst IAS: 99 species). Error bars indicate 95% Wilson confidence intervals.

Table A3.1 – Dataset used for the analyses, and list of references the information is based on. For each of the 201 species, information on 13 potential invasion traits was collected using USDA (2009a,b), BfN (2013), DAISIE (2013), GISD (2013), IUCN (2013), and NOBANIS (2013). Additional sources are given in a separate column (reference list see p. 136). Taxonomic affiliation follows Maddison & Schulz (2010). Species nomenclature follows the publications used as reference. Abbreviations: Invasion traits: 1: yes, 0: no; taxonomic group: 1: bacteria, 2: plants, 3: red algae, 4: animals, 5: fungi, 6: alveolates, 7: heterokonts; hypothetical invader types: 0: no assignment, 1: drifters, 2: fugitives, 3: establishers, 4: spreaders, 5: promoted.

Species	**Intentional transportation?**	**In IUCN Red List? (2013)**	**Transportation as diaspore?**	**Seedbank?**	**Intentional release?**	**Release adult?**	**Phenotypic plasticity?**	**Can one individual form a population?**	**More than one reproduction per year?**	**Fecundity above average?**	**Offspring in first year?**	**Intentional spread?**	**Spread as active mobile organism?**	**References**	**Taxonomic group**	**2-Cluster**	**3-Cluster**	**5-Cluster**	**Invader type**
Acacia dealbata	1	0	1	1	1	0	1	1	1	1	0	0	0	Lorenzo et al. 2010	2	1	3	5	3
Acanthaster planci	0	0	0	0	0	0	1	0	0	1	0	0	0	Babcock & Mundy 1992; Mills 2012	4	2	2	2	0
Acanthophora spicifera	0	0	0	1	0	1	1	1	1	1	1	0	0	University of Hawaii 2002	3	1	1	1	3
Acer platanoides	1	0	1	1	0	0	1	0	0	0	0	0	0	Paquette et al. 2012	2	1	1	3	0
Acridotheres tristis	1	0	0	0	1	1	0	0	1	1	1	0	1	Bennett 1986; McLain et al. 1999; Cassey 2001	4	2	2	4	4
Aedes albopictus	0	0	1	1	0	1	1	0	1	0	1	0	1	Löwenberg Neto & Navarro-Silva 2004; Reynolds et al. 2012; Yee et al. 2012	4	2	2	2	1
Ailanthus altissima	1	0	0	1	0	0	1	0	0	1	0	0	0	Landenberger et al. 2006; Mou et al. 2012	2	1	1	3	0
Alexandrium catenella	0	0	1	1	0	0	0	1	1	0	1	0	1		6	1	1	1	1
Alosa pseudoharengus	0	0	0	0	0	1	0	0	0	0	0	0	1	Carlander 1969	4	2	2	2	0
Alternanthera philoxeroides	0	0	1	0	0	1	1	1	1	0	1	0	0	Geng et al. 2006	2	1	1	1	2
Amaranthus retroflexus	0	0	1	1	0	0	1	1	0	1	1	0	0	Wang et al. 2006c	2	1	1	3	1
Ambrosia artemisiifolia	0	0	1	1	0	0	0	1	0	0	1	0	0	Lavoie et al. 2003; Brandes & Nietzsche 2006	2	1	1	3	1
Anas platyrhynchos	1	0	0	0	1	1	0	0	0	1	1	0	1	König 1967; Lever 1987; Janis & Carrano 1992	4	2	2	4	4
Andropogon virginicus	0	0	1	1	0	0	0	1	0	0	0	0	0		2	1	1	3	1
Anoplolepis gracilipes	0	0	0	0	0	1	0	1	0	0	1	0	1	Rao & Veeresh 1991	4	2	2	2	0
Anoplophora glabripennis	0	0	0	0	0	1	0	0	0	0	1	0	1	Li & Liu 1997; Hu et al. 2009	4	2	2	2	0
Aphanomyces astaci	0	0	1	0	0	1	0	1	1	0	1	0	1	Fisheries and Oceans Canada 2013	7	2	2	2	0
Aphis gossypii	0	0	0	0	0	1	1	1	1	0	1	0	1	Messing et al. 2007	4	2	2	2	0

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Balanus improvisus	0	0	1	0	0	0	0	1	1	0	1	0	0	Leppäkoski 1999; Daehne 2013	4	1	1	1	1
Batillaria attramentaria	0	0	0	0	0	1	0	0	0	0	0	0	1	Byers & Goldwasser 2001	4	2	2	2	0
Batrachochytrium dendrobatidis	0	0	1	0	0	1	0	1	1	0	1	0	1		5	2	2	2	0
Bemisia tabaci	0	0	0	0	0	1	1	0	1	0	1	0	1	Martin 1999; Guershon & Gerling 2001, 2006; Mau et al. 2007; Malumphy et al. 2009	4	2	2	2	0
Boiga irregularis	0	0	0	0	0	1	0	1	1	1	0	0	1	Fritts & Rodda 1998; Savidge et al. 2007	4	2	2	2	0
Bonnemaisonia hamifera	0	0	1	1	0	1	0	1	1	0	1	0	0		3	1	1	1	1
Branta canadensis	1	0	0	0	1	1	0	0	0	0	0	0	1	König 1967; Cassey 2001; Hayman & Hume 2002	4	2	2	4	4
Bubo virginianus	1	0	0	0	1	1	0	0	0	0	0	0	1	Schoener 1968; Bennett 1986; Myers et al. 2013	4	2	2	4	4
Bunias orientalis	1	0	1	1	0	0	0	1	1	1	1	0	0	Dietz et al. 1999	2	1	1	3	3
Caiman crocodilus	1	0	0	0	0	1	0	1	0	0	0	0	1		4	2	2	4	0
Campylopus introflexus	0	0	1	0	0	0	0	1	1	1	1	0	0		2	1	1	1	3
Canis lupus familiaris	1	0	0	0	0	1	0	0	0	0	0	0	1		4	2	2	4	0
Carcinus maenas	0	0	0	0	0	1	1	0	0	1	0	0	0	Todd et al. 2012	4	2	2	2	2
Carduelis carduelis	1	0	0	0	1	1	0	0	1	1	1	0	1	König 1966; Bennett 1986; Cassey 2001	4	2	2	4	4
Carpobrotus edulis	1	0	1	1	1	0	1	1	1	1	1	1	0	Weber & D'Antonio 1999	2	1	3	5	3
Castor canadensis	1	0	0	0	0	1	0	0	0	0	0	0	1		4	2	2	4	0
Caulerpa taxifolia	1	0	1	1	0	1	1	1	1	1	1	0	0	NIMPIS 2009	2	1	1	1	3
Ceratostoma inornatum	0	0	0	0	0	0	0	0	0	0	1	0	0		4	1	1	1	0
Cercopagis pengoi	0	0	1	1	0	0	0	1	1	0	1	0	0		4	1	1	1	1
Cervus elaphus	1	0	0	0	1	1	0	0	0	0	0	0	1	Purvis & Harvey 1995	4	2	2	4	4
Channa argus	1	0	0	0	1	1	0	0	1	0	0	0	1		4	2	2	4	4
Chromolaena odorata	1	0	1	1	0	0	1	0	0	1	0	0	0	Wang et al. 2006a	2	1	1	3	0
Chrysemys picta	1	0	0	0	1	1	1	1	0	0	0	0	1	Jackson 2002; Pearse et al. 2002; Rowe et al. 2009; Myers et al. 2013	4	2	2	4	4
Cichla kelberi	1	0	0	0	1	1	0	1	1	0	1	1	1	Fontenele 1950; Chellappa et al. 2003; Gomiero & Braga 2004	4	2	2	4	5

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Cichla ocellaris	1	0	0	0	1	0	0	0	1	0	1	1	1		4	2	2	4	5
Cinnamomum camphora	1	0	0	1	0	0	0	1	0	0	0	0	0	Duever 2005	2	1	1	3	0
Circus approximans	1	0	0	0	1	1	0	0	0	0	0	0	1		4	2	2	4	4
Cirsium arvense	0	0	1	1	0	0	1	1	1	0	1	0	0	Ryser & Eek 2000	2	1	1	3	1
Codium fragile spp. *tomentosoides*	0	0	1	0	0	1	1	1	1	0	1	0	0		2	1	1	1	2
Columba livia	1	0	0	0	0	1	0	0	1	1	0	0	1	Heinroth 1922; Bennett 1986; Cassey 2001	4	2	2	4	0
Conyza canadensis	0	0	1	0	0	0	1	1	0	1	1	0	0	Alexander et al. 2009	2	1	1	3	3
Coptotermes formosanus	0	0	0	0	0	1	0	0	0	0	1	0	1	Suiter et al. 2013	4	2	2	2	0
Cortaderia selloana	1	0	1	1	1	1	1	1	0	1	1	0	0	Vourlitis & Kroon 2013	2	1	1	3	3
Corvus splendens	1	0	0	0	1	1	0	0	1	0	0	0	1	Bennett 1986; Cassey 2001	4	2	2	4	4
Coscinodiscus wailesii	0	0	1	1	0	1	0	1	1	1	1	0	0		7	1	1	1	1
Crassula helmsii	1	0	1	1	0	1	1	1	1	1	1	0	0		2	1	1	1	3
Cronartium ribicola	0	0	1	0	0	1	0	1	1	0	1	0	0	Maloy 2003	5	1	1	1	2
Cryphonectria parasitica	0	0	1	0	0	1	0	1	1	0	1	0	0		5	1	1	1	2
Ctenopharyngodon idella	1	0	0	0	1	0	0	0	0	1	0	0	1		4	2	2	4	4
Ctenosaura similis	1	0	0	0	1	1	0	1	0	1	0	0	1	Krysko et al. 2003; Townsend et al. 2003; Myers et al. 2013	4	2	2	4	4
Cupressus macrocarpa	1	1	0	1	1	1	0	0	0	0	0	0	0		2	2	2	4	5
Cyathea cooperi	1	0	1	1	0	0	0	0	0	0	1	0	0		2	1	1	3	0
Cyclura nubila spp. *nubila*	1	1	0	0	0	1	0	1	0	0	0	0	1	Christian 1986; Lemm & Alberts 1997	4	2	2	4	0
Cygnus olor	1	0	0	0	1	1	0	0	0	1	0	0	1	Lever 1987; Janis & Carrano 1992	4	2	2	4	4
Cyprinus carpio	1	1	0	0	1	1	1	0	0	0	0	1	1	Bănărescu & Paepke 2002; Weber et al. 2012	4	2	2	4	5
Danaus plexippus	0	0	0	0	0	1	1	0	1	0	1	0	1	Solensky & Larkin 2003	4	2	2	2	0
Daphnia lumholtzi	0	0	1	1	0	0	1	1	1	0	1	0	0	Work & Gophen 1999; Burns 2000; Lennon et al. 2001	4	1	1	3	1
Dendrobates auratus	1	0	0	0	1	1	1	0	0	0	0	0	1	AmphibiaWeb 2013; Flores et al. 2013; Ostrowski & Mahn 2013	4	2	2	4	4

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Didymosphenia geminata	0	0	1	0	0	1	0	1	1	0	1	0	0		7	1	1	1	2
Dreissena polymorpha	0	0	1	0	0	0	0	0	1	1	1	0	0	Mackie et al. 1989; Borcherding 1991; Mackie 1991	4	1	1	1	1
Echinocystis lobata	1	0	1	1	0	0	0	1	0	0	1	0	0		2	1	1	3	0
Eichhornia crassipes	1	0	0	0	1	1	1	1	1	1	1	1	0	Andrade et al. 2013	2	1	3	5	3
Elaeis guineensis	1	0	0	1	0	0	0	0	1	0	0	0	0		2	1	1	3	0
Eleutherodactylus coqui	0	0	0	0	0	1	0	0	1	1	0	0	1	Kraus et al. 1999; Sin & Radford 2007; AmphibiaWeb 2013	4	2	2	2	0
Eleutherodactylus planirostris	0	0	0	0	0	1	0	0	1	0	0	0	1	AmphibiaWeb 2013	4	2	2	2	0
Elodea canadensis	1	0	0	0	1	0	1	1	1	0	1	0	0	Riis et al. 2010	2	1	3	5	3
Erigeron annuus	1	0	1	1	0	0	0	1	0	1	0	0	0	Lohmeyer & Sukopp 1992; Trtikova et al. 2010	2	1	1	3	0
Erinaceus europaeus	1	0	0	0	1	1	0	0	1	0	1	0	1	Purvis & Harvey 1995	4	2	2	4	4
Eriocheir sinensis	0	0	0	0	0	0	0	1	0	1	0	0	1		4	2	2	2	4
Eschscholzia californica	0	0	0	1	0	0	1	1	0	1	1	0	0	Leger & Rice 2003; Leger & Forister 2005	2	1	1	3	3
Felis catus	1	0	0	0	1	1	0	0	1	1	1	1	1	Purvis & Harvey 1995	4	2	2	4	5
Ficopomatus enigmaticus	0	0	1	0	0	0	0	0	1	0	1	0	0		4	1	1	1	1
Galinsoga parviflora	1	0	1	1	0	0	0	0	0	0	1	0	0		2	1	1	3	0
Gambusia affinis	1	0	0	0	1	1	1	0	1	0	1	0	1	Stockwell & Vinyard 2000	4	2	2	4	4
Glandirana rugosa	1	0	0	0	1	1	0	0	1	0	0	0	1	AmphibiaWeb 2013	4	2	2	4	4
Gracilaria salicornia	1	0	1	0	1	1	0	1	1	1	1	0	0	Oyieke 1994; Gurgel & Fredericq 2004	3	1	1	1	3
Gymnodinium mikimotoi	0	0	1	1	0	1	0	1	1	1	1	0	1		6	1	1	1	1
Gymnorhina tibicen	1	0	0	0	1	1	0	0	0	0	0	0	1	Bennett 1986; Cassey 2001	4	2	2	4	4
Halophila stipulacea	0	0	1	0	0	1	0	1	1	0	1	0	0		2	1	1	1	2
Harmonia axyridis	1	0	0	0	0	1	1	1	1	1	1	0	1	Hodek & Ceryngier 2000; Koch 2003; Bazzocchi et al. 2004; Nalepa & Weir 2007; Michie et al. 2010; Michie et al. 2011	4	2	2	2	3
Hedychium gardnerianum	1	0	1	1	0	1	0	1	1	0	1	0	0		2	1	1	1	2

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Helianthus tuberosus	1	0	0	0	0	1	0	1	1	0	1	0	0		2	1	1	1	2
Hemidactylus frenatus	0	0	0	0	0	1	0	1	1	0	0	0	1		4	2	2	2	0
Heracleum mantegazzianum	1	0	1	1	1	0	0	1	0	1	0	0	0		2	1	1	3	5
Herpestes javanicus	1	0	0	0	1	1	0	0	1	0	1	0	1	Binida-Emonds 1998	4	2	2	4	4
Hypochaeris radicata	0	0	1	1	0	0	0	0	0	0	1	0	0		2	1	1	3	1
Hypophthalmichthys molitrix	1	1	0	0	0	1	1	0	0	0	0	0	1	Coulter et al. 2013	4	2	2	4	0
Iguana iguana	1	0	0	0	1	1	0	1	0	1	0	0	1	Meshaka et al. 2007; Myers et al. 2013	4	2	2	4	4
Impatiens glandulifera	1	0	1	1	0	0	1	1	0	1	1	0	0	Pahl et al. 2013	2	1	1	3	3
Impatiens parviflora	1	0	1	1	0	0	1	1	0	0	1	0	0	Trepl 1984; Skalova et al. 2012	2	1	1	3	3
Ipomoea aquatica	0	0	0	0	0	1	0	1	1	0	1	0	0		2	1	1	1	2
Lachnellula willkommii	0	0	1	0	0	1	0	1	1	0	1	0	0		5	1	1	1	2
Lantana camara	1	0	1	1	0	0	0	1	1	1	0	0	0	Day et al. 2003; Carrion-Tacuri et al. 2011	2	1	1	3	3
Lates niloticus	1	0	0	0	1	1	0	0	0	1	0	1	1	Kegel 1999	4	2	2	4	5
Lithobates catesbeianus	1	0	0	0	1	1	0	0	1	1	0	0	1		4	2	2	4	4
Littorina littorea	0	0	0	0	0	1	1	0	0	0	0	0	1	Hollander et al. 2006	4	2	2	2	0
Lupinus polyphyllus	1	0	1	1	1	0	1	1	0	0	1	0	0	Chmelíková & Hejcman 2012; Sõber & Ramula 2013	2	1	1	3	5
Lygodium japonicum	1	0	1	1	0	0	0	1	0	1	0	0	0	Lott et al. 2003	2	1	1	3	0
Lysichiton americanus	1	0	0	0	1	1	0	0	0	0	1	0	0		2	2	2	4	5
Melilotus albus	1	0	1	1	0	0	0	1	0	0	1	0	0		2	1	1	3	0
Mesotriton alpestris	1	0	0	0	1	1	1	0	1	0	0	0	1	Bell & Bell 1995; Van Buskirk 2011	4	2	2	4	4
Micropterus salmoides	1	0	0	0	1	0	0	0	0	0	0	1	1	Carlander 1977; AnAge 2012	4	2	2	4	5
Mikania micrantha	1	0	1	1	1	1	0	1	1	1	1	0	0		2	1	1	1	3
Mimosa pigra	1	0	1	1	1	0	0	1	1	1	1	0	0		2	1	1	1	3
Mimulus guttatus	1	0	0	0	0	1	0	1	1	1	1	0	0	Holeski 2007	2	1	1	1	2
Mnemiopsis leidyi	0	0	0	0	0	0	0	1	1	1	1	0	0		4	1	1	1	3

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Molothrus ater	0	0	0	0	0	1	0	0	1	1	1	0	1		4	2	2	2	0
Molothrus bonariensis	0	0	0	0	0	1	0	0	1	1	1	0	1		4	2	2	2	0
Morella faya	1	0	1	1	0	0	0	0	0	1	0	0	0	Vitousek & Walker 1989; Arevalo et al. 2007; US Forest Service 2013	2	1	1	3	0
Muntiacus reevesi	1	0	0	0	0	1	0	0	0	0	1	0	1		4	2	2	4	0
Mus musculus	0	0	0	0	0	1	0	0	1	1	1	0	1	Ernest 2003	4	2	2	2	0
Musculista senhousia	0	0	0	0	0	1	0	0	0	1	1	0	0		4	2	2	2	2
Mustela erminea	1	0	0	0	1	1	0	0	0	0	1	0	1	Binida-Emonds 1998	4	2	2	4	4
Mustela nivalis	1	0	0	0	1	1	0	0	1	1	1	0	1	Binida-Emonds 1998	4	2	2	4	4
Mycale grandis	0	0	0	0	0	1	0	1	1	0	1	0	0		4	1	1	1	2
Myocastor coypus	1	0	0	0	0	1	0	0	1	0	1	0	1		4	2	2	2	0
Myxobolus cerebralis	0	0	1	1	0	1	0	1	1	0	1	0	0	Montana Water Center 2011	4	1	1	1	1
Neogobius melanostomus	0	0	1	0	0	0	0	0	1	0	1	0	0	Miller 2003	4	1	1	1	1
Neovison vison	1	0	0	0	0	1	0	0	0	0	0	0	1	Binida-Emonds 1998	4	2	2	4	0
Nephrolepis cordifolia	1	0	1	1	0	0	0	1	1	0	1	0	0	Center for Aquatic and Invasive Plants 2013	2	1	1	3	3
Norops sagrei	0	0	0	0	0	1	1	1	0	0	0	0	1	Sever & Hamlett 2002; Myers et al. 2013	4	2	2	2	0
Odontella sinensis	0	0	1	0	0	1	0	1	1	0	1	0	0		7	1	1	1	2
Oncorhynchus gorbuscha	0	0	0	0	0	0	0	0	0	0	0	0	1	Jeschke & Strayer 2006; AnAge 2012	4	2	2	2	4
Oncorhynchus mykiss	1	0	0	0	1	0	0	0	0	0	0	1	1	Carlander 1969	4	2	2	4	5
Oopterus soledadinus	0	0	0	0	0	1	0	1	0	0	1	0	1	Ernsting 1993; Lebouvier et al. 2005	4	2	2	2	0
Ophiostoma ulmi sensu lato	0	0	1	0	0	1	0	1	1	0	1	0	0		5	1	1	1	2
Opuntia stricta	1	0	1	1	1	1	0	1	1	1	1	0	0	Eurobodalla 2013	2	1	1	1	3
Orthodontium lineare	0	0	1	1	0	0	0	1	0	0	1	0	0		2	1	1	3	1
Oryctolagus cuniculus	1	1	0	0	1	1	0	0	1	0	1	0	1		4	2	2	4	4
Osteopilus septentrionalis	0	0	0	0	0	1	0	0	1	1	1	0	1	Masterson 2007; AmphibiaWeb 2013	4	2	2	2	0
Oxalis pes-caprae	0	0	1	0	0	0	1	1	0	0	1	0	0	Verdaguer et al. 2010	2	1	1	3	1

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Oxyura jamaicensis	1	0	0	0	0	0	0	0	0	0	0	0	1	Bennett 1986	4	2	2	2	4
Paspalum distichum	0	0	1	0	0	0	0	1	1	0	1	0	0		2	1	1	1	1
Passer domesticus	1	0	0	0	1	1	0	0	1	1	1	0	1	Heinroth 1922; Cassey 2001	4	2	2	4	4
Pasteurella multocida	0	0	0	0	0	1	0	1	1	0	1	0	0		1	1	1	1	2
Pennisetum setaceum	1	0	0	0	0	0	1	1	1	0	1	0	0	Poulin et al. 2007	2	1	3	5	3
Perca fluviatilis	1	0	0	0	1	0	1	0	0	1	0	1	1	Jeschke & Strayer 2006; Svenbäck & Eklöv 2006; Eklöv & Jonsson 2007; Kekäläinen et al. 2010a; Kekäläinen et al. 2010b	4	2	2	4	5
Petromyzon marinus	0	0	0	0	0	1	0	0	0	0	0	0	0		4	2	2	2	2
Phasianus colchicus	1	0	0	0	1	1	0	0	0	0	1	1	1	Bennett 1986; Janis & Carrano 1992	4	2	2	4	5
Phellinus noxius	0	0	1	1	0	1	0	1	1	0	1	0	0	Bartz 2007	5	1	1	1	1
Phytophthora cinnamomi	0	0	1	1	0	1	0	0	1	1	1	0	1		7	1	1	1	1
Pinus nigra	1	0	0	0	1	1	1	1	0	0	0	0	0	Richter et al. 2012	2	2	2	4	5
Pinus pinaster	1	0	0	1	0	0	1	0	0	0	0	0	0	Corcuera et al. 2011	2	1	1	3	0
Pinus strobus	1	0	0	1	1	1	0	1	0	0	0	0	0		2	2	2	4	5
Pistia stratiotes	1	0	0	0	0	1	0	1	1	0	1	0	0	Rivers 2002	2	1	1	1	2
Plasmodium relictum	0	0	0	0	0	1	0	1	1	0	1	0	0		6	1	1	1	2
Platydemus manokwari	1	0	0	0	1	1	0	1	1	0	1	0	1	Kaneda et al. 1990	4	2	2	4	4
Polistes chinensis antennalis	0	0	0	0	0	1	0	1	0	0	1	0	1	Clapperton & Lo 2000	4	2	2	2	0
Procyon lotor	1	0	0	0	1	1	0	0	0	1	0	0	1	Binida-Emonds 1998	4	2	2	4	4
Prosopis glandulosa	1	0	1	1	1	0	1	1	0	1	0	1	0	Martinez & Lopez-Portillo 2003	2	1	3	5	5
Proterorhinus marmoratus	0	0	1	0	0	0	0	0	0	0	1	0	0	Miller 2004	4	1	1	1	1
Prunus serotina	1	0	0	1	1	0	1	1	1	0	0	1	0	Abrams & Mostoller 1995	2	1	3	5	5
Pseudoscleropodium purum	1	0	1	0	0	1	0	1	1	0	1	0	0	Miller & Trigoboff 2001	2	1	1	1	2
Pseudotsuga menziesii	1	0	0	1	1	1	1	1	0	0	0	0	0	Martinez-Meier et al. 2009	2	2	2	4	5
Pueraria montana var. lobata	1	0	1	1	1	0	0	1	1	1	1	0	0		2	1	1	1	3

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Pycnonotus cafer	0	0	0	0	0	1	0	0	1	0	1	0	1	Bennett 1986; Cassey 2001	4	2	2	2	0
Python bivittatus	1	1	0	0	1	1	1	1	0	0	0	0	1	Wang et al. 2006b	4	2	2	4	4
Quercus rubra	1	0	1	1	1	0	1	1	0	1	0	1	0	Brun 1987; Abrams 1994; Dressel & Jäger 2002	2	1	3	5	5
Rangifer tarandus	1	0	0	0	1	1	0	0	0	0	0	0	1	Purvis & Harvey 1995	4	2	2	4	4
Rapana venosa	0	0	1	1	0	0	0	0	1	1	0	0	0		4	1	1	3	1
Rattus rattus	0	0	0	0	0	1	0	0	1	1	1	0	1	Millar 1981; Ernest 2003	4	2	2	2	0
Rhinella marina	1	0	0	0	1	1	1	0	1	1	0	0	1	Brown et al. 2011; Seebacher & Franklin 2011; Shine 2012	4	2	2	4	4
Rhododendrum ponticum	1	0	0	1	0	0	1	1	0	1	0	0	0	Niinemets et al. 2003	2	1	1	3	3
Robinia pseudoacacia	1	0	1	1	1	0	1	1	1	1	0	0	0	Xu et al. 2009	2	1	3	5	3
Rosa rugosa	1	0	0	1	1	0	0	1	1	0	0	1	0	Bruun 2005	2	1	3	5	5
Salvelinus namaycush	1	0	0	0	1	0	0	0	0	0	0	1	1	Carlander 1969	4	2	2	4	5
Salvinia minima	1	0	1	1	0	1	0	1	1	1	1	0	0		2	1	1	1	2
Sciurus carolinensis	1	0	0	0	1	1	0	0	1	0	1	0	1	Millar 1981; Purvis & Harvey 1995	4	2	2	4	4
Senecio inaequidens	0	0	1	1	0	0	1	1	1	1	1	0	0	Ernst 1998; Monty et al. 2013	2	1	1	3	3
Sirex noctilio	0	0	0	0	0	1	0	1	1	0	0	0	1		4	2	2	2	0
Solenopsis invicta	0	0	0	0	0	1	1	1	0	1	1	0	1	Keller & Ross 1993; Morisawa 2000; Collins & Scheffrahn 2013; Lockley 2013	4	2	2	2	0
Solidago canadensis	1	0	1	0	0	0	1	1	0	1	1	0	0	Sun et al. 2008	2	1	1	3	3
Spartina alterniflora	1	0	0	1	1	1	1	1	1	0	1	1	0	Ma & Shi 2011	2	1	3	5	5
Streptopelia decaocto	1	0	0	0	0	1	0	0	0	0	1	0	1	König 1967; Bennett 1986	4	2	2	4	0
Sturnus vulgaris	1	0	0	0	1	1	0	0	1	1	0	0	1	Martin 1995; Cassey 2001	4	2	2	4	4
Thuja occidentalis	1	0	0	1	0	0	0	0	0	0	0	0	0		2	1	1	3	0
Tilapia mariae	1	0	0	0	0	1	0	0	1	1	1	0	1	Stauffer & Gray 2004	4	2	2	2	0
Tinca tinca	1	0	0	0	1	0	0	0	0	1	0	1	1	Bănărescu 1999	4	2	2	4	5
Trachemys scripta elegans	1	0	0	0	1	1	1	1	0	0	0	0	1	Rowe et al. 2009; Ernst et al. 2013; Myers et al. 2013	4	2	2	4	4

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Species	Intentional transportation?	In IUCN Red List? (2013)	Transportation as diaspore?	Seedbank?	Intentional release?	Release adult?	Phenotypic plasticity?	Can one individual form a population?	More than one reproduction per year?	Fecundity above average?	Offspring in first year?	Intentional spread?	Spread as active mobile organism?	References	Taxonmic group	2-Cluster	3-Cluster	5-Cluster	Invader type
Trichosurus vulpecula	1	0	0	0	1	1	0	0	1	0	1	1	1		4	2	2	4	5
Trogoderma granarium	0	0	1	1	0	1	0	0	1	0	1	0	0	Harris 2009	4	1	1	1	1
Ulex europaeus	1	0	0	1	0	0	0	0	1	0	0	0	0	Buckley et al. 2003	2	1	1	3	0
Undaria pinnatifida	1	0	1	1	0	0	0	0	1	0	1	0	0	Choi et al. 2005; Schaffelke et al. 2005; Gao et al. 2013; NIMPIS 2013	7	1	1	3	0
Varanus indicus	1	0	0	0	1	1	0	0	1	0	1	0	1	Monitor-Lizards 2013	4	2	2	4	4
Varroa destructor	0	0	0	0	0	1	1	1	1	1	1	0	1	Donzé et al. 1998; Corrêa-Marques et al. 2003; East Lothian Beekeepers Association 2004; Maggi et al. 2009; Ages 2013; Ellis & Zettel Nalen 2013	4	2	2	2	3
Verbascum thapsus	1	0	0	1	0	0	1	1	0	1	0	0	0	Parker et al. 2003	2	1	1	3	3
Vibrio cholerae	0	0	0	1	0	1	0	1	1	0	1	0	1	Brunings & Gabriel 2003; Graham et al. 2004; Medical Ecology 2004	1	2	2	2	0
Vulpes vulpes	1	0	0	0	1	1	0	0	0	1	1	0	1		4	2	2	4	4
Xanthomonas citri	0	0	0	0	0	1	0	1	1	0	1	0	1	Gottwald & Graham 2005	1	2	2	2	0
Xenopus laevis	1	0	0	0	0	1	1	0	1	1	0	0	1	Gouchie et al. 2008; Walsh et al. 2009; Myers et al. 2013	4	2	2	4	0
Xylella fastidiosa	0	0	0	0	0	1	0	1	1	0	1	0	0	Liberato et al. 2011	1	1	1	1	2
Yersinia pestis	0	0	0	0	0	1	0	1	1	0	1	0	1		1	2	2	2	0
Zosterops japonicus	1	0	0	0	1	1	0	0	1	1	1	0	1		4	2	2	4	4

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Table A3.2 – Relative frequencies (%) of invasion trait values. Data are given for all species in our dataset, and for each of the seven taxonomic groups separately.

	Invasion trait	Value	All species (n = 201)	Bacteria (n = 5)	Plants (n = 70)	Red Algae (n = 3)	Animals (n = 108)	Fungi (n = 6)	Alveo-lates (n = 3)	Hetero-konts (n = 6)
Transport	Intentional transport	Yes	59	0	77	33	58	0	0	17
		No	41	100	23	67	42	100	100	83
	In IUCN Red List	Yes	3	0	1	0	5	0	0	0
		No	97	100	99	100	95	100	100	100
	Transport as diaspore	Yes	36	0	66	67	10	100	67	100
		No	64	100	34	33	90	0	33	0
	Seed bank	Yes	33	20	74	67	6	17	67	50
		No	67	80	26	33	94	83	33	50
Escape	Intentional release	Yes	36	0	31	33	45	0	0	0
		No	64	100	69	67	55	100	100	100
	Release adult	Yes	65	100	31	100	81	100	67	83
		No	35	0	69	0	19	0	33	17
Establishment	Phenotypic plasticity	Yes	28	0	47	33	21	0	0	0
		No	72	100	53	67	79	100	100	100
	One individual can form a population	Yes	52	100	81	100	25	100	100	67
		No	48	0	19	0	75	0	0	33
	More than one reproductive phase/year	Yes	56	100	49	100	51	100	100	100
		No	44	0	51	0	49	0	0	0
	Fecundity above average	Yes	38	0	46	67	36	0	33	33
		No	62	100	54	33	64	100	67	67
	Offspring in first year	Yes	61	100	63	100	51	100	100	100
		No	39	0	37	0	49	0	0	0
Spread	Intentional spread	Yes	9	0	10	0	11	0	0	0
		No	91	100	90	100	89	100	100	100
	Spread as active mobile organism	Yes	49	60	0	0	84	17	67	33
		No	51	40	100	100	16	83	33	67

Table A3.3 – Size and taxonomic composition of five clusters gained by agglomerative cluster analysis. In the clusters species are grouped according to similarity in combinations of invasion traits.

			Clusters					Total
			1	2	3	4	5	
Taxa	Bacteria	*n*	*2*	*3*	*0*	*0*	*0*	*5*
		% within taxon	40	60	0	0	0	100
		% within cluster	4	7	0	0	0	2
	Green plants	*n*	*18*	*0*	*36*	*5*	*11*	*70*
		% within taxon	26	0	51	7	16	100
		% within cluster	39	0	92	8	100	35
	Red algae	*n*	*3*	*0*	*0*	*0*	*0*	*3*
		% within taxon	100	0	0	0	0	100
		% within cluster	7	0	0	0	0	2
	Animals	*n*	*11*	*36*	*2*	*59*	*0*	*108*
		% within taxon	10	33	2	55	0	100
		% within cluster	24	88	5	92	0	54
	Fungi	*n*	*5*	*1*	*0*	*0*	*0*	*6*
		% within taxon	83	17	0	0	0	100
		% within cluster	11	2	0	0	0	3
	Alveolates	*n*	*3*	*0*	*0*	*0*	*0*	*3*
		% within taxon	100	0	0	0	0	100
		% within cluster	7	0	0	0	0	2
	Heterokonts	*n*	*4*	*1*	*1*	*0*	*0*	*6*
		% within taxon	67	17	17	0	0	100
		% within cluster	9	2	3	0	0	3
Total		*n*	*46*	*41*	*39*	*64*	*11*	*201*
		% of all species	23	20	19	32	5	100

Table A3.4 – Size and taxonomic composition of three clusters gained by agglomerative cluster analysis.

			Clusters			**Total**
			1	**2**	**3**	
Taxa	Bacteria	*n*	*2*	*3*	*0*	*5*
		% within taxon	40	60	0	100
		% within cluster	2	3	0	2
	Green plants	*n*	*54*	*5*	*11*	*70*
		% within taxon	77	7	16	100
		% within cluster	64	5	100	35
	Red algae	*n*	*3*	*0*	*0*	*3*
		% within taxon	100	0	0	100
		% within cluster	4	0	0	2
	Animals	*n*	*13*	*95*	*0*	*108*
		% within taxon	12	88	0	100
		% within cluster	15	90	0	54
	Fungi	*n*	*5*	*1*	*0*	*6*
		% within taxon	83	17	0	100
		% within cluster	6	1	0	3
	Alveolates	*n*	*3*	*0*	*0*	*3*
		% within taxon	100	0	0	100
		% within cluster	4	0	0	2
	Heterokonts	*n*	*5*	*1*	*0*	*6*
		% within taxon	83	17	0	100
		% within cluster	6	1	0	3
Total		*n*	*85*	*105*	*11*	*201*
		% of all species	42	52	5	100

Table A3.5 – Taxonomic composition of two clusters gained by agglomerative cluster analysis.

			Clusters		**Total**
			1	**2**	
Taxa	Bacteria	*n*	*2*	*3*	*5*
		% within taxon	40	60	100
		% within cluster	2	3	2
	Green plants	*n*	*65*	*5*	*70*
		% within taxon	93	7	100
		% within cluster	68	5	35
	Red algae	*n*	*3*	*0*	*3*
		% within taxon	100	0	100
		% within cluster	3	0	2
	Animals	*n*	*13*	*95*	*108*
		% within taxon	12	88	100
		% within cluster	14	90	54
	Fungi	*n*	*5*	*1*	*6*
		% within taxon	83	17	100
		% within cluster	5	1	3
	Alveolates	*n*	*3*	*0*	*3*
		% within taxon	100	0	100
		% within cluster	3	0	2
	Heterokonts	*n*	*5*	*1*	*6*
		% within taxon	83	17	100
		% within cluster	5	1	3
Total		*n*	*96*	*105*	*201*
		% of all species	48	52	100

Table A3.6 – Frequencies of species of the hypothetic invader types in the five clusters.

			Clusters					**Total**
			1	**2**	**3**	**4**	**5**	
Hypothetic invader types	Drifters	*n*	*15*	*1*	*9*	*0*	*0*	*25*
		% within type	60	4	36	0	0	100
		% within cluster	33	2	23	0	0	12
	Fugitives	*n*	*20*	*3*	*0*	*0*	*0*	*23*
		% within type	87	13	0	0	0	100
		% within cluster	43	7	0	0	0	11
	Establishers	*n*	*10*	*2*	*12*	*0*	*6*	*30*
		% within type	33	7	40	0	20	100
		% within cluster	22	5	31	0	55	15
	Spreaders	*n*	*0*	*3*	*0*	*37*	*0*	*40*
		% within type	0	8	0	≥93	0	100
		% within cluster	0	7	0	58	0	20
	Promoted	*n*	*0*	*0*	*2*	*17*	*5*	*24*
		% within type	0	0	8	71	21	100
		% within cluster	0	0	5	27	45	12
	No assignment	*n*	*1*	*32*	*16*	*10*	*0*	*59*
		% within type	2	54	27	17	0	100
		% within cluster	2	78	41	16	0	29
Total		*n*	*46*	*41*	*39*	*64*	*11*	*201*
		% of all species	23	20	19	32	5	100

Table A3.7 – Frequencies of species of the hypothetical invader types in the three clusters.

			Clusters			**Total**
			1	**2**	**3**	
Hypothetic invader types	Drifters	*n*	*24*	*1*	*0*	*25*
		% within type	96	4	0	100
		% within cluster	28	1	0	12
	Fugitives	*n*	*20*	*3*	*0*	*23*
		% within type	87	13	0	100
		% within cluster	24	3	0	11
	Establishers	*n*	*22*	*2*	*6*	*30*
		% within type	73	7	20	100
		% within cluster	26	2	55	15
	Spreaders	*n*	*0*	*40*	*0*	*40*
		% within type	0	100	0	100
		% within cluster	0	38	0	20
	Promoted	*n*	*2*	*17*	*5*	*24*
		% within type	8	71	21	100
		% within cluster	2	16	45	12
	No assignment	*n*	*17*	*42*	*0*	*59*
		% within type	29	71	0	100
		% within cluster	20	40	0	29
Total		*n*	*85*	*105*	*11*	*201*
		% of all species	42	52	5	100

Table A3.8 – Frequencies of species of the hypothetic invader types in the two clusters.

			Clusters		**Total**
			1	**2**	
Hypothetic invader types	Drifters	*n*	*24*	*1*	*25*
		% within type	96	4	100
		% within cluster	25	1	12
	Fugitives	*n*	*20*	*3*	*23*
		% within type	87	13	100
		% within cluster	21	3	11
	Establishers	*n*	*28*	*2*	*30*
		% within type	93	7	100
		% within cluster	29	2	15
	Spreaders	*n*	*0*	*40*	*40*
		% within type	0	100	100
		% within cluster	0	38	20
	Promoted	*n*	*7*	*17*	*24*
		% within type	29	71	100
		% within cluster	7	16	12
	No assignment	*n*	*17*	*42*	*59*
		% within type	29	71	100
		% within cluster	18	40	29
Total		*n*	*96*	*105*	*201*
		% of all species	48	52	100

Panel A4.1 – The shared eco-evolutionary basis of major hypotheses in invasion ecology

The concept of ‘eco-evolutionary experience’ posits that biotic interactions maintained during the evolutionary history of species influence the outcome of interactions between native and introduced species in present times, i.e. (a) the invasion success of the introduced species and (b) the responses of natives. Several major hypotheses for explaining invasion success can be directly related to this concept based on their implicit reference to the logical consequence of a species being introduced into an area where it has not evolved (for references see main text):

a) Specialized, i.e. eco-evolutionarily highly experienced native enemies of the introduced species may be missing (‘enemy release hypothesis’).

b) Reduced predation due to inexperienced native predators (herbivores) may allow the introduced species to allocate more resources to traits that increase its competitive abilities (‘evolution of increased competitive ability hypothesis’).

c) The introduced species may be inexperienced with native enemies and may therefore lack appropriate defence mechanisms (‘new associations hypothesis’).

d) Introduced species with close relatives in the target area may be less successful because native predators may already be experienced with native congeneric prey species (‘Darwin’s naturalization hypothesis’).

e) Native prey species may be unprepared, i.e. inexperienced for effectively countering novel predatory behaviour of an introduced species (‘naïve prey hypothesis’).

f) Native species may not be adapted to, i.e. may be inexperienced with specialized competitive strategies of the introduced species (‘novel weapons hypothesis’).

g) Mutualistic interactions may fail to develop because of missing experience be tween native and non-native species (‘missed mutualisms hypothesis’).

h) Mutualistic interactions between a native and non-native species may be possible, provided that the degree of experience is high enough in both interaction partners (‘mutualist facilitation hypothesis’).

i) Species that have evolved a strong commensal affiliation to humans may benefit from this eco-evolutionary experience when introduced to areas dominated by humans. This may be especially true for Eurasian species: they coevolved with Europeans and their plants, pathogens and livestock, which were dispersed all over the world during the European Imperialism period (‘human commensals and imperialism hypothesis’).

Panel A4.2 – Routine for the quantification of eco-evolutionary experience: a food web-based example

1. Identify direct interactions and single-step indirect interactions (i.e. including one intermediate species) of the focal species in the food web of its source area and in the food web of the (potential) target area (see example in Fig. A).
2. Define ecological guilds (or other appropriate ecological groupings) for each type of ecological interaction (focal species acting as prey, predator, competitor or indirect mutualist). Assign the focal species and its interaction partners in the source and target area to the ecological guilds.

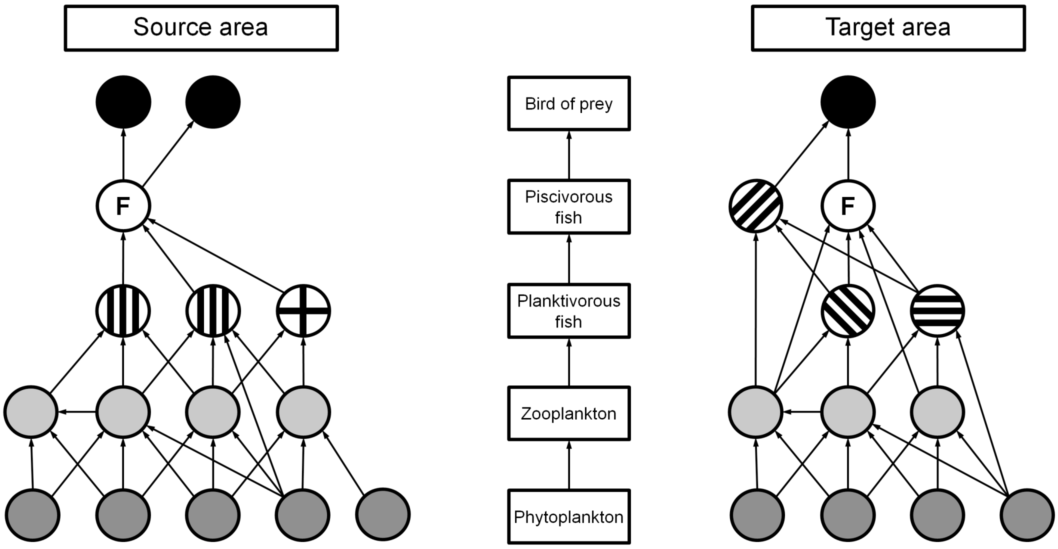

Figure A – Hypothetical food webs in freshwater lakes in source and target area. Circles represent species (F = focal species), different shading and patterning indicate different guilds (see steps 2 and 3).

Quantification of the focal species' eco-evolutionary experience ($\mathrm{xp}_{\mathrm{Focal}}$):

3. Determine the number of species that interact with the focal species per ecological guild in the source and target area, separately for each type of interaction (Table A).
4. Calculate the xp_{Focal} index (Eq. 2) for each type of interaction, obtaining the eco-evolutionary experience of the focal species regarding its interaction with resident species in the food web of the target area.

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Quantification of the resident species' eco-evolutionary experience ($xp_{Residents}$):

5. Determine the number of resident species in the target area that are members of the same ecological guild as the focal species (regardless if they interact with the focal species or not), separately for each type of interaction (Table B).
6. Calculate the $xp_{Residents}$ index (Eq. 3) for each type of interaction, obtaining the eco-evolutionary experience of the resident species community regarding its interaction with the introduced focal species.

Table A – Numbers of species per guild that interact with the focal species in the food webs of the source and target area (taken from Fig. A), and the respective eco-evolutionary experience of the focal species (xp_{Focal}) in the target area (R1-R5: predator guilds, P1-P5: prey guilds, C1-C5: competitor guilds, M1-M5: mutualist guilds).

Type of interaction Interaction partners of the focal species	**No. of species in guild *i* in source area *S***					**No. of species in guild *i* in target area *T***					xp_{Focal}
i =	*R1*	*R2*	*R3*	*R4*	*R5*	*R1*	*R2*	*R3*	*R4*	*R5*	
Predators	2	-	-	-	-	1	-	-	-	-	1.00
i =	*P1*	*P2*	*P3*	*P4*	*P5*	*P1*	*P2*	*P3*	*P4*	*P5*	
Prey	2	1	-	-	-	-	-	1	1	2	0.43
i =	*C1*	*C2*	*C3*	*C4*	*C5*	*C1*	*C2*	*C3*	*C4*	*C5*	
Competitors	-	-	-	-	-	1	1	1	-	-	0.00
i =	*M1*	*M2*	*M3*	*M4*	*M5*	*M1*	*M2*	*M3*	*M4*	*M5*	
Indirect mutualists	4	1	-	-	-	3	4	-	-	-	0.75

Table B – Number of resident species in the target area that are members of the same guild as the focal species (note that species numbers are exemplary and not directly deducible from Fig. A), and the respective eco-evolutionary experience of the native community ($xp_{Residents}$) with the focal species.

	No. of resident species in same guild as the focal species	$xp_{Residents}$
Predators	1	0.50
Prey	0	0.00
Competitors	3	0.75
Indirect mutualists	2	0.67

Table A5.1 – Expectations regarding differences and temporal dynamics in the parameters of the predation cycle when highly experienced (A) novel predators and (B) novel prey instead of their resident comparator species interact with inexperienced resident species (= high-risk scenario; cf. Fig. 5.2). Rationales for the expectations mainly focus on prey defences and predator offences discussed in Jeschke 2006 (see also Jeschke et al. 2008). Numbers in italics refer to exemplary references (listed in the last column) that lend direct or indirect support to the expected values, temporal developments and rationales.

(A) NOVEL PREDATOR

Expected difference when the interaction partner involved is the novel predator instead of the resident comparator	**Expected development of *difference* over time (with novel predator as interaction partner)***		**Rationale**	**References** (see Appendix List A5.1)
	short-term	**long-term**		
Stage 1: Search				
higher searching effort (sensu Jeschke et al. 2004, i.e. searching probability times searching intensity)	→	↓	**Expected difference:** a predator's search for the next meal can be delayed by increased digestion and/or handling times (*1*), which may result from antipredator defences in prey (*2-4*). Low experience of resident prey with the novel predator may consist of e.g. a reduced toxicity or indigestibility due to ineffective chemical defences or defences for countering attacks (e.g. *5*), potentially leading to shorter digestion and/or handling times (cf. *6-8*) and earlier resuming of searching activities in the novel predator than its resident comparator. **Expected development:** advantages of the novel predator may possibly persist over ecological time spans, e.g. because the development of more effective chemical defences in prey may require evolutionary processes (see *9; 10*).	[1] Jeschke et al. 2002 [2] Fritz & Simms 1992 [3] Ruxton et al. 2004 [4] Johnson 2011 [5] Gamradt & Kats 1996 [6] Haddaway et al. 2012 [7] Dick et al. 2013 [8] Alexander et al. 2014 [9] Brodie & Brodie 1999a [10] Cornell & Hawkins 2003
Stage 2: Encounter				
higher encounter rate (β)	↓	↓	**Expected difference:** resident prey may be inexperienced with the foraging behaviour of the novel predator and face an increased probability that its avoidance strategies to lower the encounter rate with predators (i.e. non-overlapping spatiotemporal activity patterns, e.g. by shifted activity periods, generally reduced activity, hiding in refuges, diel migration, adapted life histories; *11-14*) are unsuitable against the novel predator (see e.g. *15*). This would result in a higher encounter rate with novel predators. **Expected development:** behavioural plasticity and learning may allow prey to react appropriately to the novel predator quite rapidly by shifting spatial and temporal activity patterns (e.g. *16-19*), potentially compensating the advantage of the novel predator already within ecological time. Longer-term evolutionary adaptation to reduce encounter with predators has also been observed (*20-21*).	[11] Edmunds 1974 [12] Endler 1991) [13] Jeschke et al. 2008 [14] Dugatkin 2013 [15] Short et al. 2002 [16] McIntosh & Townsend 1994 [17] Hudgens & Garcelon 2011 [18] Lönnstedt et al. 2012 [19] Miller et al. 2014 [20] Patten & Campbell 1998 [21] Cousyn et al. 2001

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Stage 3: Detection				
higher detection probability (γ)	→	↓	**<u>Expected difference:</u>** measures of the inexperienced prey to remain undetected (e.g. regarding camouflage or movement patterns; *22-26*) may be ineffective against a novel predator (e.g. in Kakapo *vs.* feral cats; *27*), leading to a higher detection probability as compared to resident predators. **<u>Expected development:</u>** although behavioural plasticity may allow some improvement in the resident prey's response to the novel predator already within ecological time spans (e.g. in regard to more suitable movement patterns), significant improvements for the prey may often require evolutionary adaptations (e.g. improved camouflage; *28-30*).	[22] Edmunds 1974 [23] Endler 1991 [24] Ruxton et al. 2004 [25] Caro 2005 [26] Dugatkin 2013 [27] Karl & Best 1982 [28] Endler 1980 [29] Endler 1983 [30] Krebs & Davies 1993
Stage 4: Attack				
higher attack probability (δ)	↓	↓	**<u>Expected difference:</u>** detected prey can reduce the probability of being attacked e.g. by showing 'startling' warning signals (e.g. eyespots in butterflies, inflating in toads) or by engaging in otherwise attack-discouraging behaviour (e.g. shoaling and predator inspection in fish; *31-34*). A prerequisite for this is the successful recognition of the predator by the prey (*35*), but low experience of resident prey with the novel predator may mean a low ability of identifying the latter as a threat (e.g. *36-38*). This would lead to higher attack probabilities for novel than for resident predators. Note that permanent warning signals in the resident prey (e.g. aposematic colouration) are not considered a source for difference in the attack probabilities here, since in the high-risk scenario both novel and resident predators are assumed to be equally experienced and thus equally likely to react appropriately to the signals. **<u>Expected development:</u>** learning and behavioural plasticity may enable resident prey to recognize a novel predator in relatively short time (*39; 40*). Attack probabilities of resident and novel predators may thus become similar already within ecological time. Longer-term evolutionary adaptation to reduce attack probability has also been observed (e.g. *41*).	[31] Edmunds 1974 [32] Magurran et al. 1990 [33] Godin & Davis 1995 [34] Ruxton et al. 2004 [35] Carthey & Banks 2014 [36] Blumstein et al. 2002 [37] Gomez-Mestre & Diaz-Paniagua 2011 [38] Kuehne & Olden 2012 [39] Brown et al. 2011 [40] Brown et al. 2013 [41] Magurran et al. 1992
Stage 5: Consumption				
higher attack efficiency (ratio of successful to total number of attacks) (ε)	→	↓	**<u>Expected difference:</u>** inexperienced resident prey may face an increased probability that its traits for escaping attack and consumption (e.g. regarding flight behaviour, weapons, armour, disposition to fight, aggregating with conspecifics; *42-46*) are ineffective against novel predators (e.g. *47; 48*), leading to a higher attack efficiency in novel than in resident predators. **<u>Expected development:</u>** although some prey species are phenotypically plastic in that they can form inducible morphological defences that reduce predator attack efficiency (e.g. in *Daphnia* spp.; *49*), only a fraction of these defences will be effective against a novel predator. Advantages for the novel predator may thus persist at least over ecological time spans. Significant improvements for the prey may often require evolutionary adaptations (e.g. in morphology; *47; 50; 51*) and cannot be based solely on behavioural plasticity.	[42] Edmunds 1974 [43] Endler 1991 [44] Ruxton et al. 2004 [45] Caro 2005 [46] Dugatkin 2013 [47] Seeley 1986 [48] Macdonald & Harrington 2003 [49] Tollrian & Harvell 1999 [50] Freeman & Byers 2006 [51] Langkilde 2009

(B) NOVEL PREY

Expected difference when the interaction partner involved is the novel prey instead of the resident comparator	Expected development of *difference* over time (with novel prey as interaction partner)*		Rationale	References (see Appendix List A5.1)
	short-term	long-term		
Stage 1: Search				
lower searching effort (sensu Jeschke et al. 2004, i.e. searching probability times searching intensity)	→	↓	**Expected difference:** a predator's search for the next meal can be delayed by increased digestion and handling times (*52*), which may result from antipredator defences in prey (*53-56*). Low experience of resident predators with novel prey may consist e.g. in a reduced or missing immunity to the novel prey's chemical defences (*57*), resulting in reduced searching effort when preying on novel prey compared to resident prey (*58*). **Expected development:** aversion-learning may enable resident predators within relatively short time to respond to chemical defences of novel prey by avoiding it (*59; 60*). This reduces direct negative impacts for the resident predator, but does not compensate the lower searching effort for novel prey. Significant improvements for overcoming the novel prey's defences and reducing digestion and/or handling times may often require evolutionary processes (*61-65*), probably amplified by phenotypic plasticity (e.g. learning in crayfish; *66*).	[52] Jeschke et al. 2002 [53] Fritz & Simms 1992 [54] Ruxton et al. 2004 [55] Phillips & Shine 2007 [56] Johnson 2011 [57] Crossland et al. 2008 [58] Beckmann et al. 2011 [59] Webb et al. 2008 [60] Nelson et al. 2011 [61] Brodie & Brodie 1999b [62] Cornell & Hawkins 2003 [63] Phillips & Shine 2004 [64] Phillips & Shine 2006 [65] Després et al. 2007 [66] Ramalho & Anastácio 2011
Stage 2: Encounter				
lower encounter rate (β)	↓	↓	**Expected difference:** the resident predator may be inexperienced with the avoidance strategies of novel prey and face an increased probability that its foraging behaviour (e.g. regarding activity periods or diel migration; *67-70*) is less effective for encountering novel than resident prey (see *71*). This would result in lower encounter rates with novel prey. **Expected development:** behavioural plasticity may enable the resident predator within relatively short time to adopt strategies that are suitable to encounter novel prey (e.g. change in migration patterns; *72; 73*; see also *74* about learned host preferences), leading to similar encounter rates of resident predators with resident and novel prey within ecological time spans. Longer-term evolutionary adaptation to increase encounter (i.e. spatiotemporal overlap) with prey has also been observed, e.g. timing of insect emergence according to flowering of novel host plant (*75*).	[67] Endler 1991 [68] Perry & Pianka 1997 [69] Begon et al. 2006 [70] Dugatkin 2013 [71] Scharf et al. 2006 [72] Wormington & Leach 1992 [73] Petrie & Knapton 1999 [74] Barron 2009 [75] Groman & Pellmyr 2000

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Stage 3: Detection				
lower detection probability (γ)	↓	↓	**<u>Expected difference:</u>** traits of the inexperienced resident predator for prey detection (e.g. search images; *76-79*) may be ineffective to reliably detect novel prey and recognize it as such (e.g. failure of female butterflies to recognize a novel potential host plant; *80*), leading to a lower detection probability for novel than resident prey. **<u>Expected development:</u>** predator search images can be adjusted through rapid learning processes (*81; 82*), so that the probability of resident predators for detecting novel prey may become similar to that for detecting resident prey already within relatively short time.	[76] Tinbergen 1960 [77] Krebs & Davies 1993 [78] Ruxton et al. 2004 [79] Dugatkin 2013 [80] Karowe 1990 [81] Dawkins 1971 [82] Pietrewicz & Kamil 1979
Stage 4: Attack				
lower attack probability (δ)	↓	↓	**<u>Expected difference:</u>** inexperienced resident predators may respond to the unfamiliar cues of novel prey with dietary wariness (i.e. neophobia and dietary conservatism) as has been observed in various animal taxa (*83-85*). This would lead to a lower attack probability for novel prey compared to resident prey. **<u>Expected development:</u>** neophobia usually lasts for only a few minutes (*84*), dietary conservatism persists longer but may also be overcome over ecological time spans (days, months, or years; *86; 87*). Rapid inclusion of novel prey into a resident predator's diet has been observed in the field (*88*).	[83] Marples & Kelly 1999 [84] Thomas et al. 2010 [85] McMahon et al. 2014 [86] Marples et al. 2005 [87] Marples et al. 2007 [88] King et al. 2006
Stage 5: Consumption				
lower attack efficiency (ratio of successful to total number of attacks) (ε)	→	↓	**<u>Expected difference:</u>** inexperienced resident predators may face an increased probability that their traits for attacking and consuming prey (e.g. regarding attack strategy, handling behaviour, feeding morphology; *89-91*) are less effective for novel than resident prey (e.g. *92*). **<u>Expected development:</u>** advantages for the novel prey may persist over some time since significant improvements in the attacking traits of the resident predator may often require evolutionary adaptations (e.g. regarding feeding morphology; *93*) and cannot be based solely on behavioural plasticity.	[89] Endler 1991 [90] Karban & Agrawal 2002 [91] Dugatkin 2013 [92] Cattau et al. 2010 [93] Carroll et al. 2005

* Arrows indicate the expected development over time of the *difference* between resident/resident and resident/non-resident interactions, not the development of the parameter *value*.

Table A5.2 – Expectations regarding differences and temporal dynamics in additional parameters of the steady-state satiation (SSS) equation, when highly experienced (A) novel predators and (B) novel prey instead of their resident comparator species interact with inexperienced resident species (= high-risk scenario; cf. Fig. 5.2). The SSS model explicitly considers the joint influence of handling time and digestion time on the predator's searching effort. Rationales and supporting references as in Appendix Table A5.1.

(A) NOVEL PREDATOR

Expected difference when the interaction partner involved is the novel predator instead of the resident comparator	**Expected development of *difference* over time (with novel predator as interaction partner)***		**Rationale**	**References** (see Appendix List A5.1)
	short-term	**long-term**		
Stage 1: Search				
Handling time $b = t_{att}/\varepsilon + t_{eat}$				
shorter attacking time (t_{att})	→	↓	**Expected difference:** similarly to the rationale regarding attack efficiency (ε; see Appendix Table A5.1A, Stage 5), inexperienced resident prey may face an increased probability that its traits for countering attacks (e.g. regarding flight behaviour, disposition to fight, aggregating with conspecifics) are ineffective against novel predators, which would reduce the time the novel predator needs to carry out an attack. **Expected development:** advantages for the novel predator may persist over ecological time spans since significant improvements for the prey may often require evolutionary adaptations (e.g. in morphology) and cannot be based solely on behavioural plasticity.	see Table A5.1A, 'Stage 1: Search' and 'Stage 5: Consumption'
similar eating time (t_{eat})	→	→	**Expected difference:** prey defences that may affect eating time (e.g. armour, sharp spines etc.) have no different effect on novel as compared to resident predators, as both are assumed to be equally experienced with the prey (high-risk scenario). **Expected development:** a significant difference between novel and resident predator is not expected to arise over time.	see Table A5.1A, 'Stage 5: Consumption'
Digestion time $c = t_g/g$				
shorter gut retention time (t_g)	→	↓	**Expected difference:** low experience of resident prey with the novel predator may consist of e.g. ineffective chemical defences against the novel predator, resulting in shorter gut retention times (thus, shorter digestion times) in the novel predator. **Expected development:** advantages of the novel predator may persist over ecological time periods since the development of more appropriate chemical defences in resident prey may require evolutionary adaptation.	see Table A5.1A, 'Stage 1: Search'
similar gut capacity (g)†	→	→	**Expected difference:** at the onset of the novel interaction, the predator's gut capacity is a given anatomical fact that is independent of the resident prey's low experience. **Expected development:** shorter gut retention time due to ineffective chemical defences in the inexperienced prey would in principle allow the novel predator to evolve a relatively smaller gut capacity compared to the resident predator without prolonging digestion time (since $c = t_g/g$). On the other hand, improvements in the resident prey's defences against the novel predator over evolutionary time would counteract this. Overall, pronounced differences between novel and resident predators' gut capacities may thus not arise.	see Table A5.1A, 'Stage 1: Search'

(B) NOVEL PREY

Expected difference when the interaction partner involved is the novel prey instead of the resident comparator	Expected development of *difference* over time (with novel prey as interaction partner)*		Rationale	References (see Appendix List A5.1)
	short-term	long-term		
Stage 1: Search				
Handling time $b = t_{att}/ε+t_{eat}$				
longer attacking time (t_{att})	→	↓	**Expected difference:** similarly to the rationale for attack efficiency (*ε*; see Appendix Table A5.1B, Stage 5), inexperienced resident predators may face an increased probability that their traits for attacking and consuming prey (regarding attack strategy, handling behaviour, feeding morphology) are less effective for novel than resident prey, which prolongs attacking time. **Expected development:** advantages for the novel prey may persist over some time since significant improvements in the attacking traits of the resident predator may often require evolutionary adaptations (e.g. regarding feeding morphology) and cannot be based solely on behavioural plasticity.	see Table A5.1B, 'Stage 1: Search' and 'Stage 5: Consumption'
similar eating time (t_{eat})	→	→	**Expected difference:** the effectiveness of prey defences that may influence eating time (e.g. armour, sharp spines etc.) is not expected to differ significantly between novel and resident prey since both are assumed to be equally experienced with the resident predator (high-risk scenario). **Expected development:** a significant difference in the time needed for eating novel or resident prey is not expected to arise.	see Table A5.1B, 'Stage 5: Consumption'
Digestion time $c = t_g/g$				
longer gut retention time (t_g)	→	↓	**Expected difference:** low experience of the resident predator with the novel prey may consist of e.g. lower immunity to chemical defences of the novel prey, resulting in longer gut retention times (thus, longer digestion times) in the resident predator. **Expected development:** disadvantages of the resident predator may persist over ecological time spans, as changes in its digestive system to increase immunity to chemical defences probably require evolutionary adaptations that need time.	see Table A5.1B, 'Stage 1: Search'
similar gut capacity (g)[†]	→	→	**Expected difference:** at the onset of the novel interaction the predator's gut capacity is a given anatomical fact that is independent of the predator's low experience with the novel prey at that time. **Expected development:** with resident predators adapting to chemical defences of the novel prey over evolutionary time (and thus reducing again the gut retention time; see above), significant changes in the gut capacity of resident predators preying on novel prey are not expected to arise.	see Table A5.1B, 'Stage 1: Search'

* Arrows indicate the expected development over time of the *difference* between resident/resident and resident/non-resident interactions, not the development of the parameter *value*.

[†] Gut capacity is dependent on body size. For reasons of simplicity we assume here that novel predators and their resident comparators are similar in body size.

List A5.1 – Supporting references for Appendix Tables A5.1 and A5.2

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