

This Manuscript is contextually identical with the published paper:  
AMBIO (2013) 42:527-540  
DOI 10.1007/s13280-012-0379-x

# Conceptual frameworks and methods for advancing invasion ecology

Tina Heger<sup>a, b, \*</sup>, Anna T. Pahl<sup>a</sup>, Zoltan Botta-Dukát<sup>c</sup>, Francesca Gherardi<sup>d</sup>, Christina Hoppe<sup>e</sup>, Ivan Hoste<sup>f</sup>, Kurt Jax<sup>a, g</sup>, Leena Lindström<sup>h</sup>, Pieter Boets<sup>i</sup>, Sylvia Haider<sup>a</sup>, Johannes Kollmann<sup>a</sup>, Meike J. Wittmann<sup>j</sup>, Jonathan M. Jeschke<sup>a, j, k</sup>

<sup>a</sup> *Technische Universität München, Department of Ecology and Ecosystem Management, Restoration Ecology, Emil-Ramann-Str. 6, D-85350 Freising, Germany*

<sup>b</sup> *Department of Plant Sciences, University of California, One Shields Ave., Davis, CA 95616, USA*

<sup>c</sup> *MTA Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4, H-2163 Vácrátót, Hungary*

<sup>d</sup> *University of Florence, Department of Evolutionary Biology „Leo Pardi“, Via Romana 17, I-50125 Florence, Italy*

<sup>e</sup> *Goethe University of Frankfurt, Institute of Ecology, Evolution & Diversity, Plant Ecology, Max-von-Laue Str. 13, D-60438, Frankfurt, Germany*

<sup>f</sup> *National Botanic Garden of Belgium, Domein van Bouchout, B-1860 Meise, Belgium*

<sup>g</sup> *Helmholtz-Centre for Environmental Research – UFZ, Department of Conservation Biology, Permoserstr. 15, D-04318 Leipzig, Germany*

<sup>h</sup> *University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland*

<sup>i</sup> *Ghent University, Laboratory of Environmental Toxicology and Aquatic Ecology, J. Plateaustraat 22, B-9000 Ghent, Belgium*

<sup>j</sup> *Ludwig-Maximilians-University Munich, Department of Biology II, Ecology, Grosshaderner Str. 2, D-82152 Planegg-Martinsried, Germany*

<sup>k</sup> *Cary Institute of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545, USA*

\*Corresponding author. Tel.: ++49 8161 714142; fax: ++49 8161 714143.

E-mail address: [t.heger@wzw.tum.de](mailto:t.heger@wzw.tum.de) (T. Heger)

## Abstract

Invasion ecology has much advanced since its early beginnings. Nevertheless, explanation, prediction, and management of biological invasions remain difficult. We argue that progress in invasion research can be accelerated by, first, pointing out difficulties this field is currently facing and, second, looking for measures to overcome them. We see basic and applied research in

invasion ecology confronted with difficulties arising from (A) societal issues, e.g., disparate perceptions of invasive species; (B) the peculiarity of the invasion process, e.g., its complexity and context dependency; and (C) the scientific methodology, e.g., imprecise hypotheses. To overcome these difficulties, we propose three key measures: (1) a checklist for definitions to encourage explicit definitions; (2) implementation of a hierarchy of hypotheses (HoH), where general hypotheses branch into specific and precisely testable hypotheses; and (3) platforms for improved communication. These measures may significantly increase conceptual clarity and enhance communication, thus advancing invasion ecology.

**Keywords:**

communication platforms; definitions and terminology; hierarchy of hypotheses; invasive alien species; synthesis; transdisciplinarity

**INTRODUCTION**

Studying biological invasions can yield insights into numerous basic ecological, evolutionary, and biogeographical topics (Sax et al. 2005). As some invasive species threaten biodiversity, are vectors of human diseases, and cause socio-economic costs, their investigation also has an applied focus. From its beginning, invasion ecology has combined these basic and applied aspects. The first written accounts of invasive species date back to the 18th century (Chew 2006), but the publication of Elton's (1958) book "The ecology of invasions by animals and plants", which conveys an explicit conservation point of view, is generally considered to be the starting point of focused research on biological invasions (Richardson and Pyšek 2008). In the 1980s, invasion ecology emerged as a specific research field (Richardson and Pyšek 2007). This was in part due to the international program of the Scientific Committee on Problems of the Environment (SCOPE) on biological invasions (Drake et al. 1989). The program focused on three questions, again addressing basic as well as applied aspects: (i) What factors determine whether a species will become an invader or not? (ii) What are the properties that determine whether an ecological community is vulnerable or resistant to invasions? (iii) How should effective management strategies be developed?

Some answers to these questions are now available, and have been summarized in various journal articles and books (Lockwood et al. 2007; Blackburn et al. 2009; Davis 2009; Richardson 2011a). Based on Elton's work and the SCOPE program, invasion ecologists have produced plenty of hypotheses and data. New methods such as modeling approaches, multi-scale comparisons and molecular methods are being applied, and new topics such as *propagule pressure* (the pattern in which propagules arrive; Simberloff 2009) and post-introduction evolution have been raised (Richardson and Pyšek 2008). It should be expected, thus, that knowledge has increased considerably since the beginning of invasion research. Nevertheless, progress towards satisfactory explanation and prediction of invasions as well as management of invasive species is rather slow

(Puth and Post 2005; Lockwood et al. 2007; Blackburn et al. 2009; Davis 2009; Richardson 2011b; Moles et al. 2012).

Several authors have already called for an improvement of the implementation of existing knowledge into policies and management (Hulme 2006; Lodge et al. 2006). In this paper, we focus on invasion science itself: We think there is much potential for improving the effectiveness of basic and applied research on invasions. We argue that progress in invasion ecology can be accelerated by, first, explicating difficulties that basic and applied research on invasions are facing today and, second, developing measures to overcome them. By difficulties, we here mean circumstances that hinder or complicate basic or applied research. Difficulties for invasion ecology arise from: (A) society's impact and perception; (B) the peculiarity of the invasion process; and (C) the scientific methodology. Overlaps between these three domains exist, but this classification is helpful to structure our considerations. In Tables 1 to 3, we summarize difficulties of all three domains as well as measures to overcome them. Some of these difficulties and measures have been pointed out before and are covered by the references provided. Here, our focus is on new possibilities to improve the effectiveness of basic and applied research on biological invasions, especially regarding domain C.

## **DOMAIN A: DIFFICULTIES ARISING FROM SOCIETY AND ITS RELATIONSHIP TO BIOLOGICAL INVASIONS**

Society causes biological invasions, and biological invasions influence society. This feedback not only complicates effective prevention and management (A1-A4 in Table 1) but also has consequences for the scientific approach (right column in Table 1). An example is the perception of invasive species by the general public. The general public has only limited knowledge of the phenomenon of biological invasions (Gellis Communications 2008), and perception as well as evaluation of invasions are not at all homogeneous across societal groups (Fischer and van der Wal 2007; Gherardi 2011; Lambert and Rotherham 2011) (A3 in Table 1). Especially in case of deliberate introductions related to agriculture, forestry, fisheries, and biological control, species can cause benefits as well as costs (Gozlan 2008). Thus, species ranked as highly problematic by conservation scientists sometimes are regarded as not harmful or even desirable by the public. For example, conservation scientists perceive the tree of heaven (*Ailanthus altissima*) as a harmful invader with the potential to threaten native species; on the other hand, many people on the Mediterranean islands appreciate its ability to grow on dry soils and to provide shade (Bardsley and Edwards-Jones 2007).

Such disparate perceptions have consequences for applied research on invasions: research on managing invasions and strategies tailored to address actual societal needs cannot be efficient unless these needs are uncovered. An increasing amount of work already aims to include social and economic demands into invasion research (Fischer and van der Wal 2007; Berghöfer et al. 2010; Perrings et al. 2010a). Such efforts are in high demand, and more inter- and transdisciplinary collaborations should be established to foster them (Richardson 2011b; see below).

## **DOMAIN B: DIFFICULTIES ARISING FROM THE PECULIARITY OF THE INVASION PROCESS**

In addition to problems related to society, a major obstacle for research is that invasion processes are notably difficult to analyze, explain, and predict. Invasion processes are complex (Lodge 1993; Hayes and Barry 2008; B1 in Table 2) and context-dependent (Zedler and Kercher 2004; Gurevitch et al. 2008; Blackburn et al. 2009) (B2 in Table 2). This creates the need for methods that are able to explain and predict multiple interacting influences (Heger and Treppl 2003), and to take into account the history of current invasions for their explanation (Cassey et al. 2005) (see right column in Table 2).

Global transportation networks and other socio-cultural activities (such as horticulture or fishery) not only cause difficulties for the prevention and management of invasive species, but also create the need to integrate socio-cultural sciences into research (Kowarik 2003; Niggemann et al. 2009; Tatem 2009) (B3 in Table 2). One example is the spread of New Zealand bittercress (*Cardamine corymbosa*) to Europe and the U.S., which is largely due to a combination of ecological traits (e.g., active short-distance seed dispersal) and socio-economic activities that include international plant auctions and exchanges of container-grown plants among nurseries, garden centers, and private gardens (Hoste et al. 2008). An increasing number of studies already integrate socio-cultural analyses into approaches to study invasions (Dehnen-Schmutz and Williamson 2006; Skou et al., in press), and invasion ecologists increasingly collaborate with socio-cultural scientists. An example is the workshop organized by C. Kueffer, in Bielefeld, Germany, August 2012 ([http://www.uni-bielefeld.de/\(en\)/ZIF/AG/2012/08-27-Kueffer.html](http://www.uni-bielefeld.de/(en)/ZIF/AG/2012/08-27-Kueffer.html)), where half of the participants were socio-cultural scientists and the other half natural scientists. To improve effectiveness of explanation, prediction and management, similar efforts should be strengthened (see key measure 3 below).

## **DOMAIN C: CONCEPTUAL AND METHODOLOGICAL DIFFICULTIES**

Invasion ecology has to cope with several conceptual and methodological difficulties, many of which are related to or produced by society and the peculiarity of the invasion process (see right columns in Tables 1 and 2). The scientific methodology in invasion research is facing difficulties concerning the conceptual basis and theory of invasion ecology (C1 to C3 in Table 3), empirical research (C4 and C5 in Table 3), and the need for integration with other scientific disciplines and societal groups (C6 to C8 in Table 3). We will focus on some particularly important difficulties and propose three key measures to overcome them.

### **Terminology: Unclear terms and concepts**

As many other research fields, invasion ecology is still plagued by the ambiguous use of terms and unclear concepts (Richardson et al. 2011; McGeoch et al. 2012) (C1 in Table 3). Inconsistent terminology can cause difficulties when it comes to the communication of research rationales and

results, both within science, and between science and the broader public; therefore explicit definitions are needed. However, they are not equally necessary for all publications. General treatments of biological invasions (such as this publication) can cover different definitions of invasive species, whereas comparisons of sets of native and invasive species need explicit definitions and consistent applications of underlying concepts (van Kleunen et al. 2010).

Creating a single set of definitions that suits all purposes seems impossible (Hodges 2008), as different research goals create different ideas of what is peculiar about invasions (Küffer and Hirsch Hadorn 2008). We therefore suggest to accept that different stakeholders use different definitions (cf. Heger, Saul and Trepl in press). However, it is important to clarify how *alien* or *invasive species* is defined by a given person or text. We propose to use the following checklist to achieve such clarity.

### **Key measure 1: Checklist for explicit definitions**

The checklist we suggest consists of five questions that are important to define alien species, and four additional questions for defining invasive species (Box 1). Depending on the research context (e.g., basic or applied focus), different answers are possible for each question. The references included below can help deciding which answers are most reasonable for a given context.

*Question 1: How did the species arrive in areas beyond their native range? Is human-mediated transport regarded a condition to call a species alien?* If the answer is ‘yes’, it should be stated how unintentional species introductions are distinguished from natural dispersal events. In cases where information on the pathway is lacking, proxies can be used (e.g., geographical distribution, see Webb 1985). Additionally, it is helpful to state what is meant by human-mediated transport: are indirect effects of human action, e.g., habitat change, included or excluded? An excellent example clarifying this and similar aspects can be found in Pyšek et al. (2004).

*Question 2: Are continuously spreading species (‘leading edge dispersal’, Wilson et al. 2009) regarded as alien?* Climate change alters species distributions; hence spontaneous colonization events from neighboring geographic regions may become more frequent in the near future (Walther et al. 2009). If continuously spreading species are not viewed as alien, the definition will need to include a criterion to distinguish continuous from non-continuous spread. For example, Richardson et al. (2000) suggested that a new occurrence of plant species should be regarded as alien if it is more than about 100 km away from the closest native population. Another option is to consider species as alien as soon as they overcome a species-specific barrier to dispersal (Heger and Trepl 2003).

*Question 3: Are species that originate in the region by hybridization of alien and native species regarded as aliens?* In the strict sense of many definitions of alien species, these hybrids have to be regarded as natives, because they evolved in the region. If authors do not agree with this view, it should be stated clearly (see e.g. Pyšek et al. 2004).

*Question 4: Are species regarded as alien if they evolved in the region, became extinct, and were re-introduced?* When answering this question, the time scale has to be explained. Some authors argue species that were native in an area but became extinct during the last glaciation should be viewed as alien (Webb 1985; Pyšek et al. 2004).

*Question 5: Is residence time within an area regarded as an important criterion?* In this case, it is useful to specify after which residence time a species is considered to be native (see Carthey and Banks 2012).

The previous questions all relate to the term *alien species*; questions 6 to 9 can be used to clarify definitions of *invasive species*.

*Question 6: Can native species also be called invasive?* The term *invasive species* is sometimes used for species expanding their range, no matter whether they are alien or native (Myster 1993; Valéry et al. 2008; Catford et al. 2009; Carey et al. 2012). Davis (2009), as an example, proposes to focus on similarities between processes of species redistributions instead of trying to separate aliens from range-expanding native species (SPRED-ecology, pp. 191-192). It is useful to state whether this view is shared, or *invasive species* are regarded as a subset of *alien species* (see e.g. ISSG 2000 or Richardson et al. 2011 for respective definitions).

*Question 7: Do invasive species necessarily have a negative impact in their new environment?* Some definitions apply the term *invasive* to those alien species that spread, regardless of their effects in the new environment (e.g. Heger and Trepl 2003). If impact is used as a condition (as e.g. in ISSG 2000), it should be specified what kind of impact is meant, e.g., economic, social and/or ecological impact, and which is the threshold to consider the impact relevant.

*Question 8: Do invasive species have to be successful?* Some authors propose that success is an important criterion to define *invasive species* (Valéry et al. 2008). As *success* can be indicated by a large distribution, high local abundance, dominance, fast spread, or a combination of these, it should be explained which measure of success the definition uses.

*Question 9: Do invasive species have to occur in semi-natural communities?* As some alien species at first only occur in heavily modified habitats (Richardson et al. 2000), the colonization of semi-natural or natural habitats is sometimes viewed as a useful criterion to define *invasive species* (Reichard and Hamilton 1997). According to such definitions, alien species quickly spreading in agricultural habitats are excluded from the *invasive species* category.

Explicitly answering these nine questions can help solving the problem of unclear terminology. The implementation of this checklist could, for instance, be accomplished in a working group or regular symposia. Increased consciousness of a growing number of authors, editors, and reviewers will help to minimize misunderstandings and misinterpretations.

### **Invasion theory: Lack of synthesis and imprecise hypotheses**

Each of the many existing hypotheses in invasion ecology covers specific aspects of the general mechanisms behind biological invasions. Some recent studies offer ideas for a synthesis of invasion theory (Colautti and MacIsaac 2004; Blumenthal 2006; Catford et al. 2009; Davis 2009;

Gurevitch et al. 2011). These approaches each put together different pieces of available knowledge in a specific and valuable way, but each approach is limited in what it covers. Additionally, invasion ecology still struggles to overcome a taxonomic bias, especially a division into plant-oriented studies on the one hand and animal-oriented studies on the other hand (Pyšek et al. 2008; Jeschke et al. 2012a). As a result, our overall knowledge about the mechanisms driving invasions is still patchy. Although a few treatments of both invasive plants and animals are available (Blackburn et al. 2011), a general synthesis of invasion ecology is still missing (C2 in Table 3).

As an additional difficulty, studies testing widely-used hypotheses often report contradictory results (Jeschke et al. 2012b; Moles et al. 2012). This is oftentimes due to the context-dependency of invasions (see above). Contradictory results become a problem as soon as the respective hypothesis is at stake: it is not clear if hypotheses with ambiguous evidence are worth keeping, or if they should be discarded (cf. Jeschke et al. 2012b). For example, the biotic resistance hypothesis (also known as 'diversity-invasibility hypothesis') states that ecosystems with a high biodiversity are more resistant to invaders than ecosystems with a low biodiversity (Elton 1958; Levine and D'Antonio 1999; Mack et al. 2000; Fridley et al. 2007; Davis 2009). Several small-scale experiments have supported this hypothesis, whereas large-scale studies hardly ever do so (Fridley et al. 2007). The latter sometimes even show the opposite pattern of what is predicted (Levine 2000; Stohlgren et al. 2003, 2006). Second, the enemy release hypothesis (Keane and Crawley 2002), which states that the absence of enemies is one cause of invasion success, is supported by several studies (Wolfe 2002; Mitchell and Power 2003), but questioned by others (Frenzel and Brandl 2003; te Beest et al. 2009).

One reason for these contradictory results is that considerable variation exists with respect to the wording of many current hypotheses (C3a in Table 3), and studies addressing them are not always explicit about which version they focus on. If two studies claim to test a certain hypothesis but are in fact testing different variants of this hypothesis, they may have opposite conclusions even if their empirical results are similar. The biotic resistance hypothesis, for example, is sometimes formulated as above, stating that ecosystems with a high biodiversity are more resistant to invaders than ecosystems with a low biodiversity. According to another, very general formulation of this hypothesis, ecosystems with a high biodiversity and a low level of disturbance should be more resistant to invaders than ecosystems with a low biodiversity and a high level of disturbance (Jeschke and Genovesi 2011). Yet another formulation focuses on disturbance and leaves out diversity (Mack et al. 2000), and other factors have also been tested to see if they influence an ecosystem's resistance to invaders, e.g., the presence of keystone predators (Carlsson et al. 2010).

A related difficulty is that many existing versions of hypotheses are too imprecise to be actually testable (C3b in Table 3). In fact, the number of variants of some hypotheses probably keeps rising exactly because existing versions are not testable. The biotic resistance hypothesis in the version stating that ecosystems with a high biodiversity are more resistant to invaders than ecosystems with a low biodiversity can be tested only if 'biodiversity' and 'resistance' are specified.

Existing studies have quantified biodiversity in different ways, for example by measuring richness of native species (Arndt 2006; Capers et al. 2007) or evenness (Wilsey and Polley 2002; Mattingly et al. 2007). Resistance has also been quantified in different ways, for example by counting the number of invasive species (assuming that fewer invasive species will be found in resistant ecosystems as compared to other ecosystems; e.g., Arndt 2006; Capers et al. 2007), or by calculating the fraction of introduced species that have become established (Blackburn and Duncan 2001; Jeschke and Genovesi 2011). Existing studies have thus focused on different forms of biodiversity and resistance (see also Jeschke et al. 2012b), and have consequently tested different formulations of the resistance hypothesis, in most cases without stating which exact version of the hypothesis has been addressed.

Another example is the enemy release hypothesis. Its general version contains several different possible mechanisms and processes, hence no single study can be designed to test it in its full extent. Studies addressing enemy release can only focus on some of its aspects, and often do so without explicitly discussing this limitation. For example, some studies compare populations of invasive species in the new range to populations of the same species in the indigenous range and quantify infestation, i.e., abundance or diversity of predators or parasites that can be found on the species (Mitchell and Power 2003; Vignon et al. 2009). Other studies use the same comparison but quantify damage typically caused by predators, e.g., leaf damage (Lewis et al. 2006; Ebeling et al. 2008). Another approach is to compare invasive to similar or related native species, and again, in some cases infestation is quantified (Frenzel and Brandl 2003; Blakeslee and Byers 2008), in others damage (Carpenter and Cappuccino 2005; Sugiura 2010). The case is even more complicated by the fact that some comparisons analyze the importance of generalist predators (Jogesh et al. 2008), others that of specialist predators (Memmott et al. 2000; Liu et al. 2007). It is often stated that the data confirm or reject the enemy release hypothesis without stating that only some aspects have been tested (see also Davis 2011).

### **Key measure 2: A hierarchy of hypotheses (HoH)**

The difficulty of imprecise hypotheses and lacking synthesis can be overcome by what we call a hierarchy of hypotheses (HoH). We suggest arranging hypotheses in an inverted tree-like structure, in which general hypotheses (i.e., hypotheses including too many aspects to be tested in single case studies) at the top branch into more and more specific hypotheses at the bottom. The most specific hypotheses (at the bottom) are very precise, and each can be approached with case studies. An accumulation of evidence for or against individual hypotheses can then help evaluate the more general predictions represented by this branch (cf. Jeschke et al. 2012b).

A HoH is able to structure the various aspects contained within many existing hypotheses. Let us use the enemy release hypothesis as an example. Its general formulation can be situated at the top of a branch (Fig. 1). A hypothesis addressing the rate of infestation in the new compared to the native range could be situated below, and further branch into hypotheses focused on generalist or specialist predators only (Fig. 1). Other lower-level hypotheses and aspects of the enemy release



hypothesis could be fanned out in the same way; where necessary, hypotheses could also be specified with respect to certain taxa or habitats.

Such an explicit formulation of testable lower-level hypotheses could be used to structure research on biological invasions. Every study could explicitly state which lower-level hypothesis is tested, whether it is confirmed or rejected, and what that means for higher-level hypotheses. To construct a HoH for invasion ecology will not be easy, and it has to be worked out how exactly the lower-level hypotheses contribute to the rejection or confirmation of the higher-level hypotheses. We think of a HoH as an evolving structure, at all times able to integrate new insights. As soon as it is constructed, it will be much easier than it is today to see whether lower-level hypotheses for a given higher-level hypothesis reach similar levels of empirical support, or whether certain lower-level hypotheses are better supported than others. Furthermore, it would be possible to see which hypotheses apply under which environmental conditions, for which scales, for which taxonomic groups and habitats. In other words, important information would be available to decide which hypotheses are valuable as a basis for prediction and management for given conditions.

Within a HoH, higher-level hypotheses are also connected to each other. For example, the enemy release hypothesis is connected to the novel weapons hypothesis. The latter hypothesis suggests that invasive species can have a competitive advantage over native species because they possess a trait that the native species are not evolutionarily adapted to and therefore affects them negatively (Callaway and Ridenour 2004). A shared idea is that missing eco-evolutionary 'experience' of the resident species with the invader can be advantageous for alien species. We suggest calling this the 'lack of eco-evolutionary experience hypothesis' (Fig. 1).

In a HoH for invasion ecology, every existing hypothesis would find its place within an interlinked system of other hypotheses. Every hypothesis could be classified as a basic building block at a lower level (i.e., testable but with small cover and extent) or be located at a higher level. Different formulations of similar ideas (e.g., formulations of the biotic resistance hypothesis described above) could be neighbors on one level and be integrated into an overarching idea at a higher level. In this way, a novel possibility for synthesis becomes visible. Research could aim at precisely determining which hypotheses hold in which situations, finding more and more interconnections among hypotheses and ideas, and search for more higher-level theories synthesizing those at lower levels. Future research should focus on building and maintaining such a HoH. It could be implemented as an online tool and updated regularly to integrate new data and hypotheses.

### **Empirical evidence: Lack of data and biases in data collection**

In addition to conceptual issues, a lack of data to test hypotheses (McGeoch et al. 2010) is a difficulty in invasion ecology (C4 in Table 3). For example, information on failed invasions following accidental introductions is often not available, especially for plants and invertebrates, sometimes not even for vertebrates. This problem affects many hypotheses in invasion ecology (Jeschke 2009; Lockwood et al. 2009; Rodriguez-Cabal et al. 2009). Invasion ecology also lacks

homogeneous data at large spatial scales, and long-term data are rare as well (but see Meiners et al. 2004). While short-term effects of invasive species are often known, their long-term effects are rarely investigated and hard to predict (Strayer et al. 2006). The history of invasion processes sometimes can be recovered through the study of herbarium specimens in combination with molecular research and literature reviews. Model simulations can additionally help fill this gap to some degree (Strayer et al. 2006). The study of ongoing changes in the effects of invasive species is necessary for predicting future effects. Unfortunately, the collection of long-term data is often hampered by difficulties to acquire funding for more than a few years. Citizen science has proven useful to gather large amounts of data, with a spatial and temporal coverage that would be hard to achieve for individual research teams (Dickinson et al. 2012). More citizen science programs to engage the general public into invasion research should be started. Online databases such as DAISIE (Delivering Alien Invasive Species Inventories for Europe; <http://www.europe-alien.org>), GISD (Global Invasive Species Database; <http://www.issg.org/database>), or NOBANIS (European Network on Invasive Alien Species; <http://www.nobanis.org>) have proven very useful, but they can only summarize data that are actually available.

Another difficulty for data analysis is that data collection is often biased, e.g., taxonomically, geographically, or methodologically (C5 in Table 3). Research on successful invaders is concentrated in those areas where most funding is available (Wilson et al. 2007; Pyšek et al. 2008). Similarly, researchers preferentially use those research methods that are easier to put into practice. Finally, initial introduction seems to be much less studied than other phases of the invasion process (Puth and Post 2005). These difficulties could be overcome, at least partly, if review studies that summarize existing data and identify research gaps and biases, such as the one by Pyšek et al. (2008), would be undertaken more frequently. A coherent framework, like the hierarchy of hypotheses suggested above, could help structure such summaries.

### **Lack of communication with the public, and with other scientific disciplines**

In addition to the discussed possibilities for improvement of the scientific methodology of invasion ecology concerning theory and data, there is a considerable potential for improvement concerning communication. Enhanced communication of applied research results to relevant stakeholders could help advance implementation of existing knowledge into policy and management (see Driscoll et al. 2011; Jones-Walters & Çil 2011) (C6 in Table 3), and invasion ecology could profit considerably from an improved communication among scientists of different disciplines (e.g., community ecology, macroecology, biological control, weed science, conservation biology, global change biology, biogeography, and evolutionary biology; Davis et al. 2001; C7 in Table 3). A hierarchy of hypotheses could help implement knowledge exchange: a similar hierarchy could be developed for other disciplines, and these HoHs could be interconnected on a higher level.

As pointed out above, invasion processes are influenced by socio-economic and cultural activities in many different ways, which also creates the need for transdisciplinary research (C8 in

Table 3). An increasing number of studies already advance in that direction, e.g., by analyzing historic catalogues (Dehnen-Schmutz et al. 2007; Blackburn et al. 2010), by explaining patterns in alien species richness based on indicators of current and historic socio-economic conditions (Hulme 2009; Essl et al. 2010), or by considering factors like economic value of species and invasions (Born et al. 2005; Gozlan et al. 2010). Another way to bridge the gap between ecology and social sciences is to combine vector science (Carlton and Ruiz 2005) with the study of continually shifting global decentralized networks (Barabási 2002).

### **Key measure 3: Platforms for improved communication**

We suggest to establish platforms for improved communication among scientists of different disciplines and with other societal groups (Fig. 2). Conference series explicitly addressing biological invasions already exist (e.g. 'Neobiota' or 'Biolief'). By inviting contributions from non-ecological disciplines, especially social sciences, these conferences could be used as forums for integrative, transdisciplinary research. Such transdisciplinary conferences would also benefit from frequent opportunities for open discussions. Moderated discussions in small groups can strongly promote the exchange of ideas and views, and are able to yield valuable insights. Smaller workshops addressing specific inter- or transdisciplinary questions would foster exchange of views and the development of novel approaches to invasion research. To permanently establish a culture of inter- and transdisciplinary communication at invasion conferences, it might be necessary to have one or more institutions guiding the process (cf. Aronson et al. 2010 concerning integrative communication in ecological economics). Therefore, existing organizations such as Neobiota (<http://www.oekosys.tu-berlin.de/menue/neobiota/>) should be used as a starting ground for such inter- and transdisciplinary efforts. Establishing an international transdisciplinary society for invasion science could be the next step.

The internet is providing possibilities for communication that should be better utilized for invasion research. In particular, social networks could be used for increasing communication among invasion scientists (cf. Nisbet et al. 2010 for similar recommendations to enhance communication regarding climate change research). Websites can also be set-up for citizen science approaches where volunteers can post the observations of alien species on a website (Dickinson et al. 2012; <http://www.waarnemingen.be>). Websites and apps of networks that connect science and policy can be very helpful as well, e.g. the Network-Forum for Biodiversity Research Germany (NeFo, <http://www.biodiversity.de>). It has been shown that stakeholders prefer free and easily accessible information on biological invasions (Bayliss et al. 2012). Two recently established websites (<http://www.lifewatch.eu> and <http://www.congressgenetics.eu/>) offer a combination of easily accessible information and communication platforms for researchers and stakeholders involved in biodiversity management. These initiatives could serve as a guide for launching a similar website for biological invasions. The HoH as described above could become the basis for such a website. It could become an evolving online platform, integrating knowledge from different subdisciplines and providing easy access to existing knowledge for other societal groups. Email

forums, integrated in existing or newly founded organizations and invigorated at workshops and symposia, could further enhance communication within science as well as among scientists and other stakeholders.

## CONCLUSION

This contribution is meant to increase awareness about existing difficulties in basic and applied invasion research, and to motivate efforts to more efficiently push to the limits of explanation, prediction, and management. Much can be done to increase clarity in communication, within science as well as between science, management, and the public. The proposed checklist for definitions can be useful to find a common language, and the proposed networking activities will provide opportunities to meet and exchange knowledge and ideas. Finally, the implementation of a hierarchy of hypotheses in invasion ecology can sharpen and synthesize existing hypotheses and can make scientific knowledge better available and thus more useful for understanding and managing invasions.

## ACKNOWLEDGMENTS

This paper summarizes the results of many fruitful discussions during the workshop "Tackling the emerging crisis of invasion biology: How can ecological theory, experiments, and field studies be combined to achieve major progress?" (March 2010 in Benediktbeuern, Germany; workshop of the specialist-group "Theory in Ecology" of the Ecological Society of Germany, Austria and Switzerland, GfÖ), organized by TH, SH, ATP, and MJM. We thank Laura Aquiloni, Silvia Bertocchi, Sara Brusconi, Alberto Inghilesi, Christiane Koch, Giuseppe Mazza, Roberto Merciai, Gabriele Orioli, and Elena Tricarico for their valuable contributions during this workshop. Katharina Dehnen-Schmutz as well as anonymous reviewers provided many critical comments that helped to improve the manuscript. The manuscript was reviewed through Peerage of Science (<http://www.peerageofscience.org>). Stella Copeland provided language corrections. MJM acknowledges financial support from the DFG (JE 288/4-1).

## REFERENCES

- Andreu, J., M. Vilà, and P.E. Hulme. 2009. An assessment of stakeholder perception and management of noxious alien plants in Spain. *Environmental Management* 43: 1244-1255.
- Arndt, E. 2006. Niche occupation by invasive ground-dwelling predator species in Canarian laurel forests. *Biological Invasions* 8: 893-902.
- Aronson, J., J.N. Blignaut, R.S. de Groot, A. Clewell, P.P. Lowry, II, P. Woodworth, R.M. Cowling, D. Renison, et al. 2010. The road to sustainability must bridge three great divides. In: *Ecological Economics Reviews*, eds K. Limburg, and Costanza, R.
- Barabási, A.-L. 2002. *Linked. The new science of networks*: Perseus Publishing.

- Bardsley, D.K., and G. Edwards-Jones. 2007. Invasive species policy and climate change: social perceptions of environmental change in the Mediterranean. *Environmental Science and Policy*. 10: 230-242.
- Bayliss, H.R., A. Wilcox, G.B. Stewart, and N.P. Randall. 2012. Does research information meet the needs of stakeholders? Exploring evidence selection in the global management of invasive species. *Evidence & Policy* 8: 37-56.
- Berghöfer, U., R. Rozzi, and K. Jax. 2010. Many eyes on nature: diverse perspectives in the Cap Horn Biosphere Reserve and their relevance for conservation. *Ecology and Society* 15: Art. 18. [online] URL: <http://www.ecologyandsociety.org/vol15/iss1/art18/>.
- Blackburn, T.M., and R.P. Duncan. 2001. Determinants of establishment success in introduced birds. *Nature* 414: 195-197.
- Blackburn, T.M., J.L. Lockwood, and P. Cassey. 2009. *Avian Invasions*. Oxford: Oxford University Press.
- Blackburn, T.M., K.J. Gaston, and M. Parnell. 2010. Changes in non-randomness in the expanding introduced avifauna of the world. *Ecography* 33: 168-174.
- Blackburn, T.M., P. Pysek, S. Bacher, J.T. Carlton, R.P. Duncan, V. Jarosík, J.R.U. Wilson, and D.M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333-339.
- Blakeslee, A.M.H., and J.E. Byers. 2008. Using parasites to inform ecological history: Comparisons among three congeneric marine snails. *Ecology* 89: 1068-1078.
- Blumenthal, D.M. 2006. Interactions between resource availability and enemy release in plant invasion. *Ecology Letters* 9: 887-895.
- Bodey, T.W., S. Bearhop, S.S. Roy, J. Newton, and R.A. McDonald. 2010. Behavioural responses of invasive American mink *Neovison vison* to an eradication campaign, revealed by stable isotope analysis. *Journal of Applied Ecology* 47: 114-120.
- Born, W., F. Rauschmayer, and I. Bräuer. 2005. Economic evaluation of biological invasions - a survey. *Ecological Economics* 55: 321-336.
- Bremner, A., and K. Park. 2007. Public attitude to the management of invasive non-native species in Scotland. *Biological Conservation* 139: 306-314.
- Burt, J., A. Muir, J. Piovia-Scott, K. Veblen, A. Chang, J. Grossman, and H. Weiskel. 2007. Preventing horticultural introductions of invasive plants: potential efficacy of voluntary initiatives. *Biological Invasions* 9: 909-923.
- Byron, J. 2008. Safe alternatives to replace invasives in California gardens. *California Agriculture* 62: 88-89.
- Callaway, R.M., and W.M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2: 436-443.
- Capers, R.S., R. Selsky, G.J. Bugbee, and J.C. White. 2007. Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. *Ecology* 88: 3135-3143.

- Carey, M.P., B.L. Sanderson, K.A. Barnas, and J.D. Olden. 2012. Native invaders - challenges for science, management, policy, and society. *Frontiers in Ecology and the Environment* 10: 373-381.
- Carlsson, N.O.L., J.M. Jeschke, N. Holmqvist, and J. Kindberg. 2010. Long-term data on invaders: when the fox is away, the mink will play. *Biological Invasions* 12: 633-641.
- Carlton, J.T., and G.M. Ruiz. 2005. Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: *Invasive alien species. A new synthesis*, eds. H. A. Mooney, Mack, R. N., McNeely, J. A., Neville, L. E., Schei, P. J., and Waage, J. K.: Island Press.
- Carpenter, D., and N. Cappuccino. 2005. Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology* 93: 315-321.
- Carthey, A.J.R., and P.B. Banks. 2012. When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. *PLoS ONE* 7: e31804.
- Cassey, P., T.M. Blackburn, R.P. Duncan, and J.L. Lockwood. 2005. Lessons from the establishment of exotic species: a meta-analytical case study using birds. *Journal of Animal Ecology* 74: 250-258.
- Catford, J.A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22-40.
- Chew, M. 2006. *Ending with Elton: preludes to invasion biology*. Tempe, AZ: Arizona State University.
- Colautti, R.I., and H.J. MacIsaac. 2004. A neutral terminology to define 'invasive' species. *Diversity and Distributions* 10: 135-141.
- Davis, M.A. 2009. *Invasion Biology*. Oxford: Oxford University Press.
- Davis, M.A. 2011. Researching invasive species 50 years after Elton: a cautionary tale. In: *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*, eds. D. M. Richardson: Blackwell Publishing.
- Davis, M.A., K. Thompson, and J.P. Grime. 2001. Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions* 7: 97-102.
- Dehnen-Schmutz, K., and M. Williamson. 2006. *Rhododendron ponticum* in Britain and Ireland: social, economic and ecological factors in its successful invasion. *Environment and History* 12: 325-350.
- Dehnen-Schmutz, K., J. Touza, C. Perrings, and M. Williamson. 2007. The horticultural trade and ornamental plant invasions in Britain. *Conservation Biology* 21: 224-231.
- Dickinson, J.L., J. Shirk, D. Bonter, R. Bonney, R.L. Crain, J. Martin, T. Phillips, and K. Purcell. 2012. The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment* 10: 291-297.

- Drake, J.A., H.A. Mooney, F. Di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek, and M. Williamson (eds.). 1989. *Biological Invasions: a Global Perspective*. Chichester: John Wiley & Sons Ltd.
- Driscoll, C.T., L. Kathy Fallon, and K.C. Weathers. 2011. Integrating Science and Policy: A Case Study of the Hubbard Brook Research Foundation Science Links Program. *Bioscience* 61: 791-801.
- Ebeling, S.K., I. Hensen, and H. Auge. 2008. The invasive shrub *Buddleja davidii* performs better in its introduced range. *Diversity and Distributions* 14: 225-233.
- Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen & Co. Ltd.
- Essl, F., S. Dullinger, W. Rabitsch, P.E. Hulme, K. Hülber, V. Jarošík, I. Kleinbauer, F. Krausmann, et al. 2010. Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America* 108: 203-207.
- Fischer, A., and R. van der Wal. 2007. Invasive plant suppresses charismatic seabird - the construction of attitudes towards biodiversity management options. *Biological Conservation* 135: 256-267.
- Frenzel, M., and R. Brandl. 2003. Diversity and abundance patterns of phytophagous insect communities on alien and native host plants in the Brassicaceae. *Ecography* 26: 723-730.
- Fridley, J.D., J.J. Stachowicz, S. Naeem, D.F. Sax, E.W. Seabloom, M.D. Smith, T.J. Stohlgren, D. Tilman, et al. 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88: 3-17.
- Gellis Communications. 2008. Scoping study for an EU wide communications campaign on biodiversity and nature. Final report to the Commission/DG ENV.
- Gherardi, F. 2011. Public perception of invasive alien species in Mediterranean Europe. In: *Invasive and introduced plants and animals: human perceptions, attitudes and approaches to management.*, eds. R. A. Lambert, and Rotherham, I. D. London, UK: Earthscan.
- Gozlan, R.E. 2008. Introduction of non native freshwater fish: is it all bad? *Fish and Fisheries* 9: 106-115.
- Gozlan, R.E., J.R. Britton, I. Cowx, and G.H. Copp. 2010. Current knowledge on non-native freshwater fish introductions. *Journal of Fish Biology* 76: 751-786.
- Gurevitch, J., I.W. Howard, E.A. Ashton, E.A. Leger, E. Howe, E. Woo, and M. Lerdau. 2008. Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. *Biological Invasions* 10: 821-831.
- Gurevitch, J., G.A. Fox, G.M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14: 407-418.
- Hayes, K.R., and S.C. Barry. 2008. Are there any consistent predictors of invasion success? *Biological Invasions* 10: 483-506.
- Heger, T., and L. Trepl. 2003. Predicting biological invasions. *Biological Invasions* 5: 313-321.

- Heger, T., W.-C. Saul, and L. Trepl in press. What biological invasions 'are' is a matter of perspective. *Journal for Nature Conservation*.
- Hodges, K.E. 2008. Defining the problem: terminology and progress in ecology. *Frontiers in Ecology and the Environment* 6: 35-42.
- Hoste, I., R. van Moorsel, and R. Barendse. 2008. Een nieuwkomer in sierteeltbedrijven en tuinen: *Cardamine corymbosa* in Nederland en België. *Dumortiera* 93: 15-24.
- Hulme, P.E. 2006. Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* 43: 835-847.
- Hulme, P.E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10-18.
- ISSG. 2000. IUCN Guidelines for the prevention of biodiversity loss caused by alien invasive species.  
[http://intranet.iucn.org/webfiles/doc/SSC/SSCwebsite/Policy\\_statements/IUCN\\_Guidelines\\_for\\_the\\_Prevention\\_of\\_Biodiversity\\_Loss\\_caused\\_by\\_Alien\\_Invasive\\_Species.pdf](http://intranet.iucn.org/webfiles/doc/SSC/SSCwebsite/Policy_statements/IUCN_Guidelines_for_the_Prevention_of_Biodiversity_Loss_caused_by_Alien_Invasive_Species.pdf).
- Jeschke, J.M. 2009. Across islands and continents, mammals are more successful invaders than birds (Reply to Rodriguez-Cabal et al.). *Diversity and Distributions* 15: 913-914.
- Jeschke, J.M., and P. Genovesi. 2011. Do biodiversity and human impact influence the introduction or establishment of alien mammals? *Oikos* 120: 57-64.
- Jeschke, J.M., L. Gómez Aparicio, S. Haider, T. Heger, C.J. Lortie, P. Pyšek, and D.L. Strayer. 2012a. Taxonomic bias and lack of cross-taxonomic studies in invasion biology. *Frontiers in Ecology and the Environment* 10: 349-350.
- Jeschke, J.M., L. Gómez Aparicio, S. Haider, T. Heger, C.J. Lortie, P. Pyšek, and D.L. Strayer. 2012b. Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14: 1-20.
- Jogesh, T., D. Carpenter, and N. Cappuccino. 2008. Herbivory on invasive exotic plants and their non-invasive relatives. *Biological Invasions* 10: 797-804.
- Jones-Walters, L., and A. Çil. 2011. Biodiversity and stakeholder participation. *Journal for Nature Conservation* 19: 327-329.
- Keane, R.M., and M.J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164-170.
- Kowarik, I. 2003. Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. *Biological Invasions* 5: 293 - 312.
- Küffer, C., and G. Hirsch Hadorn. 2008. How to achieve effectiveness in problem-oriented landscape research: the example of research on biotic invasions. *Living Reviews in Landscape Research* 2: 2. [Online Article] URL: <http://landscaperesearch.livingreviews.org/Articles/lrlr-2008-2/>.
- Lambert, R.A., and I.D. Rotherham (eds.). 2011. *Invasive and introduced plants and animals: human perceptions, attitudes and approaches to management*. London, UK: Earthscan.



- Levine, J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* 288: 852-854.
- Levine, J.M., and C.M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- Lewis, K.C., F.A. Bazzaz, Q. Liao, and C.M. Orians. 2006. Geographic patterns of herbivory and resource allocation to defense, growth, and reproduction in an invasive biennial, *Alliaria petiolata*. *Oecologia* 148: 384-395.
- Liu, H., P. Stiling, and R.W. Pemberton. 2007. Does enemy release matter for invasive plants? evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. *Biological Invasions* 9: 773-781.
- Lockwood, J.L., M.F. Hoopes, and M.P. Marchetti. 2007. *Invasion Ecology*. Malden, USA: Blackwell Publishing.
- Lockwood, J.L., P. Cassey, and T.M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15: 904-910.
- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133-137.
- Lodge, D.M., S. Williams, H.J. MacIsaac, K.R. Hayes, B. Leung, S.E. Reichard, R.N. Mack, P.B. Moyle et al. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* 16: 2035-2054.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710.
- Mattingly, B.W., R. Hewlate, and H.L. Reynolds. 2007. Species evenness and invasion resistance of experimental grassland communities. *Oikos* 116: 1164-1170.
- McGeoch, M.A., S.H.M. Butchart, D. Spear, E. Marais, E.J. Kleynhans, A. Symes, J. Chanson, and M. Hoffmann. 2010. Global indicators of biological invasions: species numbers, biodiversity impact and policy responses. *Diversity and Distributions* 16: 95-108.
- McGeoch, M.A., D. Spear, E.J. Kleynhans, and E. Marais. 2012. Uncertainty in invasive alien species listing. *Ecological Applications* 22: 959-971.
- Meiners, S.J., M.L. Cadenasso, and S.T.A. Pickett. 2004. Beyond biodiversity: individualistic controls of invasion in a self-assembled community. *Ecology Letters* 7: 121-126.
- Memmott, J., S.V. Fowler, Q. Paynter, A.W. Sheppard, and P. Syrett. 2000. The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica* 21: 213-222.
- Mitchell, C.E., and A.G. Power. 2003. Release of invasive plants from fungal and viral pathogens. *Nature* 421: 625-627.

- Moles, A.T., H. Flores-Moreno, S.P. Bonser, D.I. Warton, A. Helm, L. Warman, D.J. Eldridge, E. Jurado, et al. 2012. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology* 100: 116-127.
- Moore, J.L., T.M. Rout, C.E. Hauser, D. Moro, M. Jones, C. Wilcox, and H.P. Possingham. 2010. Protecting islands from pest invasion: optimal allocation of biosecurity resources between quarantine and surveillance. *Biological Conservation* 143: 1068-1078.
- Myster, R.M. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. *Botanical Reviews*. 59: 251-272.
- Niggemann, M., J. Jetzkowitz, S. Brunzel, M.C. Wichmann, and R. Bialozyt. 2009. Distribution patterns of plants explained by human movement behaviour. *Ecological Modelling* 220: 1339-1346.
- Nisbet, M.C., M.A. Hixon, K.D. Moore, and M. Nelson. 2010. Four cultures: new synergies for engaging society on climate change. *Frontiers in Ecology and the Environment* 8: 329-331.
- Perrings, C., H.A. Mooney, and M. Williamson (eds.). 2010a. *Bioinvasions and globalization. Ecology, economics, management, and policy*. Oxford: Oxford University Press.
- Perrings, C., S. Burgiel, M. Lonsdale, H.A. Mooney, and M. Williamson. 2010b. Globalization and bioinvasions: the international policy problem. In: *Bioinvasions and globalization. Ecology, economics, management, and policy*, eds. C. Perrings, Mooney, H. A., and Williamson, M. Oxford: Oxford University Press.
- Puth, L.M., and D.M. Post. 2005. Studying invasion: have we missed the boat? *Ecology Letters* 8: 715-721.
- Pyšek, P., D.M. Richardson, M. Rejmánek, G.L. Webster, M. Williamson, and J. Kirschner. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131-143.
- Pyšek, P., D.M. Richardson, J. Pergl, V. Jarosik, Z. Sixtova, and E. Weber. 2008. Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution* 23: 237-244.
- Reichard, S.H., and C.W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* 11: 193-203.
- Richardson, D.M. (ed.). 2011a. *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. Chichester: Wiley-Blackwell.
- Richardson, D.M. 2011b. Invasion science: the roads travelled and the roads ahead. In: *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*, eds. D. M. Richardson: Wiley-Blackwell.
- Richardson, D.M., and P. Pyšek. 2007. Elton, C.S. 1958: The ecology of invasions by animals and plants. London: Methuen. *Progress in Physical Georaphy* 31: 659-666.
- Richardson, D.M., and P. Pyšek. 2008. Fifty years of invasion ecology - the legacy of Charles Elton. *Diversity and Distributions* 14: 161-168.
- Richardson, D.M., P. Pyšek, M. Rejmánek, M.G. Barbour, F.D. Panetta, and C.J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93-107.

- Richardson, D.M., P. Pyšek, and J.T. Carlton. 2011. A compendium of essential concepts and terminology in invasion ecology. In: *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*, ed. D. M. Richardson: Wiley-Blackwell.
- Rodriguez-Cabal, M., N. Barrios-Garcia, and D. Simberloff. 2009. Across island and continents, mammals are more successful invaders than birds (Reply). *Diversity and Distributions* 15: 911-912.
- Sax, D.F., J.H. Brown, E.P. White, and S.D. Gaines. 2005. The dynamics of species invasions. Insights into the mechanisms that limit species diversity. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography*, eds. D. F. Sax, Stachowicz, J. J., and Gaines, S. D. Sunderland: Sinauer.
- Simberloff, D. 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution and Systematics* 40: 81-102.
- Skou, A.M.T., S. Pauleit, and J. Kollmann (in press) Tracing the introduction history of a potentially invasive ornamental shrub – variation in frost hardiness and climate change. *Nordic Journal of Botany*.
- Stohlgren, T.J., D.T. Barnett, and J. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1: 11-14.
- Stohlgren, T.J., C. Jarnevich, G.W. Chong, and P.H. Evangelista. 2006. Scale and plant invasions: a theory of biotic acceptance. *Preslia* 78: 405-426.
- Strayer, D.L., V.T. Eviner, J.M. Jeschke, and M.L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* 21: 645-651.
- Sugiura, S. 2010. Associations of leaf miners and leaf gillers with island plants of different residency histories. *Journal of Biogeography* 37: 237-244.
- Tatem, A.J. 2009. The worldwide airline network and the dispersal of exotic species: 2007–2010. *Ecography* 32: 94-102.
- te Beest, M., N. Stevens, H. Olf, and W.H. van der Putten. 2009. Plant-soil feedback induces shifts in biomass allocation in the invasive plant *Chromolaena odorata*. *Journal of Ecology* 97: 1281-1290.
- Valéry, L., F. Hervé, J.-C. Levfeuvre, and D. Simberloff. 2008. In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions* 10: 1345–1351.
- van Kleunen, M., W. Dawson, D. Schlaepfer, J.M. Jeschke, and M. Fischer. 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters* 13: 947-958.
- Verbrugge, L.N.H., R.S.E.W. Leuven, and G.v.d. Velde. 2010. Evaluation of international risk assessment protocols for exotic species. *Series of Reports on Environmental Science*. Radboud University Nijmegen.
- Vignon, M., P. Sasal, and R. Galzin. 2009. Host introduction and parasites: a case study on the parasite community of the peacock grouper *Cephalopholis argus* (Serranidae) in the Hawaiian Islands. *Parasitology Research* 104: 775-782.

- Walther, G.-R., A. Roques, P.E. Hulme, M.T. Sykes, P. Pyšek, I. Kühn, M. Zobel, S. Bacher et al. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* 24: 686-693.
- Webb, D.A. 1985. What are the criteria for presuming native status? *Watsonia* 15: 231-236.
- Wilsey, B.J., and H.W. Polley. 2002. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters* 5: 676-684.
- Wilson, J.R.U., S. Proches, B. Braschler, E.S. Dixon, and D.M. Richardson. 2007. The (bio)diversity of science reflects the interests of society. *Frontiers in Ecology and the Environment* 5: 409-414.
- Wilson, J.R.U., E.E. Dormontt, P.J. Prentis, A.J. Lowe, and D.M. Richardson. 2009. Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology & Evolution* 24: 136-144.
- Wolfe, L.M. 2002. Why Alien Invaders Succeed: Support for the Escape-from-Enemy Hypothesis. *The American Naturalist* 160: 705-711.
- Zedler, J.B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* 23: 431-452.

## AUTHOR BIOGRAPHIES

**Tina Heger** is a postdoctoral researcher at Technische Universität München, Germany and University of California, Davis, USA. She is interested in conceptual ecology and biological invasions. Her current research focusses on the influence of evolutionary legacy on invasion success.

*Address:* Technische Universität München (TUM), Department of Ecology and Ecosystem Management, Restoration Ecology, Emil-Ramann-Str. 6, D-85350 Freising, Germany.  
e-mail: t.heger@wzw.tum.de

**Anna T. Pahl** is a doctoral candidate in Restoration Ecology at the Technische Universität München. Her research in invasion ecology is mainly focused on the relevance of changes in the community context for the invasion success of alien plants.

*Address:* Technische Universität München (TUM), Department of Ecology and Ecosystem Management, Restoration Ecology, Emil-Ramann-Str. 6, D-85350 Freising, Germany.  
e-mail: a.pahl@wzw.tum.de

**Zoltan Botta-Dukát** is a senior researcher at the MTA Centre for Ecological Research. His main research topics are community assembly and biological invasion.

*Address:* MTA Centre for Ecological Research, Alkotmány 2-4, H.2163 Vácrátót, Hungary  
e-mail: botta-dukát.zoltan@okologia.mta.hu

**Francesca Gherardi** is a professor of zoology and conservation biology at the Department of Biology, University of Florence, Italy. Her interests are focused on invasion biology, biodiversity conservation, and eco-ethology.

*Address:* Department of Biology, University of Florence, Via Romana 17, I-50125 Florence, Italy.  
e-mail: francesca.gherardi@unifi.it

**Christina Hoppe** is a doctoral candidate at the Institute of Ecology, Evolution and Diversity at the Goethe University of Frankfurt. Her main research interests include seed dispersal strategies of plant species, invasion ecology and conservation biology.

*Address:* Goethe University of Frankfurt, Institute for Ecology, Evolution & Diversity, Max-von-Laue-Str. 13, D-60438 Frankfurt am Main, Germany.  
e-mail: hoppe@bio.uni-frankfurt.de

**Ivan Hoste** studied history at Ghent University and has a job at the National Botanic Garden of Belgium since 1997. His research interests include the alien flora of Western Europe and the 19th- and 20th-century history of botany in Belgium.

*Address:* National Botanic Garden of Belgium, Domein van Bouchout, B-1860 Meise, Belgium.  
e-mail: ivan.hoste@br.fgov.be

**Kurt Jax** is a senior scientist at the Helmholtz-Centre for Environmental Research - UFZ, Germany, and professor of ecology at the Technische Universität München. His research interests are the theory and philosophy of ecology, with a special emphasis on linking the natural sciences and the humanities with respect to these fields.

*Address:* Helmholtz-Centre for Environmental Research - UFZ, Department of Conservation Biology, Permoserstr. 15, D-04318 Leipzig, Germany.  
e-mail: kurt.jax@ufz.de

**Leena Lindström** is a University lecturer in Ecology and Evolutionary Biology at the University of Jyväskylä and her team is part of the Finnish Academy funded Centre of Excellence in Biological Interactions Research. Her research interests include evolutionary ecology of species invasions.

*Address:* Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland.  
e-mail: leena.m.lindstrom@jyu.fi

**Pieter Boets** is a PhD student at the department of Applied Ecology, Laboratory of Environmental Toxicology and Aquatic Ecology at Ghent University, Belgium. His research interest is related to the impact and spread of alien macroinvertebrates in inland waters in Flanders (Belgium). Based

on a combination of modelling techniques and laboratory experiments, he tries to gain insight into the complex ecology of invasive species.

*Address:* Laboratory of Environmental Toxicology and Aquatic Ecology, Ghent University, J. Plateaustraat 22, B-9000 Ghent, Belgium.

e-mail: pieter.boets@ugent.be

**Sylvia Haider** is a postdoctoral researcher at the Martin Luther University Halle Wittenberg, Germany. Her research focus lies on plant invasions in mountains with a special emphasis on distribution patterns and adaptation processes. She is part of the Consortium of the Mountain Invasion Research Network (MIREN, <http://www.miren.ethz.ch>).

*Address:* Martin Luther University Halle Wittenberg, Institute of Biology, Geobotany and Botanical Garden, Am Kirchtor 1, D-06108 Halle (Saale), Germany.

e-mail: Sylvia.haider@botanik.uni-halle.de

**Johannes Kollmann** is a professor in restoration ecology at the Technische Universität München. His scientific interest is focused on various aspects of ecological restoration, including plant provenances used for restoration and invasive alien plants.

*Address:* Technische Universität München (TUM), Department of Ecology and Ecosystem Management, Chair of Restoration Ecology, D-85350 Freising, Germany.

e-mail: jkollmann@wzw.tum.de

**Meike J. Wittmann** is a PhD student in biology at the University of Munich (LMU) where she develops stochastic models for the dynamics of introduced populations. More generally, she is interested in mathematical modeling in ecology and population genetics.

*Address:* Ludwig-Maximilians-Universität München, Department of Biology II, Großhaderner Str. 2, D-82152 Planegg-Martinsried, Germany

e-mail: wittmann@bio.lmu.de

**Jonathan M. Jeschke** is Principal Investigator at Technische Universität München, Germany, and Visiting Scientist at the Cary Institute of Ecosystem Studies, Millbrook, New York, USA. He held research positions at Ludwig-Maximilians-Universität München, Germany; Cary Institute of Ecosystem Studies, Millbrook, New York, USA; and University of Helsinki, Finland. His research interests focuses on biological invasions, other novel organisms, biodiversity, predator-prey interactions, and other basic and applied ecological topics.

*Address:* Technische Universität München (TUM), Department of Ecology and Ecosystem Management, Restoration Ecology, Emil-Ramann-Str. 6, D-85350 Freising, Germany.

e-mail: jonathan.jeschke@gmx.net

1 **Table 1** Invasion ecology is confronted with three domains of difficulties. Domain A: Difficulties arising from society and its relationship to  
 2 biological invasions, measures that can be taken to overcome them and consequences for the scientific approach of invasion ecology; letters and  
 3 numbers in parentheses refer to Table 3.

	<b>Difficulty</b>	<b>Measures</b>	<b>Consequences for the scientific approach</b>
A1	Deliberate introductions, influenced by commercial interests and changing fashions	<ul style="list-style-type: none"> <li>• Risk assessment protocols</li> <li>• Black, white and grey lists<sup>1</sup></li> <li>• International cooperation to prevent trade with risky species<sup>2</sup></li> <li>• Raising public awareness<sup>3</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Commercial interests and changing fashions should be considered for explanation and prediction (C8)</li> </ul>
A2	Accidental introductions, promoted by globalization	<ul style="list-style-type: none"> <li>• Quarantine measures<sup>4</sup></li> <li>• International cooperation to prevent accidental introductions<sup>2</sup></li> <li>• Raising public awareness<sup>3</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Changes in transportation pathways should be considered for explanation and prediction (C8)</li> </ul>
A3	Inconsistent evaluation of invasive species	<ul style="list-style-type: none"> <li>• Development of management strategies based on knowledge about public attitudes<sup>5</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Public attitudes should be investigated and considered (C8)</li> </ul>
A4	Little motivation for management measures due to little prospect of success <sup>6</sup>	<ul style="list-style-type: none"> <li>• Improve information about feasibility of management strategies<sup>7</sup></li> </ul>	<ul style="list-style-type: none"> <li>• Need for clear management guidelines (C6)</li> </ul>

4

<sup>1</sup> Verbrugge et al. 2010

<sup>2</sup> Perrings et al. 2010b

<sup>3</sup> Bremner and Park 2007, Burt et al. 2007, Byron 2008

<sup>4</sup> Mack et al. 2000, Moore et al. 2010

<sup>5</sup> Fischer and van der Wal 2007

<sup>6</sup> Andreu et al. 2009

<sup>7</sup> Bodey et al. 2010

**Table 2** Invasion ecology is confronted with three domains of difficulties. Domain B: Difficulties caused by the peculiarity of the invasion process, and consequences for the scientific approach of invasion ecology; letters and numbers in parentheses refer to Table 3.

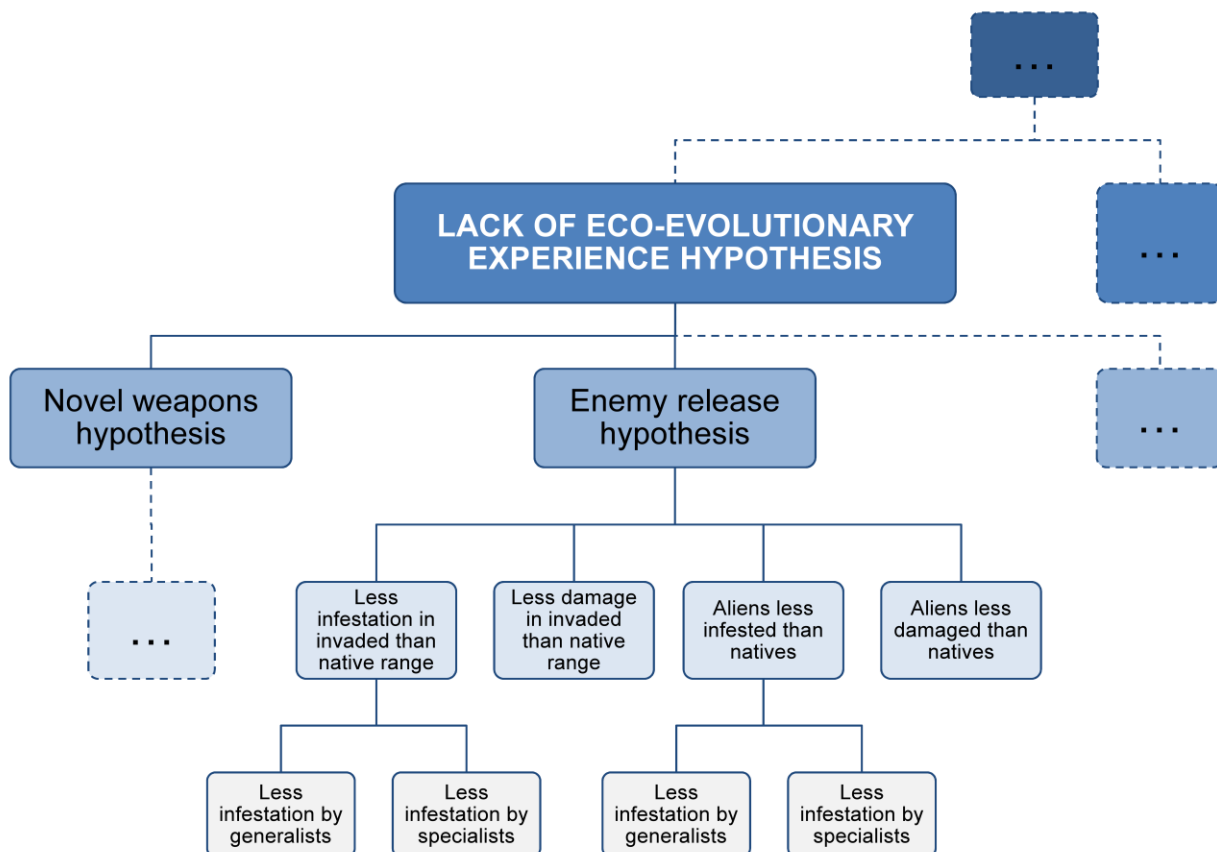
	<b>Difficulty</b>	<b>Consequences for the scientific approach</b>
B1	Complexity: many different factors interact in determining invasion success	<ul style="list-style-type: none"> <li>• Synthesis needed to integrate the interacting influence of multiple factors (C2)</li> </ul>
B2	Context dependence: invader success varies in time and space	<ul style="list-style-type: none"> <li>• Historic data are relevant (C4)</li> <li>• Case studies needed, but also synthesis (C2)</li> </ul>
B3	Cultural influences at each stage of the process	<ul style="list-style-type: none"> <li>• Socio-cultural sciences have to be integrated for explanation and prediction (C8)</li> </ul>



**Table 3** Invasion ecology is confronted with three domains of difficulties. Domain C: Conceptual and methodological difficulties, and measures to meet them. C1 to C3 relate to the conceptual basis and theory of invasion ecology, C4 and C5 to empirical research, and C6 to C8 to the need of integration with other scientific disciplines and societal groups. Letters and numbers in parentheses refer to difficulties given in Tables 1, 2.

	<b>Difficulty</b>	<b>Measures</b>
C1	Terminology: unclear concepts and definitions	<ul style="list-style-type: none"> <li>• Explicit definitions (see checklist in Box 1)</li> </ul>
C2	Insufficient synthesis; sub-division of invasion ecology (e.g., taxonomic groups)	<ul style="list-style-type: none"> <li>• Hierarchy of hypotheses (HoH) with precise, testable hypotheses at lowest level</li> </ul>
C3	Imprecise hypotheses (a) different versions of hypotheses (b) lack of testability	<ul style="list-style-type: none"> <li>• HoH</li> </ul>
C4	Lack of data to test hypotheses (a) lack of data on unsuccessful introductions (b) lack of large-scale experimental data (c) lack of long-term data	<ul style="list-style-type: none"> <li>• Funding of large-scale and long-term research</li> <li>• ‘Indirect’ methods (e.g., retrospective analyses and model simulations instead of long-term experiments)</li> <li>• Online databases</li> <li>• Citizen science and monitoring programs by the general public</li> </ul>
C5	Bias in data collection (a) invasion events (most research on successful species in areas with high density of researchers) (b) methods of data collection	<ul style="list-style-type: none"> <li>• Frequent reviews with connection to HoH; aim: identification of gaps and biases</li> </ul>
C6	Necessity of communication of research results to concerned stakeholders (A4)	<ul style="list-style-type: none"> <li>• Focus on output valuable for applications</li> <li>• Up-to-date networks and platforms</li> <li>• Joint conferences and discussions</li> </ul>
C7	Complexity (B1) creates the need to integrate other biological subdisciplines	<ul style="list-style-type: none"> <li>• Integration of HoH into other disciplines</li> <li>• Joint conferences and discussions</li> </ul>
C8	Influence of socio-economic and cultural processes on invasions (A1, A2, B3) creates the need for transdisciplinary research	<ul style="list-style-type: none"> <li>• Communication and collaboration with researchers of humanities and social sciences</li> <li>• Joint conferences and discussions</li> </ul>

**Fig. 1** Sketch of a possible hierarchy of hypotheses (HoH) for invasion ecology. Overarching ideas branch into more precise, better testable hypotheses at lower levels. ‘Infestation’ means abundance or diversity of predators or parasites that can be found on the species. Empty boxes indicate that the hierarchy may be extended.



**Fig. 2** Possibilities to improve communication among scientists of different disciplines, managers, politicians, and other stakeholders (represented by different colors).



**Box 1** Checklist for definitions: questions that should be answered when defining *alien* or *invasive species*.

<b>ALIEN SPECIES</b>	1. Is human-mediated transport a necessary criterion?
	<p>If yes:</p> <ul style="list-style-type: none"> <li>❖ How are unrecorded, unintentional introductions distinguished from natural dispersal?</li> <li>❖ Does human mediation include indirect effects such as habitat change?</li> </ul>
	2. Are species that continuously expand their range regarded as aliens?
	<p>If not:</p> <ul style="list-style-type: none"> <li>❖ Which criterion is used to distinguish continuous from non-continuous spread (e.g., distance between populations, existence of a barrier to dispersal)?</li> </ul>
	3. Are species that originate in the region by hybridization of alien and native species regarded as aliens?
	4. Are species regarded as aliens if they evolved in the region, became extinct, and were reintroduced?
	5. Are species regarded as aliens even if they have been present in the new region for quite a long time?
	<p>If not:</p> <ul style="list-style-type: none"> <li>❖ After which time period do we consider them to be native?</li> </ul>
<b>INVASIVE SPECIES</b>	6. Can native species also be invasive, or are invasive species a subset of alien species?
	7. Is impact a necessary criterion?
	<p>If yes:</p> <ul style="list-style-type: none"> <li>❖ How is impact defined? Which is the threshold to consider an impact relevant?</li> </ul>
	8. Is success a necessary criterion?
	<p>If yes:</p> <ul style="list-style-type: none"> <li>❖ How is success defined? Indicators may be large distribution, high local abundance, or fast spread.</li> </ul>
	9. Is occurrence in natural habitats a necessary criterion?