Creating and evaluating hypothesis networks in invasion biology

Inaugural-Dissertation

to obtain the academic degree

Doctor rerum naturalium (Dr. rer. nat.)

submitted to the Department of Biology, Chemistry and Pharmacy

of Freie Universität Berlin

by

M.Sc. M.A. Martin Enders

2019

This work was written from May 2015 to October 2019 under the supervision of Prof. Dr. Jonathan M. Jeschke.

1. Gutachter: Prof. Dr. Jonathan M. Jeschke

2. Gutachter: Prof. Dr. Marc-Thorsten Hütt

Disputation am 27.01.2020

ACKNOWLEDGEMENTS

Many thanks to Jonathan and Tina for believing in this work and supporting me with it. Frank and Marc-Thorsten for working with me and teaching me a lot in programming. Christian Kummer and Christian Dürnberger for philosophical support. Also, I want to thank the Foundation of German Business (sdw) for giving me a three-year scholarship and ideational support. Further financial support was provided by the German Federal Ministry of Education and Research (BMBF) within the Collaborative Project "Bridging in Biodiversity Science - BIBS" (funding number 01LC1501A-H). In addition, I want to thank all my co-authors, my working group, especially Stefan Linzmaier for sharing an office with me, and my family & friends.

CONTENTS

0. Summary 5
0. Zusammenfassung 6
1. General Introduction 8
  1.1. Motivation 8
  1.2. Invasion biology 8
  1.3. Biases in invasion biology 10
  1.4. Further challenges in invasion biology 11
  1.5. Previous works and other maps of science 12
  1.6. Bibliometrics 13
  1.7. Network analysis 14
  1.8. Aims of this work 15
2. A Network of Invasion Hypotheses 16
3. Drawing a map of invasion biology based on a network of hypotheses 28
  3.1. Appendix 43
4. A citation-based map of concepts in invasion biology 69
5. A conceptual map of invasion biology 90
  5.1. Appendix 120
6. Discussion 125
  6.1. The problem with maps 125
  6.2. The trait network 127
  6.3. The survey network 127
  6.4. The bibliometric network 128
  6.5. Comparing trait and survey networks with the bibliometric network 129
  6.6. The consensus network 129
  6.7. Problems in visualization 130
  6.8. Conclusions 131
  6.9. Further work 133
  6.10. Coda 134
7. Publications with author contributions 135
8. Literature cited 136
9. Curriculum Vitae 142

0. Summary

Invasion biology is a relatively young sub-discipline of biology. Despite the fact that the idea was established in Charles Darwin's book 'On the origin of species', the field was only founded a hundred years later with Charles Elton. Since the middle of the 1990s, the field has substantially grown in size. Accordingly, the number of hypotheses and concepts about biological invasions has substantially increased, and some of them are similar to each other, others are not supported by empirical evidence. The aim of this work was to develop and apply methods to create networks of hypotheses and concepts that visualize the field of invasion biology. The thesis contains four different methods and their resulting networks. Due to the nature of the topic, this work is interdisciplinary. The topics range from biology and its way to find categories (chapter 2), over social science (chapters 3 & 5) to bibliometrics (chapter 4). Also, this work had to overcome challenges in visualizing the emerging networks (see chapter 6.1). The method presented and applied in chapter 2 is a straightforward possibility to structure hypotheses based on their traits and characteristics. This method resulted in a hypothesis network with several clusters of hypotheses. For chapter 3, a survey approach was applied to create hypothesis networks. The participants of the survey were experts in the field of invasion biology. Surprisingly, the results showed that experts in invasion biology seem to have no consistent idea of their research field and therefore no clear, consistent inner map of invasion biology. With additional analyses, however, we were able to create networks of the best-known hypotheses and concepts in invasion biology seen by the participating experts. In chapter 4, we looked at co-citations of the key papers related to the major invasion hypotheses. This approach led to two clear maps of the field (one for each of the two applied analysis methods). Finally, in chapter 5, we created a hypothesis network based on a workshop we held in Berlin. This network emerged from a Delphi-based consensus approach that we developed. We also applied an advanced cluster-finding algorithm here that clusters links between nodes in the network instead of clustering nodes which is done by traditional cluster-finding algorithms. The advanced algorithm thus allows nodes to be in more than one cluster. This network based on the consensus approach and analyzed with the link-clustering algorithm has a better resolution and provides more information than the other networks presented in this thesis. I conclude this thesis with a discussion of the benefits and drawbacks of each network and its underlying approach. It seems that the best approaches to create a useful hypothesis network of a research field are those presented in chapters 4 and 5, i.e. the co-citation and consensus approaches. A co-citation based network reveals how a research field such as invasion biology is seen by scientists who work in the field and how they cite publications. But there are no strict rules for citation and therefore this approach is based on trust in scientifically correct citations. The risk of a strong bias is reduced in case of the consensus approach, as the resulting network is based on the combined perspective of a sizeable number of experts. This seems to be the best way to structure existing hypotheses of invasion biology right now. A future important step is to apply this and possibly other approaches in other research fields.

0. Zusammenfassung

Die Invasionsbiologie ist eine relativ junge Unterdisziplin der Biologie. Trotz der Tatsache, dass die Idee in Charles Darwins Buch "On the origin of species" begründet war, wurde das Feld erst einhundert Jahre später mit Charles Elton begründet. Seit Mitte der 1990er Jahre ist das Feld erheblich gewachsen. Dementsprechend hat die Anzahl der Hypothesen und Konzepte zu biologischen Invasionen erheblich zugenommen, und einige von ihnen ähneln sich, andere werden nicht durch empirische Evidenz gestützt. Ziel dieser Arbeit war es, Methoden zu entwickeln und anzuwenden, um Netzwerke von Hypothesen und Konzepten zu erstellen, die das Gebiet der Invasionsbiologie visualisieren. Die Arbeit enthält vier verschiedene Methoden und die daraus resultierenden Netzwerke. Aufgrund der Art des Themas ist diese Arbeit interdisziplinär. Die Themen reichen von der Biologie und ihrem Weg zur Kategorisierung (Kapitel 2) über die Sozialwissenschaften (Kapitel 3 und 5) bis hin zur Bibliometrie (Kapitel 4). Diese Arbeit musste auch die Herausforderungen bei der Visualisierung der entstehenden Netzwerke bewältigen (siehe Kapitel 6.1). Die in Kapitel 2 vorgestellte und angewandte Methode ist eine nahe liegende Möglichkeit, Hypothesen anhand ihrer Merkmale und Eigenschaften zu strukturieren. Diese Methode führte zu einem Hypothesennetzwerk mit mehreren Hypothesenclustern. Für das 3. Kapitel wurde ein Erhebungsansatz angewendet, um Hypothesennetzwerke zu erstellen. Die Teilnehmer der Umfrage waren Experten auf dem Gebiet der Invasionsbiologie. Überraschenderweise zeigten die Ergebnisse, dass Experten der Invasionsbiologie offenbar keine einheitliche Vorstellung von ihrem Forschungsgebiet und daher keine klare, einheitliche innere Karte der Invasionsbiologie haben. Mit zusätzlichen Analysen konnten wir jedoch Netzwerke der

bekanntesten Hypothesen und Konzepte in der Invasionsbiologie erstellen, wie sie von den teilnehmenden Experten gesehen wurden. In Kapitel 4 haben wir uns die Ko-Zitationen der wichtigsten Veröffentlichungen im Zusammenhang mit den Hypothesen der Invasionsbiologie angesehen. Dieser Ansatz führte zu zwei übersichtlichen Karten des Feldes (eine für jede der beiden angewandten Analysemethoden). Schließlich haben wir in Kapitel 5 ein Hypothesennetzwerk erstellt, das auf einem Workshop basiert, den wir in Berlin organisiert hatten. Dieses Netzwerk ist aus einem von uns entwickelten Delphi-basierten Konsensus-Ansatz hervorgegangen. Wir haben hier auch einen fortschrittlichen Cluster-Finding-Algorithmus angewendet, der Verbindungen zwischen Knoten im Netzwerk gruppiert, anstatt Knoten zu gruppieren, was durch herkömmliche Cluster-Finding-Algorithmen erfolgt. Der erweiterte Algorithmus ermöglicht es somit, dass sich Knoten in mehr als einem Cluster befinden. Dieses auf dem Konsensansatz basierende und mit dem Link-Clustering-Algorithmus analysierte Netzwerk hat eine bessere Auflösung und liefert mehr Informationen als die anderen in dieser Arbeit vorgestellten Netzwerke. Ich schließe diese Arbeit mit einer Diskussion der Vor- und Nachteile jedes Netzwerks sowie der jeweils zugrunde liegenden Methode. Es scheint, dass die besten Ansätze zur Schaffung eines nützlichen Hypothesennetzwerks auf einem Wissenschaftsgebiet die in den Kapiteln 4 und 5 vorgestellten sind. Ein Ko-Zitation-basiertes Netzwerk (Kapitel 4) zeigt, wie ein Forschungsgebiet wie die Invasionsbiologie von Wissenschaftlern, die auf diesem Gebiet arbeiten, gesehen wird und wie sie Veröffentlichungen zitieren. Da es jedoch keine strengen Zitierregeln gibt, basiert diese Arbeit auf dem Vertrauen in wissenschaftlich korrekte Zitationen. Das Risiko einer starken Verzerrung wird im Falle des Konsensansatzes (Kapitel 5) verringert, da das resultierende Netzwerk auf der kombinierten Perspektive einer beträchtlichen Anzahl von Experten basiert. Dies scheint der derzeit beste Weg zu sein, um die Hypothesen der Invasionsbiologie zu strukturieren. Ein nächster wichtiger Schritt ist nun die Anwendung dieses und möglicherweise anderer Ansätze in anderen Forschungsbereichen.

1. General Introduction

1.1. Motivation

The motivation for this work was to produce and provide a map of science and a method to structure research fields. The most fitting explanation was written in Enders and Jeschke (2018):

> *It is said that before Napoleon Bonaparte went into battle, he sat in a big sandbox, planning all his battle moves with miniature figures in advance (Botham, 2006). Sure, Napoleon took it too far, but the concept of visualizing a battle on a map of the surroundings wasn´t that extravagant. This is also the idea behind networks of invasion biology: to see the bigger picture behind it, the connections, similarities and dissimilarities at once, to plan your next move – in this case regarding research or management of biological invasions. To see the bigger picture in the field of invasion biology is getting more and more important, especially when considering the progress of the field in the last 25 years. We have reached a point at which we produce more information every day but seem to have lost the general overview of the field.*

A way to provide an overview of research fields is urgently needed because it seems that the experts of many fields are in danger to lose themselves in the myriads of hypotheses and concepts of these fields, and this leads to a waste of money, knowledge and time (Jeschke et al. 2019). This is at least the case for the field of invasion biology. Using this discipline as a case study, this thesis aimed to develop and apply different ways of making such a map/network of a science field and analyze the benefits and drawbacks of each method.

1.2. Invasion biology

Invasion biology is a part of ecology that focuses on the introduction, establishment and spread of species in a new habitat (Lockwood et al. 2013). One of its goals is to find reasons for the success of some non-native species. It is a discipline that grew very slowly at first. In the 19th century, early concepts on non-native species were mentioned, for example in Charles Darwin's book "On the origin of species by means of natural selection" (Darwin 1859). Further concepts were introduced by the Swiss botanist Albert Thellung in the early 20th century (Kowarik and Pyšek 2012), and then by Charles Elton (1958) and others until the 1950s, however there was still too little work on the topic to recognize a distinct research field. Possibly due to a growing consciousness for ecosystems in a changing world (Meadows et al. 1972) and in human responsibilities (Jonas 1979), interest in invasion biology strongly increased since the late 20th century (Richardson and Pyšek 2008; Gurevitch et al. 2011). It has also influenced other research fields; for example, concepts and hypotheses of invasion biology are used in restoration ecology, landscape ecology, urban ecology or risk assessments of genetically modified organisms (Jeschke et al. 2013). For this work, a hypothesis is defined as by Heger et al. (2019, p. 30): an "[a]ssumption or proposed explanation that is in principle testable."

Nowadays, concepts and hypotheses of invasion biology are used in different fields of science (e.g. renaturation ecology, landscape ecology) (Lowry et al. 2013). This loose usage of the concepts and hypotheses could lead to a blurry picture of this field of science. But besides this, the rich cornucopia of hypotheses includes also some rotten fruits. For example, hypotheses that have a low level of empirical support, such as the tens rule (Williamson and Brown 1986; Jeschke and Strayer 2005) are still being used. Further, some other biases have found their way into invasion biology like a decline effect (time bias) described by Jeschke et al. (2012a), which is a decline in support for a hypothesis over time; or a geographical bias (Lowry et al. 2013), as most studies concerning invasive species are done in North America or Europe; and a taxonomic and habitat bias, as most studies in the field focus on terrestrial plants (Pyšek et al. 2008; Jeschke and Heger 2018). For these reasons which are further detailed in the next sections, a map of the field is urgently needed especially when one looks at the consequences that biological invasions have on biodiversity.

According to Collen et al. (2012), non-native species are, after pollution and the loss of habitats, the third biggest threat of biodiversity in invertebrates. In the recent report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), invasive species are also listed as one of the biggest biodiversity threats (Brondizio et al. 2019; see also McGeoch et al. 2010), and the Convention on Biological Diversity (a Convention of the United Nations) sees the urge to fight non-native species (United Nations 2002) in its agreements.

Biodiversity thereby means much more than the "diversity of species". I follow the definition of biodiversity proposed by the Convention on Biological Diversity (CBD) in 1992 in Rio de Janeiro:

> "Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems.” United Nations CBD (1992)

1.3. Biases in invasion biology

There are many biases in research focused on biological invasions. They can be structured into at least four different groups: (i) geographic bias, (ii) taxonomic bias, (iii) habitat bias and (iv) chronological bias. Other biases exist as well, for example publication biases, but I do not focus on them here for the sake of brevity.

1.3.1. Geographic bias

There is a significant imbalance between areas where invasions are taking place and areas where invasions are being investigated. Most of the studies are from Northern America or from Western Europe (Lowry et al. 2013), not where the impacts of invasions are strongest (Bellard and Jeschke 2016). The survey network (chapter 3) also shows this bias in the composition of the participants. The strong focus on North America and Western Europe could is likely caused by financial reasons and by the fact that most researchers are still based there (cf. Tydecks et al. 2018).

1.3.2. Taxonomic bias

Pyšek et al. (2008; Jeschke et al. 2012b; Jeschke and Heger 2018) showed that there is also a bias concerning the studied species. Almost half (48.3%) of the studies focus on plants. With 36.3% come invertebrates in second place. This leads to an under-representation of other species and also to a bias in the hypotheses and concepts. These hypotheses and concepts are not necessarily robust and useable for every taxon (Jeschke and Heger 2018).

1.3.3. Habitat bias

Similar to the taxonomic bias, there is a habitat bias. Many hypotheses and concepts focus their attention on terrestrial plants (on average >80%; cf. Jeschke and Heger 2018). This leads, like the taxonomic bias, to an overrepresentation of studies in terrestrial habitats.

Therefore, the hypotheses are well tested for terrestrial plants, but this is not the case for every habitat or taxa.

1.3.4. Chronological bias

Although many hypotheses initially (shortly after being postulated) receive a great deal of empirical support, this level of support can decrease significantly over time (Jeschke et al., 2012). This leads to a possible temporal data distortion or time-shifted perception: new hypotheses get a lot of empirical support and only over time get empirically refuted. This can also mean that hypotheses we still see as valid could be empirically refuted, but are still in use (see tens rule).

1.4. Further challenges in invasion biology

In addition to these biases, there are several other challenges that invasion biology has to cope with, particularly concerning the applied methods, concepts and the listing of invasive species. This section gives a short overview of such difficulties.

1.4.1. Conceptual and methodological difficulties

In this category falls the terminology, which means unclear terms and concepts. Unclear terminology can cause problems in communication with the broader public, other scientists, in the science itself and with decision-makers. This is a problem not only in invasion biology, but also in ecology in general and probably also in many other fields of science. So, for example, a negative connotation of some terms like “invaders”, “aliens” or “weeds” for non-native species can lead to problems in communication with non-scientists (Hodges 2008; Heger et al. 2013).

1.4.2. Imprecise hypotheses

Invasion biology has, as shown in the following chapters, many hypotheses that are rather similar, but focused on different aspects or nuances of a step in the invasion process. The problem is that every testing of a hypothesis has a slight variation in the wording of that hypothesis. It can thus happen that two studies claim to test the same hypothesis, i.e. they use the same name of a hypothesis, but actually test different concepts, because the researchers carrying out the studies had different perspectives of what the hypothesis posits. As a result, they may offer completely different interpretations of their data: even if their results are qualitatively similar, one study could argue the results support the hypothesis, whereas the other study could argue it questions the hypothesis (Heger et al. 2013). It is thus important to explicitly define a hypothesis one is testing; this is done for every chapter of this thesis. The hierarchy-of-hypotheses (HoH) approach (Jeschke et al. 2012a; Heger et al. 2013; Jeschke and Heger 2018; Heger et al. 2019) is a helpful tool in this respect. In the HoH approach, hypotheses are split in an inverted tree-like structure: on the top is the most general idea of this hypothesis and if you go deeper, it divides into different aspects. Through this approach, scientists could easily define which aspect of a hypothesis they are studying.

1.4.3. Lack of data

There is a lack of data to test hypotheses (McGeoch et al. 2010a). Invasion biology lacks information on failed invasions, homogeneous data at large spatial scales, long-term data and accidental introductions of plants and invertebrates (Heger et al. 2013). This affects many hypotheses in invasion biology (Jeschke 2008; Lockwood et al. 2009). Short-term effects of non-native species are often known, but their long term effects are hardly studied and even harder to predict. These effects could mean genetic, physiological or behavioral ones which could affect the outcome of an invasion (Strayer et al. 2006). As Strayer et al. (2006) wrote: “we need to include time in our thinking about invaders”.

1.5. Previous works and other maps of science

Science maps allow to visually explore disciplines including their biases and difficulties. One could say that the visualization of science was established in the 18th century, although in a different way than today. At this time, the maps showed more information on a ‘classical’ map with geographic properties, like the spread of the cholera in London. Also at this time, another line of mapping evolved that lacked geographic properties. Especially with the appearance of bibliometric studies (see below, section 1.6.), non-geographical maps were created. In recent times, the development of the internet and more computing power to work with large-scale data sets paved the way for more complex maps (c.f. Börner 2010).

The maps created for invasion biology in this thesis are science maps because they ‘visually encode the structure and evolution of scholarly knowledge’ (Börner 2010), but can be separated by the scale they look at. On the smallest scale, there are works who look at the deeper structure of hypotheses and try to create an in-depth structure of a concept or hypothesis. Heger and Jeschke (2014) and Schulz et al. (2019) did this for the enemy release hypothesis (Keane and Crawley 2002) by dividing the hypothesis into different sub-hypotheses to show different aspects of it. These visualizations follow the HoH approach mentioned above (Jeschke et al. 2012; Heger et al. 2013; Jeschke and Heger 2018; Heger et al. 2019). In the book ‘Invasion biology: hypotheses and evidence’ (Jeschke and Heger 2018), 13 hypotheses were split into sub-hypotheses in a hierarchical structure and combined with more than 1100 empirical studies testing them.

Maps where also created for other disciplines in science, for example, chemistry (Boyack et al. 2007). On a higher scale, there are conceptual or structural frameworks. These frameworks can be done visually, like this work, or in another, non-visual, way like in Catford et al. (2009) or Gurevitch et al. (2011). Such frameworks aim for a way to arrange the field in a useful way.

The biggest scale is a network of the field of sciences (Boyack et al. 2005). These maps are mostly produced by data from the science citation index and use huge amounts of data of citations or bibliographic coupling (cf. Börner (2010)). There are also science maps that are not concerned with academic science at all. For example, Klavans and Boyack (2014) studied domains of 125,000 non-profit organizations in the United States to cluster and show the structure of altruistic groups in the US. Please note that in this work the words “maps” and “networks” were used in a similar way: “network” is the more technical term and better describes how the map is methodologically constructed, whereas the term “map” focuses on the purpose as a navigation tool. A misconception in the use of the word map could be coming from the common usage of the word map for a geographical map. But this strict usage is outdated for at least 100 years, and the field of science maps has further evolved.

1.6. Bibliometrics

Bibliometrics is the field of science concerning the statistical analysis of bibliographic data, mainly of scientific journals. Despite early works by Lotka (1926) on the productivity of authors and the first citation analysis by Gross and Gross (1927), the work by Bradford (1934) on the distribution of articles in journals, the book ‘little science, big science’ by de Sola Price (1963) and the invention of the Science Citation Index (SCI) in 1961, the field of bibliometrics was not established before the 1970s. Bibliometrics is nowadays a fundamental part of recognizing and evaluating the productivity of a scientist, a journal or a field of science, even although such metrics can have key drawbacks (Jeschke et al. 2019). This process goes from simple counting of citations or papers to more complex models. Also, to see citations and co-citations in a field of science bibliometrics are crucial (cf. Havemann (2016)). Especially the results of citation and co-citation analyses could be visualized as networks. The 21st century brought the advance of many methods for clustering networks (Fortunato 2010; Xie, Kelley, & Szymanski 2013; Amelio and Pizzuti 2014). To cluster a network means to use algorithms that identify groups of nodes that are more connected within their group than to the rest of the network. Some of these methods were also applied for topic identification (Börner 2015).

1.7. Network analysis

To structure a network, Newman and Girvan (2004) introduced so-called 'modularity' as an evaluation function of a graph partition. The resulting groups of nodes, i.e. clusters, should be more connected with their own cluster than to the rest of the network. For this clustering, several algorithms were introduced. These algorithms, which separate a network, can, in turn, be categorized into several types. The following algorithms were used in this thesis: (1) The Girvan and Newman (2002) algorithm as an example of divisive clustering. It recursively detects links with high edge betweenness and removes them from the network. The clustering dendrogram is cut at the partition with maximum modularity. (2) Clauset et al. (2004) proposed to set each node as a cluster and then merge those two subgraphs that give the highest gain in modularity; this is repeated until there is no gain in modularity anymore. Again, the clustering dendrogram is cut at the partition with maximum modularity. (3) Quite similar is the approach introduced by Brandes et al. (2008); it maximizes modularity applying an optimization algorithm from integer linear programming. (4) The Louvain algorithm designed by Blondel et al. (2008) which very quickly maximizes partition modularity by combining and separating clusters. (5) The “walk trap” algorithm suggested by Pons and Latapy (2005) assumes a random walker gets trapped in communities and calculates these “traps”. (6) The divisive spectral algorithm suggested by Newmann (2006) which also maximizes modularity with help of the eigenvector values. And (7) finally, the most sophisticated approach, the link-clustering algorithm designed by Havemann et al. (2019). This algorithm clusters a network not by the nodes but by the links, which results in nodes that are members of more than one cluster. Of course, there are way more algorithms to cluster a network, but for this work only the most well-known and common were chosen (1-6) plus the advanced algorithm to cluster links (7).

1.8. Aims of this work

The aims of this thesis are threefold: First, find different ways to create a network to visualize a field of science; in this case, the field of science is invasion biology. Second, compare the resulting networks. And finally, evaluate the different networks concerning their overall usefulness, their resolution and the question(s) they address. The thesis structure is depicted in Figure 1. It shows how the four chapters are connected to each other. All of these four chapters' overarching aim is to find a useful, repeatable way to structure a field of science, and they all use hypotheses in invasion biology as a case example.

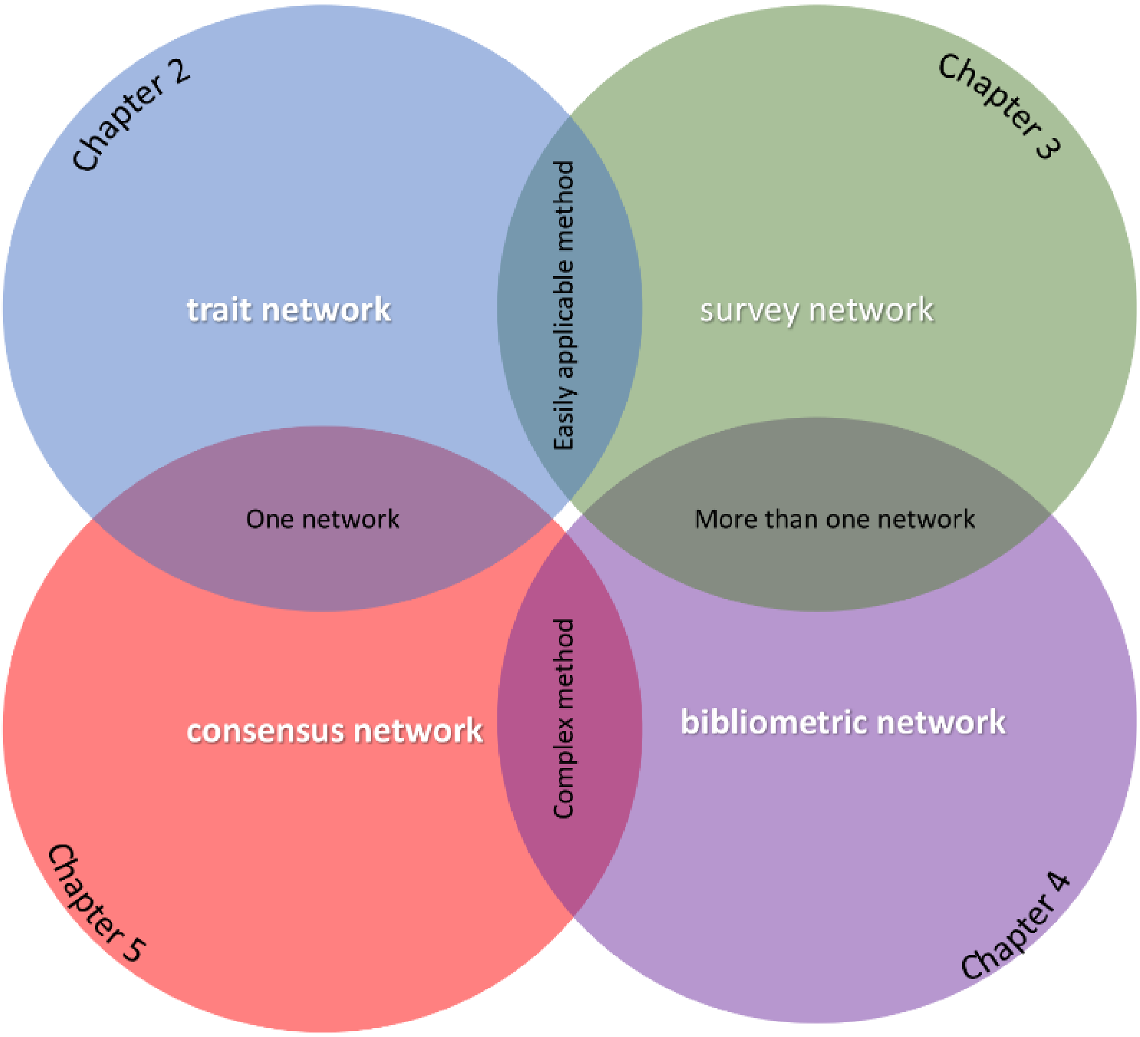

Figure 1 Venn-diagram of the chapters in this work.

2. A Network of Invasion Hypotheses

This chapter was published in the book *Invasion Biology: Hypotheses and Evidence* (Jeschke and Heger 2018) and was printed there as chapter 7. It was written with Prof. Dr. Jonathan Jeschke from Freie Universität Berlin and Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB). The idea for this method of using ‘traits’ to construct a network was first applied in my Bachelor thesis at Ludwig-Maximilians University in the year 2012.

Published as: Enders, M. and Jeschke, J. M. (2018). A Network of Invasion Hypotheses. Invasion Biology: Hypotheses and Evidence. J. M. Jeschke and T. Heger, eds. Wallingford, CABI**:** 49-59.

7

A Network of Invasion Hypotheses

Martin Enders[1,2,3]* and Jonathan M. Jeschke[1,2,3]
[1]Freie Universität Berlin, Institute of Biology, Berlin, Germany; [2]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany; [3]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

Abstract

Hypotheses of research disciplines are typically not isolated from each other but share similarities. In a broad sense as defined here, they form an important part of the theoretical–conceptual understanding of a given topic, e.g. invasion hypotheses *sensu lato* represent an important part of our understanding of biological invasions. Dynamic research disciplines such as invasion biology have so many hypotheses that it is even hard for experts to keep track, and researchers from other disciplines as well as policymakers, managers and other interested people find it extremely complicated to get to grips with invasion hypotheses. To tackle this situation, we argue that it is useful to define key hypotheses and visualize their relationships. We define 35 of the arguably most common invasion hypotheses and outline three approaches to create hypothesis networks that visualize the similarities and dissimilarities between hypotheses: (i) the bibliometric approach; (ii) the survey approach; and (iii) the matrix approach. The latter approach is in the focus of this chapter. It is centred around a matrix that represents the characteristics or traits of each hypothesis. Here we assigned such traits to 35 invasion hypotheses based on 13 trait categories. We then calculated the similarities between them and created a hypothesis network visualizing these similarities. With the same trait matrix, we created a smaller network focused on the 12 hypotheses featured in this book. This network thus illustrates the relationships between these 12 hypotheses and can be used as a map for the following chapters.

Introduction

It is said that before Napoleon Bonaparte went into battle he sat in a big sandbox, planning all his battle moves with miniature figures in advance (Botham, 2006). Sure, Napoleon took it too far, but the concept of visualizing a battle on a map of the surroundings wasn't that extravagant. This is also the idea behind networks of invasion biology: to see the bigger picture behind it, the connections, similarities and dissimilarities at once, to plan your next move – in this case regarding research or management of biological invasions. To see the bigger picture in the field of invasion biology is getting more and more important, especially when considering the progress of the field in the last 25 years. We have reached a point at which we produce more information every day but seem to have lost the general overview of the field. This is why the field of invasion biology needs something to order it, for example a map of the field. Networks seem to be promising tools to create useful maps of this and other research fields (Jeschke, 2014).

---

* Corresponding author. E-mail: enders.martin@gmx.net

© CAB International 2018. *Invasion Biology: Hypotheses and Evidence*
(eds J.M. Jeschke and T. Heger)

There are different possible approaches to create networks, each of them with their own benefits and disadvantages. We outline three such approaches (this list is, of course, not exhaustive) and will concentrate on the third one of these for the remainder of this chapter:

1. *Bibliometric approach*: Here, the full text or meta-data of publications are analysed and used to build a network based on citations, co-citations or collaborations between working groups, or on content similarity by comparing key phrases. The nodes in such a network can be authors, journals or (sub-) disciplines. See de Solla Price (1965) or Börner (2010) for examples of applications of this approach.
2. *Survey approach*: The idea here is to use the judgement of different experts on the similarities and dissimilarities of hypotheses in a research field. This procedure was already used for the field of invasion biology by Enders *et al.* (2018) who developed an online questionnaire asking experts in the field about similarities and dissimilarities between 33 common invasion hypotheses. Each hypothesis was defined and a short explanation provided (based on and extending Catford *et al.*, 2009; a further extension is provided in this chapter, see Table 7.1). Participants were asked to choose up to three hypotheses that they know best. The survey then took the chosen hypotheses and randomly paired them with other hypotheses; the participants were asked about their similarities or dissimilarities. From the results, different networks were created using different formulae for calculating between-hypotheses similarity.
3. *Matrix approach*: This approach compares characteristics (i.e. traits) of ideas in a specific field. If two hypotheses share a number of characteristics beyond a certain threshold, they are termed 'similar', and a connection between these hypotheses is drawn in the network. This approach will be explained in detail in the next section using invasion hypotheses as an example.

All approaches can be applied in any field of research where a number of key hypotheses exist. It is quite surprising that such approaches have only been rarely applied, even though Naisbitt's quote 'we are drowning in information but starved for knowledge' is over three decades old now (p. 24 in Naisbitt, 1982). We urgently need tools to synthesize the increasing amounts of information in order to make them more accessible and usable. It is the goal of this chapter to contribute to the development of such tools by focusing on one possible approach, the one we termed 'matrix approach'.

Methods

Applying the matrix approach, we first defined 35 common invasion hypotheses. This list of definitions was based on Catford *et al.* (2009), references cited therein and further sources cited in Table 7.1. For Enders *et al.* (2018) we extended the list provided in Catford *et al.* (2009); for this chapter we extended it once more, resulting in the list provided in Table 7.1. Please note, however, that there are further invasion hypotheses (see e.g. Chapter 17, this volume, and Ricciardi *et al.*, 2013).

We then developed a matrix containing traits for each hypothesis in 13 categories (Table 7.2). The category 'lag time' describes the time period that the mechanism or effect represented by a hypothesis needs, starting from the introduction of a non-native species. We differentiated very short (++), relatively short (+), intermediate (+–), relatively long (–) and very long (– –) lag times. The next two categories were 'propagule pressure' and 'other human actions' and are summarized under human interference. These and all following categories were classified as either very important (++), somewhat important (+) or not important (empty cell) for a given hypothesis. The following three categories describe ecosystem properties: 'habitat modification', caused by either humans, non-native or native species or abiotic factors; available 'resources' in the new ecosystem; and other 'ecosystem properties'. The following three categories come under the header biotic interactions: 'enemies', 'mutualism' and 'competition'. They

Table 7.1. List of 35 common invasion hypotheses and how we defined them.

Hypothesis	Definition	Key reference(s)
Adaptation (ADP)	The invasion success of non-native species depends on the adaptation to the conditions in the exotic range before and/or after the introduction. Non-native species that are related to native species are more successful in this adaptation.	Duncan and Williams (2002)
Biotic acceptance aka 'the rich get richer' (BA)	Ecosystems tend to accommodate the establishment and coexistence of non-native species despite the presence and abundance of native species.	Stohlgren *et al.* (2006)
Biotic indirect effects (BID)	Non-native species benefit from different indirect effects triggered by native species.	Callaway *et al.* (2004)
Biotic resistance aka diversity-invasibility hypothesis (BR)	An ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity.	Elton (1958), Levine and D'Antonio (1999)
Darwin's naturalization (DN)	The invasion success of non-native species is higher in areas that are poor in closely related species than in areas that are rich in closely related species.	Darwin (1859)
Disturbance (DS)	The invasion success of non-native species is higher in highly disturbed than in relatively undisturbed ecosystems.	Elton (1958), Hobbs and Huenneke (1992)
Dynamic equilibrium model (DEM)	The establishment of a non-native species depends on natural fluctuations of the ecosystem, which influences the competition of local species.	Hutson (1979)
Empty niche (EN)	The invasion success of non-native species increases with the availability of empty niches in the exotic range.	MacArthur (1970)
Enemy inversion (EI)	Introduced enemies of non-native species are less harmful for them in the exotic than the native range, owing to altered biotic and abiotic conditions.	Colautti *et al.* (2004)
Enemy of my enemy aka accumulation-of-local-pathogens hypothesis (EE)	Introduced enemies of a non-native species are less harmful to the non-native as compared to the native species.	Eppinga *et al.* (2006)
Enemy reduction (ERD)	The partial release of enemies in the exotic range is a cause of invasion success.	Colautti *et al.* (2004)
Enemy release (ER)	The absence of enemies in the exotic range is a cause of invasion success.	Keane and Crawley (2002)
Environmental heterogeneity (EVH)	The invasion success of non-native species is high if the exotic range has a highly heterogeneous environment.	Melbourne *et al.* (2007)
Evolution of increased competitive ability (EICA)	After having been released from natural enemies, non-native species will allocate more energy in growth and/or reproduction (this re-allocation is due to genetic changes), which makes them more competitive.	Blossey and Nötzold (1995)
Global competition (GC)	A large number of different non-native species is more successful than a small number.	Colautti *et al.* (2006)

continued

Table 7.1. *continued*

Hypothesis	Definition	Key reference(s)
Habitat filtering (HF)	The invasion success of non-native species in the new area is high if they are pre-adapted to this area.	Darwin (1859)
Human commensalism (HC)	Species that are living in close proximity to humans are more successful in invading new areas than other species.	Jeschke and Strayer (2006)
Ideal weed (IW)	The invasion success of a non-native species depends on its specific traits (e.g. life-history traits).	Elton (1958), Reimánek and Richardson (1996)
Increased resource availability (IRA)	The invasion success of non-native species increases with the availability of resources.	Sher and Hyatt (1999)
Increased susceptibility (IS)	If a non-native species has a lower genetic diversity than the native species, there will be a low probability that the non-native species establishes itself.	Colautti *et al.* (2004)
Invasional meltdown (IM)	The presence of non-native species in an ecosystem facilitates invasion by additional species, increasing their likelihood of survival or ecological impact.	Simberloff and Von Holle (1999), Sax *et al.* (2007)
Island susceptibility hypothesis (ISH)	Non-native species are more likely to become established and have major ecological impacts on islands than on continents.	Jeschke (2008)
Limiting similarity (LS)	The invasion success of non-native species is high if they strongly differ from native species and it is low if they are similar to native species.	MacArthur and Levins (1967)
Missed mutualisms (MM)	In their exotic range, non-native species suffer from missing mutualists.	Mitchell *et al.* (2006)
New associations (NAS)	New relationships between non-native and native species can positively or negatively influence the establishment of the non-native species.	Colautti *et al.* (2004)
Novel weapons (NW)	In the exotic range, non-native species can have a competitive advantage against native species because they possess a novel weapon, i.e. a trait that is new to the resident community of native species and therefore affects them negatively.	Callaway and Ridenour (2004)

Opportunity windows (OW)	The invasion success of non-native species increases with the availability of empty niches in the exotic range and the availability of these niches fluctuates spatio-temporally.	Johnstone (1986)
Plasticity hypothesis (PH)	Invasive species are more phenotypically plastic than non-invasive or native ones.	Richards *et al.* (2006)
Propagule pressure (PP)	A high propagule pressure (a composite measure consisting of the number of individuals introduced per introduction event and the frequency of introduction events) is a cause of invasion success.	Lonsdale (1999), Lockwood *et al.* (2013)
Reckless invader aka ‘boom-bust’ (RI)	A non-native species that is highly successful shortly after its introduction can get reduced in its population or even extinct over time due to different reasons (such as competition with other introduced species or adaptation by native species).	Simberloff and Gibbons (2004)
Resource-enemy release (RER)	The non-native species is released from its natural enemies and can spend more energy in its reproduction, and invasion success increases with the availability of resources.	Blumenthal (2006)
Sampling (SP)	A large number of different non-native species is more likely to become invasive than a small number owing to interspecific competition. Also the species identity of the locals is more important than the richness in terms of the invasion of an area.	Crawley *et al.* (1999)
Shifting defence hypothesis (SDH)	After having been released from natural specialist enemies, non-native species will allocate more energy in cheap (energy-inexpensive) defences against generalist enemies and less energy in expensive defences against specialist enemies (this re-allocation is due to genetic changes); the energy gained in this way will be invested in growth and/or reproduction, which makes the non-native species more competitive.	Doorduin and Vrieling (2011)
Specialist–generalist (SG)	Non-native species are more successful in a new region if the local predators are specialists and local mutualists are generalists.	Callaway *et al.* (2004)
Tens rule (TEN)	Approximately 10% of species successfully take consecutive steps of the invasion process.	Williamson and Brown (1986), Williamson (1996)

Table 7.2. Matrix with traits of 35 invasion hypotheses in 13 different categories.

	1	2	3	4	5	6	7	8	9	10	11	12	13
		Human interference		Ecosystem properties			Biotic interactions			Invader traits			
Hypothesis	Lag Time	Propagule pressure	Other human actions	Habitat modification	Resources	Other ecosystem properties	Enemies	Mutualism	Competition	Phylogenetic distance	Functional novelty	Evolution	Other invader traits
Adaptation [ADP]	+	+		+	+		+	+	+	++	++		++
Biotic acceptance [BA]	+-			++	+	++	+	+	+				
Biotic indirect effects [BID]	--	+		+	+	+	++	++	++				
Biotic resistance [BR]	++						++		++				
Dynamic equilibrium model [DEM]	+-	+	+	+	+	++			++				
Darwin’s Naturalization [DN]	+-						++	++	++	++	++	+	+
Disturbance [DS]	+-	+	++	++	++	++							
Enemy of my enemy [EE]	-	+					++		++				
Enemy Inversion [EI]	++			+	+	+	+	+	+				
Evolution of increased competitive ability [EICA]	-						++		++	+	+	++	
Empty niche [EN]	++	+	+	++	+	++							++
Enemy release [ER]	++						++			+	+		
Enemy reduction [ERD]	++						++			+	+		
Environmental heterogeneity [EVH]	+-	+		+	+	+	+	+	+				
Global competition [GC]	+-	++						+	++				
Human commensalism [HC]	+-	++	++	++	++	++							
Habitat filtering [HF]	++	+		+			+	+	+	++	++	++	++
Invasional meltdown [IM]	--	++	+	++	++	++	+	++	++				
Increased resource availability [IRA]	+-	+	+		++	++			++				
Increased susceptibility [IS]	++	+					+		+			+	++
Island susceptibility hypothesis [ISH]	+-		+		+	+	++		++				
Ideal weed [IW]	++	+									+		++
Limiting similarity [LS]	++	+					+	+	+	++	++	+	+
Missed mutualisms [MM]	+-	+						++					
New associations [NAS]	+-	+					+	+	+				
Novel weapons [NW]	++	+					++		++	++	++	++	++
Opportunity windows [OW]	+-		+	+	++	++							++
Plasticity hypothesis [PH]	++						++	++	++			++	++
Propagule pressure [PP]	+-	++											
Resource-enemy release [RER]	+-	+	+		++	++	++		++				
Reckless invader [RI]	-				+	+	+	+	+		+	+	+
Shifting defence hypothesis [SDH]	+						++		++			+	+
Specialist-generalist [SG]	+-	+					++	++					
Sampling [SP]	+-	++				+	+	+	++				
Tens rule [TEN]	+-	++											

describe to which degree each type of interaction is important for the mechanism or effect represented by a hypothesis. Finally, four categories represent different invader traits: 'phylogenetic distance' between the non-native and resident species; 'functional novelty' of the non-native species, e.g. based on the concept of eco-evolutionary experience (Saul *et al*., 2013; Saul and Jeschke, 2015); 'evolution' of the non-native species after its introduction; and 'other invader traits' (e.g. life-history traits).

We assessed the similarity of each hypothesis with every other hypothesis by calculating the percentage of shared traits. For this calculation, we excluded categories where both hypotheses had empty cells because an empty cell for both hypotheses cannot be considered a shared trait. If a threshold was reached, a connection was made. In this way, we created two networks. The first network includes all 35 evaluated hypotheses, and connections were made if two hypotheses shared at least 25% of their traits. We clustered the network using yEd's (2017) natural groups algorithm (which is based on the edge-betweenness clustering method proposed by Girvan and Newman, 2005). This resulted in four clusters, three of which were large and one (containing propagule pressure, global competition, missed mutualisms and the tens rule) small. For clarity, we included the one small cluster in the closest bigger cluster. The second network focused on the 12 hypotheses featured in the following chapters of this book – here, thick connections were made for a threshold of 25% and thin connections for a threshold of 15%.

Results and Discussion

Matrix network for 35 invasion hypotheses

The matrix network (Fig. 7.1) contains a total of 35 nodes (= number of hypotheses) and 151 edges (connections) between them. The average number of connections for a hypothesis is 8.6 ± 2.46 (SD). The three most connected hypotheses (with the highest degree centrality) are resource-enemy release (13 connections), environmental heterogeneity and new associations (both with 12 connections). Enemy reduction and enemy release are the hypotheses with the fewest connections (four connections).

All hypotheses in the purple group (see Fig. 7.1) consider human interference to be important or very important ('+' or '++' in columns 2 or 3 in Table 7.2). Taking all hypotheses, most of those hypotheses that consider human interference to be very important ('++' in columns 2 or 3 in Table 7.2) are in the network's purple group: disturbance, global competition, human commensalism, invasional meltdown, propagule pressure and the tens rule; only the sampling hypothesis is not in the purple group, yet it has as many connections to hypotheses in the purple group as it has to hypotheses in the red group, thus it is between these two groups. All of the hypotheses in the red cluster consider mutualism as an important factor: all 10 hypotheses for which this is the case ('+' in column 8 in Table 7.1) are included in the red group, which does not contain any other hypotheses. The green cluster includes most hypotheses that consider enemies (predators or parasites) to be particularly important: 10 of the 13 hypotheses for which this is the case ('++' in column 7 in Table 7.1) are in this group. Out of the 11 hypotheses in this group, only one hypothesis does not explicitly consider enemies to be very important. This hypothesis – ideal weed – is characterized by very short time lags, which is also true for other hypotheses in the green group. Thus, the green cluster mainly includes hypotheses with a focus on enemies, or the lack thereof, of non-native species and on short time lags.

Matrix network for the 12 hypotheses featured in this book

The matrix network of the 12 hypotheses (Fig. 7.2) contains 27 edges. Darwin's naturalization hypothesis and the phenotypic

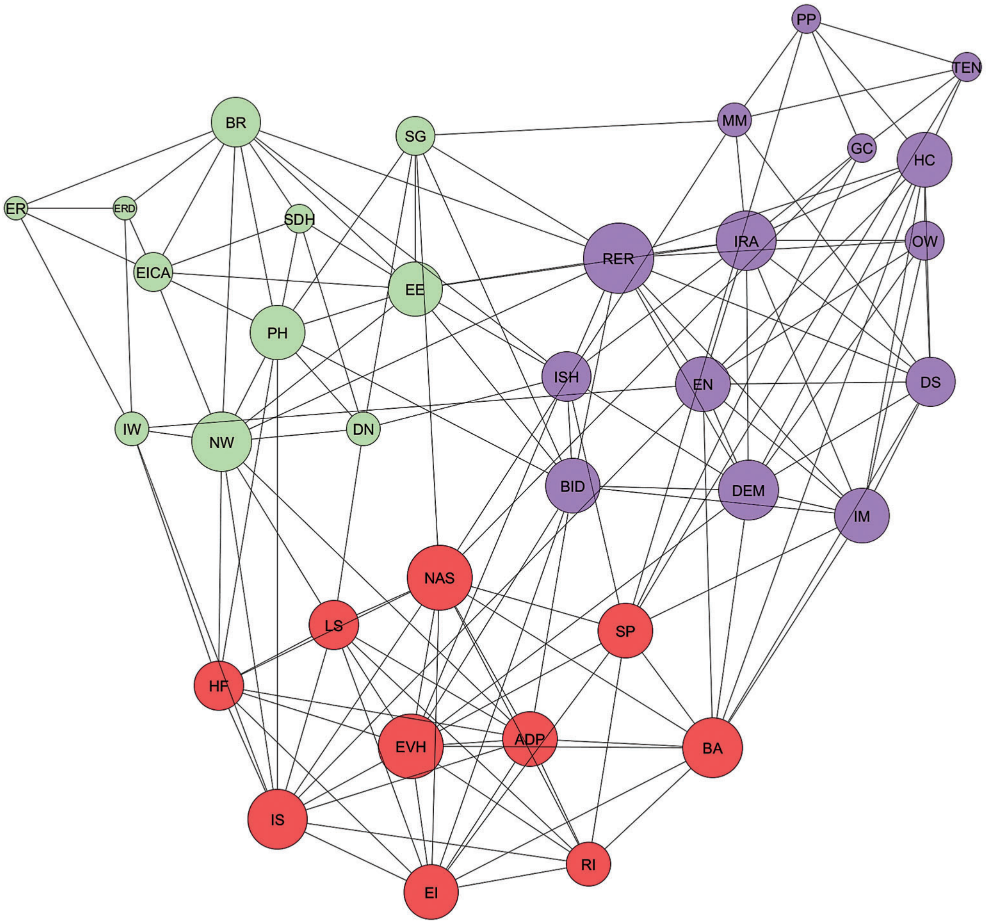

Fig. 7.1 Network with all 35 hypotheses evaluated in this chapter. Connected hypotheses share at least 25% of their traits (the exact spatial position of each hypothesis is arbitrary). Groups of hypotheses are represented by different colours and the size of each circle represents the degree centrality of the hypothesis. Hypothesis names are abbreviated as follows: ADP = adaptation, BA = biotic acceptance, BID = biotic indirect effects, BR = biotic resistance, DN = Darwin's naturalization, DS = disturbance, DEM = dynamic equilibrium, EN = empty niche, EI = enemy inversion, EE = enemy of my enemy, ERD = enemy reduction, ER = enemy release, EVH = environmental heterogeneity, EICA = evolution of increased competitive ability, GC = global competition, HF = habitat filtering, HC = human commensalism, IW = ideal weed, IRA = increased resource availability, IS = increased susceptibility, IM = invasional meltdown, ISH = island susceptibility hypothesis, LS = limiting similarity, MM = missed mutualisms, NAS = new associations, NW = novel weapons, OW = opportunity windows, PH = plasticity hypothesis, PP = propagule pressure, RI = reckless invader, RER = resource-enemy release, SP = sampling, SDH = shifting defence hypothesis, SG = specialist–generalist, TEN = tens rule.

plasticity hypothesis (both seven connections) are the most connected hypotheses (i.e. with the highest degree centrality) in this smaller network. In contrast, limiting similarity, propagule pressure and the tens rule are the least connected hypotheses with two connections each. All of these 12 hypotheses will be explored in detail in the following chapters, and we will come back to this network in the synthesizing Chapter 17.

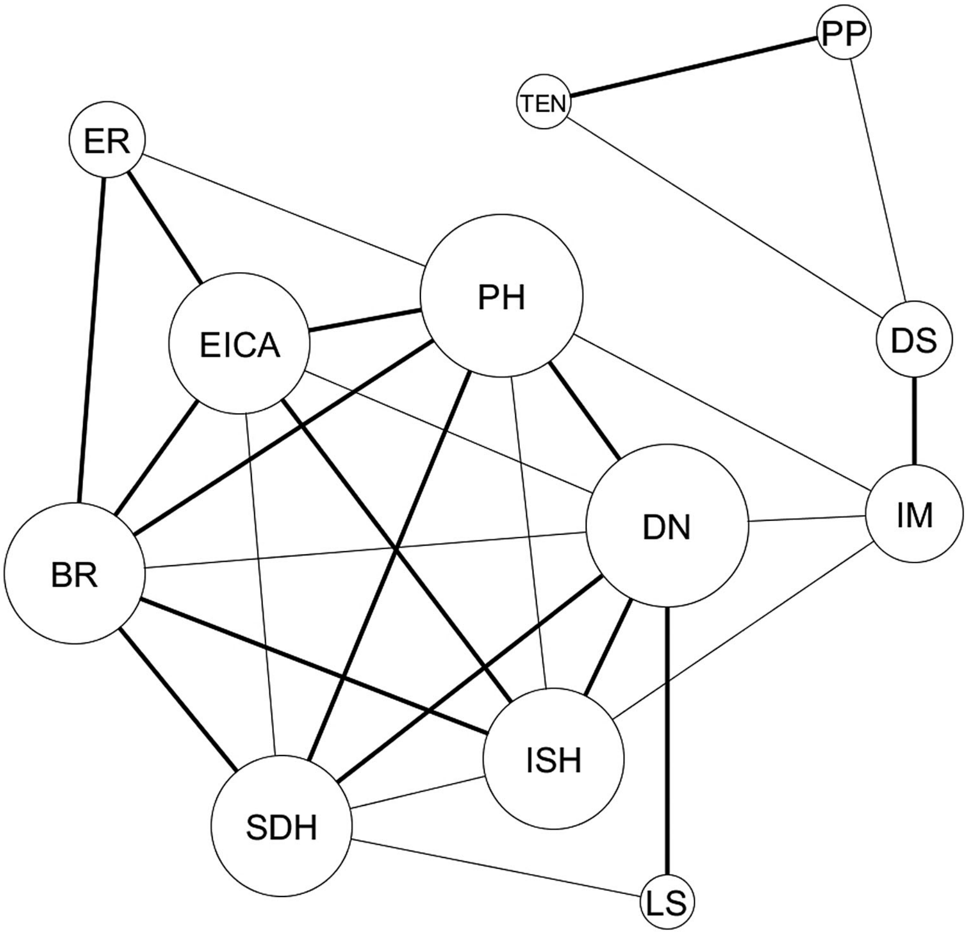

Fig. 7.2. Network with the 12 hypotheses featured in this book. Connected hypotheses share at least 15% of their traits, and connections are thick if they share at least 25% of their traits (otherwise as Fig. 7.1).

Conclusions

The benefits of hypothesis networks are obvious: in addition to providing a map with the main hypotheses of a field, the most central and connected hypotheses can be easily identified. Furthermore, they can convey, depending on the way they are created, much additional valuable information, e.g. hidden similarities among hypotheses, contradictions between hypotheses, thematic groups and, if the release or 'birth date' of hypotheses is considered, developments in the field: when were hypotheses born, which branches of hypothesis networks are particularly thriving and which ones are basically dead ends?

Yet there is need for much additional research on approaches for creating such networks and on the best way to interpret them. For instance, one can see from the results presented in this chapter that it depends on the number of nodes which hypotheses are the ones with the highest degree centrality. Also, there are different methods to create hypothesis networks as mentioned in the Introduction section. Each of these methods can be specified and fitted depending on the specific goals one wants to achieve with the network, e.g. a bibliometric network can be created based on simple co-authorships or co-citations but also based on full publication texts. The same is true for the survey approach: in Enders *et al.* (2018), we used different mathematical metrics to create different networks based on the survey results. Also, the characteristics of the hypotheses given in Table 7.1 can be mathematically analysed in different ways to create yet different hypothesis networks. Thus, one can imagine numerous, apparently reasonable approaches to create hypothesis networks. We have just started to explore this issue and hope others will join us in order to identify the most useful approaches depending on the goal one wants to achieve with a given network. More generally speaking, hypothesis networks seem to be one promising tool for synthesizing the increasing amounts of information in research fields such as invasion biology, yet they need to be further developed and combined with additional synthesis tools.

References

Blumenthal, D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecology Letters* 9, 887–895.

Blossey, B. and Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* 83, 887–889.

Börner K. (2010) *Atlas of Science – Visualizing What we Know.* MIT Press, London.

Botham, N. (2006) *The book of useless information*. Berkeley, London.

Callaway, R.M. and Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2, 436–443.

Callaway, R.M., Thelen, G.C., Rodriguez, A. and Holben, W.E. (2004) Soil biota and exotic plant invasion. *Nature* 427, 731–733.

Catford, J.A., Jansson, R. and Nilsson, C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15, 22–40.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. and MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7, 721–733.

Colautti, R., Grigorovich, I. and MacIsaac, H. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions* 8, 1023–1037.

Crawley, M.J., Brown, S.L., Heard, M.S. and Edwards, G.R. (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* 2, 140–148.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* Murray, London.

de Solla Price, D.J. (1965) Networks of scientific papers. *Science* 149, 510–515.

Doorduin, L.J. and Vrieling, K. (2011) A review of the phytochemical support for the shifting defence hypothesis. *Phytochemistry Reviews* 10, 99–106.

Duncan, R.P. and Williams, P.A. (2002) Ecology: Darwin's naturalization hypothesis challenged. *Nature* 417, 608–609.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Enders, M., Hütt, M.-T. and Jeschke, J.M. (2018) Drawing a map of invasion biology based on a network of hypotheses. *Ecosphere*. DOI: 10.1002/ecs2.2146.

Eppinga, M.B., Rietkerk, M., Dekker, S.C., De Ruiter, P.C. and Van der Putten, W.H. (2006) Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. *Oikos*, 114, 168–176.

Girvan, M. and Newman, M.E.J. (2005) Community structure in social and biological networks. *Proceedings of the National Academy of Sciences USA* 99, 7821–7826.

Hobbs, R.J. and Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6, 324–337.

Hutson, M.A. (1979) A general hypothesis of species diversity. *American Naturalist* 113, 81–101.

Jeschke, J.M. (2008) Across islands and continents, mammals are more successful invaders than birds. *Diversity and Distributions* 14, 913–916.

Jeschke, J.M. (2014) General hypotheses in invasion ecology. *Diversity and Distributions*, 20, 1229–1234.

Jeschke, J.M. and Strayer, D.L. (2006) Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology* 12, 1608–1619.

Johnstone, I.M. (1986) Plant invasion windows: a time-based classification of invasion potential. *Biological Reviews* 61, 369–394.

Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17, 164–170.

Levine, J.M. and D'Antonio, C.M. (1999) Elton revisited: A review of evidence linking diversity and invisibility. *Oikos* 87, 15–26.

Lockwood, J.L., Hoopes, M.F. and Marchetti, M.P. (2013) *Invasion ecology*, 2nd edn. Wiley-Blackwell, Chichester, UK.

Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536.

MacArthur, R. and Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101, 377–385.

MacArthur, R. H. (1970) Species packing and competitive equilibrium for many species. *Theoretical Population Biology* 1, 1–11.

Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M. *et al.* (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* 10, 77–94.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G. *et al.* (2006) Biotic interactions and plant invasions. *Ecology Letters* 9, 726–740.

Naisbitt, J. (1982) *Megatrends: Ten New Directions Transforming our Lives.* Warner Books, New York.

Reimánek, M. and Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology* 77, 1655–1661.

Ricciardi, A., Hoopes, M.F., Marchetti, M.P. and Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83, 263–282.

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. and Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9, 981–993.

Saul, W.-C., Jeschke, J.M. (2015) Eco-evolutionary experience in novel species interactions. *Ecology Letters* 18, 236–245.

Saul, W.-C., Jeschke, J.M. and Heger, T. (2013) The role of eco-evolutionary experience in invasion success. *NeoBiota* 17, 57–74.

Sax, D.F., Stachowicz, J.J., Brown, J. H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M. M. *et al.* (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* 22, 465–471.

Sher, A.A. and Hyatt, L.A. (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion, *Biological Invasions* 1, 107–114.

Simberloff, D. and Gibbons, L. (2004) Now you see them, now you don't! – Population crashes of established introduced species. *Biological Invasions* 6, 161–172.

Simberloff, D. and Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1, 21–32.

Stohlgren, T.J., Jarnevitch, C., Chong, G.W. and Evangelista, P.H. (2006) Scale and plant invasions: a theory of biotic acceptance. *Preslia* 78, 405–426.

Williamson, M. (1996) *Biological Invasions*. Chapman & Hall, London.

Williamson, M. and Brown, K.C. (1986) The analysis and modelling of British invasions. *Philosophical Transactions of the Royal Society* 314, 505–522.

yEd (2017) yEd Graph Editor. yWorks the diagramming company.

3. Drawing a map of invasion biology based on a network of hypotheses

This paper was a collaboration with Prof. Dr. Marc-Thorsten Hütt from Jacobs University Bremen and Prof. Dr. Jonathan Jeschke from Freie Universität Berlin and Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) and was published in Ecosphere (2018). The survey was held during my Master thesis at Technische Universität München in 2015. The data of the survey was taken, revisited and newly analyzed for this work.

Published as: Enders, M., Hütt, M.-T. Jeschke, J. M. (2018). Drawing a map of invasion biology based on a network of hypotheses. Ecosphere: e02146.

esa ECOSPHERE

Drawing a map of invasion biology based on a network of hypotheses

Martin Enders,[1,2,3,4,]† Marc-Thorsten Hütt,[5] and Jonathan M. Jeschke[1,2,3,4]

[1]Department of Biology, Chemistry, Pharmacy, Institute of Biology, Freie Universität Berlin, Königin-Luise-Str. 1-3, Berlin, 14195 Germany
[2]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, Berlin, 12587 Germany
[3]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, Berlin, 14195 Germany
[4]Department of Ecology and Ecosystem Management, Restoration Ecology, Technische Universität München, Emil-Ramann-Str. 6, Freising-Weihenstephan, 85350 Germany
[5]Department of Life Sciences and Chemistry, Computational Systems Biology, Jacobs University Bremen, Campus Ring 1, Bremen, 28759 Germany

Citation: Enders, M., M.-T. Hütt, and J. M. Jeschke. 2018. Drawing a map of invasion biology based on a network of hypotheses. Ecosphere 9(3):e02146. 10.1002/ecs2.2146

Abstract. Invasion biology is a thriving ecological research field, and confusingly many hypotheses, concepts, and ideas about biological invasions populate today's literature. Moreover, some of these hypotheses are very similar, whereas others contradict each other. It is not clear whether in such a situation a plausible global relational structure—or map—of these hypotheses emerges in the minds of the involved researchers and, if so, how this map can be reliably reconstructed from the expertise of individuals. Here, we report results of an online survey with 357 experts on invasion biology and several reconstructions of such a map. Using the distance information between hypotheses provided in the survey, the resulting network is essentially random. This finding implies that invasion biologists currently do not have a joint vision how invasion hypotheses are related to each other. However, the pattern of pairwise familiarities between the hypotheses in the survey yields joint-mentions networks with highly non-random features. These networks allow us to assign conceptual roles to many of the hypotheses in the field on purely topological grounds. Such hypothesis networks can help everyone interested in research fields to understand their conceptual structure. They can serve as maps of research fields.

Key words: biological invasions; concepts; defining invasion hypotheses; hypothesis network; invasive alien species.

Received 22 January 2018; accepted 24 January 2018. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** enders.martin@gmx.net

INTRODUCTION

When you visit a city such as Munich in Germany for the first time in your life without a smartphone or traditional map, you might be able to find your way from the central train station to the Oktoberfest. Maybe you would also find your way to the "Marienplatz" (city center), but you would definitely miss out some beautiful spots. Without a traditional map or Google Maps, visitors of a city such as Munich, Bremen, or Berlin can quickly become lost. The only true alternative to such an external map is an internal mental map acquired by visiting a city's locations on a regular basis. This is not only true for cities but also for research disciplines where researchers can become lost in a multitude of concepts and hypotheses. This leads to the intriguing general question: Do researchers have a clear, detailed, and unambiguous map of their scientific field in their minds?

For one specific scientific field, we here use a questionnaire to probe the representation of such a knowledge map in the scientific community.

We took the discipline of invasion biology as a case example. This discipline focuses on non-native species and emerged in the 1990s when the number of publications on the topic started to massively increase (Richardson and Pyšek 2008). The first ideas, concepts, and hypotheses about biological invasions date back to previous centuries (Darwin 1859), and Elton's (1958) book, *The ecology of invasions by animals and plants*, includes many ideas that are influential in the field until today. Other concepts and hypotheses were formulated later (Jeschke 2014), and many of them are now populating the literature. Several challenges have emerged with the raising number of invasion hypotheses, for instance: (1) it is becoming increasingly unclear what the central concepts and hypotheses are of the field; (2) some hypotheses have different names but represent the same, or a very similar, basic concept (Catford et al. 2009); (3) some hypotheses completely contradict each other, and there is confusion about which of these hypotheses are empirically better supported; and (4) hypotheses that are not empirically supported keep being used (Jeschke et al. 2012*a*).

An important task for a discipline populated by many hypotheses is to develop synthesis tools that provide an overview or map of existing hypotheses. Such an overview can then be connected with meta-analyses to discriminate those hypotheses that are empirically supported from those that are not (Jeschke and Heger 2018). It can also be connected to a larger atlas of scientific disciplines (Börner 2015). There are several possible approaches to synthesize existing hypotheses, for example, based on bibliometric analyses, expert surveys, or conceptual meta-frameworks (Catford et al. 2009, Gurevitch et al. 2011, Saul et al. 2013, Börner et al. 2015).

For this study, we developed an online questionnaire covering 33 common invasion hypotheses and asking experts which invasion hypotheses they know best and how similar these are to other invasion hypotheses. Based on the answers, we are addressing the three following questions: (1) Which are the best-known and most central invasion hypotheses? (2) Do invasion biologists agree on the similarity or dissimilarity of hypotheses and already have a joint map or network of invasion hypotheses in mind (i.e., an internal map)? (3) If this is not the case, what would be a promising candidate for an explicit, external map, or network of invasion hypotheses? To our knowledge, this is the first study following such an approach, within ecology or beyond, that creates hypothesis networks based on a survey among experts in the field. A first, rather rudimentary hypothesis network was presented by Jeschke (2014) for invasion biology, and a second one was created based on a matrix with characteristics of hypotheses (Enders and Jeschke 2018).

METHODS

Survey among invasion biologists

We compiled a list of 33 common invasion hypotheses and defined each hypothesis (Table 1). Key references for compiling this list were as follows: Catford et al. (2009), Lamarque et al. (2011), Jeschke et al. (2012*a, b*), Jeschke (2014), Lockwood et al. (2013), Lowry et al. (2013), and references given in Table 1. The survey was available on the Internet site https://www.soscisurvey.de/ for a month, from 12 November 2014 to 12 December 2014. Links to the questionnaire were sent out to invasion biologists and ecologists by using different mailing lists (Ecolog-L, Alien-List, ISSG-Members-List) and was, all in all, well received (357 participants, 102 complete surveys [i.e., also including personal information such as continent of residence or age]). The first question that was asked was as follows: "Which of the following Hypotheses in Invasion biology do you know best?" The participants could choose a maximum of three hypotheses out of the 33 listed ones. A definition was provided for each hypothesis (see Table 1). We programmed the survey, so that hypotheses selected by the participants were randomly paired with other hypotheses, and the participants were asked as follows: "From your perspective, how similar are the following two hypotheses? [selected hypothesis] and [random hypothesis]?" The participant could pick from a scale from 1 "*These hypotheses completely contradict each other*" through 5; "*No relationship between these hypotheses*" to 9; *"These hypotheses are extremely similar to each other."* Based on the responses, we created three different networks of invasion hypotheses, which are further outlined below. In the survey, participants were also asked about their continent of residency, age (in 10-yr steps), current academic position, and time since PhD. The

Table 1. List of 33 common invasion hypotheses and how they were defined in the survey (key references provided here were not given in the survey in order to minimize the amount of text in the survey).

Hypothesis and key reference(s)	Definition
Adaptation (ADP; Duncan and Williams 2002)	The invasion success of non-native species depends on the adaptation to the conditions in the exotic range before and/or after the introduction. Non-native species that are related to native species are more successful in this adaptation
Biotic acceptance aka "the rich get richer" (BA; Stohlgen et al. 2006)	Ecosystems tend to accommodate the establishment and coexistence of non-native species despite the presence and abundance of native species
Biotic indirect effects (BID; Callaway et al. 2004)	Non-native species benefit from different indirect effects triggered by native species
Biotic resistance aka diversity-invasibility hypothesis (BR; Elton 1958, Levine and D'Antonio 1999)	An ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity
Darwin's naturalization (DN; Darwin 1859)	The invasion success of non-native species is higher in areas that are poor in closely related species than in areas that are rich in closely related species
Disturbance (DS; Elton 1958, Hobbs and Huenneke 1992)	The invasion success of non-native species is higher in highly disturbed than in relatively undisturbed ecosystems
Dynamic equilibrium (DEM; Hutson 1979)	The establishment of a non-native species depends on natural fluctuations of the ecosystem, which influences the competition of local species
Empty niche (EN; MacArthur 1970)	The invasion success of non-native species increases with the availability of empty niches in the exotic range
Enemy inversion (EI; Colautti et al. 2004)	Introduced enemies of non-native species are less harmful for them in the exotic than the native range, due to altered biotic and abiotic conditions
Enemy of my enemy aka accumulation-of-local-pathogens hypothesis (EE; Eppinga et al. 2006)	Introduced enemies of a non-native species are less harmful to the non-native as compared to the native species
Enemy reduction (ERD; Colautti et al. 2004)	The partial release of enemies in the exotic range is a cause of invasion success
Enemy release (ER; Keane and Crawley 2002)	The absence of enemies in the exotic range is a cause of invasion success
Environmental heterogeneity (EVH; Melbourne et al. 2007)	The invasion success of non-native species is high if the exotic range has a highly heterogeneous environment
Evolution of increased competitive ability (EICA; Blossey and Nötzold 1995)	After having been released from natural enemies, non-native species will allocate more energy in growth and/or reproduction (this re-allocation is due to genetic changes), which makes them more competitive
Global competition (GC; Colautti et al. 2006)	A large number of different non-native species is more successful than a small number
Habitat filtering (HF; Darwin 1859)	The invasion success of non-native species in the new area is high if they are pre-adapted to this area
Human commensalism (HC; Jeschke and Strayer 2006)	Species that are living in close proximity to humans are more successful in invading new areas than other species
Ideal weed (IW; Elton 1958, Rejmánek and Richardson 1996)	The invasion success of a non-native species depends on its specific traits (e.g. life-history traits)
Increased resource availability (IRA; Sher and Hyatt 1999)	The invasion success of non-native species increases with the availability of resources
Increased susceptibility (IS; Colautti et al. 2004)	If a non-native species has a lower genetic diversity than the native species, there will be a low probability that the non-native species establishes itself
Invasion meltdown (IM; Simberloff and Holle 1999, Sax et al. 2007)	The presence of non-native species in an ecosystem facilitates invasion by additional species, increasing their likelihood of survival or ecological impact
Island susceptibility hypothesis (ISH; Jeschke 2008)	Non-native species are more likely to become established and have major ecological impacts on islands than on continents
Limiting similarity (LS; MacArthur and Levins 1967)	The invasion success of non-native species is high if they highly differ from native species, and it is low if they are similar to native species
Missed mutualisms (MM; Colautti et al. 2004, Mitchell et al. 2006)	In their exotic range, non-native species suffer from missing mutualists
New associations (NAS; Colautti et al. 2004)	New relationships between non-native and native species can positively or negatively influence the establishment of the non-native species
Novel weapons (NW; Callaway and Ridenour 2004)	In the exotic range, non-native species can have a competitive advantage against native species because they possess a novel weapon, i.e. a trait that is new to the resident community of native species and therefore affects them negatively
Opportunity windows (OW; Johnstone 1986)	The invasion success of non-native species increases with the availability of empty niches in the exotic range, and the availability of these niches fluctuates spatio-temporally

(Table 1. *Continued*)

Hypothesis and key reference(s)	Definition
Propagule pressure (PP; Lockwood et al. 2005)	A high propagule pressure (a composite measure consisting of the number of individuals introduced per introduction event and the frequency of introduction events) is a cause of invasion success
Reckless invader (RI; Simberloff and Gibbons 2004)	A non-native species that is highly successful shortly after its introduction can get reduced in its population or even extinct over time due to different reasons (such as competition with other introduced species or adaptation by native species)
Resource-enemy release (RER; Blumenthal 2006)	The non-native species is released from its natural enemies and can spend more energy in its reproduction, and invasion success increases with the availability of resources
Specialist-generalist (SG; Callaway et al. 2004)	Non-native species are more successful in a new region if the local predators are specialists and local mutualists are generalists
Sampling (SP; Crawley et al. 1999)	A large number of different non-native species is more likely to become invasive than a small number due to interspecific competition. Also the species identity of the locals is more important than the richness in terms of the invasion of an area
Tens rule (TEN; Williamson and Brown 1986, Williamson 1996)	Approximately 10% of species successfully take consecutive steps of the invasion process

geographic bias we observed among survey participants (Appendix S1: Fig. S1) was quite similar to the results described by Pyšek et al. (2008) for publications within invasion biology. The e-mail lists we used to send out the survey (Ecolog-L, run by the Ecological Society of America; Aliens-L, run by the IUCN Invasive Species Specialist Group; ISSG-Members-List, received by members of the IUCN Invasive Species Specialist Group) are based in North America, Europe, and Australia/New Zealand, but experts worldwide receive e-mails sent through them. Also, these lists are arguably the most relevant ones globally on the topic for experts in the field of invasion biology.

Similarity–dissimilarity networks

We used the similarity between invasion hypotheses that the participants indicated by answering the questions, "From your perspective, how similar are the following two hypotheses?" In the network, we connected two hypotheses if the mean values taken from the participants' answers related to these hypotheses were either below 3 (contradictory hypotheses) or above 7 (similar hypotheses). This network is the only one of the three networks that can discriminate between similar and contradictory hypotheses. It is also the only conscious network; it illustrates similarities and dissimilarities between hypotheses that the experts are readily aware of.

To address potential differences between the academic background of participants and resulting hypothesis networks, we also created similarity–dissimilarity networks with participants who specified their academic position (1) as PhD candidate, postdoc or higher, or (2) as other (e.g., managers or students). Furthermore, we created alternative networks with only positive connections (using a threshold of 7) and with thresholds below 2 (contradictory hypotheses) and above 8 (similar hypotheses).

Joint-mentions networks A and B

We used the number of joint mentions of hypotheses to the question which hypotheses the experts know best as an alternative for constructing networks. In other words, we say that hypotheses that are frequently well-known by the same people have a higher degree of similarity compared to hypotheses that are rarely well-known by the same people. Such joint-mentions networks are unconscious networks, as they are not based on the answers to the survey questions related to similarity and dissimilarity of hypotheses. The joint-mentions networks are thus networks based on local information that have been reconstructed from the co-occurrences of two hypotheses in the data.

Let H_i denote the total number of mentions of hypothesis i in the set of replies, and H_{ij} the joint mentions of hypotheses i and j. It should be noted that sometimes a hypothesis i was given as the sole expertise of a given survey participant, whereas sometimes two or three hypotheses, say i, j, and k, were given as expertise (thus contributing to three entries in the joint-mentions matrix: H_{ij}, $H_{ik,}$ and H_{jk}). Therefore, in general we do not have $\sum_j H_{ij} = H_i$.

We used two metrics for translating the co-occurrence counts into a score and then into a network. In the first metric which underlies joint-mentions network A, the absolute number of co-occurrence counts (normalized to values between 0 and 1) was used. This leads to pronounced hubs as the dominant topological feature. Mathematically, the observed number H_{ij} of joint mentions of two hypotheses i and j was compared with the maximal number of joint mentions that could have been observed given the number of individual mentions of each hypothesis, that is, $\min(H_i, H_j)$. An example where such a normalization is frequently used is in the evaluation of co-activations of cortical areas in Computational Neuroscience (Müller-Linow et al. 2008). The matrix we used for creating the joint-mentions network A thus has the following entries:

$$s_{ij}^{(A)} = \frac{H_{ij}}{\min(H_i, H_j)}. \tag{1}$$

Using this normalization, joint-mentions network A shows the connected mentions of the hypotheses and therefore indicates which hypotheses are used together in the minds of scientists and in practical work. Appendix S1: Fig. S2 shows a histogram of the entries $s_{ij}^{(A)}$ from Eq. 1. Zeros and diagonal elements have been removed in order to focus on the non-trivial entries of the matrix. In order to arrive at a (binary) adjacency matrix (and hence the joint-mentions network A), we need to select a binarization threshold s_T. Visual inspection of this distribution suggests $s_T = 0.2$, that is, the minimum after the first dominant peak.

The second metric which underlies joint-mentions network B compares the score with an expected score based on randomized data. In this case, the network's degree distribution is not as broad and additional topological features of the hypotheses emerge. We use relative frequencies as estimates of these probabilities; that is, $p_i = H_i/\sum_j H_j$ is the probability of mentioning hypothesis i at random. Relatedly, $p_{ij} = H_{ij}/\sum_{kl} H_{kl}$ serves as an estimate of the probability of jointly mentioning hypotheses i and j. We compare this probability p_{ij} of joint mentions of two hypotheses i and j with the expectation of joint mentions based on randomly drawing pairs of hypotheses from a pool, where a hypothesis i occurs with the probability p_i. This expectation then is $p_i p_j$. In other words, joint-mentions network B shows the probability of hypotheses chosen together and so the probability of hypotheses used together in any situation. Similar normalizations are the basis of, for example, the mutual information used in information theory (Shannon 1948). The matrix leading to joint-mentions network B thus has the following entries:

$$s_{ij}^{(H)} = \frac{p_{ij}}{p_i p_j} \tag{2}$$

Appendix S1: Fig. S3 shows a histogram of the entries $s_{ij}^{(H)}$ from Eq. 2. While the first normalization requires somewhat arbitrarily selecting a threshold in order to determine the links in the joint-mentions network A, in the second normalization here the value 1 is a natural choice of such a threshold, as values above 1 indicate that the observed joint-mentions count of the two hypotheses is higher than expected at random. It would also have been possible to use weighted graphs instead of a binary adjacency matrix. However, for the latter a much richer choice of analysis methods is available.

Identifying communities within networks

A community within a network is a set of nodes with a large number of links among themselves (many intracommunity links) and only comparatively few links to the rest of the network (i.e., to other communities; few intercommunity links). We calculated communities within the programming environment Mathematica. We used a modularity-maximizing algorithm (i.e., an iterative search for maximizing the Girvan-Newman modularity measure; Girvan and Newman 2002) for community detection.

RESULTS

Well-known invasion hypotheses & statistics about survey participants

The age of most participants ranged between 30 and 70 yr, where the age class 40–49 yr was less well represented than other age classes (Appendix S1: Fig. S1). Similarly, participants had a range of academic positions, and time since PhD (including no PhD yet) varied as well. Thus, participants included students, practitioners, PhD candidates, postdocs, and professors.

Some hypotheses were significantly more frequently selected by survey participants than others: The distribution of the number of times each hypothesis was selected significantly differed from an equal distribution (Pearson's chi-squared test, $\chi^2 = 483.65$, df = 32, $P < 0.001$; Fig. 1). The three most frequently selected hypotheses were as follows: enemy release (ER, 150 times selected), propagule pressure (PP, 135 times), and disturbance (DS, 102 times). It is similar for survey participants who specified their academic position as PhD candidate or higher where ER and PP were followed by BR (red columns in Fig. 1). For participants specifying their academic position as other (managers, students, etc.), the three most frequently selected hypotheses were PP, DS, and ER (blue columns in Fig. 1). There was a strong and significant correlation between the number of times that hypotheses were selected by academic vs. non-academic survey participants (Appendix S1: Fig. S7; $r_S = 0.78$, $P < 0.001$, Spearman's rank correlation test).

Similarity–dissimilarity networks

The main similarity–dissimilarity network has a total of 137 connections (edges) between hypotheses which are differentiated by color and thickness: The thickness of a line represents the strength of a similarity (black) or contradiction (red), respectively (Fig. 2). Despite that there should be no difference which hypothesis is mentioned first in the question, "From your perspective, how similar are the following two hypotheses?" there were sometimes different results for hypotheses pairs if one of the two hypotheses was mentioned first. In such cases, the more extreme result (stronger similarity or dissimilarity) was taken. In one case (NAS-DEM),

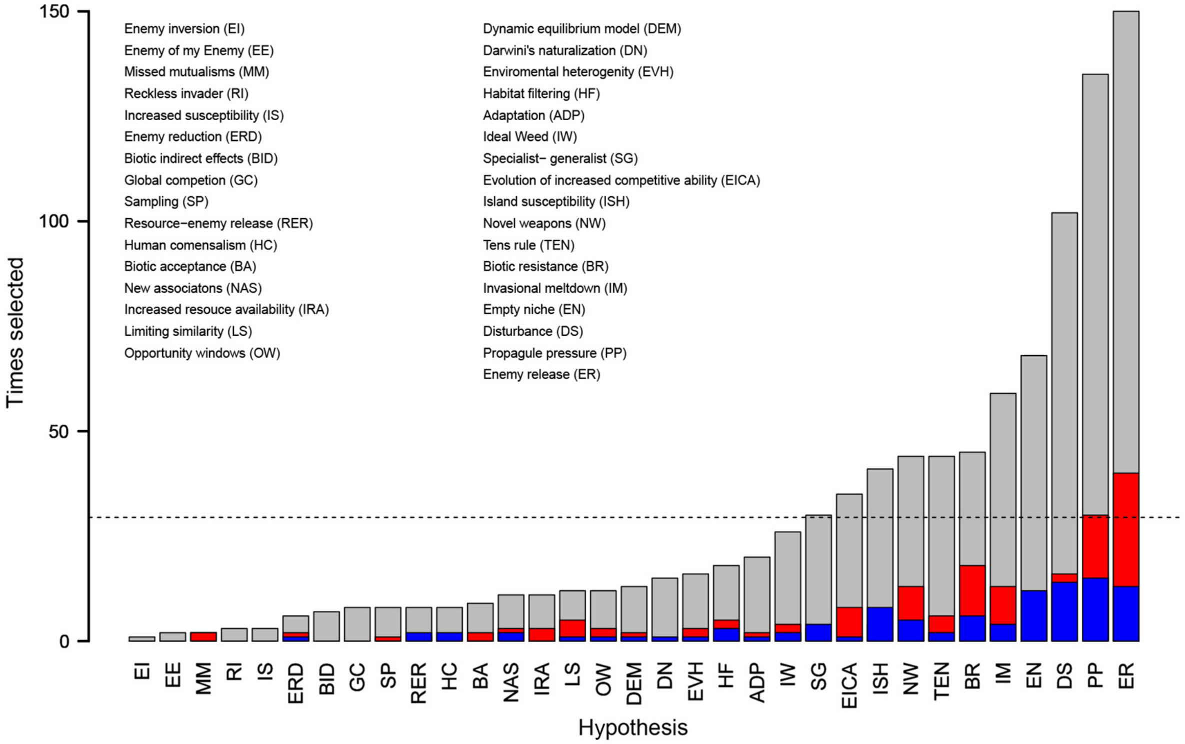

Fig. 1. Number of times each hypothesis was selected by survey participants as those they know best (the dashed line indicates the average across all 33 hypotheses). The red bars indicate the number of times each hypothesis was selected by survey participants who specified their academic position as PhD candidate or higher. The blue bars indicate the number of times each hypothesis was selected by survey participants who specified their academic position as other (e.g., managers or students). The remaining gray part in each bar indicates selections by survey participants who did not specify their academic position.

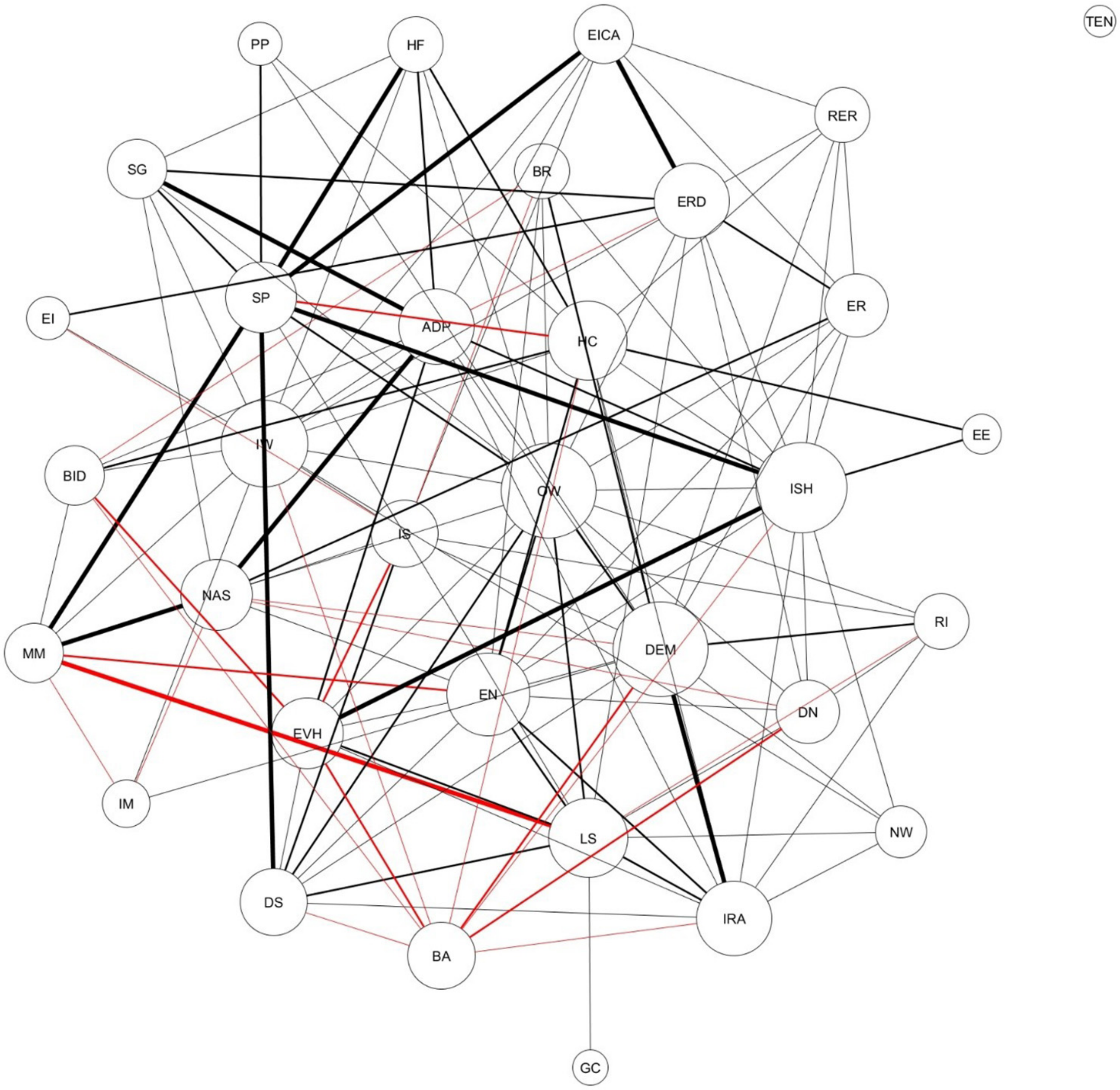

Fig. 2. The similarity–dissimilarity network of invasion hypotheses, based on the participants' responses how similar hypotheses are. Line thickness indicates the level of similarity (black lines) or dissimilarity (red lines) between hypotheses. The degree centrality of a hypothesis is indicated by the size of its circle. Since this network is similar to a random network (see main text and Appendix S1), it cannot be reasonably divided into communities of hypotheses within the network. This was only possible for the joint-mentions networks.

survey participants indicated similarities as well as dissimilarities; here, the more frequent answer was taken. Such differences are probably due to different interpretations of the question: "From your perspective, how similar are the following two hypotheses?" For example, similarity between two hypotheses could mean compliance in the topic or a compliance in the point of view.

In general, there was a large range of answers to the question how similar two given hypotheses are. To illustrate this huge variation among answers, we plotted the minimum value of an answer against the maximum value for all hypotheses pairs (Appendix S1: Fig. S4).

The three hypotheses with the highest degree centrality (i.e., the highest number of connections) in the similarity–dissimilarity network are as follows: opportunity windows (OW), dynamic equilibrium (DEM, both 16 connections), and island susceptibility hypothesis (ISH, 15 connections), but several other hypotheses also have high degrees. The average degree centrality for a hypothesis in this network is 8.30 ± 4.09 (SD). The most isolated hypothesis is the tens rule which has no connections here. Surprisingly, the network reconstructed from the quantitative information has many features of a random graph (see Appendix S1 and below for more information). However, when only local information ("Name the hypotheses from the list you are familiar with") is used, non-random networks emerge, which allow us to topologically characterize the role each hypothesis has in shaping the scientific field under consideration.

We also created similarity–dissimilarity networks using only answers of participants who specified their academic position: either (1) PhD candidate or higher (academic network; Appendix S1: Fig. S9) or (2) other (e.g., managers or students, non-academic network; Appendix S1: Fig. S10). In addition to the strong correlation between the number of times that hypotheses were selected by academic vs. non-academic survey participants (see above), there was also a significant correlation between the degree centralities of hypotheses in the two networks (Appendix S1: Fig. S8; $r_S = 0.46$, $P = 0.01$, Spearman's rank correlation test). Since many survey participants did not indicate their academic position, these two networks are based on fewer information than other networks generated here.

Furthermore, we created a similarity–dissimilarity network based on positive answers only (Appendix S1: Fig. S11). In this network, two hypotheses are isolated (tens rule, TEN, and biotic acceptance, BA), and OW is the hypothesis with the highest degree centrality (16 connections) followed by the DEM and the ISH (both 14 connections).

Finally, we applied stricter thresholds for the similarity–dissimilarity network, using a threshold of 2 for contradictory hypotheses and a threshold of 8 for similar hypotheses (Appendix S1: Fig. S12). In this network, five hypotheses are isolated, and the overall number of edges was low.

Joint-mentions networks A and B

The joint-mentions network A is dominated by the three most central nodes: ER (21 connections), DS, and PP (both 19 connections; Fig. 3). The next following hypothesis is empty niche (EN) with 10 connections, with all other hypotheses having only up to seven connections. One hypothesis has no connection: enemy inversion (EI). Overall, this network has 83 connections, and the average number of connections for a hypothesis is 5.03 ± 4.95 (SD).

The last network we created was the joint-mentions network B. It has 107 connections, and the hypotheses with the highest degree centrality are specialist–generalist (SG, 11 connections) and environmental heterogeneity (EVH, 10 connections; Fig. 4). Here, the average number of connections for a hypothesis is 6.45 ± 2.28 (SD).

Comparing well-known with central hypotheses

When comparing the degree centrality of each hypothesis with the number of times it was selected by survey participants as the ones they know best, there was no significant correlation in the similarity–dissimilarity network shown in Fig. 2 (Pearson's correlation coefficient $r = -0.14$, $P = 0.40$; Appendix S1: Fig. S5a). The same was true for joint-mentions network B ($r = 0.03$, $P = 0.82$; Appendix S1: Fig. S5c). However, the degree centrality was significantly correlated with the number of times a hypothesis was selected in joint-mentions network A ($r = 0.89$, $P < 0.001$; Appendix S1: Fig. S5b).

DISCUSSION

Well-known and central invasion hypotheses

The best-known invasion hypotheses among the survey participants were enemy release, propagule pressure, and disturbance. As further outlined below, the joint-mentions network A is, among the networks compared here, best suited to reveal the most central hypotheses in the field. In this network, well-known invasion hypotheses also have a high degree centrality.

In a systematic review, Lowry et al. (2013) demonstrated differences in the number of studies on different invasion hypotheses. Their results cannot be easily compared to ours because a systematic review documents the past,

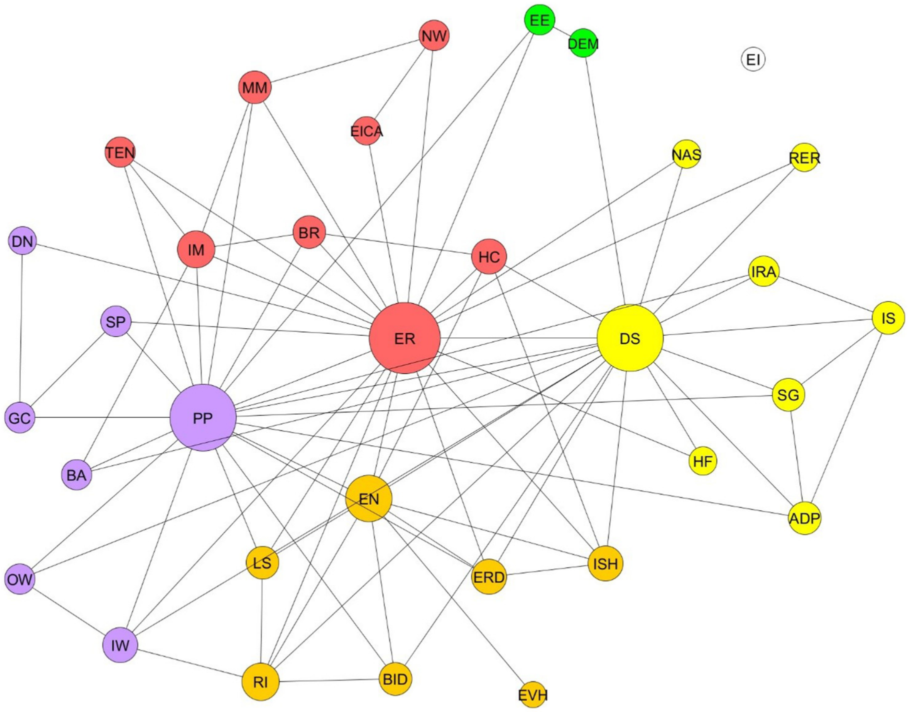

Fig. 3. The joint-mentions network A of invasion hypotheses, based on the participants' responses which hypotheses they know best and standardized by the number of mentions of hypotheses. The degree centrality of a hypothesis is indicated by the size of its circle, and colors indicate different hypothesis communities.

as it covers all publications until the date when the review was done, whereas a survey as reported here is a snapshot of the present time when the survey was done. Also, Lowry et al. partly used different terms and definitions for their hypotheses, whereas we followed and extended Catford et al. (2009) in our terminology. Nonetheless, the most frequently selected hypotheses in our survey are also well investigated according to Lowry et al. (2013).

The three best-known hypotheses according to our survey and the most central ones according to the joint-mentions network A—PP, ER, and DS—represent important aspects of biological invasions: While the propagule pressure hypothesis represents the principal importance of human action (humans transport propagules of invaders, either intentionally or unintentionally), the enemy release and disturbance hypotheses represent the importance of classical ecological interactions: ER related to interactions with other biota and DS related to interactions with abiotic factors.

Do invasion biologists already have a map or network of invasion hypotheses in mind?

The similarity–dissimilarity network showed that there is no clear joint map of the field of invasion biology in the heads of people working in this field. The range of the answers varied widely (Appendix S1: Fig. S4), and the similarity–dissimilarity network resulting from these answers lacks a clear structure and shows random features (Fig. 2). This visual impression is supported by statistical comparisons of the similarity–dissimilarity network with an Erdős-Rényi (ER) random graph (Erdős and Rényi 1959) with 100 nodes and a connectivity of 0.1. The connectivity in the ER graph is the probability of each possible (undirected) link to be present. In this completely random graph, where no other influences shape the topological features, the degree essentially determines centrality, leading to a high correlation of these features (and to a high correlation of the two centralities). Furthermore, the clustering coefficient and the betweenness centrality are negatively correlated

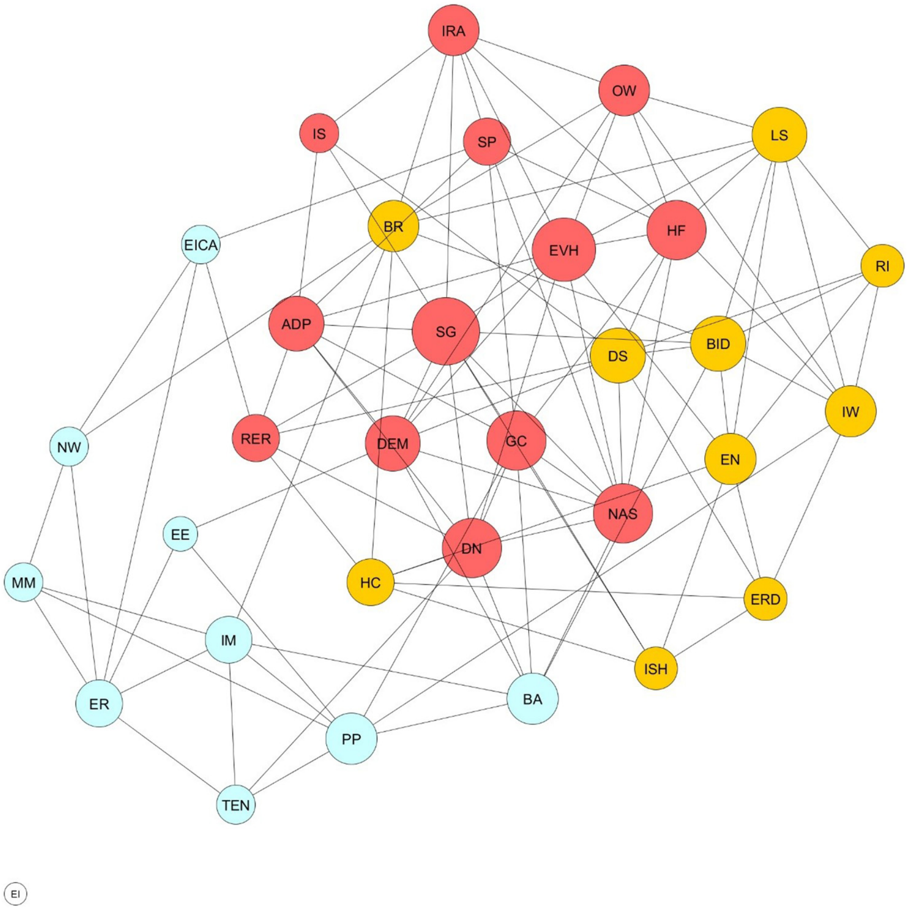

Fig. 4. The joint-mentions network B of invasion hypotheses, based on the participants' responses which hypotheses they know best and standardized by the expected numbers of joint mentions. The degree centrality of a hypothesis is indicated by the size of its circle, and colors indicate different hypothesis communities.

(Appendix S1: Figs. S13–S15). Similar patterns were observed for the similarity–dissimilarity network (Appendix S1: Figs. S16–S18). We also performed quantitative statistical analysis which confirmed that both the main similarity–dissimilarity network (Fig. 2) and the one restricted to positive connections between hypotheses (Appendix S1: Fig. S11) are similar to random networks (details are provided in Appendix S1). These analyses were not performed for the other similarity–dissimilarity networks due to the lower number of participants in case of the networks for different academic degrees and the many isolated hypotheses as well as low number of edges in case of the network for the thresholds 2 and 8. The comparisons to random networks suggest that we can negate our question (2) above: Do invasion biologists agree on the similarity or dissimilarity of hypotheses and already have a joint map or network of invasion hypotheses in mind (i.e., an internal map)?

What would be a promising candidate for a map or network of invasion hypotheses?

Detailed analyses of topological properties of the hypotheses in the two joint-mentions networks lead to a remarkably detailed characterization of the role of these hypotheses. These analyses are outlined in Appendix S1 and revealed, for instance, interesting sub-networks or communities characterized by a higher number of connections within than outside the community. The question on which the joint-mentions networks A and B were based on was which hypotheses the participants know best or work with. Hence, the probability if you work with one of the hypotheses in a community, to know or work with another of the same community, is higher than for hypotheses in different communities.

The joint-mentions network A has four communities, and the four most central hypotheses (ER, PP, DS, and EN) are these communities' central pillars. Furthermore, each central hypothesis and thus each community represents different factors that can benefit an invasion: The human factor is represented by propagule pressure (in purple, Fig. 3), the loss of parasites and predators is represented by enemy release (in red), and disturbances (either anthropogenic or non-anthropogenic, in yellow) and empty niches (in orange) are represented by the respective hypotheses. Within the communities, there is a variety of different hypotheses representing different factors for a successful invasion.

The joint-mentions network B has three communities. The first one (in red, Fig. 4) contains the hypotheses with the highest degrees, for example, SG, EVH, and NAS; the second community (in yellow) contains hypotheses with intermediate numbers of connections such as disturbance, limiting similarity, and biotic indirect effects; and the third community (in blue) is characterized by hypotheses with a low degree centrality, for example, enemy inversion, invasion meltdown, and the tens rule. All three communities include hypotheses focusing on biotic and abiotic factors and unlike joint-mentions network A are not dominated by hypotheses with a great degree. The joint-mentions network B has a richer, more intricate structure than joint-mentions network A, beyond the dominance of a few prominent nodes.

There are other important differences among the networks. In particular, the similarity–dissimilarity network can discriminate between similar and contradictory hypotheses, whereas the joint-mentions networks do not show contradictions between hypotheses. Another key difference is that the similarity–dissimilarity network is based on the direct, conscious answers of the survey participants how similar hypotheses are, whereas the joint-mentions networks are based on the unconsciously given information about the similarity of hypotheses. We argue that the former information could be biased due to intellectual–psychological reasons or since the participants were saturated with questions when being asked to indicate similarities between hypotheses (these questions were asked in the middle of the survey); being saturated or tired of questions can lead to unreliable survey data, which could also explain the range in the answers (Faulbaum et al. 2009). Furthermore, these questions might not have been straightforward to answer for all survey participants. The unconsciously given information as a response to the first survey question does not suffer from these problems: (1) The participants should have been more focused, as they were not exhausted by other questions; (2) the first question did not require any specific knowledge of invasion hypotheses (Porst 2009). We thus argue that the unconsciously provided information in responding to this question is more robust.

From this perspective, it may not surprise that the two joint-mentions networks, which are based on arguably more robust data, show a clearer picture of similarities between hypotheses than the similarity–dissimilarity network. But the two joint-mentions networks differ: Popular hypotheses have a higher likelihood for being mentioned together than less popular hypotheses, and the two normalizations applied for creating joint-mentions network A and B (Eqs. 1, 2 above) separate popular vs. similar hypotheses. This separation is fully achieved for joint-mentions network B, whereas in case of joint-mentions network A, popular hypotheses still have higher degree centralities than other hypotheses as illustrated in Fig. 3 (cf. Fig. 1). This incomplete separation of popularity vs. similarity may, however, be useful because the central hypotheses in such networks are like big cities on regular maps: These are the well-known hypotheses and landmarks that many people will look for first when inspecting the network.

Both Eqs. 1, 2 seem reasonable and have proven useful, although in other fields and for other purposes. Joint-mentions network B shows the probability of hypotheses chosen together and so the probability of hypotheses used together in any situation. This network seems to be better suited to visualize the structure among the hypotheses of the field such as sub-networks. Depending on which feature is more important, one might choose joint-mentions network A or B. However, more networks based on different approaches (e.g., bibliometric analyses) are clearly needed before making decisions about the best-suited network(s) or map(s) for the field.

Future Perspectives

This study is an early step toward a fully functional network of invasion hypotheses. Our approach was based on a survey among experts in the field. An alternative approach based on a matrix with characteristics of hypotheses was recently applied by Enders and Jeschke (2018), and other approaches, for example, based on bibliometrics, should be explored as well.

Hypothesis networks could prove very useful for invasion biology and—in extended versions—for other disciplines, as it is a powerful synthesis tool that provides an overview of the hypotheses and thus the theory of the field (Jeschke 2014). One of the main benefits of visualizing similarities and dissimilarities between hypotheses is to reduce redundancy in the field: Such a network allows researchers to quickly identify (1) hypotheses with different names that represent the same, or a very similar, basic idea or concept; and (2) hypotheses that contradict each other. Connecting the network with a database for meta-analytic approaches will also allow identifying and discarding zombie hypotheses (Fox 2001), so that the field can better focus on those hypotheses that are actually supported empirically. More generally, hypothesis networks can serve as maps of research fields and will benefit everyone interested in the topic, not only scientists but also managers and decision-makers, teachers and their students, etc. Such networks could be complemented with other navigation tools, so that we do not get lost in the myriad of concepts and hypotheses that nowadays populate invasion biology and other disciplines.

ACKNOWLEDGMENTS

We thank Jane Catford and Tina Heger for contributing ideas to the survey, sociologist Carolin Thiem for practical help with the questionnaire and Florian Ruland for discussions about the statistical analyses. We are also grateful to the numerous invasion ecologists who participated in the survey: Linda Auker, Vit Kukolja, Lindsey Sargent, Bilgenur Baloğlu, Anne-Céline Granjon, Dreux Watermolen, Michael Putnam, Denny Fernandez del Viso, Emily Rauschert, Jesse R. Blanchard, Alex Latzka, Adam Mitchell, Jordan M. Marshall, Andrew Kramer, Matthew R. O'Neil, Noah Blumenthal, Phil Cowan, Erin Jo Tiedeken, Michael Millane, Sarah Nyikos, Chris Habeck, Tom Horton, Andrea R. Litt, Johannes Kollmann, Felicia Miranda Fischer, and many anonymous participants. Financial support was provided by the Foundation of German Business (sdw) to ME and the Deutsche Forschungsgemeinschaft (DFG, JE 288/9-1, JE 288/9-2) to JMJ.

LITERATURE CITED

Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. Journal of Ecology 83:887–889.

Blumenthal, D. M. 2006. Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9:887–895.

Börner, K. 2015. Atlas of knowledge: anyone can map. MIT Press, Cambridge, Massachusetts, USA.

Börner, K., T. N. Theriault, and K. W. Boyack. 2015. Mapping science introduction: past, present and future. Bulletin of the Association for Information Science and Technology 41:12–16.

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.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben. 2004. Soil biota and exotic plant invasion. Nature 427:731–733.

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.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8:1023–1037.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters 2:140–148.

Darwin, C. 1859. On the origin of species by means of natural selection. J. Murray, London, UK.

Duncan, R. P., and P. A. Williams. 2002. Ecology: Darwin's naturalization hypothesis challenged. Nature 417:608–609.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Enders, M., and J. M. Jeschke. 2018. A network of invasion hypotheses. Pages 49–59 *in* J. M. Jeschke and T. Heger, editors. Invasion biology: hypotheses and evidence. CABI, Wallingford, UK.

Eppinga, M. B., M. Rietkerk, S. C. Dekker, P. C. De Ruiter, and W. H. Van der Putten. 2006. Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114:168–176.

Erdős, P., and A. Rényi. 1959. On random graphs. Publicationes Mathematicae 6:290–297.

Faulbaum, F., P. Prüfer, and M. Rexroth. 2009. Was ist eine gute Frage? Die systematische Evaluation der Fragenqualität. Springer VS, Wiesbaden, Germany.

Fox, J. 2001. Zombie ideas in ecology. Oikos Blog. http://oikosjournal.wordpress.com/2011/06/17/zombie-ideas-in-ecology/.

Girvan, M., and M. E. J. Newman. 2002. Community structure in social and biological networks. Proceedings of the National Academy of Sciences of the United States of America 99:7821–7826.

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.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion—implications for conservations. Conservation Biology 6:324–337.

Hutson, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Jeschke, J. M. 2008. Across islands and continents, mammals are more successful invaders than birds. Diversity and Distributions 14:913–916.

Jeschke, J. M. 2014. General hypotheses in invasion ecology. Diversity and Distributions 20:1229–1234.

Jeschke, J. M., L. Gómez Aparicio, S. Haider, T. Heger, C. J. Lortie, P. Pyšek, and D. L. Strayer. 2012*a*. Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14:1–20.

Jeschke, J. M., L. Gómez Aparicio, S. Haider, T. Heger, C. J. Lortie, P. Pyšek, and D. L. Strayer. 2012*b*. Taxonomic bias and lack of cross-taxonomic studies in invasion biology. Frontiers in Ecology and the Environment 10:349–350.

Jeschke, J. M., and T., Heger, editors. 2018. Invasion biology: hypotheses and evidence. CABI, Wallingford, UK.

Jeschke, J. M., and D. L. Strayer. 2006. Determinants of vertebrate invasion success in Europe and North America. Global Change Biology 12:1608–1619.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Reviews of the Cambridge Philosophical Society 61:369–394.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17:164–170.

Lamarque, L. J., S. Delzon, and C. J. Lortie. 2011. Tree invasions: a comparative test of the dominant hypotheses and functional traits. Biological Invasions 13:1969–1989.

Levine, J. M., and C. M. D’Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20:223–228.

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. Invasion ecology. Wiley-Blackwell, Chichester, West Sussex, UK.

Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3:182–196.

MacArthur, R. 1970. Species packing and competitive equilibrium for many species. Theoretical Population Biology 1:1–11.

MacArthur, R., and R. Levins. 1967. Limiting similarity convergence and divergence of coexisting species. American Naturalist 101:377–385.

Melbourne, B. A., et al. 2007. Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? Ecology Letters 10:77–94.

Mitchell, C. E., et al. 2006. Biotic interactions and plant invasions. Ecology Letters 9:726–740.

Müller-Linow, M., C. C. Hilgetag, and M. T. Hütt. 2008. Organization of excitable dynamics in hierarchical biological networks. PLoS Computational Biology 4:e1000190.

Porst, R. 2009. Fragebogen: ein Arbeitsbuch. Springer, Wiesbaden, Germany.

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.

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77:1655–1661.

Richardson, D. M., and P. Pyšek. 2008. Fifty years of invasion ecology: the legacy of Charles Elton. Diversity and Distributions 14:161–168.

Saul, W.-C., J. M. Jeschke, and T. Heger. 2013. The role of eco-evolutionary experience in invasion success. NeoBiota 17:57–74.

Sax, D. F., et al. 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology & Evolution 22:465–471.

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal 27:379–423.

Sher, A. A., and L. A. Hyatt. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. Biological Invasions 1:107–114.

Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't: population crashes of established introduced species. Biological Invasions 6:161–172.

Simberloff, D., and B. V. Holle. 1999. Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1:21–32.

Stohlgen, T. J., C. Jarnevitch, and G. W. Chong. 2006. Scale and plant invasions: a theory of biotic acceptance. Preslia 78:405–426.

Williamson, M. H. 1996. Biological invasions. Chapman & Hall, London, UK.

Williamson, M. H., and K. C. Brown. 1986. The Analysis and modeling of british invasions. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 314: 505–522.

DATA ACCESSIBILITY

The raw data underlying this study are available via FU Box (https://box.fu-berlin.de/index.php/s/NPUmwSEotcFMvWk).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2146/full

3.1. Appendix

The appendix for the publication published as: Enders, M., Hütt, M.-T. Jeschke, J. M. (2018). Drawing a map of invasion biology based on a network of hypotheses. Ecosphere: e02146.

The appendix is also available at:

https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.2146

Supplementary material

Drawing a map of invasion biology based on a network of hypotheses

Martin Enders, Marc-Thorsten Hütt and Jonathan M. Jeschke

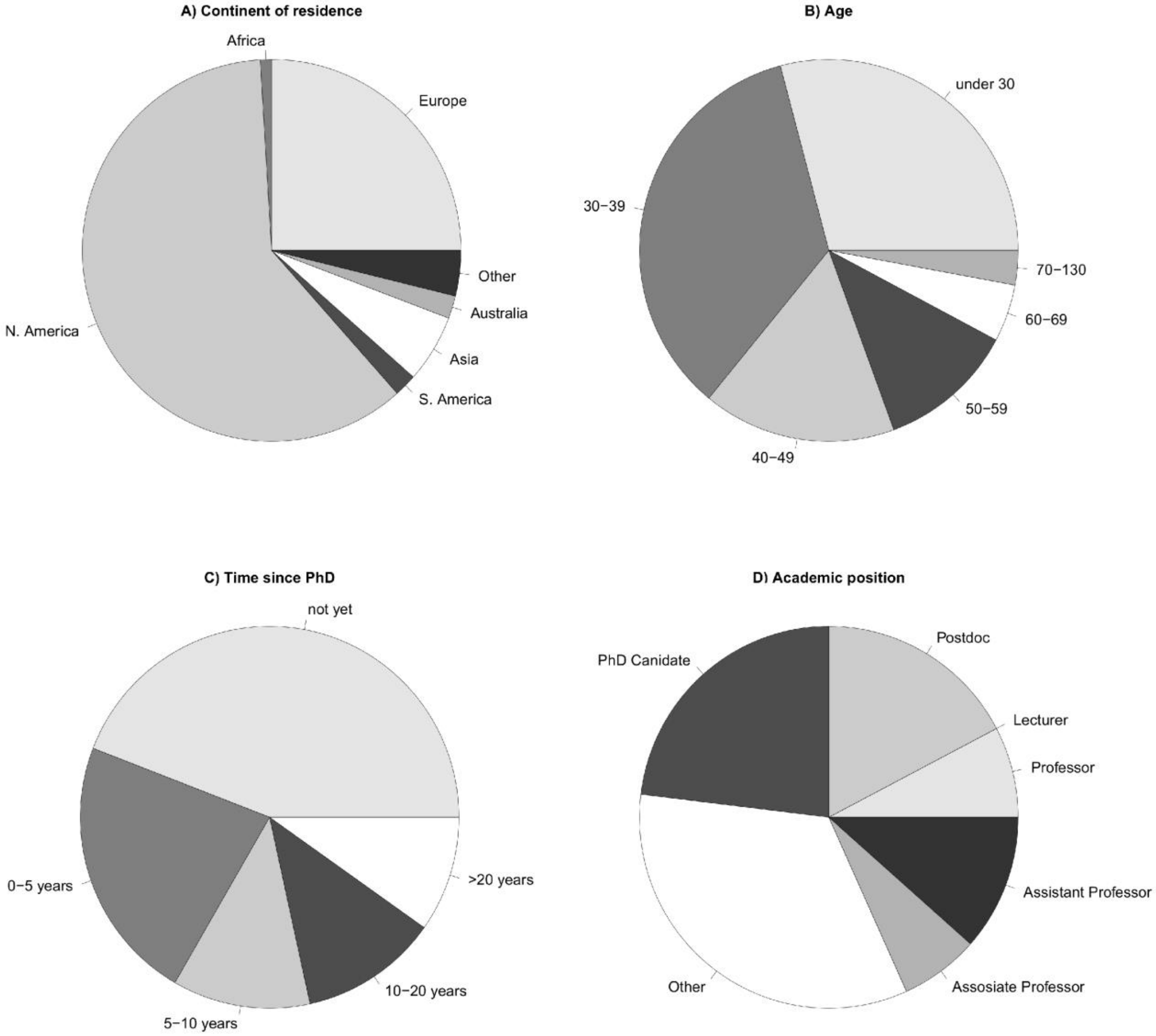

Figure S1. Continent of residency of the survey participants (a), age distribution (b), current academic position (c) and time since PhD (d). Figures indicate the number of survey participants ticking the respective category – these numbers are lower than the total number of survey participants, as not all participants chose to provide this information: n = 104 (a), n = 103 (b), n = 102 (c), n = 129 (d).

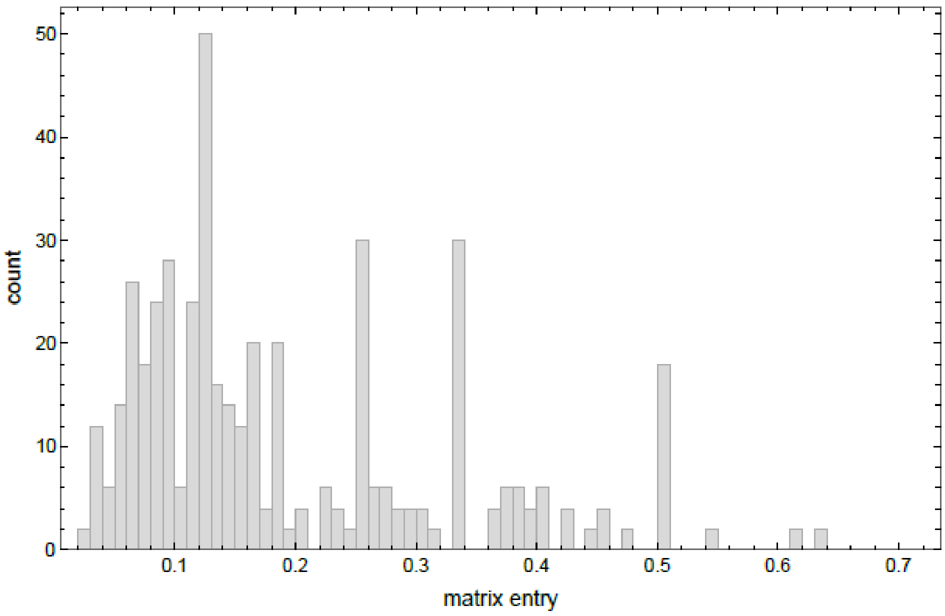

Figure S2. Histogram of matrix entries $s_{ij}^{(A)}$ for normalization A (joint-mentions network A). Zeros and diagonal elements have been removed.

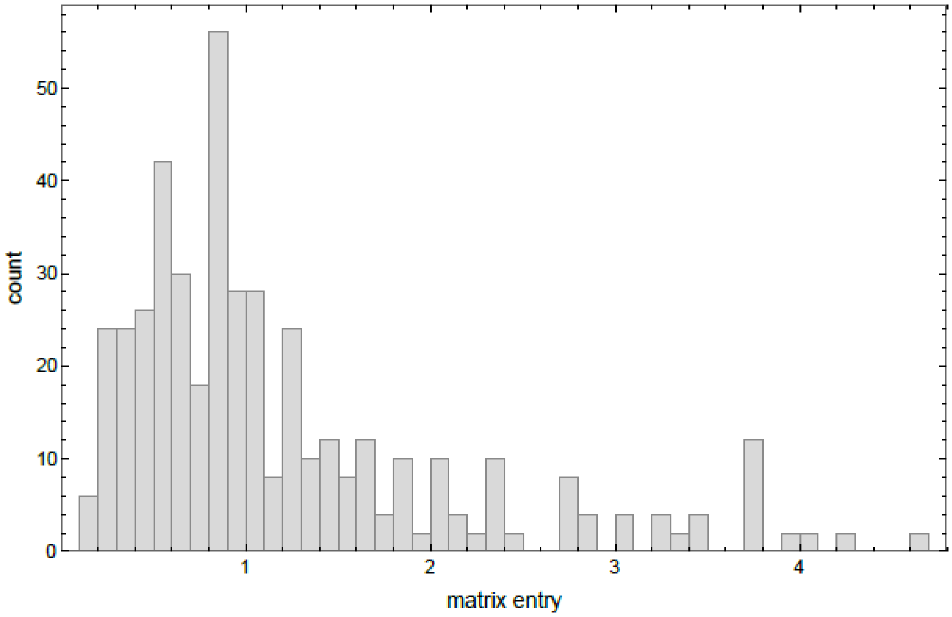

Figure S3. Histogram of matrix entries $s_{ij}^{(B)}$ for normalization B (joint-mentions network B). Zeros and diagonal elements have been removed.

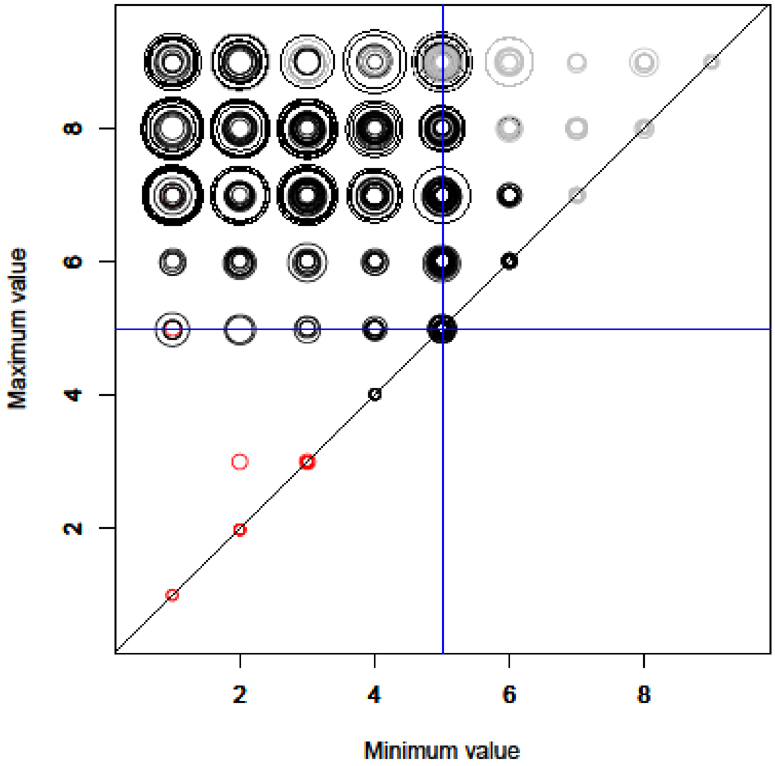

Figure S4. Minimum and maximum values of the survey answers to the question how similar two given hypotheses are. Similarity bonds in the network are indicated in gray, dissimilarity bonds in red and no bond in black. The size indicates the number of answers for a given hypotheses pair. In case of a strong congruence among the answers, the circles would lie on or be close to the vertical line, as minimum and maximum values should be similar.

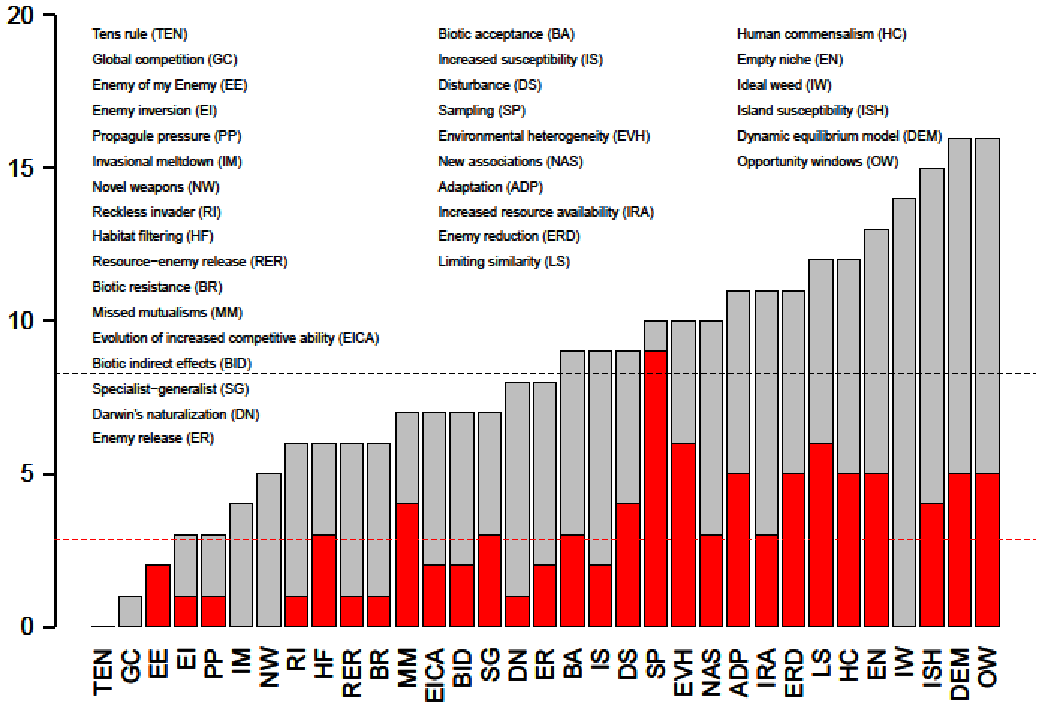

Figure S5. Degree centrality of the hypotheses in the similarity-dissimilarity network based on thresholds 3 and 7 compared to the network based on thresholds 2 and 8 (in red). Dashed lines indicates the average number of connections across all 33 hypotheses.

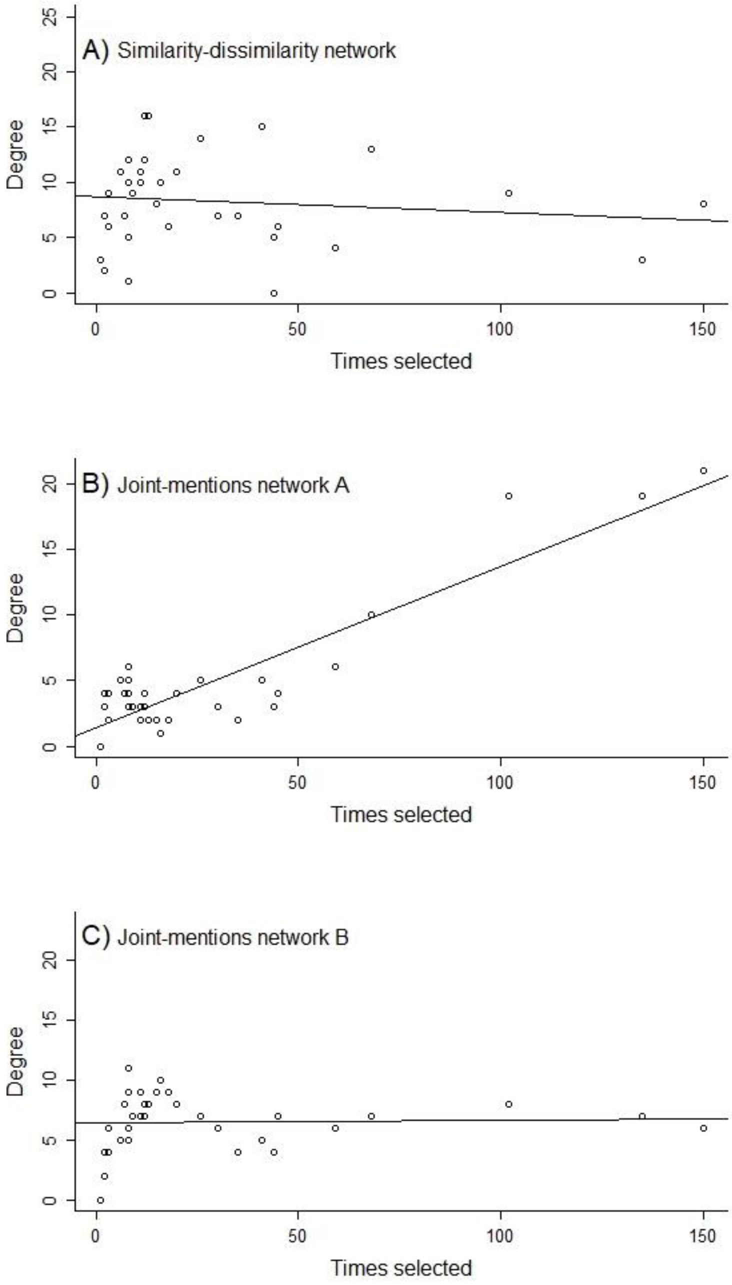

Figure S6. Comparisons between the number of times each hypothesis was selected by participants as those they know best and the degree centrality of this hypothesis in (a) the similarity-dissimilarity network (r = -0.12, p = 0.49), (b) the joint-mentions network A (r = 0.89, p = <0.001) and (c) the joint-mentions network B (r = 0.03, p =0.82). The two hypotheses that were most frequently selected are enemy release and propagule pressure (cf. Fig. 1).

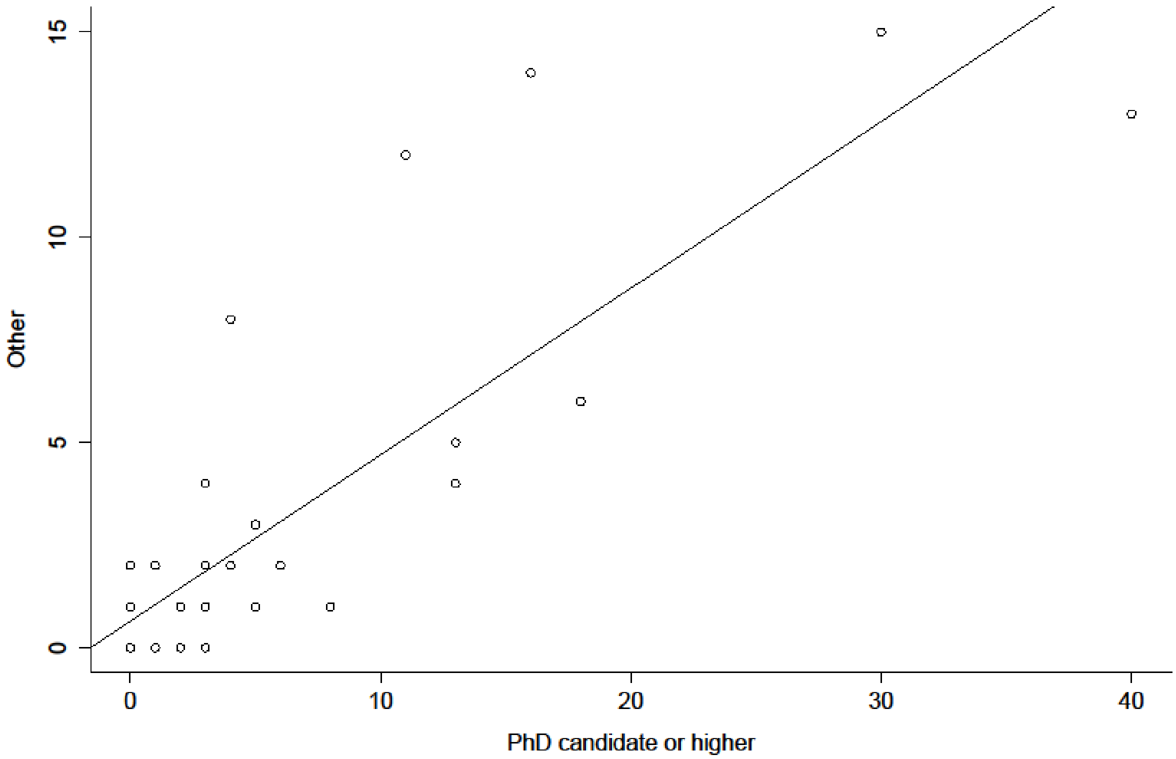

Figure S7. Correlation between the number of times that hypotheses were selected as those they know best by survey participants who specified their academic position as “Other” (y-axis) and those who indicated to be a PhD candidate or higher (x-axis).

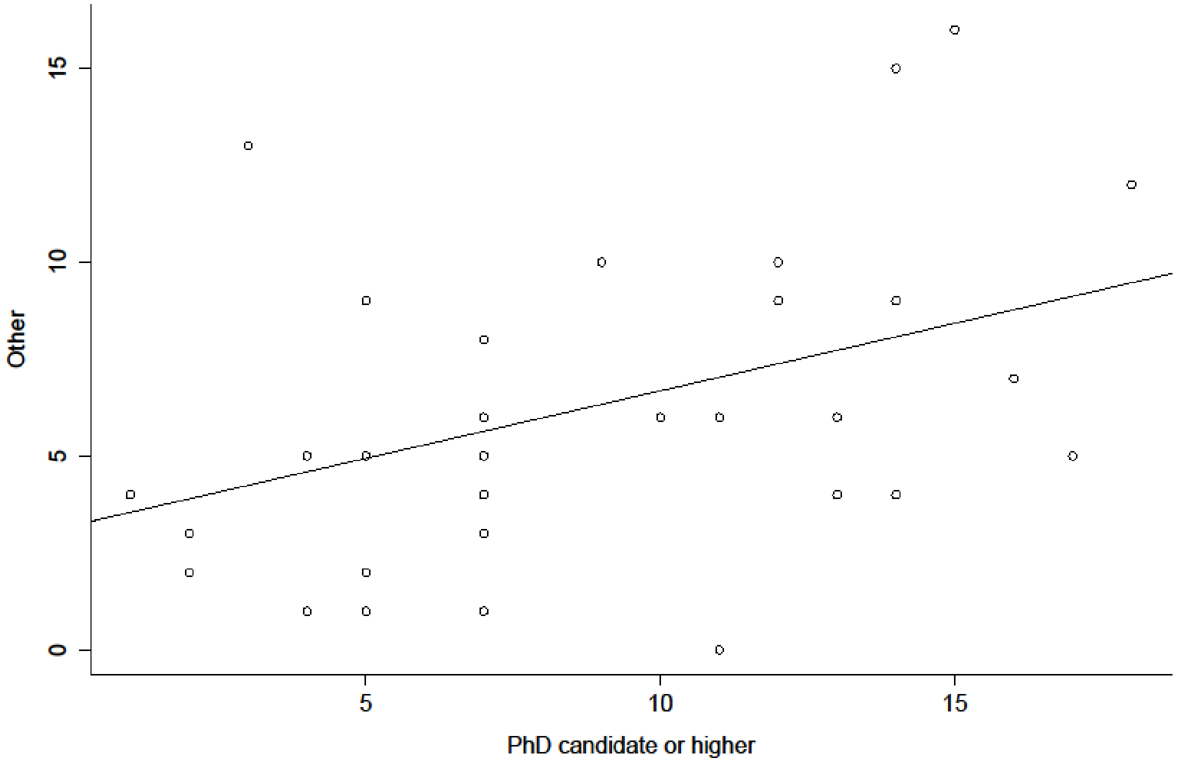

Figure S8. Correlation between the degree centrality of hypotheses in the similarity-dissimilarity networks based on answers by survey participants who specified their academic position as "Other" (y-axis) and those who indicated to be a PhD candidate or higher (x-axis).

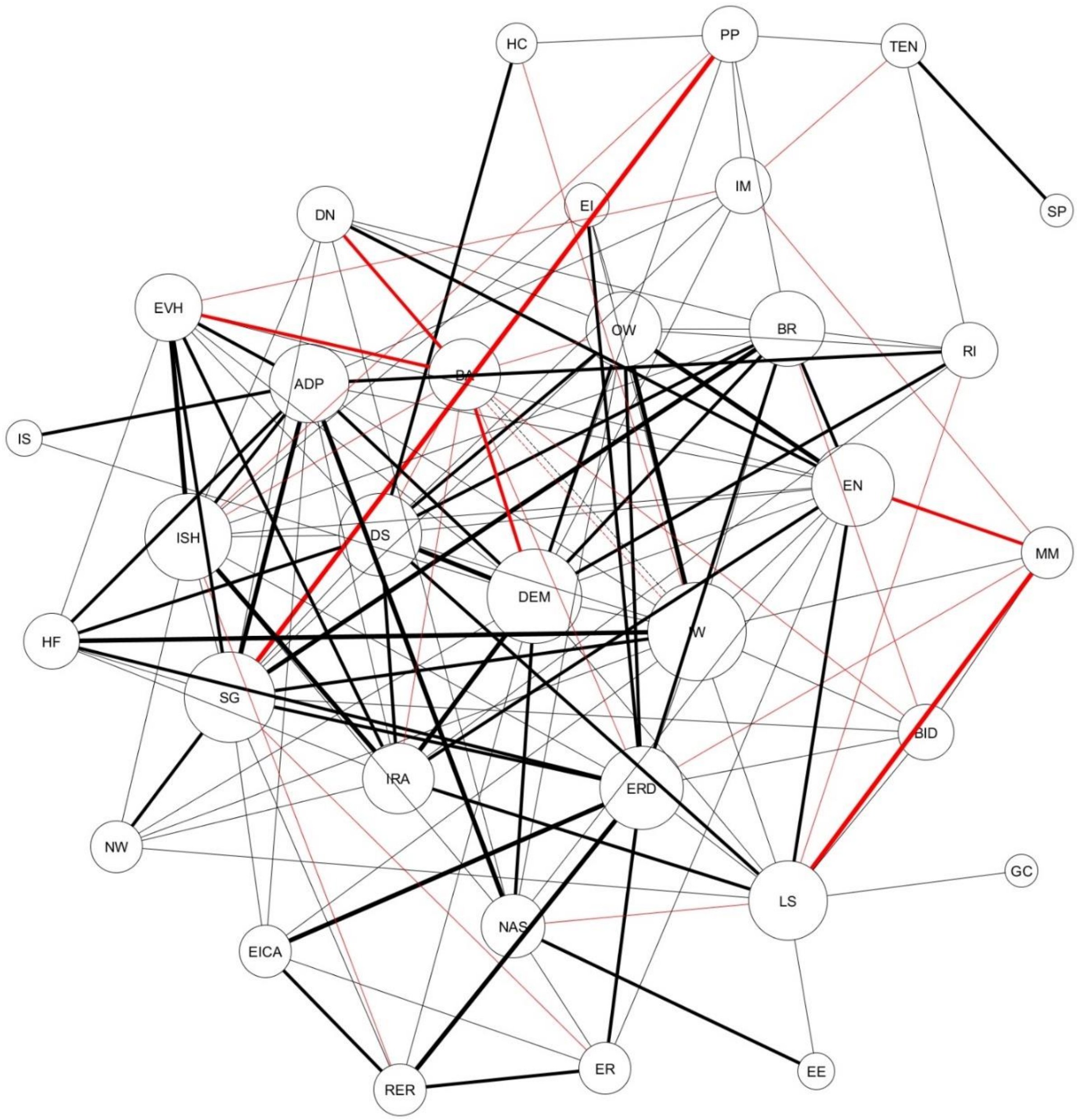

Figure S9. The similarity-dissimilarity network based on answers from participants who specified their academic status as PhD candidate, postdoc or higher (i.e., participants who specified their status as “Other” or who did not specify it were excluded here).

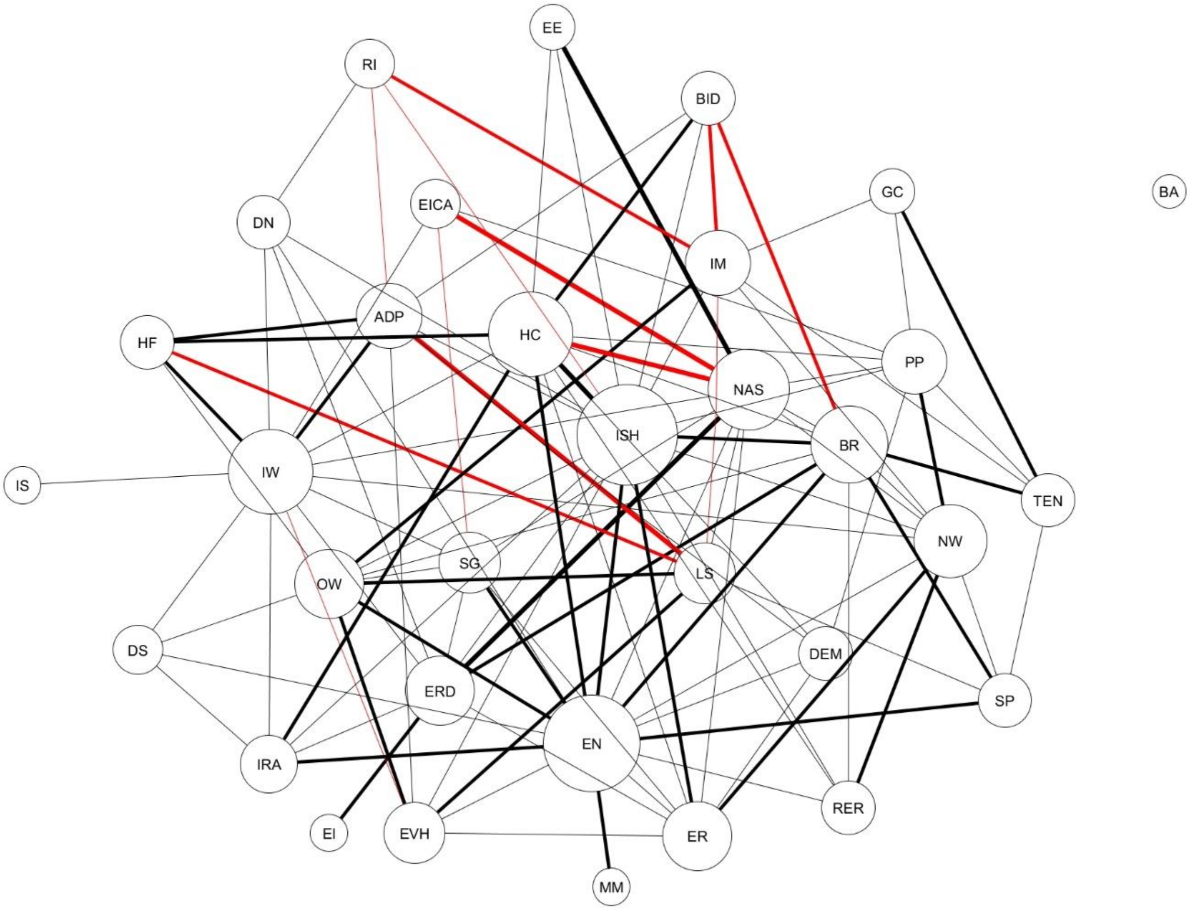

Figure S10. The similarity-dissimilarity network based on answers of participants who specified their academic status as “Other”.

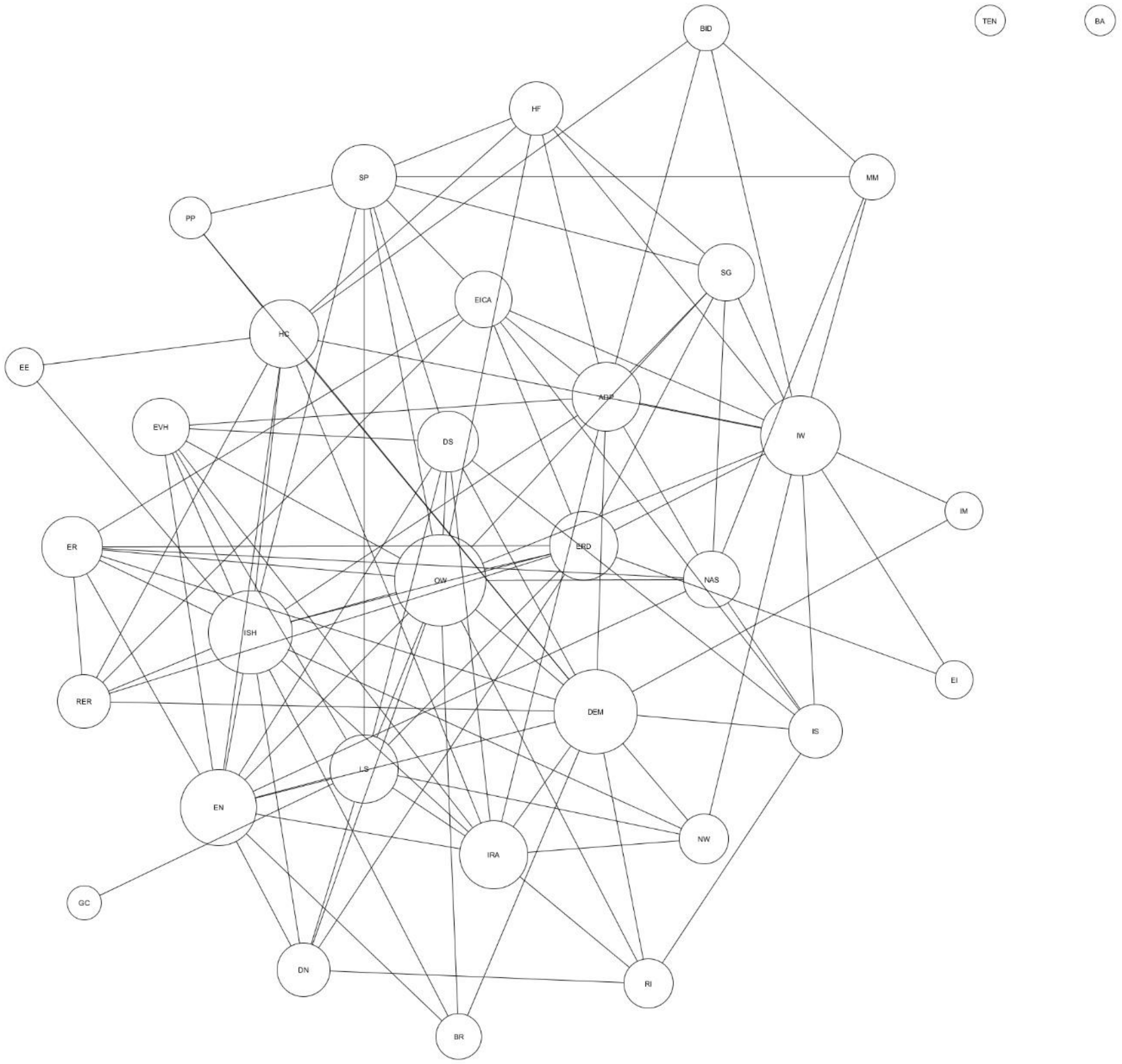

Figure S11. The similarity-dissimilarity network based on only positive answers.

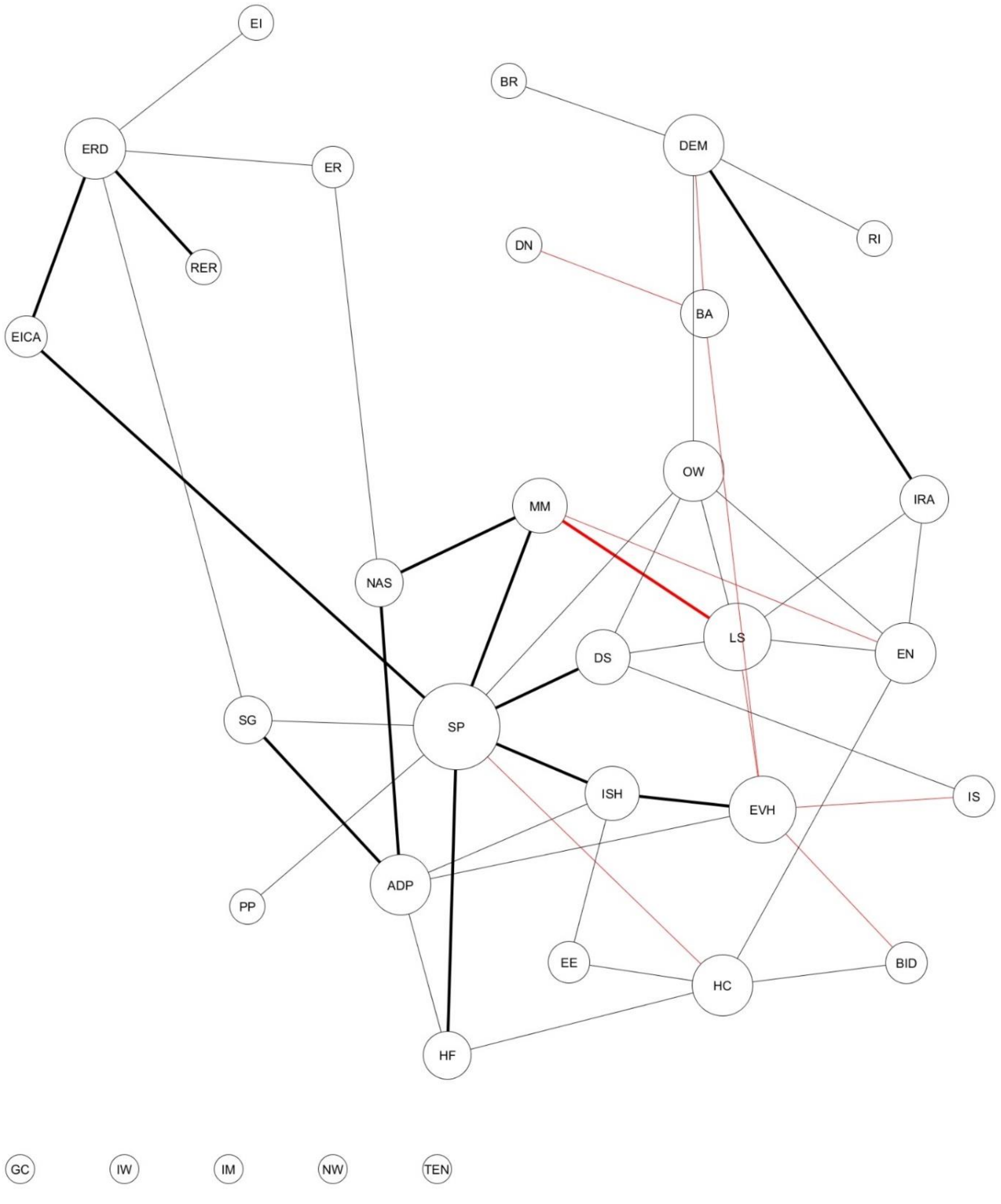

Figure S12. The similarity-dissimilarity network using a threshold for 2 for contradictory hypotheses and a threshold of 8 for similar hypotheses.

Statistical analyses of networks

Given the three network representations derived from the survey results, two key questions need to be addressed: (1) Do certain hypotheses stand out topologically? Can they be characterized on the basis of their topological features such that the roles of the hypotheses within the scientific discipline can be better understood? (2) Are the topological features of these networks rather random or do they possess clear non-random properties? These questions are addressed in the statistical analyses.

In order to characterize each node i in a network (question 1), we will use the degree k_i, the betweenness centrality b_i, the clustering coefficient c_i and the eigenvector centrality e_i. While the degree of a node is simply the number of neighbors, the betweenness centrality b_i of a node i is the percentage of shortest paths from any node to any other node in the graph, which pass through this node i (Freeman 1977). The clustering coefficient c_i of node i is the percentage of links among the neighbors of node i (Watts and Strogatz 1998). In contrast to the betweenness centrality, where all nodes contribute equally (via their shortest paths) to the computation of a node's centrality, in the case of the eigenvector centrality a link of a node to a high-score neighbor is more relevant than a link to a low-score neighbor. Google's PageRank is a variant of this eigenvector centrality (Brin and Page 1998). These centralities are of particular importance for dynamical processes on graphs, as they can be associated to the node visiting probabilities of a random walk on the graph. Technically, the quantities e_i form the eigenvector of the graph's adjacency matrix belonging to the largest eigenvalue, i.e. the Perron-Frobenius eigenvector (Newman 2003).

To address whether the topological features of the networks are rather random (question 2), we computed the correlation coefficient r for each pair of topological quantities discussed above (degree with betweenness centrality, D–BC; eigenvector centrality with betweenness centrality, EC–BC; clustering coefficient with betweenness centrality, CC–BC). We then generated large sets of Erdős-Rényi (ER) random graphs (null model NM1), each with the same number of nodes and edges as the hypotheses network under consideration. For these graphs, we computed the average correlation coefficient $\langle r \rangle$, as well as its standard deviation σ_r, yielding a z-score, $z_r = (r - \langle r \rangle) / \sigma_r$. A z-score between –1 and +1 indicates that the correlation coefficient r between the topological quantities observed in the hypothesis networks cannot be distinguished from random graphs. A z-score with $1 < |z| < 2$ can be interpreted as a correlation coefficient close to those in random graphs (less than two standard deviations away). Larger values of $|z|$ suggest significant deviations from random graphs. Furthermore, we performed the same numerical experiment using a large set of switch-randomized graphs (null model NM 2; see e.g. Milo et al. (2002), Fretter et al. (2012)), thus not only conserving the total number of nodes and edges, but also the degree sequence of the graph (i.e. the degree of each nodes).

Erdős-Rényi (ER) random network

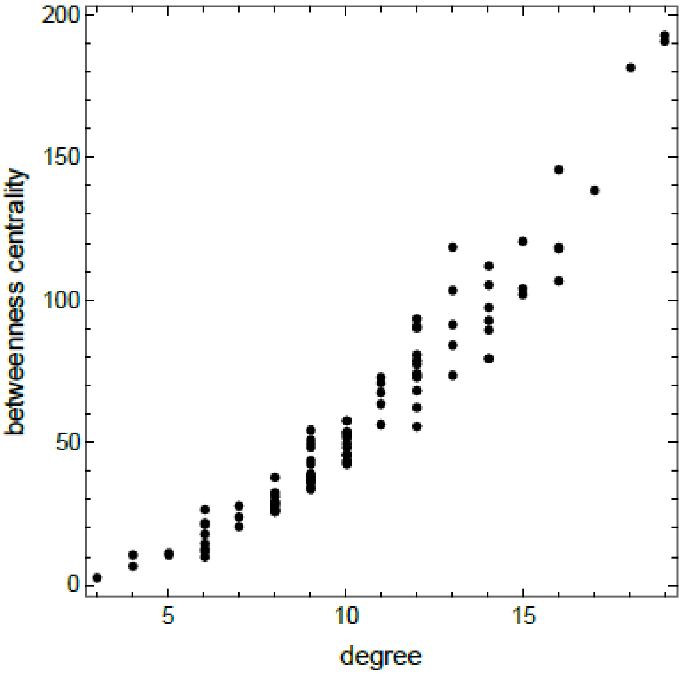

Figure S13. Betweenness centrality vs. degree for the nodes of the random ER network.

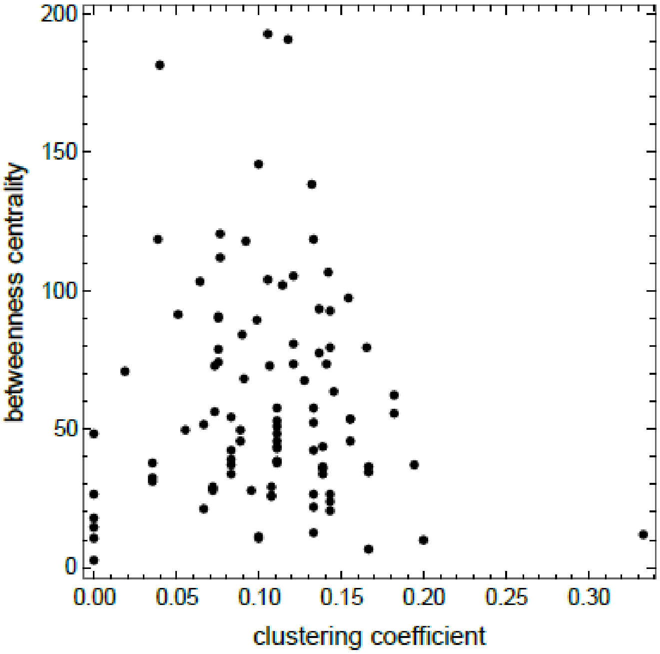

Figure S14. Betweenness centrality vs. clustering coeffcient for the nodes of the random ER network.

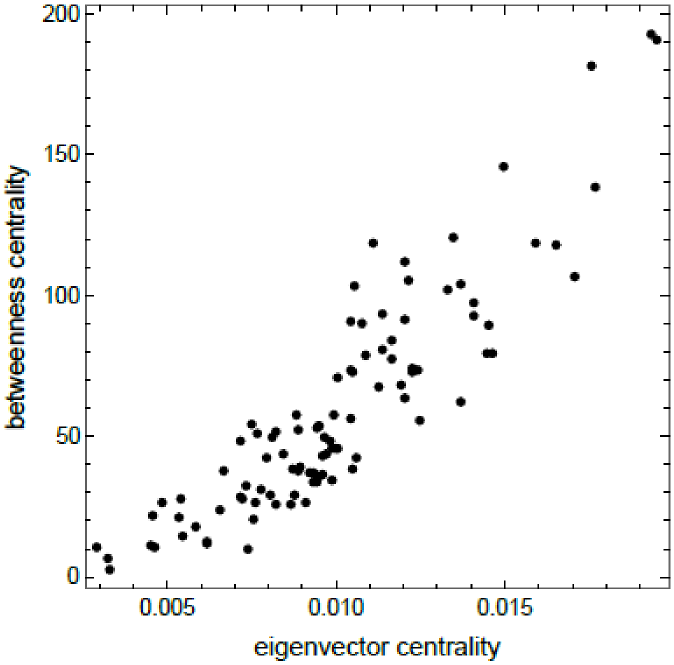

Figure S15. Betweenness centrality vs. eigenvector centrality for the nodes of the random ER network.

Statistical analysis of the similarity-dissimilarity networks

Figure S16 shows the node’s betweenness centrality against the node degree for all nodes (hypotheses) in the main similarity-dissimilarity network shown in Fig. 2 in the manuscript. In Figure S17, the betweenness centrality is shown against the clustering coefficient, while Figure S18 compares the two centralities, the eigenvector centrality and the betweenness centrality.

In order to assess the similarity to a random network, which is suggested by these scatter plots (compare with Figures S13-15), we performed the numerical experiments described above. Tables S1 and S2 show the correlation coefficients, as well as the z-scores with respect to both null models for the three pairs of topological quantities for the main similarity-dissimilarity network (Fig. 2 in the paper, using values 1-3 and 7-9) and the modified similarity-dissimilarity network based on positives values only (using values 7-9; Fig. S11). The z-scores in Table S1 indicate that the latter similarity-dissimilarity network indeed shows no significant deviations from random graphs. For the main similarity-dissimilarity network (Table S2), the correlation between the clustering coefficient and the betweenness centrality shows a deviation from each of the sets of random graphs, but all other z-scores confirm the random features of this network. The weaker negative correlation of the lustering coefficient and the betweenness centrality could be due to the slightly higher modularity of the similarity-dissimilarity network (Girvan-Newman index of 0.201; see Girvan and Newman (2002) for the definition of the index) compared to random graphs.

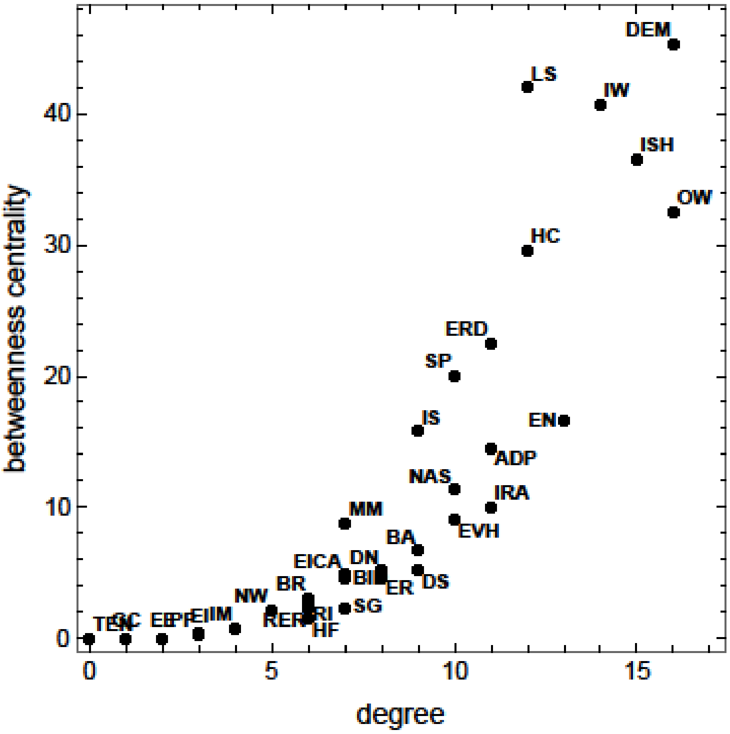

Figure S16. Betweenness centrality vs. degree for the nodes of the similarity-dissimilarity network.

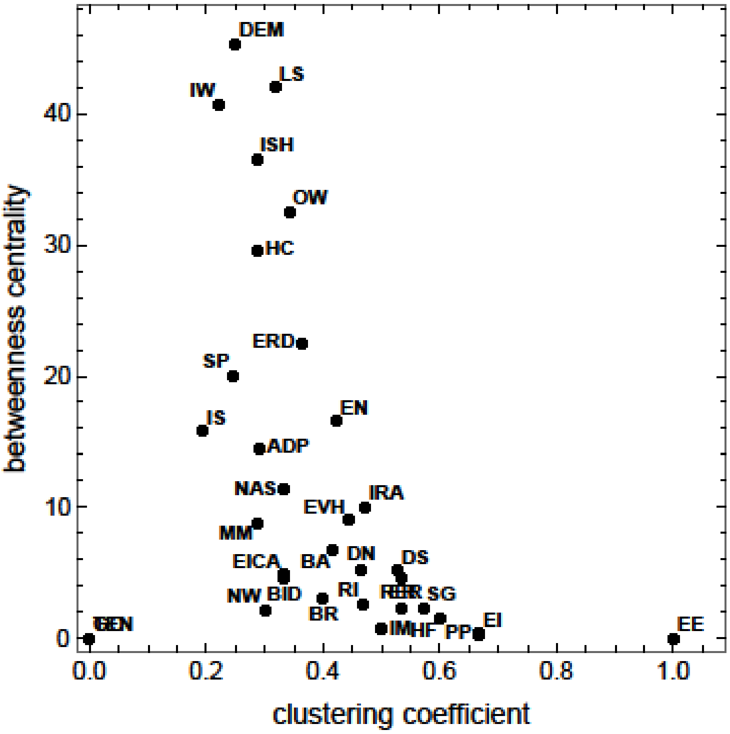

Figure S17. Betweenness centrality vs. clustering coeffcient for the nodes of the similarity-dissimilarity network.

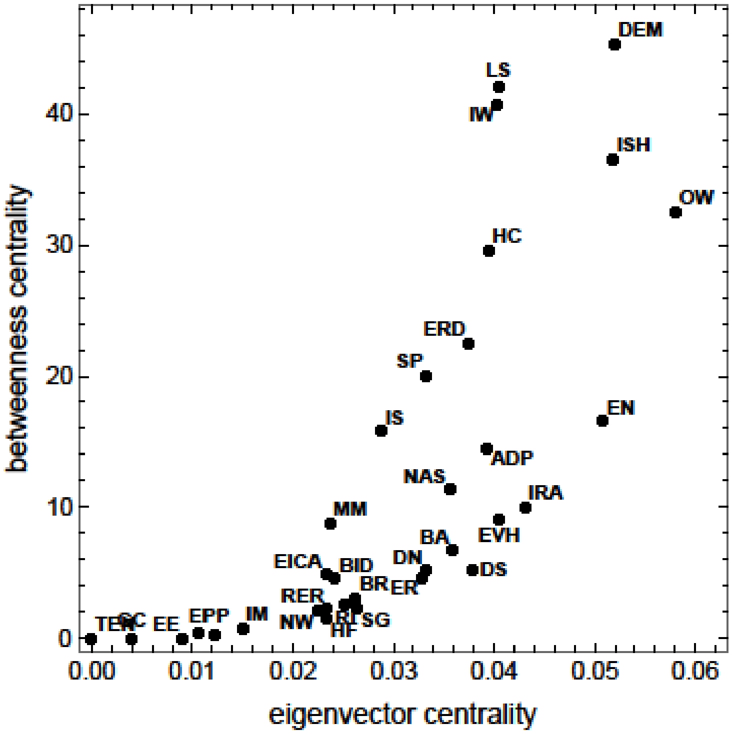

Figure S18. Betweenness centrality vs. eigenvector centrality for the nodes of the similarity-dissimilarity network.

Table S1. Correlation coefficients between topological properties for the similarity-dissimilarity network based on scores 7-9, together with the z-scores derived from ER graphs (null model NM 1) and from switch-randomized graphs (null model NM 2). For each null model, z-scores are based on 1000 graphs. D: degree, BC: betweenness centrality, EC: eigenvector centrality, CC: clustering coefficient.

Property	**Correlation**	**z-score (NM 1)**	**z-score (NM 2)**
D–BC	0:871148	–0.0361625	0.133177
EC–BC	0.750786	–0.327436	–0.824518
CC–BC	–0.517281	–1.03688	–1.02059

Table S2: Same as Table S1, but for the main similarity-dissimilarity network based on scores 1-3 and 7-9.

Property	**Correlation**	**z-score (NM 1)**	**z-score (NM 2)**
D–BC	0.854399	–0.645742	0.17137
EC–BC	0.743479	–0.755784	–0.297047
CC–BC	–0.656414	–2.35288	–3.33159

Statistical analysis of the joint-mentions network A

Figure S19 shows the node's betweenness centrality against the node degree for all nodes (hypotheses) in the joint-mentions network A. In Figure S20, the betweenness centrality is shown against the clustering coefficient, while Figure S21 compares the two centralities, the eigenvector centrality and the betweenness centrality. The joint-mentions network A is dominated by four hypotheses that clamp the network. For a better view on the structure each figure is also zoomed in on the rest of the hypotheses without the four dominating hypotheses. Regarding the potential similarity to a random network, all z-scores indicate a moderate but systematic deviation from randomness across all topological indicators (Table S3).

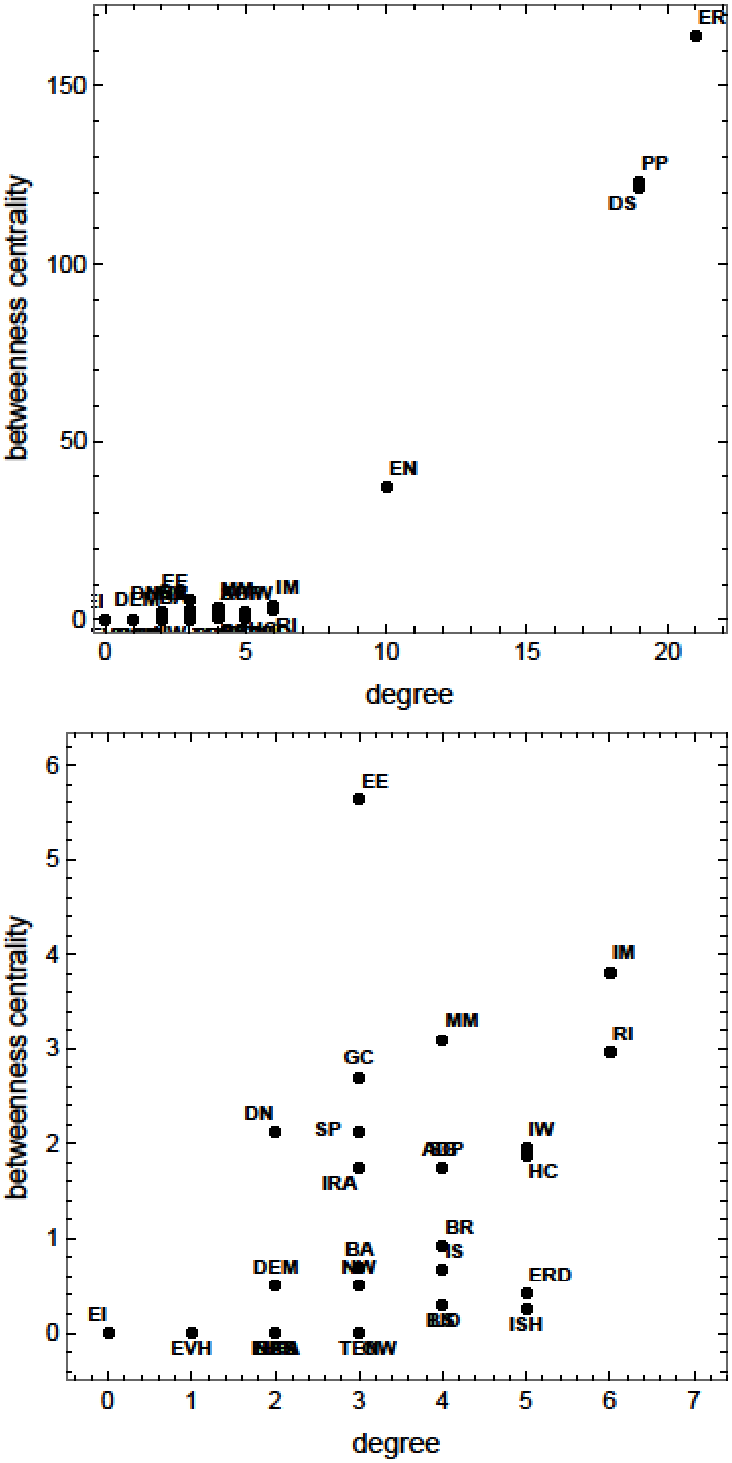

Figure S19. Betweenness centrality vs. degree vs. for the nodes of the joint-mentions-network A. For a better view on the structure each figure is also zoomed in on the rest of the hypotheses without the four outliners (below).

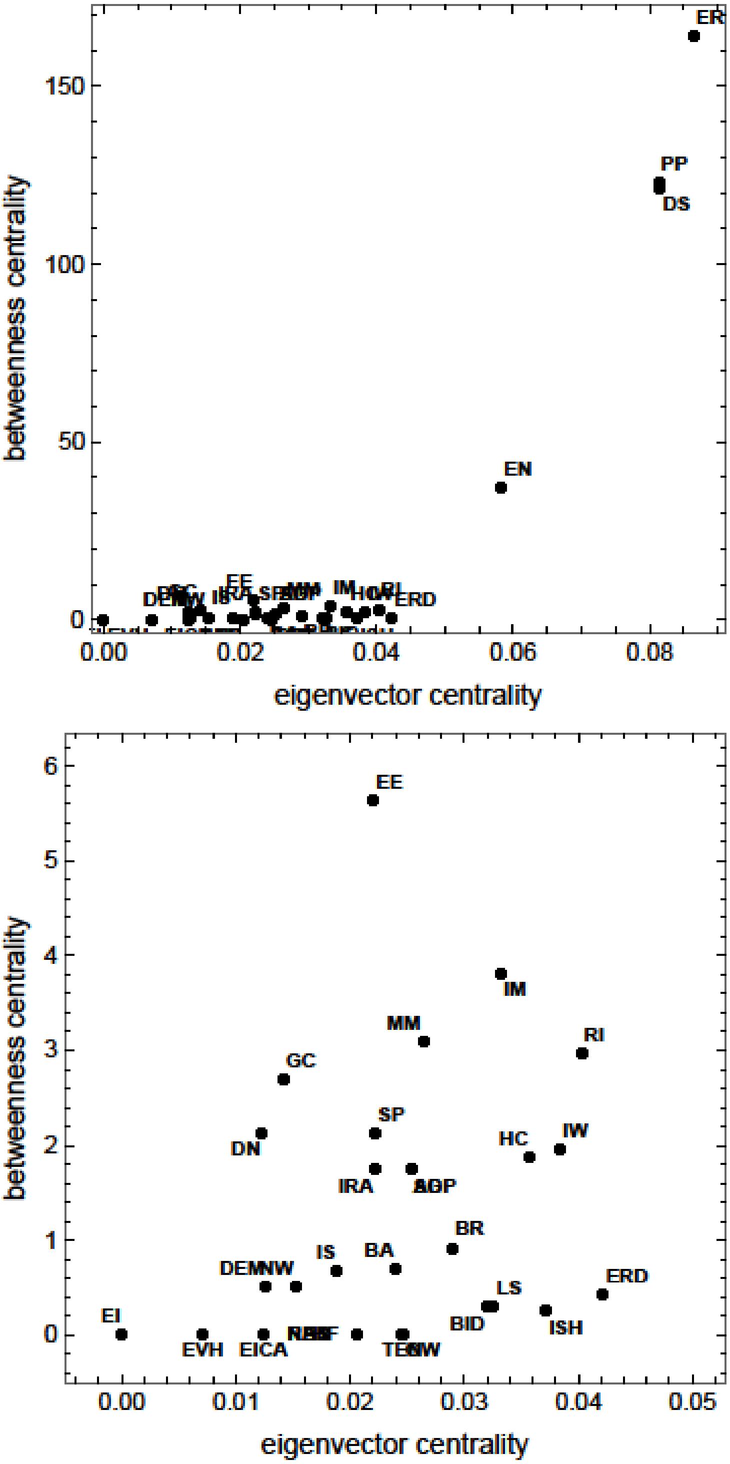

Figure S20. Betweenness centrality vs. clustering coefficient for the nodes of the joint-mentions network A. For a better view on the structure each figure is also zoomed in on the rest of the hypotheses without the four outliners (below).

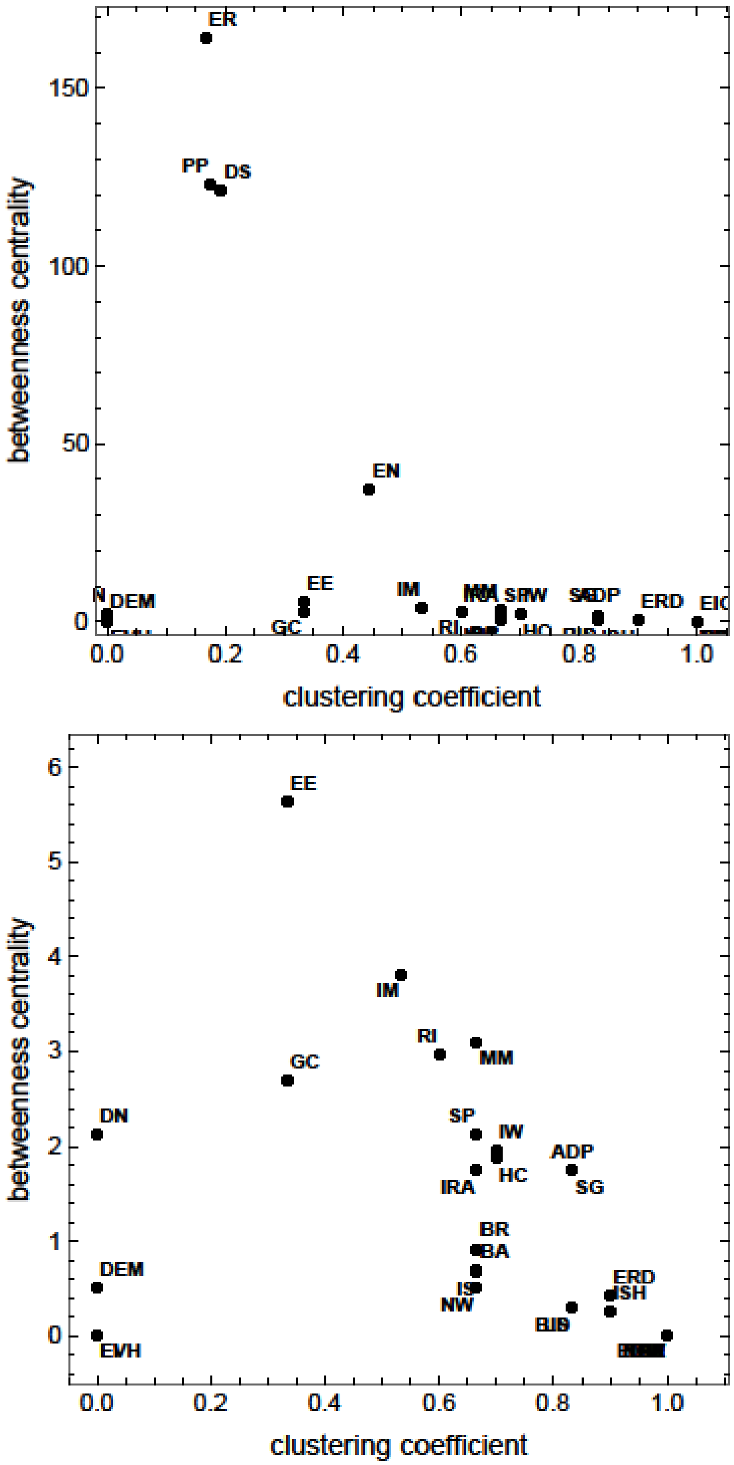

Figure S21. Betweenness centrality vs. eigenvector centrality for the nodes of the joint-mentions network B. For a better view on the structure each figure is also zoomed in on the rest of the hypotheses without the four outliners (below).

Table S3. As Table S1, but for joint-mentions network A.

Property	Correlation	z-score (NM 1)	z-score (NM 2)
D–BC	0.959959	1.58967	–1.04517
EC–BC	0.867749	1.64308	–2.89482
CC–BC	–0.773808	–1.93993	–3.35674

Statistical analysis of the joint-mentions network B

Figure S22 shows the node's betweenness centrality against the node degree for all nodes (hypotheses) in the joint-mentions network B. In Figure S23, the betweenness centrality is shown against the clustering coefficient, while Figure S24 compares the two centralities, the eigenvector centrality and the betweenness centrality. Visually inspecting these figures, we find evidence for hidden integrators with a comparatively low or intermediate degree, but a high betweenness centrality (for example BR and PP), organizers of cohesive groups with a low betweenness centrality, but a high clustering coefficient (for example RI), as well as structural integrators with a high betweenness centrality but intermediate eigenvector centrality (like BR and PP) vs. dynamical integrators with a high eigenvector centrality but intermediate betweenness centrality (like SG, EVH and NAS). In general, the community structure of a network is an interesting topological characterization, as it suggests relevant sub-networks that may be discussed individually. For the hypotheses networks discussed here, this is of particular relevance, as a strong modularity may be indicative of the existence of different scientific 'schools', with a stronger dissemination and exchange within than with other 'schools'.

The joint-mentions network B shows a drastic deviation from random graphs in almost all topological indicators, except for the correlation between clustering coefficient and betweenness centrality (see Table S4). As indicated above, this quantity could be affected by the modularity of the networks (Girvan-Newman index of 0.34).

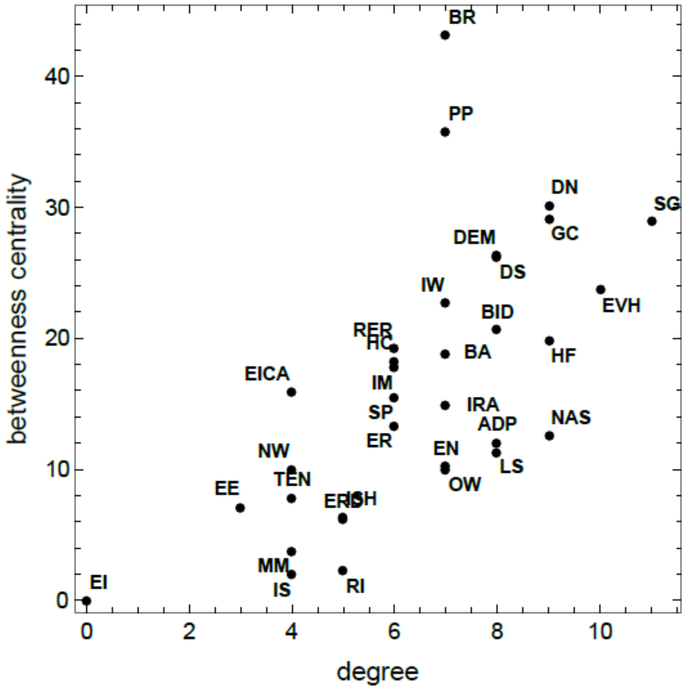

Figure S22. Betweenness centrality vs. degree for the nodes of the joint-mentions network B.

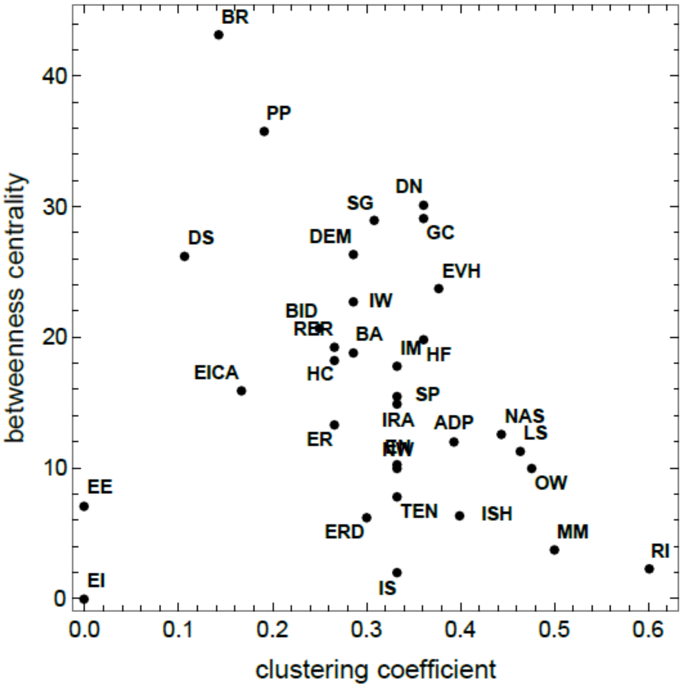

Figure S23. Betweenness centrality vs. clustering coefficient for the nodes of the joint-mentions network B.

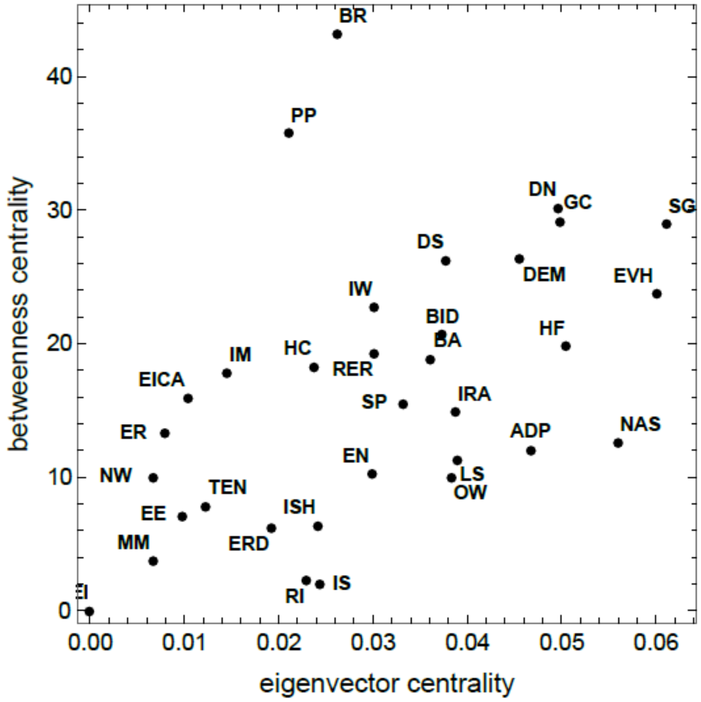

Figure S24. Betweenness centrality vs. eigenvector centrality for the nodes of the joint-mentions network B.

Table S4. As Table S1, but for the joint-mentions network B.

Property	**Correlation**	**z-score (NM 1)**	**z-score (NM 2)**
D–BC	0.656206	-5.19909	-17.2986
EC–BC	0.476911	-4.36896	-9.10713
CC–BC	-0.608896	-1.58043	-0.790375

Supplementary References

Brin, S. and L. Page 1998. The anatomy of a large-scale hypertextual web search engine. *Computer Networks and ISDN Systems* 30: 107-117.

Freeman, L. C. 1977. A set of measures of centrality based on betweenness. *Sociometry* 40: 35-41.

Fretter, C., M. Muller-Hannemann and M. T. Hütt 2012. Subgraph fluctuations in random graphs. *Physical Review E* 85(5), 056119.

Girvan, M. and M. E. J. Newman 2002. Community structure in social and biological networks. *Proceedings of the National Academy of Sciences of the United States of America* 99(12): 7821-7826.

Milo, R., S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii and U. Alon 2002. Network motifs: Simple building blocks of complex networks. *Science* 298(5594): 824-827.

Newman, M. E. J. 2003. The structure and function of complex networks. *Siam Review* 45: 167-256.

Watts, D. J. and S. H. Strogatz 1998. Collective dynamics of 'small-world' networks. *Nature* 393: 440-442.

4. A citation-based map of concepts in invasion biology

This paper was a collaboration with Dr. Frank Havemann from Humboldt-Universität zu Berlin and Prof. Dr. Jonathan Jeschke from Freie Universität Berlin and Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) and was published in NeoBiota (2019).

Published as: Enders M, Havemann F, Jeschke JM (2019) A citation-based map of concepts in invasion biology. NeoBiota 47: 23-42.

NeoBiota 47: 23–42 (2019)
doi: 10.3897/neobiota.47.32608
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

A citation-based map of concepts in invasion biology

Martin Enders[1,2,3], Frank Havemann[4], Jonathan M. Jeschke[1,2,3]

1 *Freie Universität Berlin, Department of Biology, Chemistry, Pharmacy, Institute of Biology, Königin-Luise-Str. 1–3, 14195 Berlin, Germany* **2** *Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany* **3** *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, 14195 Berlin, Germany* **4** *Humboldt-Universität zu Berlin, Philosophische Fakultät, Institut für Bibliotheks- und Informationswissenschaft, Dorotheenstr. 26, 10099 Berlin, Germany*

Corresponding author: *Martin Enders* (enders.martin@gmx.net)

Academic editor: *Robert Colautti* | Received 21 December 2018 | Accepted 23 May 2019 | Published 19 June 2019

Citation: Enders M, Havemann F, Jeschke JM (2019) A citation-based map of concepts in invasion biology. NeoBiota 47: 23–42. https://doi.org/10.3897/neobiota.47.32608

Abstract

Invasion biology has been quickly expanding in the last decades so that it is now metaphorically flooded with publications, concepts, and hypotheses. Among experts, there is no clear consensus about the relationships between invasion concepts, and almost no one seems to have a good overview of the literature anymore. Similar observations can be made for other research fields. Science needs new navigation tools so that researchers within and outside of a research field as well as science journalists, students, teachers, practitioners, policy-makers, and others interested in the field can more easily understand its key ideas. Such navigation tools could, for example, be maps of the major concepts and hypotheses of a research field. Applying a bibliometric method, we created such maps for invasion biology. We analysed research papers of the last two decades citing at least two of 35 common invasion hypotheses. Co-citation analysis yields four distinct clusters of hypotheses. These clusters can describe the main directions in invasion biology and explain basic driving forces behind biological invasions. The method we outline here for invasion biology can be easily applied for other research fields.

Keywords

bibliometric methods, biological invasions, concepts, invasion biology, invasion science, map, navigation tools, network of invasion hypotheses

Introduction

When you are visiting a city, you can usually find some important places by yourself, for example the central station, a supermarket, and maybe even a few touristic highlights. A better way, however, would be that a friend draws you a map with the places in the city you are interested in. Then you would also find the small French café, the little arthouse cinema, and the restaurant serving delicious oriental food. But this map will be limited by your friend's knowledge of her district. What if you want to visit another part of the city? You will find yourself in the same position as before. Therefore, an even better way is to ask several people who live in different areas of the city. In this way, you can get a detailed picture of the whole city and, if you are lucky, even find the best brewed coffee in the city.

The same is true when you start in a new research field. Enders et al. (2018) showed that the field of invasion biology can be seen as such a big city in which many of its inhabitants, i.e. invasion biologists, have no clear picture of the whole city; their knowledge seems to be limited to their immediate field of interest within invasion biology. What is the solution for a problem like this? Suppose you have no good tourist guide at hand, then you need to observe where other tourists go to and follow them. For a research field, this would be an analysis of citations made by specialists.

Authors of a scholarly paper cite publications and other sources they assume to be relevant for the topic of their paper. Thus, scholarly papers form a huge network, a view already propagated by one of the fathers of bibliometrics (de Solla Price 1965). The identification of topics in bibliographies is an old problem in bibliometrics. Starting with co-citation analysis (Marshakova 1973; Small 1973; Small and Sweeny 1985), important recent developments include hybrid approaches that combine citation-based and term-based techniques (Glenisson et al. 2005; Glänzel and Thijs 2017), and term-based probabilistic methods (topic modelling, Yau et al. 2014). The 21st century brought the advance of many methods for clustering in networks (Fortunato 2010; Xie et al. 2013; Amelio and Pizzuti 2014). Some of these methods were also applied to citation networks (Gläser et al. 2017; Velden et al. 2017), and topic identification is often accompanied by visualization of the topic landscape (Börner 2015).

For this publication, we analysed co-citations of invasion hypotheses in research papers of the last two decades. Co-citation analysis was independently introduced by Irina Marshakova (1973) and Henry Small (1973) (see also Havemann 2016). Because there are no strict rules for citing, they had to solve the problem of noise in co-citation data. Irina Marshakova compared the observed absolute co-citation numbers with expected numbers in a null model of independent random citing and only accepted co-citation links between cited sources that are more frequently co-cited than in 95% of random trials in the null model. In other words, she assumed binomial distributions of co-citation numbers and chose a significance level of 95%. Henry Small, on the other hand, reduced noise by using thresholds of relative co-citation measures (Jaccard and Salton index). Also, other relative measures of co-citation strengths were used (Gmür 2003; Egghe and Leydesdorff 2009; Boyack and Klavans 2010). In a recent study, Trujillo and Long (2018) used absolute co-citation numbers as a similarity measure and created a sequence of nested co-citation networks by setting different thresholds for this measure. In invasion biology or related research fields, however, no citation-based map of major concepts and hypotheses does, to our knowledge, currently exist.

Invasion biology is a discipline that grew very slowly at first. In the 19th century, early concepts on non-native species were mentioned (Cadotte 2006), for example in Darwin's (1859) book "On the origin of species by means of natural selection". Further concepts were introduced by the Swiss botanist Albert Thellung (Kowarik and Pyšek 2012), Elton (1958) and others until the 1950s; however, there was still too little work on the topic to recognize a distinct research field. Possibly due to a growing consciousness for ecosystems in a changing world (Meadows et al. 1972) and in human responsibilities (Jonas 1979), interest in invasion biology strongly increased since the late 20th century (Richardson and Pyšek 2008). It has also influenced other research fields; for example, concepts and hypotheses of invasion biology are used in restoration ecology, landscape ecology, urban ecology, or risk assessments of genetically modified organisms (Jeschke et al. 2013; Lowry et al. 2013).

Our study aims were twofold. First, we wanted to find a suitable map of the field of invasion biology based on co-citation analysis. Second, we aimed to compare this map to those created with two other approaches: a map based on an assessment of the characteristics ("traits") of hypotheses (Enders and Jeschke 2018), and one based on an online survey (Enders et al. 2018).

Methods

We defined 35 common concepts and hypotheses in invasion biology and their representing key publications (Table 1). This list is based on Enders and Jeschke (2018) and Enders et al. (2018), which are in turn based on Catford et al. (2009). For clarity, we only give one key publication per hypothesis. One paper is the key publication for four hypotheses (EI, ERD, IS, NAS), and another paper for two hypotheses (SG, BID) (Table 1). Thus, Table 1 includes 31 key publications.

A first hint about relationships between our key publications can be obtained from their direct citation links, but this approach is limited by the small sample size of publications. As there is some randomness in the act of citation, a larger sample size is useful. Using bibliographic coupling relations between key papers, i.e., analysing to which degree their reference lists overlap, has the same drawback.

An alternative approach, which we applied here, is co-citation analysis, where joint citations of key papers are analysed, using all publications of the field. This approach can thus draw from a much larger dataset.

We downloaded all 10,430 records citing any of our key publications from the Web of Science (WoS, as licensed for Freie Universität Berlin, March 2017). Variants of referencing key papers were identified semi-automatically with the help of an R-script provided by Felix Mattes. For example, missing or wrong author initials or wrong page numbers were corrected in this way. Then we determined the yearly citation and co-citation numbers of all key publications. We expect higher numbers of key papers cited in review papers which diminishes the weight of each co-citation. Therefore, we excluded reviews from the analysis.

Key invasion papers are also cited outside of invasion biology. We excluded such outside-of-the-field papers from co-citation analysis, as invasion hypotheses are primarily applied in invasion biology and we expect that peculiarities of their relationships are discussed within the field, whereas joint citations by publications outside of the field are less reliable for assessing such relationships. We defined papers belonging to the field as those that are returned by the term search proposed by Vaz et al. (2017):

"Ecological invasion" or "Biological invasion*" or "Invasion biology" or "Invasion ecology" or "Invasive species" or "Alien species" or "Introduced species" or "Non-native species" or "Nonnative species" or "Nonindigenous species" or "Non-indigenous species" or "Allochthonous species" or "Exotic species".*

Using this term search on 28.08.2017 in the WoS returned 30,731 records. After excluding 1,769 review papers, 28,962 papers remained in the sample. These are mainly primary research communications (28,295) and have mainly been published after 1990 (28,841; i.e. 99.6%). Figure 1 displays the time distribution of the sample of these 28,841 invasion biology papers in the WoS. In the 1990s, the number of papers in the field has remained small. We therefore restricted our analysis to the time period 1999–2017. Thus, we ended up with a sample of 1,518 invasion biology papers that cite at least two of our key publications listed in Table 1. The sample includes 1501 research articles, mainly in journals but also 39 in conference proceedings and five in books. In addition, we have eight letters and nine editorials. The time distribution of the sample is displayed in Figure 2.

Salton's cosine

In the n-dimensional vector space with one dimension per citing paper, each cited source i can be represented by a vector v_{ik} ($k = 1, ..., n$) with $v_{ik} = 1$ if paper k cites source i and $v_{ik} = 0$ otherwise. The Salton index $S(i, j)$ of two sources is a similarity measure defined as the cosine of the angle between the two source vectors (Hamers et al. 1989). Translated into the language of set theory, it can be calculated as:

$$S(i,j) = \frac{\left|c_i \cap c_j\right|}{\sqrt{\left|c_i\right| \cdot \left|c_j\right|}}, \qquad (1)$$

where c_i is the set of papers citing source publication i. Salton's cosine gives values in the interval [0, 1]. Co-citations are usually determined within reference lists of citing publications c_i published during a given year. Due to heavily fluctuating citation num-

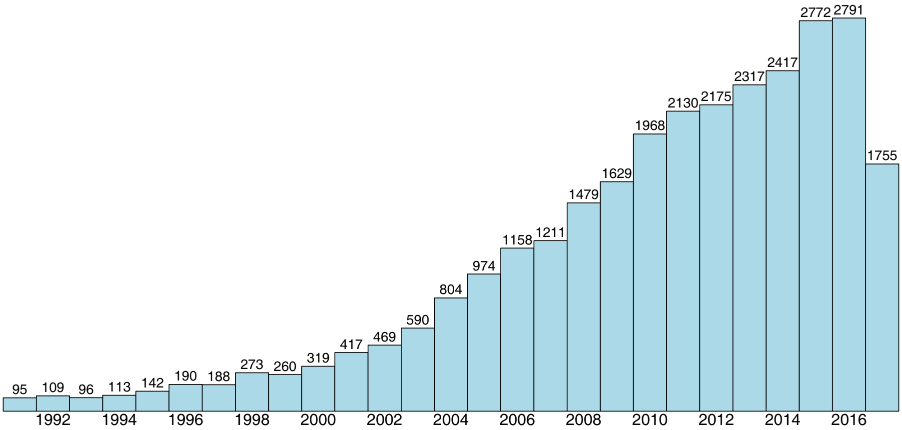

Figure 1. Numbers of publications in invasion biology, using the same search term as Vaz et al. (2017) in the Web of Science. The number of publications in 2017 is relatively low because the search was performed within this year, on 28 August 2017.

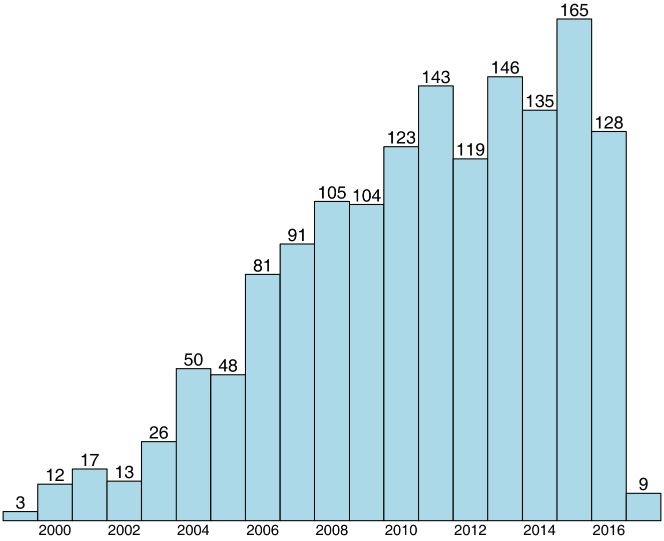

Figure 2. Number of publications per year that cite at least two of the key papers given in Table 1. This sample of 1518 publications was analysed in detail here; it is a subset of the publications shown in Figure 1.

bers, we combined several years to get broader citation windows. Due to this change, a challenge was that two key papers *i* and *j* published within the citation window in different years $y_i < y_j$ have different chances to be cited: older papers have more opportunities to be cited than younger papers. We made their chances to be cited as equal as possible by reducing the set c_i to citing papers published from year y_j on.

Table 1. List of 35 common invasion hypotheses and how we defined them (cf. Catford et al. 2009; Enders and Jeschke 2018; Enders et al. 2018).

Hypothesis		Description	Key reference
ADP	Adaptation	The invasion success of non-native species depends on the adaptation to the conditions in the exotic range before and/or after the introduction. Non-native species that are related to native species are more successful in this adaptation.	Duncan and Williams (2002)
BA	Biotic acceptance aka “the rich get richer”	Ecosystems tend to accommodate the establishment and coexistence of non-native species despite the presence and abundance of native species.	Stohlgren et al. (2006)
BID	Biotic indirect effects	Non-native species benefit from different indirect effects triggered by native species.	Callaway et al. (2004)
BR	Biotic resistance aka diversity-invasibility hypothesis	An ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity.	Levine and D’Antonio (1999)
DEM	Dynamic equilibrium model	The establishment of a non-native species depends on natural fluctuations of the ecosystem, which influences the competition of local species.	Huston (1979)
DN	Darwin’s naturalization	The invasion success of non-native species is higher in areas that are poor in closely related species than in areas that are rich in closely related species.	Daehler (2001)
DS	Disturbance	The invasion success of non-native species is higher in highly disturbed than in relatively undisturbed ecosystems.	Hobbs and Huenneke (1992)
EE	Enemy of my enemy aka accumulation-of-local-pathogens hypothesis	Introduced enemies of a non-native species are less harmful to the non-native as compared to the native species.	Eppinga et al. (2006)
EI	Enemy inversion	Introduced enemies of non-native species are less harmful for them in the exotic than the native range, due to altered biotic and abiotic conditions.	Colautti et al. (2004)
EICA	Evolution of increased competitive ability	After having been released from natural enemies, non-native species will allocate more energy in growth and/or reproduction (this re-allocation is due to genetic changes), which makes them more competitive.	Blossey and Nötzold (1995)
EN	Empty niche	The invasion success of non-native species increases with the availability of empty niches in the exotic range.	MacArthur (1970)
ER	Enemy release	The absence of enemies in the exotic range is a cause of invasion success.	Keane and Crawley (2002)
ERD	Enemy reduction	The partial release of enemies in the exotic range is a cause of invasion success.	Colautti et al. (2004)
EVH	Environmental heterogeneity	The invasion success of non-native species is high if the exotic range has a highly heterogeneous environment.	Melbourne et al. (2007)
GC	Global competition	A large number of different non-native species is more successful than a small number.	Colautti et al. (2006)
HC	Human commensalism	Species that are living in close proximity to humans are more successful in invading new areas than other species.	Jeschke and Strayer (2006)
HF	Habitat filtering	The invasion success of non-native species in the new area is high if they are pre-adapted to this area.	Weiher and Keddy (1995)
IM	Invasional meltdown	The presence of non-native species in an ecosystem facilitates invasion by additional species, increasing their likelihood of survival or ecological impact.	Simberloff and Von Holle (1999)
IRA	Increased resource availability	The invasion success of non-native species increases with the availability of resources.	Sher and Hyatt (1999)
IS	Increased susceptibility	If a non-native species has a lower genetic diversity than the native species, there will be a low probability that the non-native species establishes itself.	Colautti et al. (2004)
ISH	Island susceptibility hypothesis	Non-native species are more likely to become established and have major ecological impacts on islands than on continents.	Jeschke (2008)
IW	Ideal weed	The invasion success of a non-native species depends on its specific traits (e.g. life-history traits).	Rejmánek and Richardson (1996)

Hypothesis		Description	Key reference
LS	Limiting similarity	The invasion success of non-native species is high if they strongly differ from native species, and it is low if they are similar to native species.	MacArthur and Levins (1967)
MM	Missed mutualisms	In their exotic range, non-native species suffer from missing mutualists.	Mitchell et al. (2006)
NAS	New associations	New relationships between non-native and native species can positively or negatively influence the establishment of the non-native species.	Colautti et al. (2006)
NW	Novel weapons	In the exotic range, non-native species can have a competitive advantage against native species because they possess a novel weapon, i.e. a trait that is new to the resident community of native species and therefore affects them negatively.	Callaway and Ridenour (2004)
OW	Opportunity windows	The invasion success of non-native species increases with the availability of empty niches in the exotic range, and the availability of these niches fluctuates spatio-temporally.	Johnstone (1986)
PH	Plasticity hypothesis	Invasive species are more phenotypically plastic than non-invasive or native ones.	Richards et al. (2006)
PP	Propagule pressure	A high propagule pressure (a composite measure consisting of the number of individuals introduced per introduction event and the frequency of introduction events) is a cause of invasion success.	Lockwood et al. (2005)
RER	Resource-enemy release	The non-native species is released from its natural enemies and can spend more energy in its reproduction, and invasion success increases with the availability of resources.	Blumenthal (2006)
RI	Reckless invader aka "boom-bust"	A non-native species that is highly successful shortly after its introduction can get reduced in its population or even extinct over time due to different reasons (such as competition with other introduced species or adaptation by native species).	Simberloff and Gibbons (2004)
SDH	Shifting defence hypothesis	After having been released from natural specialist enemies, non-native species will allocate more energy in cheap (energy-inexpensive) defenses against generalist enemies and less energy in expensive defenses against specialist enemies (this re-allocation is due to genetic changes); the energy gained in this way will be invested in growth and/or reproduction, which makes the non-native species more competitive.	Doorduin andVrieling (2011)
SG	Specialist-generalist	Non-native species are more successful in a new region if the local predators are specialists and local mutualists are generalists.	Callaway et al. (2004)
SP	Sampling	A large number of different non-native species is more likely to become invasive than a small number due to interspecific competition. Also, the species identity of the locals is more important than the richness in terms of the invasion of an area.	Crawley et al. (1999)
TEN	Tens rule	Approximately 10% of species successfully take consecutive steps of the invasion process.	Williamson and Brown (1986)

Communities in networks

Clusters of highly cited sources containing often co-cited sources are assumed to represent knowledge bases of current research fronts (Small and Sweeny 1985). Such clusters are particularly useful for constructing conceptual maps that should serve as navigation tools for research fields, as they group similar concepts and hypotheses in one cluster. Especially in the last two decades, several clustering methods have been developed in network science (see Fortunato (2010) for a review). Clusters (also called modules or communities) of nodes in networks should have many internal links and comparatively few external links. In the case of weighted networks, not the number of external and internal links is compared but the sum of their weights. Identifying clusters in a network is a way of investigating its inner structure.

For the case of disjoint communities, Newman and Girvan (2004) introduced "modularity" as an evaluation function of a graph partition. It compares the actual number of internal edges of each community with the number expected in a null model without community structure. In the usual null model, each vertex is expected to have the same degree as in the original graph.

We compared the results of different algorithms for community detection from the packages SNA (Handcock et al. 2003) and igraph (Csardi and Nepusz 2006) in R (R Development Core Team 2008), which can be categorized into several types. (1) The Girvan and Newman (2002) algorithm is an example of divisive clustering (igraph function cluster_edge_betweenness). It recursively detects links with high edge betweenness and removes them from the network. The clustering dendrogram is cut at the partition with maximum modularity. (2) Clauset et al. (2004) proposed to set each node as a cluster and then merge those two subgraphs that give the highest gain in modularity; this is repeated until there is no gain in modularity anymore (igraph function cluster_fast_greedy). Again, the clustering dendrogram is cut at the partition with maximum modularity. (3) Quite similar is the approach introduced by Brandes et al. (2008) (igraph function cluster_optimal). It maximizes modularity applying an optimization algorithm from integer linear programming. (4) We also applied the Louvain algorithm designed by Blondel et al. (2008) that very quickly maximizes partition modularity (igraph function cluster_louvain), (5) the "walk trap" algorithm suggested by Pons and Latapy (2005) that assumes a random walker gets trapped in communities and calculates these "traps" (igraph function cluster_walktrap), and (6) a divisive spectral algorithm suggested by Newmann (2006) which also maximizes modularity (igraph function cluster_leading_eigen).

Beside global evaluation functions like modularity, there are also functions that evaluate cohesion and separation of each community. A community *C* is well separated from the rest of the network if the escape probability of a random walker is small (Fortunato 2010). It is given by the ratio of the sum of external degrees of a community's nodes to the sum of their total degrees:

$$P_{esc}(C) = \frac{k_{out}(C)}{k(C)} . \tag{2}$$

The weak definition of a community after Radicchi et al. (2004) is fulfilled when the total internal degree is greater than the total external degree. The requirements are fulfilled if $P_{esc} < 0.5$. The strong community definition requires that every node has a stronger internal than external connection.

Results

We analysed different time periods (time steps of 1–5 years), but the results varied too much to get a clear picture. This means that the edges between the nodes varied from period to period. Obviously, in different years relationships between different concepts and

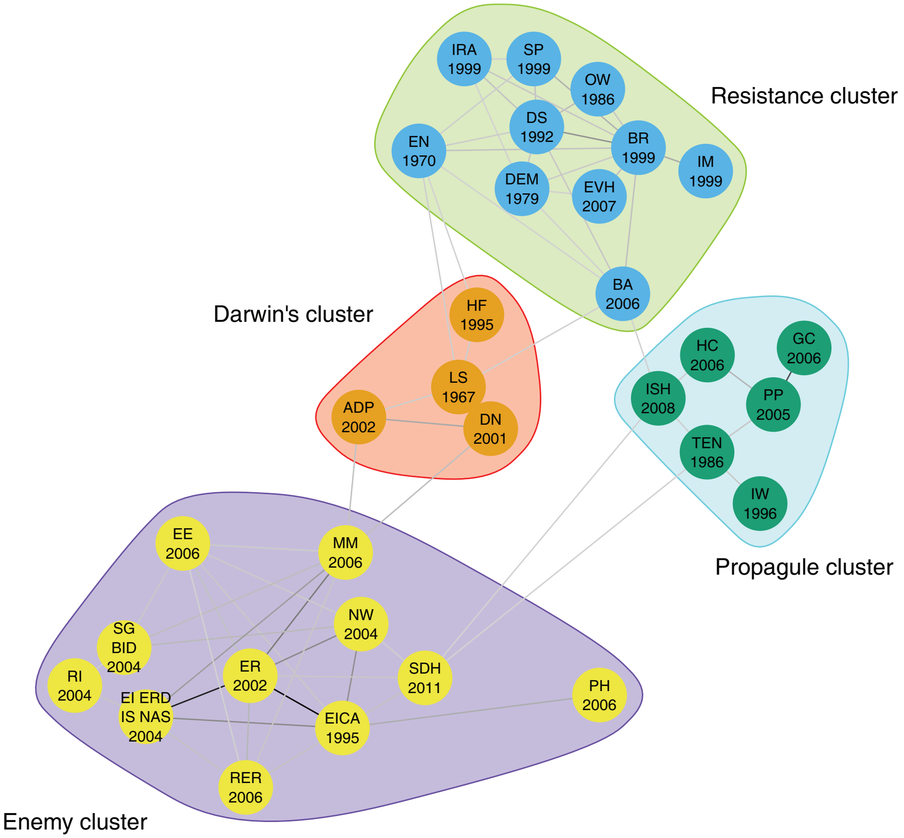

Figure 3. Partition of co-citation network *M* with maximum modularity q = 0.520. Links are weighted with significant co-citation numbers of hypothesis papers (significance level 95%, cf. text). For acronyms of hypotheses see Table 1.

hypotheses were discussed in the literature. We decided to accumulate the data from 1999 to 2017 to get a clearer, cumulative picture of relationships between invasion hypotheses.

We constructed two co-citation networks of our 31 key papers. Network *M* is based on Marshakova (1973) where accepted links are weighted by co-citation numbers (Fig. 3). Following Small and Sweeny (1985) in network *S*, we weighted all links with Salton's cosine and omitted links with a cosine below a threshold of 0.1 (Fig. 4). This threshold was chosen to receive a clearer picture of the graph and to have no unconnected nodes.

We compared the results obtained with different clustering algorithms (Table 2). In both networks, maximum modularity was achieved by a partition with four clusters. The partitions in *M* and *S* differ only in the membership of the plasticity hypothesis (PH), which switches between two clusters. We named the four clusters obtained in both networks by the most prominent principle of their hypotheses (Figs 3, 4; Table 3): *Darwin's cluster*, *resistance cluster*, *propagule cluster* and *enemy cluster*.

Table 2. Partitions of co-citation networks *M* and *S* obtained by different algorithms maximizing modularity.

Algorithm	Number of clusters		Modularity	
	M-network	*S*-network	*M*-network	*S*-network
Cluster_optimal	4	4	0.520	0.463
Fast_greedy	4	4	0.520	0.463
Louvain	4	4	0.520	0.463
Leading_eigen	6	4	0.502	0.441
Edge_betweenness	3	5	0.464	0.428
Walktrap	4	5	0.520	0.430

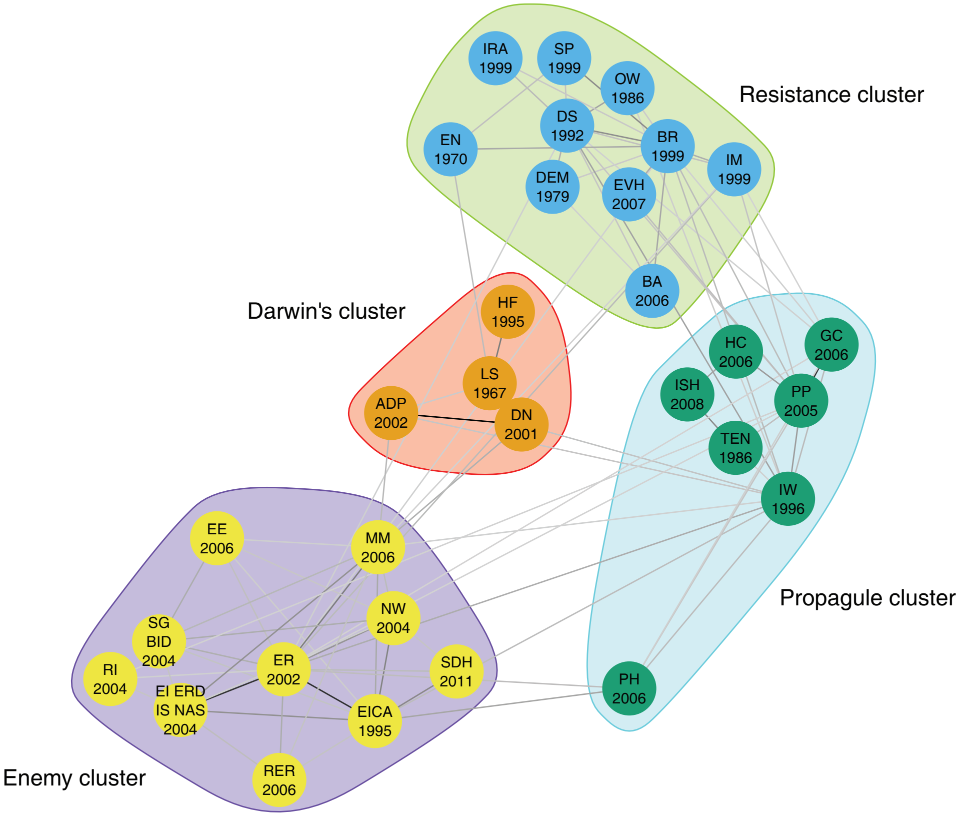

Figure 4. Partition of co-citation network *S* with maximum modularity q = 0.463. Links are weighted with Salton's cosine of co-citation numbers of hypothesis papers above a minimum threshold of 0.1 (cf. text). For acronyms of hypotheses see Table 1.

The plasticity hypothesis (PH) switches between the enemy and the propagule cluster. In the *M*-network, PH has no links to the propagule cluster because the numbers of co-citations with papers of the cluster are not significant on the 95%-level.

The best partition of network *M* has modularity 0.520 (see Fig. 3) and its clusters are communities in the weak *and* strong sense. The best partition of network *S* (Fig. 4) has modularity 0.463 and its clusters are communities in the weak sense, two of them also in the strong sense (*Darwin's* and *enemy* cluster). Since the key papers for IW (ideal weed)

Table 3. Partitions of co-citation networks *M* and *S* with maximum modularity. The key papers (see Table 1 for details) are ranked in their clusters by internal strength. Also, escape probability P_{esc} is displayed for each cluster (cf. Figs 3, 4).

Network *M*		**Network *S***	
Hypothesis-paper	**Internal strength**	**Hypothesis-paper**	**Internal strength**
Darwin´s cluster			
P_{esc}(C) = 0.27		P_{esc}(C) = 0.24	
Adaptation (ADP 2002)	54	Darwin‘s naturalization (DN 2001)	0.77
Darwin‘s naturalization (DN 2001)	53	Adaptation (ADP 2002)	0.76
Limiting similarity (LS 1967)	19	Limiting similarity (LS 1967)	0.57
Habitat filtering (HF 1995)	6	Habitat filtering (HF 1995)	0.32
Niche cluster			
P_{esc}(C) = 0.02		P_{esc}(C) = 0.25	
Biotic resistance (BR 1999)	243	Biotic resistance (BR 1999)	1.75
Disturbance (DS 1992)	163	Disturbance (DS 1992)	1.28
Sampling (SP 1999)	63	Sampling (SP 1999)	0.57
Invasional meltdown (IM 1999)	44	Biotic acceptance (BA 2006)	0.45
Increased resource availability (IRA 1999)	38	Dynamic equilibrium model (DEM 1979)	0.41
Opportunity windows (OW 1986)	37	Empty niche (EN 1970)	0.35
Biotic acceptance (BA 2006)	36	Invasional meltdown (IM 1999)	0.34
Empty niche (EN 1970)	33	Opportunity windows (OW 1986)	0.34
Dynamic equilibrium model (DEM 1979)	31	Increased resource availability (IRA 1999)	0.29
Environmental heterogeneity (EVH 2007)	24	Environmental heterogeneity (EVH 2007)	0.20
Propagule cluster			
P_{esc}(C) = 0.01		P_{esc}(C) = 0.38	
Propagule pressure (PP 2005)	186	Propagule pressure (PP 2005)	1.28
Global competition (GC 2006)	141	Global competition (GC 2006)	0.78
Human commensalism (HC 2006)	38	Ideal weed (IW 1996)	0.66
Tens rule (TEN 1986)	28	Tens rule (TEN 1986)	0.54
Island susceptibility hypothesis (ISH 2008)	11	Island susceptibility hypothesis (ISH 2008)	0.50
Ideal weed (IW1996)	10	Human commensalism (HC 2006)	0.46
		Plasticity hypothesis (PH 2006)	0.40
Enemy cluster			
P_{esc}(C) = 0.02		P_{esc}(C) = 0.14	
Enemy release (ER 2002)	652	Enemy release (ER 2002)	2.41
Evolution of increased competitive ability (EICA 1995)	465	Evolution of increased competitive ability (EICA 1995)	1.98
Enemy inversion, Enemy reduction, Increased susceptibility, New associations	357	Enemy inversion, Enemy reduction, Increased susceptibility, New associations (EI; ERD; IS; NAS 2004)	1.58
Missed mutualism	196	Missed mutualism (MM2006)	1.37
Novel weapons	192	Novel weapons (NW 2004)	1.30
Resource-enemy release (RER 2006)	81	Specialist-generalist, Biotic indirect effects (SG; BID 2004)	1.04
Specialist-generalist, Biotic indirect effects (SG; BID 2004)	67	Enemy of my enemy aka accumulation-of-local-pathogens hypothesis (EE 2006)	0.69
Enemy of my enemy aka accumulation-of-local-pathogens hypothesis (EE 2006)	60	Resource-enemy release (RER 2006)	0.62
Plasticity hypothesis (PH 2006)	41	Shifting defence hypothesis (SDH 2011)	0.58
Shifting defence hypothesis (SDH 2011)	35	Reckless invader aka “boom-bust” (RI 2004)	0.24
Reckless invader aka “boom-bust” (RI 2004)	20		

and IM (invasional meltdown) have stronger external than internal connections, the *niche* and *propagule* cluster do not meet the strong definition here. In general, the centrality of a node in an unweighted graph can be measured by its degree. The analogy in weighted networks is called the *strength* of the node and is defined as the sum of weights of its links. The centrality within a subgraph is then the sum of weights of the node's internal links and can be called its *internal strength* which we use for ranking papers in Table 3.

Discussion

The clusters of networks *M* and *S* are remarkably similar. Two of the four clusters in each network are even identical, namely the concept clusters focused on eco-evolutionary and phylogenetic relationships between non-native and resident species (*Darwin's cluster*) and the concept cluster focused on biotic resistance of ecosystems against non-native species (*resistance cluster)*. Comparing these two networks further, one can see that the other two concept clusters differ just in the membership of PH, the plasticity hypothesis. In one case (*M*-network), PH is in the concept cluster focused on species relationships (*enemy cluster*). In the other case (*S*-network), PH is a member of the concept cluster focused on introduction and species traits (*propagule cluster*).

What are the implications from the networks?

The networks visualize how invasion biologists have seen their research field during the last two decades. Essentially, the networks suggest four broad themes that are represented by the four clusters. One core idea comes from evolutionary biology; it highlights the importance of eco-evolutionary relationships between non-native and resident species, and the capability of species to adapt to new environments (evolutionary perspective, *Darwin's cluster*). A second core idea is the possibility that ecosystems can be resistant, or not, against non-native species based on their characteristics (ecosystem perspective, *resistance cluster*). A third core idea is that species interactions such as host-parasite or predator-prey interactions (including the loss of such interactions in the exotic environment, i.e., enemy release) are very important for understanding biological invasions (species-interactions perspective, *enemy cluster*). Finally, the most recent core idea is that human action is principally influencing biological invasions, which can thus only be understood by studies bridging different research fields (Richardson and Pyšek 2008; Kueffer 2017) (interdisciplinary perspective; *propagule cluster*). Following this line of thought, the discipline of invasion biology is now sometimes called *invasion science*, reflecting that it is not simply a biological subdiscipline but stretches towards other disciplines including social sciences and economics (Richardson and Ricciardi 2013).

Strongly connected hypothesis pairs

Some of the hypotheses in our networks are particularly strongly connected. In this section, we highlight one strongly connected hypothesis pair for each of the four clusters, and outline whether these connections are reasonable.

In *Darwin's cluster*, the two hypotheses adaptation (ADP) and Darwin's naturalization hypothesis (DN) are very strongly connected. The two key publications for these hypotheses included in Table 1 were published at roughly the same time (2001 and 2002). However, DN has its origin in the mid-19th century in what is probably biology's most famous publication of all times (Darwin 1859). As Darwin's book is mainly cited for other reasons than DN, we used another publication as the key paper for DN. The main reason for the strong connection between the hypotheses DN and ADP based on their co-citation in so many papers might be that both hypotheses are contradicting each other (Table 1) and are jointly called *Darwin's naturalization conundrum* (Diez et al. 2008).

In the *resistance cluster*, there is a particularly strong connection between biotic resistance (BR) and the disturbance hypothesis (DS). These two hypotheses are in fact logically linked. According to DS, the invasion success of non-native species is higher in highly disturbed than in relatively undisturbed ecosystems (Table 1). In other terms, highly disturbed ecosystems show lower resistance against non-native species than relatively undisturbed ecosystems. Thus, both hypotheses focus on the resistance of ecosystems against non-native species; BR does so with a focus on biodiversity, and DS with a focus on disturbance (Jeschke and Heger 2018). Another link between the two hypotheses is that disturbance can reduce biodiversity.

In the *propagule cluster*, the propagule pressure hypothesis (PP) is very strongly connected to global competition (GC). The latter hypothesis is actually based on PP (Catford et al. 2009), which explains that these concepts are often jointly cited.

Finally in the *enemy cluster*, the enemy release hypothesis (ER) and EICA hypothesis are particularly strongly connected. This can also be easily explained, as EICA uses enemy release as an underlying assumption (Table 1).

Which network is the better map?

Although the clusters of the two networks are very similar, the better map is in our opinion the *M*-network. This is due to the following two reasons. First, the *M*-network has 25% less edges compared to the *S*-network which results in a clearer picture. Second, the clusters in the *M*-network are better separated from each other than in the *S*-network; all clusters in the *M*-network are communities in the strong sense, but this is only true for two clusters in the *S*-network.

Comparing the network to previous works

In comparison to the other two networks published by Enders and Jeschke (2018) and Enders et al. (2018), the networks of this publication are way clearer. Compared with the similarity-dissimilarity network in Enders et al. (2018), which was created based on an online survey, the *M*- and *S*-networks have fewer connections and clearer, distinct clusters. Apparently, the survey participants had different views on the relationships between invasion hypotheses, possibly because invasion biology has so many hypotheses now that it is hard for researchers to know them all; the similarity-dissimilarity network in Enders et al. (2018) used direct responses given by the survey participants when being asked for hypothesis pairs how similar they are. If participants often simply guessed the similarity of hypothesis pairs, one would expect a random network to emerge from the answers, and this is what Enders et al. (2018) found. This problem was circumvented for two other networks in Enders et al. (2018), joint-mentions networks A and B, which are only based on hypotheses that the survey participants indicated to know best. These networks are clearer than the similarity-dissimilarity network; however, they do not seem to be as useful maps as the networks *M* and *S* presented here. They are not as clear, there clusters have a lower modularity (ca 0.25 for both networks; Enders et al. 2018), and their clusters are not communities in the strong sense.

The network in Enders and Jeschke (2018), which was created by traits of the concepts and hypotheses, has three clusters consisting of concepts with a focus on (i) human interference, (ii) mutualisms, and (iii) enemies (predators or parasites). The modularity is relatively high (ca 0.4) but still lower than for the two networks shown here. Also, the clusters are not communities in the strong sense. This network also seems to be less suitable to serve as a map of the field than the networks shown here, particularly the *M*-network.

Conclusions and outlook

The co-citation approach has proven useful to construct conceptual maps of the field of invasion biology. These maps, particularly the *M*-network, are clearer than previous maps created with other approaches. Efforts to create such conceptual maps that highlight relationships between major concepts within a research field are currently limited. In fact, we are unaware of other attempts to create such maps. This lack of conceptual maps means that researchers lack navigation tools which would help them identify where their work is located within a given research field such as invasion biology. The results of a recent online survey among >350 invasion biologists suggest that the participants lack a "joint vision how invasion hypotheses are related to each other" (Enders et al. 2018). This resembles the situation that invasion biologists lack a common map of the field, which also implies that they do not know where their own work is located in comparison to other studies in the field. The utility of conceptual maps and other navigation tools for research fields thus seems obvious, and it is of course not restricted to invasion biology. Such maps can be provided as interactive visualization tools (https://www.hi-knowledge.org, Jeschke et al. 2018).

But the conceptual maps constructed for this study are early steps on the way towards advanced navigation tools. An important next step would be to allow for concepts and hypotheses to be included in more than one cluster, so that they can take the role of cluster-connecting concepts. To take this next step, a cluster-finding-algorithm that allows overlapping communities should be considered. Furthermore, we have thus far applied three different approaches to create conceptual maps. Other approaches can be imagined as well, for example based on a Delphi-approach in which a group of experts follows multiple iterative steps to create a consensus map. Further work should also involve the expansion of the network to include maps of related fields. In this way, a larger map, or atlas of science (see also Börner 2010, 2015; Kitcher 2011) can be generated that highlights linkages between fields by way of shared broader concepts, such as diversity, stability or the ecological niche (Jeschke 2014). Such a larger atlas of science will undoubtedly foster inter- and transdisciplinary collaboration.

Data accessibility

The R script underlying this study is available via Dryad (https://doi.org/10.5061/dryad.d2q07t6).

Acknowledgements

We thank Felix Mattes for providing an R-script to identify variants of reference strings in the Web of Science. Financial support was provided by the Foundation of German Business (sdw) to ME and the Deutsche Forschungsgemeinschaft (DFG, JE 288/9-2) to JMJ.

References

Amelio A, Pizzuti C (2014) An evolutionary approach for image segmentation. Evolutionary Computation 22: 525–557. https://doi.org/10.1162/EVCO_a_00115

Blondel VD, Guillaume JL, Lambiotte R, Lefebvre E (2008) Fast unfolding of communities in large networks. Journal of Statistical Mechanics-Theory and Experiment 10: 10008. https://doi.org/10.1088/1742-5468/2008/10/P10008

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. Journal of Ecology 83: 887–889. https://doi.org/10.2307/2261425

Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9: 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x

Börner K (2010) Atlas of Science: Visualizing What We Know. MIT Press, Cambridge/Massachusetts.

Börner K (2015) Atlas of knowledge: anyone can map. MIT Press, Cambridge/Massachusetts.

Boyack KW, Klavans R (2010) Co-citation analysis, bibliographic coupling, and direct citation: which citation approach represents the research front most accurately? Journal of the American Society for Information Science and Technology 61: 2389–2404. https://doi.org/10.1002/asi.21419

Brandes U, Delling D, Gaertler M, Gorke R, Hoefer M, Nikoloski Z, Wagner D (2008) On modularity clustering. IEEE Transactions on Knowledge and Data Engineering 20: 172–188. https://doi.org/10.1109/TKDE.2007.190689

Cadotte MW (2006) Darwin to Elton: early ecology and the problem of invasive species. In: Cadotte MW, Mcmahon SM, Fukami TE (Eds) Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature. Springer (Dordrecht): 15–33. https://doi.org/10.1007/1-4020-4925-0_2

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2: 436–443. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731–733. https://doi.org/10.1038/nature02322

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15: 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Clauset A, Newman MEJ, Moore C (2004) Finding community structure in very large networks. Physical Review E 70: 066111. https://doi.org/10.1103/PhysRevE.70.066111

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023–1037. https://doi.org/10.1007/s10530-006-9007-7

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721–733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Crawley MJ, Brown SL, Heard MS, Edwards GR (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters 2: 140–148. https://doi.org/10.1046/j.1461-0248.1999.00056.x

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal Complex Systems 1695. http://igraph.org

Daehler CC (2001) Darwin's naturalization hypothesis revisited. American Naturalist 158: 324–330. https://doi.org/10.1086/321316

Darwin C (1859) On the Origin of Species by Means of Natural Selection. Murray (London).

de Solla Price DJ (1965) Networks of scientific papers. Science 149: 510–515. https://doi.org/10.1126/science.149.3683.510

Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters 11: 674–681. https://doi.org/10.1111/j.1461-0248.2008.01178.x

Doorduin LJ, Vrieling K (2011) A review of the phytochemical support for the shifting defence hypothesis. Phytochemistry Reviews 10: 99–106. https://doi.org/10.1007/s11101-010-9195-8

Duncan RP, Williams PA (2002) Darwin's naturalization hypothesis challenged. Nature 417: 608–609. https://doi.org/10.1038/417608a

Egghe L, Leydesdorff L (2009) The relation between Pearson's correlation coefficient *r* and Salton's cosine measure. Journal of the American Society for Information Science and Technology 60: 1027–1036. https://doi.org/10.1002/asi.21009

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen (London). https://doi.org/10.1007/978-1-4899-7214-9

Enders M, Jeschke JM (2018) A network of invasion hypotheses. In: Jeschke JM, Heger T (Eds) Invasion Biology: Hypotheses and Evidence. CABI, Wallingford, 49–59. https://doi.org/10.1079/9781780647647.0049

Enders M, Hütt M-T, Jeschke JM (2018) Drawing a map of invasion biology based on a network of hypotheses. Ecosphere 9: e02146. https://doi.org/10.1002/ecs2.2146

Eppinga MB, Rietkerk M, Dekker S, De Ruiter PC, Van der Putten WH (2006) Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114: 168–176. https://doi.org/10.1111/j.2006.0030-1299.14625.x

Fortunato S (2010) Community detection in graphs. Physics Reports-Review Section of Physics Letters 486: 75–174. https://doi.org/10.1016/j.physrep.2009.11.002

Girvan M, Newman MEJ (2002) Community structure in social and biological networks. Proceedings of the National Academy of Sciences of the United States of America 99: 7821–7826. https://doi.org/10.1073/pnas.122653799

Glänzel W, Thijs B (2017) Using hybrid methods and 'core documents' for the representation of clusters and topics: the astronomy dataset. Scientometrics 111: 1071–1087. https://doi.org/10.1007/s11192-017-2301-6

Gläser J, Glänzel W, Scharnhorst A (2017) Same data – different results? Towards a comparative approach to the identification of thematic structures in science. Scientometrics 111: 981–998. https://doi.org/10.1007/s11192-017-2296-z

Glenisson P, Glanzel W, Persson O (2005) Combining full-text analysis and bibliometric indicators: a pilot study. Scientometrics 63: 163–180. https://doi.org/10.1007/s11192-005-0208-0

Gmür M (2003) Co-citation analysis and the search for invisible colleges: a methodological evaluation. Scientometrics 57: 27–57. https://doi.org/10.1023/A:1023619503005

Hamers L, Hemeryck Y, Herweyers G, Janssen M, Kettrs H, Rousseau R, Vanhoutte A (1989) Similarity measures in scientometric research: the Jaccard index versus Salton's cosine formula. Information Processing & Management 25: 315–318. https://doi.org/10.1016/0306-4573(89)90048-4

Handcock MS, Hunter DR, Butts CT, Goodreau SM, Morris M (2003) Statnet: Software tools for the Statistical Modeling of Network Data. http://statnetproject.org

Havemann F (2016) Einführung in die Bibliometrie. Gesellschaft für Wissenschaftsforschung, Berlin.

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion – implications for conservation. Conservation Biology 6: 324–337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x

Huston M (1979) A general hypothesis of species diversity. American Naturalist 113: 81–101. https://doi.org/10.1086/283366

Jeschke JM (2008) Across islands and continents, mammals are more successful invaders than birds. Diversity and Distributions 14: 913–916. https://doi.org/10.1111/j.1472-4642.2008.00488.x

Jeschke JM (2014) General hypotheses in invasion ecology. Diversity and Distributions 20: 1229–1234. https://doi.org/10.1111/ddi.12258

Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. Global Change Biology 12: 1608–1619. https://doi.org/10.1111/j.1365-2486.2006.01213.x

Jeschke, JM, Heger T (2018) Invasion biology: hypotheses and evidence. CABI,Wallingford. https://doi.org/10.1079/9781780647647.0000

Jeschke JM, Keesing F, Ostfeld RS (2013) Novel organisms: comparing invasive species, GMOs, and emerging pathogens. Ambio 42: 541–548. https://doi.org/10.1007/s13280-013-0387-5

Jeschke JM, Enders M, Bagni M, Jeschke P, Zimmermann M, Heger T (2018) Hi-Knowledge.org. https://hi-knowledge.org [accessed 6 May 2019]

Johnstone IM (1986) Plant invasion windows – a time-based classification of invasion potential. Biological Reviews 61: 369–394. https://doi.org/10.1111/j.1469-185X.1986.tb00659.x

Jonas H (1979) Das Prinzip Verantwortung: Versuch einer Ethik für die technologische Zivilisation. Insel Verlag, Frankfurt am Main.

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Kitcher P (2011) Science in a democratic society. Prometheus (Amherst/NY).

Kowarik I, Pysek P (2012) The first steps towards unifying concepts in invasion ecology were made one hundred years ago: revisiting the work of the Swiss botanist Albert Thellung. Diversity and Distributions 18: 1243–1252. https://doi.org/10.1111/ddi.12009

Kueffer C (2017) Plant invasions in the Anthropocene. Science 358: 724–725. https://doi.org/10.1126/science.aao6371

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15–26. https://doi.org/10.2307/3546992

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223–228. https://doi.org/10.1016/j.tree.2005.02.004

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3: 1835–1835. https://doi.org/10.1002/ece3.431

MacArthur R (1970) Species packing and competitive equilibrium for many species. Theoretical Population Biology 1: 1–11. https://doi.org/10.1016/0040-5809(70)90039-0

MacArthur R, Levins R (1967) Limiting similarity convergence and divergence of coexisting species. American Naturalist 101: 377–385. https://doi.org/10.1086/282505

Marbach-Ad G, Schaefer KL, Kumi BC, Friedman LA, Thompson KV and Doyle MP (2012) Development and evaluation of a prep course for chemistry graduate teaching assistants at a research university. Journal of Chemical Education 89: 865–872. https://doi.org/10.1021/ed200563b

Marshakova IV (1973) System of document connections based on references. Nauchno-Tekhnicheskaya Informatsiya Seriya 2 – Informatsionnye Protsessy i Sistemy 6: 5.

Meadows DH, Club of Rome and Project on the predicament of mankind (1972) The Limits to Growth a Report for the Club of Rome's Project on the Predicament of Mankind. Universe Books, New York. https://doi.org/10.1349/ddlp.1

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10: 77–94. https://doi.org/10.1111/j.1461-0248.2006.00987.x

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecology Letters 9: 726–740. https://doi.org/10.1111/j.1461-0248.2006.00908.x

Newman MEJ (2006) Modularity and community structure in networks. Proceedings of the National Academy of Sciences of the United States of America 103: 8577–8582. https://doi.org/10.1073/pnas.0601602103

Newman, MEJ, Girvan M (2004) Finding and evaluating community structure in networks. Physical Review E 69: 026113. https://doi.org/10.1103/PhysRevE.69.026113

Pons P, Latapy M (2005) Computing communities in large networks using random walks. Computer and Information Sciences – Iscis 2005 Proceedings 3733: 284–293. https://doi.org/10.1007/11569596_31

Radicchi F, Castellano C, Cecconi F, Loreto V, Parisi D (2004) Defining and identifying communities in networks. Proceedings of the National Academy of Sciences of the United States of America 101: 2658–2663. https://doi.org/10.1073/pnas.0400054101

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655–1661. https://doi.org/10.2307/2265768

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Richardson DM, Pyšek P (2008) Fifty years of invasion ecology – the legacy of Charles Elton. Diversity and Distributions 14: 161–168. https://doi.org/10.2307/2997649

Richardson DM, Ricciardi A (2013) Misleading criticisms of invasion science: a field guide. Diversity and Distributions 19: 1461–1467. https://doi.org/10.1111/ddi.12150

Sher AA, Hyatt LA (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. Biological Invasions 1: 107–114. https://doi.org/10.1023/A:1010050420466

Simberloff D, Van Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21–32. https://doi.org/10.1023/A:1010086329619

Simberloff D, Gibbons L (2004) Now you see them, now you don't – population crashes of established introduced species. Biological Invasions 6: 161–172. https://doi.org/10.1023/B:BINV.0000022133.49752.46

Small H (1973) Cocitation in the scientific literature: a new measure of the relationship between two documents. Journal of the American Society for Information Science 24: 265–269. https://doi.org/10.1002/asi.4630240406

Small H, Sweeney E (1985) Clustering the *science citation index* using co-citations. 1. A comparison of methods. Scientometrics 7: 391–409. https://doi.org/10.1007/BF02017157

Stohlgren TJ, Jarnevitch C, Chong GW (2006) Scale and plant invasions: a theory of biotic acceptance. Preslia 78: 405–426.

Trujillo CM, Long TM (2018) Document co-citation analysis to enhance transdisciplinary research. Science Advances 4: e1701130. https://doi.org/10.1126/sciadv.1701130

Vaz AS, Kueffer C, Kull CA, Richardson DM, Schindler S, Munoz-Pajares AJ, Vicente JR, Martins J, Hui C, Kuhn I, Honrado JP (2017) The progress of interdisciplinarity in invasion science. Ambio 46: 428–442. https://doi.org/10.1007/s13280-017-0897-7

Velden T, Boyack KW, Gläser J, Koopman R, Scharnhorst A,Wang SH (2017) Comparison of topic extraction approaches and their results. Scientometrics 111: 1169–1221. https://doi.org/10.1007/s11192-017-2306-1

Weiher E, Keddy PA (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74: 159–164. https://doi.org/10.2307/3545686

Williamson MH, Brown KC (1986) The analysis and modeling of British invasions. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 314: 505–522. https://doi.org/10.1098/rstb.1986.0070

Xie JR, Kelley S, Szymanski BK (2013) Overlapping community detection in networks: The state-of-the-art and comparative study. ACM Computing Surveys 45. https://doi.org/10.1145/2501654.2501657

Yau CK, Porter A, Newman N, Suominen A (2014) Clustering scientific documents with topic modeling. Scientometrics 100: 767–786. https://doi.org/10.1007/s11192-014-1321-8

5. A conceptual map of invasion biology

This paper was a collaboration 29 co-authors (see below) and was submitted to Global Ecology and Biogeography.

A conceptual map of invasion biology: integrating hypotheses into a consensus network

Running head: Consensus map of invasion biology

Martin Enders[a,b,c], Frank Havemann[d], Florian Ruland[a,b,c], Maud Bernard-Verdier[a,b,c], Jane A. Catford[e], Lorena Gómez-Aparicio[f], Sylvia Haider[g,h], Tina Heger[c,i,j], Christoph Kueffer[k,l], Ingolf Kühn[m,n,o], Laura A. Meyerson[p], Camille Musseau[a,b,c], Ana Novoa[q], Anthony Ricciardi[r,l], Alban Sagouis[a,b,c], Conrad Schittko[c,i], David L. Strayer[s], Montserrat Vilà[t], Franz Essl[u,v], Philip E. Hulme[w], Mark van Kleunen[x,y], Sabrina Kumschick[l,z], Julie L. Lockwood[aa], Abigail L. Mabey[bb], Melodie McGeoch[cc], Estíbaliz Palma[dd], Petr Pyšek[q,ee], Wolf-Christian Saul[l,v], Florencia A. Yannelli[l] and Jonathan M. Jeschke[a,b,c]

[a]Freie Universität Berlin, Department of Biology, Chemistry, Pharmacy, Institute of Biology, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

[b]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587 Berlin, Germany

[c]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, 14195 Berlin, Germany

[d]Humboldt-Universität zu Berlin, Philosophische Fakultät, Institut für Bibliotheks- und Informationswissenschaft, Dorotheenstr. 26, 10099 Berlin, Germany

[e]Department of Geography, King’s College London, London, WC2B 4BG, UK

[f]Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, LINCGlobal, Av. Reina Mercedes 10, 41012, Sevilla, Spain

[g]Martin Luther University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle (Saale), Germany

[h]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[i]University of Potsdam, Biodiversity Research / Botany, Maulbeerallee 2a, 14469 Potsdam, Germany

[j]Technical University of Munich, Restoration Ecology, Freising, Germany

[k]Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 16, CH-8092 Zurich, Switzerland

[l]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

[m]Helmholtz Centre for Environmental Research – UFZ, Dept. Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle (Saale), Germany

[n]Martin Luther University Halle-Wittenberg, Institute of Biology/Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle (Saale), Germany

[o]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[p]The University of Rhode Island, Department of Natural Resources Science, Kingston, RI 02881, USA

[q] Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-252 43 Průhonice, Czech Republic

[r]Redpath Museum, McGill University, Montreal, Quebec H3A 0C4, Canada

[s]Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA; Graham Sustainability Institute, University of Michigan, Ann Arbor, MI 48104, USA

[t]Estación Biológica de Doñana (EBD-CSIC), Av. Américo Vespucio 26, 41092, Sevilla, Spain.

[u]Department of Botany and Biodiversity Research, University Vienna, Rennweg 14, 1030 Vienna, Austria

[v]Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Matieland 7602, South Africa

[w]Bio-Protection Research Centre, Lincoln University, Lincoln, Canterbury 7647, New Zealand

[x]Ecology, Department of Biology, University of Konstanz, Universitätsstrasse 10, D-78457 Konstanz, Germany

[y]Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China

[z]South African National Biodiversity Institute, Kirstenbosch National Botanical Gardens, Claremont 7735, South Africa

[aa]Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, New Jersey, 08901, USA

[bb]Ocean and Earth Science, National Oceanography Centre, University of Southampton, European Way, Southampton, SO14 3ZH, UK

[cc]School of Biological Sciences, Monash University, Clayton 3800, Victoria, Australia

[dd]School of BioSciences, The University of Melbourne, Parkville 3010 VIC, Australia

[ee]Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic

Paper type: Concept

Abstract

Background and Aims

Since its emergence in the mid-20th century, invasion biology has matured into a productive research field addressing questions of fundamental and applied importance. Not only has the number of empirical studies increased through time, but so has the number of competing, overlapping and, in some cases, contradictory hypotheses about biological invasions. To make these contradictions and redundancies explicit, and to gain insight into the field's current theoretical structure, we applied a Delphi approach to create a consensus network of 39 existing invasion hypotheses.

Results

The resulting network was analyzed with a link-clustering algorithm that revealed five *concept clusters* (Resource availability, Biotic interaction, Propagule, Trait, and Darwin's cluster) representing complementary areas in the theory of invasion biology. The network also displays hypotheses that link two or more clusters, called *connecting hypotheses,* which are important in determining network structure. The network indicates hypotheses that are logically linked either positively (77 connections of support) or negatively (that is, they contradict each other; 6 connections).

Significance

The network visually synthesizes how invasion biology's predominant hypotheses are conceptually related to each other and thus reveals an emergent structure – a *conceptual map* – that can serve as a navigation tool for scholars, practitioners and students, both inside and outside of the field of invasion biology, and guide the development of a more coherent foundation of theory. Additionally, the outlined approach can be more widely applied to create a conceptual map for the larger fields of ecology and biogeography.

Keywords: biological invasions, concepts, consensus map, Delphi method, invasion science, invasion theory, navigation tools, network analysis

Introduction

The first author’s grandfather was a master electrician working for the city of Munich, Germany, whose daily work consisted of repairing streetlights and other electrical devices for public use. One of his most impressive skills was his ability to intimately recall the details of every place in his district. By combining his knowledge with that of co-workers familiar with other districts, one could have created a complete map of the city that would allow anyone to confidently navigate its streets. In many ways a research field is quite similar to a city where its major questions and hypotheses represent subunits comparable to city districts. Such subunits can be represented on a map, whether of a city or a research field, the latter allowing scientists inside and outside of the field to better orient themselves and navigate their own research interests. Such a map would also be useful for students, teachers, policy-makers and managers, as it would allow them to efficiently identify the elements of science most pertinent to their interests and goals.

Some previous conceptual maps of science take the form of networks, and cover multiple disciplines; that is, they chart science as a whole and show how different disciplines relate to each other (Börner, 2010, 2015). These maps usually do not focus on the theory of any one discipline and thus do not represent the myriads of hypotheses and concepts of each research field. Given that concepts and hypotheses form the backbone of scientific inquiry, we posit that it is useful to simultaneously create conceptual maps within research disciplines to visualize the relationships among key hypotheses (Jeschke, 2014). Consensus maps identify the degree to which hypotheses are similar, competing or contradictory, and use this information to aggregate them into broader clusters.

Consensus maps in the form of networks can be particularly useful for disciplines with many hypotheses, where even researchers within the field tend to be restricted to specific research silos and thereby increasingly unaware of similar hypotheses in the field. An example for such a discipline is invasion biology. Since the emergence of the field with the publication of Charles Elton’s book in 1958 and sustained research programs developed in the 1990s (Richardson & Pyšek, 2008), it has accumulated an impressive number of hypotheses and concepts until today (summarized in e.g. Catford et al. (2009); Jeschke & Heger (2018); Schulz et al. (2019)). A recent online survey indicated that many invasion biologists appear to be knowledgeable about hypotheses and concepts they are directly working with, but do not demonstrate a consistent understanding of the relationship among these and other concepts in the field (Enders et al., 2018). A network of concepts, representing a conceptual map of invasion biology, would thus provide much-needed orientation and navigation. Because maps can take the form of networks, we use both terms in a similar way: *network* is the more technical term and better describes how the map is methodologically constructed, whereas the term *map* focuses on the purpose as a navigation tool.

Several approaches have previously been used to visualize a network of invasion hypotheses, though they have some limitations. These attempts build on past work that highlighted commonalities among invasion hypotheses, though did not visualize them (Catford et al., 2009). First, Enders et al. (2018) created a network by asking researchers which hypotheses they knew best. This approach assumes that if many researchers state that they know a given pair of hypotheses very well, these hypotheses probably have something in common, and can thus be connected in a network. This is a “black box” approach, as it is unclear why researchers often know a certain pair of hypotheses well and what this connection means.

Second, Enders & Jeschke (2018) assessed the conceptual similarity of hypotheses by classifying which factors are highlighted as most important for the invasion success of non-native species. The resulting table characterizing the hypotheses (based on 7) was then used to create a network showing conceptual overlaps. A weakness of this approach is that the classification was based on the assessments of very few experts, namely the authors of Catford et al. 2009 (n = 3) and Enders and Jeschke 2018 (n = 2).

Finally, Enders et al. (2019) applied a bibliometric approach to create a network of invasion hypotheses. In their network, two hypotheses are connected if key publications featuring these hypotheses are frequently cited together. Co-citation analysis was recently also applied by Trujillo and Long (2018) who created a sequence of nested co-citation networks (these are not hypothesis networks, though). The application of co-citation analysis for creating hypothesis networks has three main limitations: (i) a publication may be cited for reasons other than the hypothesis that it refers to; (ii) it is not possible to discriminate among hypotheses that support one another and those that contradict one another; and (iii) especially in large, complex fields, research areas that are logically connected are not always bibliographically connected (Swanson, 1986).

To overcome the limitations of these approaches, we here present a novel consensus approach based on the Delphi method to create a network of invasion hypotheses that capitalizes on the expertise of a group of invasion biologists who work on different topics and various taxonomic groups and habitats. The approach can be generally applied to any research field, thus invasion biology is used as a case example here. In a Delphi method, the opinions of a group of experts converge towards a consensus in several steps during which the experts revise their opinion based on an anonymized summary of all experts' opinions (Häder & Häder, 2000). In the resulting consensus network, we identified hypothesis clusters by applying a state-of-the-art link-clustering algorithm.

Methods

Consensus approach

Our approach to creating a consensus network of invasion hypotheses consists of nine steps (Steps 4 to 8 represent the Delphi approach; Figure 1). In Step 1, a group of 29 experts in invasion biology were assembled to ensure a breadth of experience, wide taxonomic knowledge and geographic scope. Given the high level of expertise needed for the task, of the 29 experts, 15 were senior scientists (52%), 10 postdocs or on a similar level (34%), and four were PhD students (14%). Gender representation was roughly equal with 14 male (48%) and 15 female (52%) group members. Of the 29 experts, 19 were based in Europe (66%), four in North America (14%), three in Africa (10%) and three in Australasia (10%). Eighteen of these 29 invasion biologists plus Frank Havemann, an expert on network analysis, met in Berlin on 12–13th February 2018. The European location of the meeting (and associated logistical constraints) resulted in the over-representation of European researchers. Follow-up communications with all participants were done via e-mail.

In Step 2, the moderators (ME, FR and JMJ) compiled a list of 39 hypotheses and concepts related to the invasion stages of introduction, establishment and spread, with reference to the respective original publication author/s and year (Table 1). This list, which expanded the 33 hypotheses listed by Enders et al. (2018) by six additional hypotheses considered to be influential by the experts, is to our knowledge the most extensive list of invasion hypotheses compiled to date.

In Step 3, we asked the experts to build their own version of the network. Each of the 29 experts was given the option of following one of two approaches: (a) to draw a network of the 39 hypotheses, with similar hypotheses connected by a black line, contradictory hypotheses connected by a red line, and other hypotheses (which are not logically linked) unconnected; or (b) to assess the similarity of hypotheses in a matrix by giving a value of 1 for a pair of similar hypotheses, a value of −1 for contradictory hypotheses, and 0 for hypotheses that are not logically linked, not even in a contradictory way. Hypothesis pairs could be left aside and indicated with 'NA' if an expert felt uncomfortable making a decision about the similarity of these hypotheses. However, this option was rarely chosen by the participants (0.53%). Each expert then individually sent their network or matrix to the moderators.

A key aspect of Step 3 is that researchers may have a different interpretation of the terms "similar" and "contradictory". We collectively agreed that both terms mean two hypotheses are logically linked; we call them "similar" if they are positively linked, and "contradictory" if they are negatively linked. Beyond this definition, participants were free to decide what a "logical link" means. This freedom allowed us to capture the diverse backgrounds and perspectives of individuals in the group. Most participants evaluated a logical link primarily based on the ecological mechanisms described in the hypotheses (e.g. hypotheses are logically linked if they both consider a certain type of biotic interaction), whereas some respondents included the level of organization (genotype, individual, population, community) or the indirect effects of an invasion in their link evaluation. Others considered which hypothesis gave rise to, or were cited by, another hypothesis; or to which degree the knowledge of one hypothesis substantially informs our understanding of another (e.g. understanding the enemy release hypothesis can be seen as fundamental for understanding the enemy reduction hypothesis), especially if the outcomes of both hypotheses go in the same direction (e.g. lack of enemies increases invasion success).

In Step 4, the moderators received the individual assessments and calculated the percentage of respondents who indicated hypotheses that are logically linked either positively (+1, i.e. similar hypotheses) or negatively (-1, i.e. contradictory hypotheses). For this calculation, NA scores were excluded. For example, given the entries for a hypothesis pair are: 0, 0, 1, −1, 1, −1, NA, 0, 1,1, NA, 1, the percentage of +1 or −1 values compared to zeros for this response set would be 7/10 = 0.7 (2×NA, 3×0, 5×1, 2×−1). We then determined the sign of the connection (positive or negative) based on the majority of individual entries. In the example before, there are 5 entries with +1 and 2 entries with −1, thus the overall sign of the connection is positive. The overall score for this hypothesis pair would thus be +0.7. We never found that the number of negative and positive signs were the same; in such a case, we would have asked the experts to re-assess the connection. The final action in Step 4 was to discriminate (i) hypothesis pairs for which most participants agreed that the hypotheses are either similar (overall value >0.65), contradictory (<−0.65) or not logically linked (value between −0.35 and 0.35) from (ii) hypothesis pairs for which the entries were inconclusive (value close to ±0.5: between −0.65 and −0.35, or between 0.35 and 0.65). The value of ±0.65 as a decision rule was set by the group.

In Step 5, all participants were asked to re-inspect hypothesis pairs with inconclusive entries (that was the case for 52 hypothesis pairs) and to individually send their revised network or matrix to the moderators.

In Step 6, the moderators calculated an overall hypothesis network based on the links among hypotheses, using the R statistical environment version 3.1.0 (R core development Team 2018) and packages ‘sna’ (Handcock et al., 2003), ‘reshape2’ (Wickham, 2007) and ‘igraph’ (Csardi & Nepusz, 2006) (see below for details) and shared it with all participants.

In Step 7, the participants inspected the overall network, and those who disagreed with any element explained their reason for this disagreement by sending an individual e-mail to the moderators who then shared the collected and anonymized feedback with the group.

In Step 8, participants inspected their assessments again based on this feedback and sent their final network or matrix to the moderators if any changes were made. All individual networks are provided in Table S1.

In Step 9, the moderators calculated final values for the link between each pair of hypotheses (Table S1) and constructed the final hypothesis network.

Clustering approach

To reveal the inner structure of a network, it is helpful to group the nodes (in our case: the hypotheses) of the network into clusters. A common way of doing so is node clustering, for which various algorithms exist (Fortunato, 2010). We applied four established node-clustering algorithms which, however, led to different network clusters (see Appendix, Figure S1). These inconsistencies were largely due to the fact that some hypotheses did not seem to be part of any single cluster, but were instead bridging clusters. We therefore decided to apply a link-clustering method instead (Ahn et al., 2010; Evans & Lambiotte, 2009), an approach that allows for nodes to be members of multiple clusters. Link clustering is thus more flexible than node clustering where each node can only be in one cluster (see the Appendix for details).

Clusters of links induce node communities whereby the membership grade of each node to community L is given by the portion of its internal links $\frac{k_i^{in}(L)}{k_i}$ (see below for details). Because we assumed that pairs of similar hypotheses identified in one region of the network are independent of hypothesis pairs in other regions, we chose a local approach to link clustering, where each link set L is evaluated independently from the rest of the network . Local link clustering allows for communities not only to overlap in boundary nodes but also in inner nodes. One measure for evaluating link clusters is the escape probability of the link-node-link random walker. This random walker — introduced by Evans & Lambiotte — is the translation of the ordinary random walker into the world of link clustering. The walker starts from a link, goes randomly to one of its nodes, and then to one of the links of this node. If the escape probability is low, then L is a link set that is well separated from the rest of the network (Havemann et al., 2017). The escape probability of a link-node-link random walker is given by:

$$P_{esc}(L) = \frac{\sigma(L)}{k_{in}(L)} \qquad \text{(eq. 1)}$$

with

$$\sigma(L) = \sum_{i=1}^{n} \frac{k_i^{in}(L) k_i^{out}(L)}{k_i} \qquad \text{(eq. 2)}$$

and

$$k_{in}(L) = \sum_{i=1}^{n} k_i^{in}(L) \qquad \text{(eq. 3)}$$

(Havemann et al., 2017); $k_i^{in}(L)$ and $k_i^{out}(L)$ are the internal and external degrees of node i with respect to link set L. Their sum is the node's total degree

$$k_i = k_i^{in}(L) + k_i^{out}(L) \qquad \text{(eq. 4).}$$

Since our hypothesis network is small, and the disjoint clusters are already very suggestive, we were able to avoid the random components in the evolutionary approach of Havemann et al. (2017) and only made local searches in the cost landscape of P_{esc} starting from the five disjoint clusters as seed link sets. Local searches go on the steepest path to the next local minimum in the cost landscape. In each step of a local search, we added this link to the set that resulted in the minimum cost. After reaching a local minimum, we continued the search, because cost landscapes are rough, and we did not want to get trapped in a local minimum that is only a few steps away from a deeper one. After expanding link sets, we excluded links until we found the final hypothesis clusters with the lowest escape probability. Further information on this approach is provided in Havemann et al. (2017).

Results

The resulting consensus network included (a) five clusters covering 32 of the 39 hypotheses, (b) six *connecting hypotheses* acting as bridges between clusters (human commensalism, HC, connecting three clusters; and resource-enemy release, RER, increased resource availability, IRA, reckless invader, RI, biotic indirect effects, BID, and empty niche, EN, each connecting two clusters) and (c) one hypothesis not connected with any other hypothesis in the network (increased susceptibility, IS, with the closest connection with polyploidy hypothesis, PO; link = 0.48; Table S1) (Fig. 2).

We named the five clusters the (i) “Biotic interaction cluster” accounting for 9 full-member hypotheses (i.e. without connecting hypotheses), (ii) “Darwin’s cluster” (7 full-member hypotheses), (iii) “Trait cluster” (6 full-member hypotheses) (iv) “Propagule cluster” (6 full-member hypotheses) and (v) “Resource availability cluster” (4 full-member hypotheses) (Fig. 2). The Trait cluster is actually nested in Darwin’s cluster (cf. Fig. S2), hence one could also consider Darwin’s cluster to include 13 full-member hypotheses that are further separated into two sub-clusters. For simplicity, though, and because none of the other clusters include sub-clusters, we do not usually discriminate between first- and second-level clusters here.

Discussion

Hypothesis clusters

Each of the five clusters we identified encapsulates a main explanation for the invasion success of non-native species. The commonality among the hypotheses in the Biotic interaction cluster is the role of interspecific (mostly negative) interactions in species invasion success. Most hypotheses in this cluster assume that natural enemies (i.e. predators, herbivores, parasites and pathogens) control species populations, so when a species is introduced to a new area, populations thrive because enemies are left behind. Similarly, Schulz et al. (2019) recently offered a framework of hypotheses focusing on how enemies/antagonists affect invasion success. The lack of specific enemies in the recipient location gives an advantage to non-native over native species (enemy release, ER) despite generalist enemies also reducing their success. Some hypotheses in this cluster posit that enemy release allows non-native individuals to reallocate resources from defenses against natural enemies towards growth, fitness and competitive ability (evolution of increased competitive ability, EICA; shifting defense hypothesis, SDH). Mutualistic interactions with native species (e.g. pollinators, seed dispersers, mycorrhiza) also increase invasion success (Richardson et al., 2000), whereas interspecific competition with the native species (reckless invader, RI) or a lack of mutualists (i.e. those missing compared to the invader's home range) impede it (missed mutualism, MM).

The hypotheses in the Resource availability cluster associate invasion success with invader access to resources, which is affected by abiotic and biotic conditions and their interaction (Catford et al. 2009 and references therein). The first three hypotheses (increased resource availability, IRA; disturbance, DS; opportunity windows, OW) center on temporary increases in resource availability, which can result from a decline in resource uptake in the community and/or an increase in supply. Increased resource availability (IRA) and disturbance (DS) focus on fluctuations through time, whereas opportunity-windows (OW) considers fluctuations in both space and time. High resource availability, even if only temporary, enables invader populations to become established, from which point they can continue to grow and spread. The dynamic equilibrium model (DEM) centers on interactions between disturbance and productivity, which collectively affect resource availability and strength of resource competition, and thus opportunities for invasion. While the underlying mechanism is arguably the same (sufficient resource availability), environmental heterogeneity (EVH) is phenomenological and pattern-based, unlike the first four process-based hypotheses. EVH essentially attributes invasion success to incomplete resource uptake by the resident community. This is because communities in ecosystems with high environmental heterogeneity are less likely to be saturated, such that associated resources remain unused (or under-used). These available resources provide ripe opportunities for (effectively competition-free) invasion by species having the appropriate niche. Environmental heterogeneity (EVH) is strongly linked with the empty niche hypothesis (EN; which follows Elton's rather than Hutchinson's niche concept, cf. Pulliam (Pulliam, 2000)), a connecting concept between the Resource availability cluster and Darwin's cluster (Fig. 2).

Many of the hypotheses in Darwin's cluster have an eco-evolutionary perspective on biological invasions, which highlights the importance of the species' evolutionary legacy in shaping the outcome of biotic interactions that result from species introductions. This is true for the ecological imbalance (EIM) hypothesis which focuses on the evolutionary characteristics of both the recipient region and potential donor regions. Another example is ecological naivety (ENA), which is also known as evolutionary naivety. Ecological niches are shaped evolutionarily, and many hypotheses in this cluster are related to species' niches, either that of the non-native species arriving in an ecosystem or that of the species assemblage composing the native community. Indeed, several of these hypotheses propose that non-native species could only establish and potentially become invasive if they can occupy niches different from those of the native species, a theoretical concept developed by Shea and Chesson (Shea & Chesson, 2002). In practice, niche similarity or divergence has been characterized by species' functional traits, given their link to resource acquisition, evolutionary fitness and ecosystem processes (Divíšek et al., 2018; Vidal-Garcia & Keogh, 2017; Wang et al., 2018), or by species relatedness, assuming that species niches are conserved in phylogenies (Prinzing et al., 2001; Thuiller et al., 2010). In other words, invasion success and impacts are, according to these hypotheses, related to dissimilarities in the non-native species characteristics with respect to the recipient community and thus, associated with their resource use in the new environment. Furthermore, the relation between species evolution, niche space and species traits explains why we found the Trait cluster to be nested in Darwin's cluster.

The Trait cluster includes six hypotheses related to how traits differ between successful and unsuccessful non-native species. This is a topic of long-standing interest within invasion biology, from its very onset, as it is thought that certain species traits are associated with invasiveness (H.G. Baker, 1974 ; Capellini et al., 2015; Mahoney et al., 2015; Pyšek & Richardson, 2007; van Kleunen et al., 2010). The hypotheses included within this cluster consider traits that can help non-native species to generally become invasive (ideal weed, IW), to compete with native species (novel weapons, NW), or to adapt to the novel conditions found in their introduced ranges (also in the cluster is adaption, ADP; polyploidy hypothesis, PO; plasticity hypothesis, PH; habitat filtering, HF).

Finally, the hypotheses in the Propagule cluster relate the numbers of introduced non-native species or individuals to the probability that they will establish self-sustaining populations or expand their geographical ranges in the invaded region. The propagule pressure hypothesis (PP) operates at the population level and suggests that the likelihood of a non-native population being able to establish increases with the number of individuals of that species being introduced. Several potential mechanisms underpin the propagule pressure hypothesis, all of which invoke the ability of larger numbers of individuals to overcome random, stochastic forces to ensure population persistence. The other five hypotheses operate at the community level and suggest that greater numbers of species are likely to establish and spread if greater numbers of species are introduced (colonization pressure, CP, (Lockwood et al., 2005). Similar to the propagule pressure hypothesis, these hypotheses assume that the chance of some species experiencing favorable ecological conditions increases with greater numbers of species introductions.

Connecting hypotheses

While clusters of hypotheses can reflect fertile areas of similar research questions, *connecting hypotheses* are nodes that apparently overlap with, or logically connect, two or more clusters. Thus, these nodes offer logical links between major areas of research within the field. For example, the increased resource availability (IRA) hypothesis connects the Resource availability and Biotic interaction clusters. The former cluster is concerned with changing conditions and opportunities, such as shifts in resource uptake and supply, whereas the latter cluster emphasizes the importance of a favorable biotic context in which enemies no longer constrain the population growth of the invader. In particular, non-native species must often co-opt limiting resources from native competitors in order to reproduce sustainably; thus, the IRA hypothesis is linked to the Biotic interaction cluster. Similarly, the human commensalism hypothesis (HC) logically connects to the Trait cluster by recognizing the importance of trait plasticity and pre-adaptation for surviving human-mediated disturbances and land-use (e.g. agriculture), and for exploiting human transportation systems. Human commensalism also implies greater opportunities for propagule dispersal, hence the link to the Propagule cluster. Finally, human commensalism reflects the ability of successful invaders to opportunistically exploit human-mediated disturbance events – which promote enemy release and resource release via the loss of resident predators and competitors.

Comparison with previous hypothesis networks in invasion biology

Some papers previously categorized hypotheses and concepts in invasion biology (e.g. Catford et al. (2009); Gurevitch et al. (2011); Schulz et al. (2019)) or visualized them in the form of networks (Enders et al., 2019; Enders et al., 2018; Enders & Jeschke, 2018). As already mentioned, although useful for providing a first overview, these previous approaches to create hypothesis networks in invasion biology had several limitations that were overcome by our consensus approach. In particular, here a fairly large and diverse group of experts constructing the consensus network were offered the opportunity to discuss why they consider hypotheses to be logically linked, and they could differentiate between positive linkages, negative linkages or unlinked hypotheses. Another advantage is that the consensus approach, unlike quantitative bibliometric approaches, does not depend on a large literature database. Finally, the consensus approach relates to how the concepts are being currently used in practice, and presently perceived and interpreted by experts working in the field. This is in contrast to the bibliometric approach which is based on historic citation patterns.

The networks resulting from the consensus approach used in this paper and those from previous bibliometric approaches (see Enders et al., 2019) are quite similar; however, due to the outlined benefits of the consensus approach, we recommend the latter to create networks of hypotheses and concepts in a research field.

Conclusions

Our hypothesis network visualizes the conceptual structure of the research field of invasion biology. It displays relationships among invasion hypotheses that can in turn be tested with empirical studies. A next step should be to offer both the network and empirical studies as interactive tools online. This would be an opportunity to (a) bridge the gap between theoretical-conceptual and empirical work, and (b) offer a visual and user-friendly interface to explore the knowledge of the field. In this way, it would be immediately visible which hypotheses are empirically supported under which circumstances, particularly when dividing the 39 hypotheses into more specific sub-hypotheses following the hierarchy-of-hypotheses approach (Jeschke & Heger, 2018). A first step in this direction is available at the website www.hi-knowledge.org.

The clusters in the network provide a clear, simplified summary of the main mechanisms that, according to current theory, govern the introduction, establishment and spread of invasive species. The clustering highlights that the field is currently dominated by attention to antagonistic interactions between invaders and natives; it recognizes the probabilistic nature of invasions through spatiotemporal variation in biotic and abiotic conditions (Resource availability cluster), as well as in propagule supply and filtering (Propagule cluster); and part of the foundation of the field is built upon venerable hypotheses arising from Darwin and Elton (cf. Table 1). This method could also be used to identify temporal trends in the concepts, i.e. when hypotheses were proposed and coined, and when they experienced most empirical examination. One might see moving waves of research effort through the network as research fashions and techniques change.

Further, a hypothesis network such as the one constructed here can guide a researcher working on one hypothesis to explore potentially relevant ideas and literature concerning hypotheses that are nearby in the cluster, and to highlight important co-variables that should be used in analyses that might otherwise be overlooked. The researcher will also be pointed to critical research and knowledge gaps.

Finally, a hypothesis network avoids the formulation of additional repetitive hypotheses. Anyone who wants to propose a new hypothesis or mechanism to the field can consult the network to see where the new contribution would be located and if it overlaps with existing ones.

The consensus approach outlined here can be applied to any research field. We strongly encourage its application particularly in disciplines where, as in invasion biology, there are so many hypotheses and concepts that it is hard to gain an overview without a navigation tool like a hypothesis network. Connecting an increasing number of hypothesis networks could facilitate cross-disciplinary research by revealing overlaps and joint ideas, enhancing the understanding of basic ideas and transfer of knowledge. A resulting growing atlas of knowledge could thus help address complex problems like multi-causality in biodiversity change (Sala et al., 2000; Settele et al., 2005), and to build a solid basis for tackling the current environmental crisis. Such an atlas would also reveal hypotheses and concepts that connect disciplines, helping researchers to find out if colleagues from another discipline have already come up with concepts and ideas to potentially solve challenges in their own field. Therefore, we call on researchers across scientific disciplines to create conceptual maps for their fields. Let’s then connect these maps to jointly build an atlas of knowledge.

Acknowledgments

Financial support was provided by the Foundation of German Business (sdw) to ME; by the German Federal Ministry of Education and Research (BMBF) within the Collaborative Project "Bridging in Biodiversity Science - BIBS" (funding number 01LC1501A-H) to ME, AS, CM, CS, MBV and TH; and by the Deutsche Forschungsgemeinschaft (DFG, JE 288/9-2) to JMJ. SK, FAY and WCS acknowledge support from Stellenbosch University’s DST-NRF Centre of Excellence for Invasion Biology (C•I•B), MV from Belmont Forum-BiodivERsA project InvasiBES (PCI2018-092939) funded by the Spanish Ministerio de Ciencia, Innovación y Universidades. SK acknowledges financial support from the South African National Department of Environment Affairs through its funding to the Invasive Species Programme of the South African National Biodiversity Institute. AN and PP were supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and the long-term research development project RVO 67985939 (The Czech Academy of Sciences). LGA acknowledges support from the MICINN project INTERCAPA (CGL-2014- 56739-R), FE and JMJ from the BiodivERsA-Belmont Forum Project “Alien Scenarios” (FWF project no I 4011-B32, BMBF project 01LC1807B) and AR acknowledges funding from the Natural Sciences and Engineering Research Council of Canada.

Data Accessibility Statement

The data created in this study and underlying the presented analyses are freely available online in the Supporting Information accompanying this publication:

https://onlinelibrary.wiley.com/doi/full/XXXXX/XXXXXX

References

Ahn, Y. Y., Bagrow, J. P., & Lehmann, S. (2010). Link communities reveal multiscale complexity in networks. *Nature, 466*, 761-U711. doi:10.1038/nature09182

Baker, H. G. (1965). Characteristics and modes of origin of weeds. In H. G. Baker & G. L. Stebbins (Eds.), *The genetics of colonizing species; proceedings* (pp. 147–168). New York: Academic Press.

Baker, H. G. (1974). The evolution of weeds. *Annual Review of Ecology and Systematics 1–24. , 5*, 1–24.

Blossey, B., & Nötzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants - a hypothesis. *Journal of Ecology, 83*, 887-889. doi:10.2307/2261425

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters, 9*, 887-895.

Bollen, J., Van de Sompel, H., Hagberg, A., Bettencourt, L., Chute, R., Rodriguez, M. A., & Balakireva, L. (2009). Clickstream Data Yields High-Resolution Maps of Science. *Plos One, 4*, e4803. doi:ARTN e4803 10.1371/journal.pone.0004803

Börner, K. (2010). *Atlas of science : visualizing what we know*. Cambridge, Massachusetts: MIT Press.

Börner, K. (2015). *Atlas of knowledge : anyone can map*. Cambridge, Massachusetts: MIT Press

Callaway, R. M., & Ridenour, W. M. (2004). Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment, 2*, 436-443. doi:10.2307/3868432

Callaway, R. M., Thelen, G. C., Rodriguez, A., & Holben, W. E. (2004). Soil biota and exotic plant invasion. *Nature, 427*, 731-733. doi:10.1038/nature02322

Capellini, I., Baker, J., Allen, W. L., Street, S. E., & Venditti, C. (2015). The role of life history traits in mammalian invasion success. *Ecology Letters*, *18*, 1099-1107. doi:10.1111/ele.12493

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions, 15*, 22-40. doi:10.1111/j.1472-4642.2008.00521.x

Colautti, R. I., Grigorovich, I. A., & MacIsaac, H. J. (2006). Propagule pressure: A null model for biological invasions. *Biological Invasions, 8*, 1023-1037. doi:10.1007/s10530-005-3735-y

Colautti, R. I., Ricciardi, A., Grigorovich, I. A., & MacIsaac, H. J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters, 7*, 721-733. doi:10.1111/j.1461-0248.2004.00616.x

Crawley, M. J., Brown, S. L., Heard, M. S., & Edwards, G. R. (1999). Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters, 2*, 140-148.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. InterJournal. http://igraph.org

Daehler, C. C. (2001). Darwin's naturalization hypothesis revisited. *American Naturalist, 158*, 324-330. doi:10.1086/321316

Darwin, C. (1859). *On the origin of species by means of natural selection, or, The preservation of favoured races in the struggle for life*. London: J. Murray.

Diamond, J., & Case, T. J. (1986). Overview: introductions, extinctions, exterminations, and invasions. In J. Diamond & T. J. Case (Eds.), *Community Ecology* (pp. 65–79). New York: Harper and Row.

Divíšek, J., Chytry, M., Beckage, B., Gotelli, N. J., Lososova, Z., Pysek, P., Richardson, D. M., & Molofsky, J. (2018). Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nature Communications, 9*. doi:ARTN 4631 10.1038/s41467-018-06995-4

Doorduin, L. J., & Vrieling, K. (2011). A review of the phytochemical support for the shifting defence hypothesis. *Phytochemistry Reviews, 10*, 99-106. doi:10.1007/s11101-010-9195-8

Duncan, R. P., & Williams, P. A. (2002). Ecology - Darwin's naturalization hypothesis challenged. *Nature, 417*, 608-609. doi:10.1038/417608a

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London: Methuen.

Enders, M., Havemann, F., & Jeschke, J. M. (2019). A citation-based map of concepts in invasion biology. *NeoBiota, 47*, 23-42.

Enders, M., Hütt, M.-T., & Jeschke, J. M. (2018). Drawing a map of invasion biology based on a network of hypotheses. *Ecosphere, 9*, e02146. doi:10.1002/ecs2.2146

Enders, M., & Jeschke, J. M. (2018). A Network of Invasion Hypotheses. In J. M. Jeschke & T. Heger (Eds.), *Invasion Biology: Hypotheses and Evidence* (pp. 49-59). Wallingford: CABI.

Eppinga, M. B., Rietkerk, M., Dekker, S. C., De Ruiter, P. C., & Van der Putten, W. H. (2006). Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. *Oikos, 114*, 168-176. doi:10.1111/j.2006.0030-1299.14625.x

Evans, T. S., & Lambiotte, R. (2009). Line graphs, link partitions, and overlapping communities. *Physical Review E, 80*. doi:ARTN 016105 10.1103/PhysRevE.80.016105

Fortunato, S. (2010). Community detection in graphs. *Physics Reports-Review Section of Physics Letters, 486*, 75-174. doi:10.1016/j.physrep.2009.11.002

Fridley, J. D., & Sax, D. F. (2014). The imbalance of nature: revisiting a Darwinian framework for invasion biology. *Global Ecology and Biogeography, 23*, 1157-1166. doi:10.1111/geb.12221

Gurevitch, J., Fox, G. A., Wardle, G. M., Inderjit, & Taub, D. (2011). Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters, 14*, 407-418. doi:10.1111/j.1461-0248.2011.01594.x

Häder, M., & Häder, S. (2000). *Die Delphi-Technik in den Sozialwissenschaften Methodische Forschungen und innovative Anwendungen* (Häder M. & H. S. Eds.). Wiesbaden, Germany: VS Verlag für Sozialwissenschaften.

Handcock, M. S., Hunter, D. R., Butts, C. T., Goodreau, S. M., & Morris, M. (2003). statnet: Software tools for the Statistical Modeling of Network Data. http://statnetproject.org

Havemann, F., Gläser, J., & Heinz, M. (2017). Memetic search for overlapping topics based on a local evaluation of link communities. *Scientometrics, 111*, 1089-1118.

Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, diversity, and invasion - implications for conservations. *Conservation Biology, 6*, 324-337. doi:10.1046/j.1523-1739.1992.06030324.x

Huston, M. (1979). A general hypothesis of species diversity. *The American Naturalist, 113*, 81 - 101.

Jeschke, J. M. (2008). Across islands and continents, mammals are more successful invaders than birds. *Diversity and Distributions, 14*, 913-916. doi:10.1111/j.1472-4642.2008.00488.x

Jeschke, J. M. (2014). General hypotheses in invasion ecology. *Diversity and Distributions, 20*, 1229-1234. doi:10.1111/ddi.12258

Jeschke, J. M., & Heger, T. (2018). *Invasion biology: hypotheses and evidence*. Wallingford: CABI.

Jeschke, J. M., & Strayer, D. L. (2006). Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology, 12*, 1608-1619. doi:10.1111/j.1365-2486.2006.01213.x

Johnstone, I. M. (1986). Plant invasion windows - a time-based classification of invasion potential. *Biological Reviews of the Cambridge Philosophical Society, 61*, 369-394. doi:10.1111/j.1469-185X.1986.tb00659.x

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution, 17*, 164-170. doi:10.1016/S0169-5347(02)02499-0

Levine, J. M., & D'Antonio, C. M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos, 87*, 15-26. doi:10.2307/3546992

Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution, 20*, 223-228. doi:10.1016/j.tree.2005.02.004

Lockwood, J. L., Cassey, P., & Blackburn, T. M. (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. doi:10.1111/j.1472-4642.2009.00594.x

MacArthur, R. (1970). Species packing and competitive equilibrium for many species. *Theoretical Population Biology, 1*, 1-11.

MacArthur, R., & Levins, R. (1967). Limiting similarity convergence and divergence of coexisting species. *American Naturalist, 101*, 377-385. doi:10.1086/282505

Mahoney, P. J., Beard, K. H., Durso, A. M., Tallian, A. G., Long, A. L., Kindermann, R. J., Nolan, N. E., Kinka, D., & Mohn, H. E. (2015). Introduction effort, climate matching and species traits as predictors of global establishment success in non-native reptiles. *Diversity and Distributions, 21*, 64-74. doi:10.1111/ddi.12240

Melbourne, B. A., Cornell, H. V., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A. L., Hall, R. J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K., & Yokomizo, H. (2007). Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters, 10*, 77-94. doi:10.1111/j.1461-0248.2006.00987.x

Mitchell, C. E., Agrawal, A. A., Bever, J. D., Gilbert, G. S., Hufbauer, R. A., Klironomos, J. N., Maron, J. L., Morris, W. F., Parker, I. M., Power, A. G., Seabloom, E. W., Torchin, M. E., & Vazquez, D. P. (2006). Biotic interactions and plant invasions. *Ecology Letters, 9*, 726-740. doi:10.1111/j.1461-0248.2006.00908.x

Prinzing, A., Durka, W., Klotz, S., & Brandl, R. (2001). The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society B-Biological Sciences, 268*, 2383-2389. doi:DOI 10.1098/rspb.2001.1801

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters, 3*, 349-361. doi:DOI 10.1046/j.1461-0248.2000.00143.x

Pyšek, P., & Richardson, D. M. (2007). Traits associated with invasiveness in alien plants: where do we stand? . In W. e. Nentwig (Ed.), *Biological Invasions* (pp. 97-125). Berlin,Germany: Springer-Verlag.

Rejmánek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology, 77*, 1655-1661. doi:10.2307/2265768

Ricciardi, A., & Atkinson, S. K. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters, 7*, 781-784. doi:10.1111/j.1461-0248.2004.00642.x

Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J., & Pigliucci, M. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters, 9*, 981-993. doi:10.1111/j.1461-0248.2006.00950.x

Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., & Rejmanek, M. (2000). Plant invasions - the role of mutualisms. *Biological Reviews, 75*, 65-93. doi:Doi 10.1017/S0006323199005435

Richardson, D. M., & Pyšek, P. (2008). Fifty years of invasion ecology - the legacy of Charles Elton. *Diversity and Distributions, 14*, 161-168. doi:10.1111/j.1472-4642.2008.00464.x

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Biodiversity - Global biodiversity scenarios for the year 2100. *Science, 287*, 1770-1774. doi:DOI 10.1126/science.287.5459.1770

Schulz, A. N., Lucardi, R. D., & Marsico, T. D. (2019). Successful invasions and failed biocontrol: The role of antagonistic species Interactions. *BioScience*, 1-14. doi:10.1093/biosci/biz075

Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M., Kunin, W., Marion, G., O'Connor, M., Petanidou, T., Peterson, K., Potts, S., Pritchard, H., Pysek, P., Rounsevell, M., Spangenberg, J., Steffan-Dewenter, I., Sykes, M., Vighi, M., Zobel, M., & Kuhn, I. (2005). ALARM: Assessing LArge-scale environmental Risks for biodiversity with tested Methods. *Gaia-Ecological Perspectives for Science and Society, 14*, 69-72. doi:10.14512/gaia.14.1.20

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution, 17*, 170-176. doi:Doi 10.1016/S0169-5347(02)02495-3

Sher, A. A., & Hyatt, L. A. (1999). The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biological Invasions, 1*, 107-114.

Simberloff, D., & Gibbons, L. (2004). Now you see them, now you don't - population crashes of established introduced species. *Biological Invasions, 6*, 161-172. doi:10.1023/B:Binv.0000022133.49752.46

Simberloff, D., & Holle, B. V. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions, 1*, 21-32.

Stohlgren, T. J., Jarnevitch, C., & Chong, G. W. (2006). Scale and plant invasions: a therory of biotic acceptance. *Preslia, 78*, 405-426.

Swanson, D. R. (1986). Undiscovered Public Knowledge. *Library Quarterly, 56*, 103-118. doi:Doi 10.1086/601720

te Beest, M., Le Roux, J. J., Richardson, D. M., Brysting, A. K., Suda, J., Kubešová, M., & P., P. (2012). The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany, 109*.

Team, R. D. C. (2008). R: A language and environment for

statistical computing. . Vienna, Austria: R Foundation for Statistical Computing

http://www.R-project.org.

Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Munkemuller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions, 16*, 461-475. doi:10.1111/j.1472-4642.2010.00645.x

Trujillo, C. M., & Long, T. M. (2018). Document co-citation analysis to enhance transdisciplinary research. *Science Advances, 4*. doi:ARTN e1701130 10.1126/sciadv.1701130

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters, 13*, 235-245. doi:10.1111/j.1461-0248.2009.01418.x

Vidal-Garcia, M., & Keogh, J. S. (2017). Invasive cane toads are unique in shape but overlap in ecological niche compared to Australian native frogs. *Ecology and Evolution, 7*, 7609-7619. doi:10.1002/ece3.3253

Wang, T., Hu, J. T., Wang, R. Q., Liu, C. H., & Yu, D. (2018). Tolerance and resistance facilitate the invasion success of Alternanthera philoxeroides in disturbed habitats: A reconsideration of the disturbance hypothesis in the light of phenotypic variation. *Environmental and Experimental Botany, 153*, 135-142. doi:10.1016/j.envexpbot.2018.05.011

Weiher, E., & Keddy, P. A. (1995). Assembly Rules, Null Models, and Trait Dispersion - New Questions Front Old Patterns. *Oikos, 74*, 159-164. doi:Doi 10.2307/3545686

Wickham, H. (2007). Reshaping Data with the reshape Package (Version 12). Journal of Statistical Software. http://www.jstatsoft.org/v21/i12/

Williamson, M. H., & Brown, K. C. (1986). The analysis and modeling of British invasions. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 314*, 505-522. doi:10.1098/rstb.1986.0070

Table 1. List of 39 common invasion hypotheses and how they were defined for this study [adapted from Catford et al. (2009) and Enders et al. (2018)].

Hypothesis		Description	Key reference(s)
ADP	Adaptation	The invasion success of non-native species depends on the adaptation to the conditions in the exotic range before and/or after the introduction. Non-native species that are related to native species are more successful in this adaptation.	Duncan & Williams (2002)
BA	Biotic acceptance aka “the rich get richer”	Ecosystems tend to accommodate the establishment and coexistence of non-native species despite the presence and abundance of native species.	Stohlgren et al. (2006)
BID	Biotic indirect effects	Non-native species benefit from different indirect effects triggered by native species.	Callaway et al. (2004)
BR	Biotic resistance aka diversity-invasibility hypothesis	An ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity.	Elton (1958); Levine & D'Antonio (1999)
CP	Colonization pressure	Colonization pressure is defined as the number of species introduced to a given location. As colonization pressure increases, the number of established or invasive non-native species in that location is predicted to increase.	Lockwood et al. (2009)
DEM	Dynamic equilibrium model	The establishment of a non-native species depends on natural fluctuations of the ecosystem, which influences the competition of local species.	Huston (1979)

DN	Darwin’s naturalization	The invasion success of non-native species is higher in areas that are poor in closely related species than in areas that are rich in closely related species.	Daehler (2001); Darwin (1859)
DS	Disturbance	The invasion success of non-native species is higher in highly disturbed than in relatively undisturbed ecosystems.	Elton (1958); Hobbs & Huenneke (1992)
EIM	Ecological imbalance	Invasion patterns are a function of the evolutionary characteristics of both the recipient region and potential donor regions. Species from regions with highly diverse evolutionary lineages are more likely to become successful invaders in less diverse regions.	Fridley & Sax (2014)
ENA	Ecological naivety aka evolutionary naivety	The impact of a non-native species on biodiversity is influenced by the evolutionary experience of the invaded community. Thus, the largest impacts are caused by species (e.g. predators, herbivores, pathogens) invading systems where no phylogenetically or functionally similar species exist.	Diamond & Case (1986); Ricciardi & Atkinson (2004)
EE	Enemy of my enemy aka accumulation-of-local-pathogens hypothesis	Introduced enemies of a non-native species are less harmful to the non-native than to the native species.	Eppinga et al. (2006)
EI	Enemy inversion	Introduced enemies of non-native species are less harmful for them in the exotic than the native range, due to altered biotic and abiotic conditions.	(Colautti et al., 2004)

EICA	Evolution of increased competitive ability	After having been released from natural enemies, non-native species will allocate more energy in growth and/or reproduction (this re-allocation is due to genetic changes), which makes them more competitive.	Blossey & Nötzold (1995)
EN	Empty niche	The invasion success of non-native species increases with the availability of empty niches in the exotic range.	MacArthur (1970)
ER	Enemy release	The absence of enemies in the exotic range is a cause of invasion success.	Keane & Crawley (2002)
ERD	Enemy reduction	The partial release of enemies in the exotic range is a cause of invasion success.	Colautti et al. (2004)
EVH	Environmental heterogeneity	The invasion success of non-native species is high if the exotic range has a highly heterogeneous environment.	Melbourne et al. (2007)
GC	Global competition	A large number of different non-native species is more successful than a small number.	Colautti et al. (2006)
HC	Human commensalism	Species that live in close proximity to humans are more successful in invading new areas than other species.	Jeschke & Strayer (2006)
HF	Habitat filtering	The invasion success of non-native species in the new area is high if they are pre-adapted to this area.	Weiher & Keddy (1995)
IM	Invasional meltdown	The presence of non-native species in an ecosystem facilitates invasion by additional species, increasing their likelihood of survival or ecological impact.	Simberloff & von Holle (1999)
IRA	Increased resource availability	The invasion success of non-native species increases with the availability of resources.	Sher & Hyatt (1999)

IS	Increased susceptibility	If a non-native species has a lower genetic diversity than the native species, there will be a low probability that the non-native species establishes itself.	Colautti et al. (2004)
ISH	Island susceptibility hypothesis	Non-native species are more likely to become established and have major ecological impacts on islands than on continents.	Jeschke (2008)
IW	Ideal weed	The invasion success of a non-native species depends on its specific traits (e.g. life-history traits).	H. G. Baker (1965); Rejmánek & Richardson (1996)
LS	Limiting similarity	The invasion success of non-native species is high if they strongly differ from native species, and low if they are similar to native species.	MacArthur & Levins (1967)
MM	Missed mutualisms	In their exotic range, non-native species suffer from missing mutualists.	Mitchell et al. (2006)
NAS	New associations	New relationships between non-native and native species can positively or negatively influence the establishment of the non-native species.	Colautti et al. (2006)
NW	Novel weapons	In the exotic range, non-native species can have a competitive advantage against native species because they possess a novel weapon, i.e. a trait that is new to the resident community of native species and therefore affects them negatively.	Callaway & Ridenour (2004)
OW	Opportunity windows	The invasion success of non-native species increases with the availability of empty niches in the exotic range, and the availability of these niches fluctuates spatio-temporally.	Johnstone (1986)

PH	Plasticity hypothesis	Invasive species are more phenotypically plastic than non-invasive or native ones.	Richards et al. (2006)
PO	Polyploidy hypothesis	Polyploid organisms, particularly plants, are predicted to have an increased invasion success, since polyploidy can lead to higher fitness during the establishment phase and/or increased potential for subsequent adaptation.	te Beest et al. (2012)
PP	Propagule pressure	A high propagule pressure (a composite measure consisting of the number of individuals introduced per introduction event and the frequency of introduction events) is a cause of invasion success.	Lockwood et al. (2005)
RER	Resource-enemy release	The non-native species is released from its natural enemies and can spend more energy in its reproduction, and invasion success increases with the availability of resources.	Blumenthal (2006)
RI	Reckless invader aka “boom-bust”	A population of a non-native species that is highly successful shortly after its introduction can decline or disappear over time due to different reasons (such as competition with other introduced species or adaptation by native species).	D. Simberloff & Gibbons (2004)
SDH	Shifting defence hypothesis	After having been released from natural specialist enemies, non-native species will allocate more energy in cheap (energy-inexpensive) defenses against generalist enemies and less energy in expensive defenses against specialist enemies (this re-allocation is due to genetic changes); the energy gained in this way will be invested in growth and/or reproduction, which makes the non-native species more competitive.	Doorduin & Vrieling (2011)

SG	Specialist-generalist	Non-native species are more successful in a new region if the local predators are specialists and local mutualists are generalists.	Callaway et al. (2004)
SP	Sampling	A large number of different non-native species is more likely to become invasive than a small number due to interspecific competition. Also, the species identity of the locals is more important than the richness in terms of the invasion of an area.	Crawley et al. (1999)
TEN	Tens rule	Approximately 10% of species successfully take consecutive steps of the invasion process.	Williamson & Brown (1986)

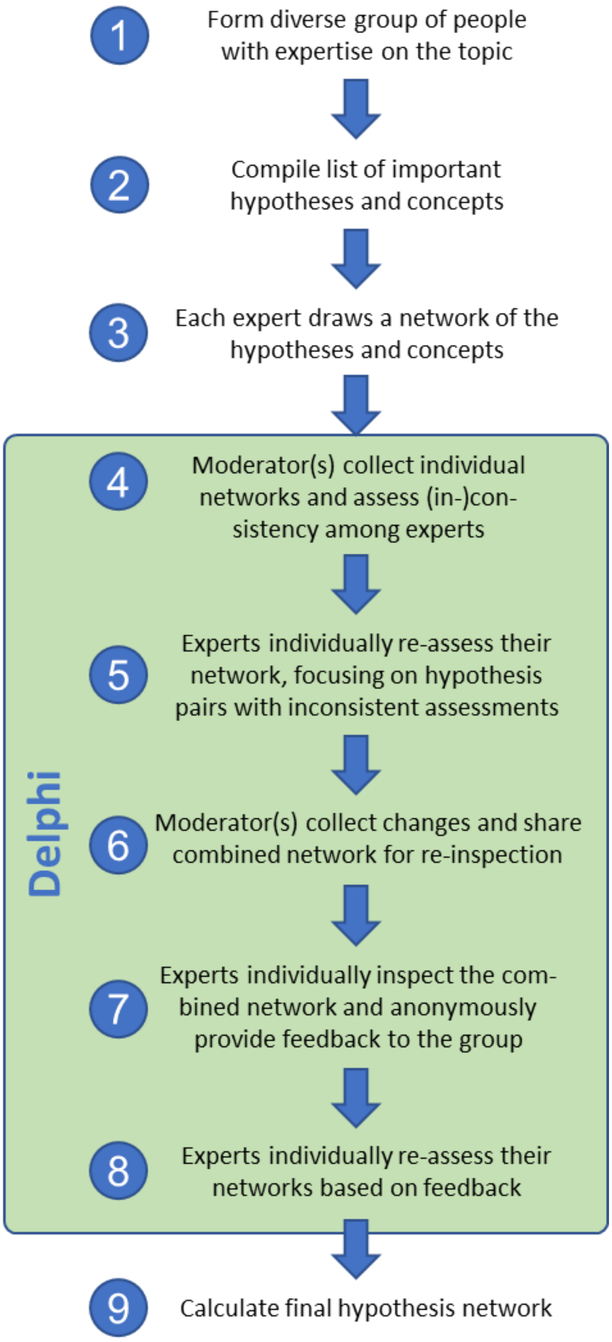

Figure 1. Description of the consecutive steps to create a consensus network of hypotheses and concepts. While we applied this approach for the field of invasion biology, it can be easily applied for other research fields as well.

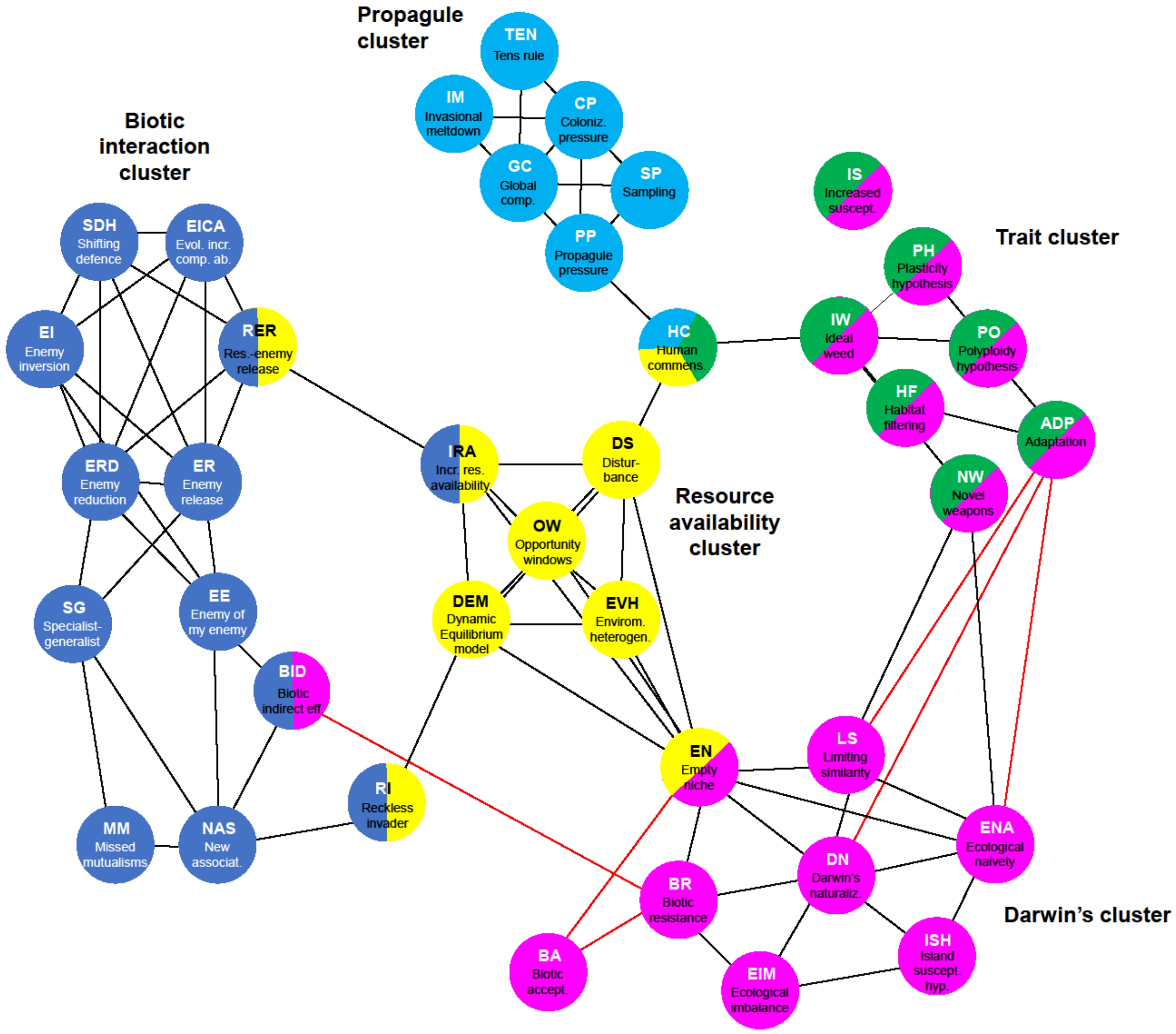

Figure 2. Network of 39 common hypotheses in invasion biology, clusters calculated with the local link-clustering algorithm (hypothesis names are abbreviated as in Table 1 where details on each hypothesis are provided). Colors indicate membership of hypotheses to *concept clusters*. The representation is simplified in that, for example, the node empty niche (EN) appears to be split into two equal parts, while it actually belongs slightly more in Darwin's cluster (6/11 = 55%) than in the Resource availability cluster (5/11 = 45%); see Fig. S2 for details. Similar hypotheses are connected with black lines, whereas contradictory hypotheses are connected with red lines.

5.1. Appendix

Submitted to Global Ecology and Biogeography as: Enders M, Havemann F, Ruland F, Bernard-Verdier M, Catford J, Gomez-Aparicio L, Haider S, Heger T, Kueffer C, Kühn IM, L. A., Musseau C, Novoa A, Ricciardi A, Sagouis A, Schittko C, Strayer DL, Montserrat V, Essel F, Hulme P, van Kleuen M, Kumschick S, Lockwood JL, Mabey AL, McGeoch M, Palma E, Pyšek P, Saul W-C, Yannelli FA, Jeschke JM (submitted) A conceptual map of invasion biology: integrating hypotheses into a consensus network.

Supplementary Material to Enders et al.: A conceptual map of invasion biology: integrating hypotheses into a consensus network

Classical clustering approach: node clustering

A classical clustering approach for network analysis is node clustering where nodes are clustered rather than their links (the alternative link-clustering approach that we used for Figure 2 clusters links rather than nodes). We tested the utility of node clustering for our hypothesis network, applying four algorithms commonly used to detect network structures: (i) the Girvan and Newman (2002) algorithm (igraph function 'cluster_edge_betweenness'); (ii) an algorithm proposed by Clauset et al. (2004) (igraph function 'cluster_fast_greedy'); (iii) the "Walktrap" algorithm suggested by Pons and Latapy (2005) (igraph function 'cluster_walktrap'); and (iv) an algorithm suggested by Newmann (2006) (igraph function 'cluster_leading_eigen').

The clusters returned by these four established algorithms were inconsistent (Fig. S1). These inconsistencies were largely due to the fact that some hypotheses did not seem to be part of any single cluster but were instead bridging clusters. For example, the human commensalism hypothesis (HC) seems to connect three clusters, but each algorithm assigned it to a different single cluster, as these ordinary algorithms are unable to split nodes into several clusters.

One possible solution to overcome these inconsistencies is to inspect the results of these different algorithms and combine them manually by identifying (a) stable clusters, i.e. those groups of nodes that are assigned to the same cluster by all algorithms, and (b) nodes that are assigned to different clusters (*connecting concepts*). However, link clustering has become available as an alternative and more elegant approach for identifying stable clusters and connecting concepts, so we used it in this study.

References

Clauset, A., Newman, M. E. J., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E, 70,* 066111. doi:ARTN 066111 10.1103/PhysRevE.70.066111

Girvan, M., & Newman, M. E. J. (2002). Community structure in social and biological networks. *Proceedings of the National Academy of Sciences of the United States of America, 99,* 7821-7826. doi:10.1073/pnas.122653799

Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 8577-8582. doi:10.1073/pnas.0601602103

Pons, P., & Latapy, M. (2005). Computing communities in large networks using random walks. *Computer and Information Sciences - Iscis 2005, Proceedings*, *3733*, 284-293.

Additional supplementary figures

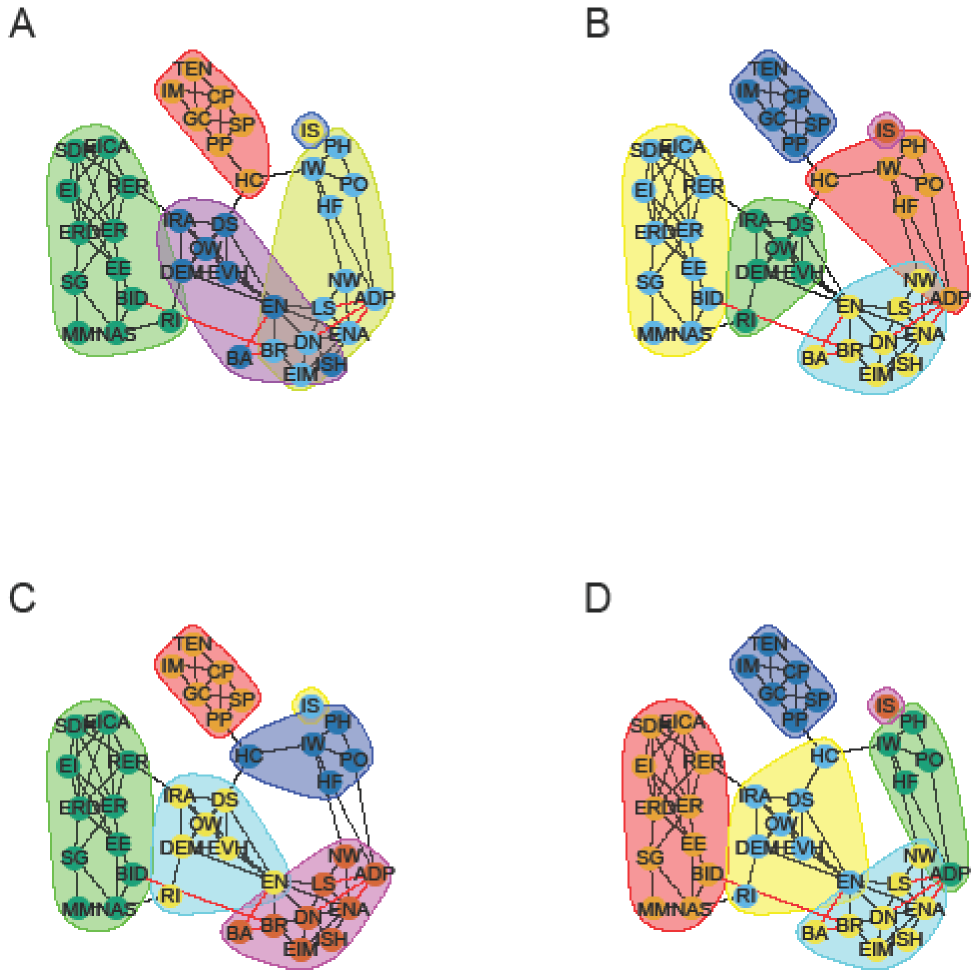

Figure S1. Results of four established algorithms to find node clusters in the network of 39 invasion hypotheses. The algorithms achieved similar levels of modularity: (A) 0.599 (edge betweenness), (B) 0.611 (fast greedy), (C) 0.613 (leading eigen), (D) 0.612 (Walktrap). Similar hypotheses are connected with grey lines, whereas contradictory hypotheses are connected with red lines. See Table 1 in the main article for a description of the hypotheses.

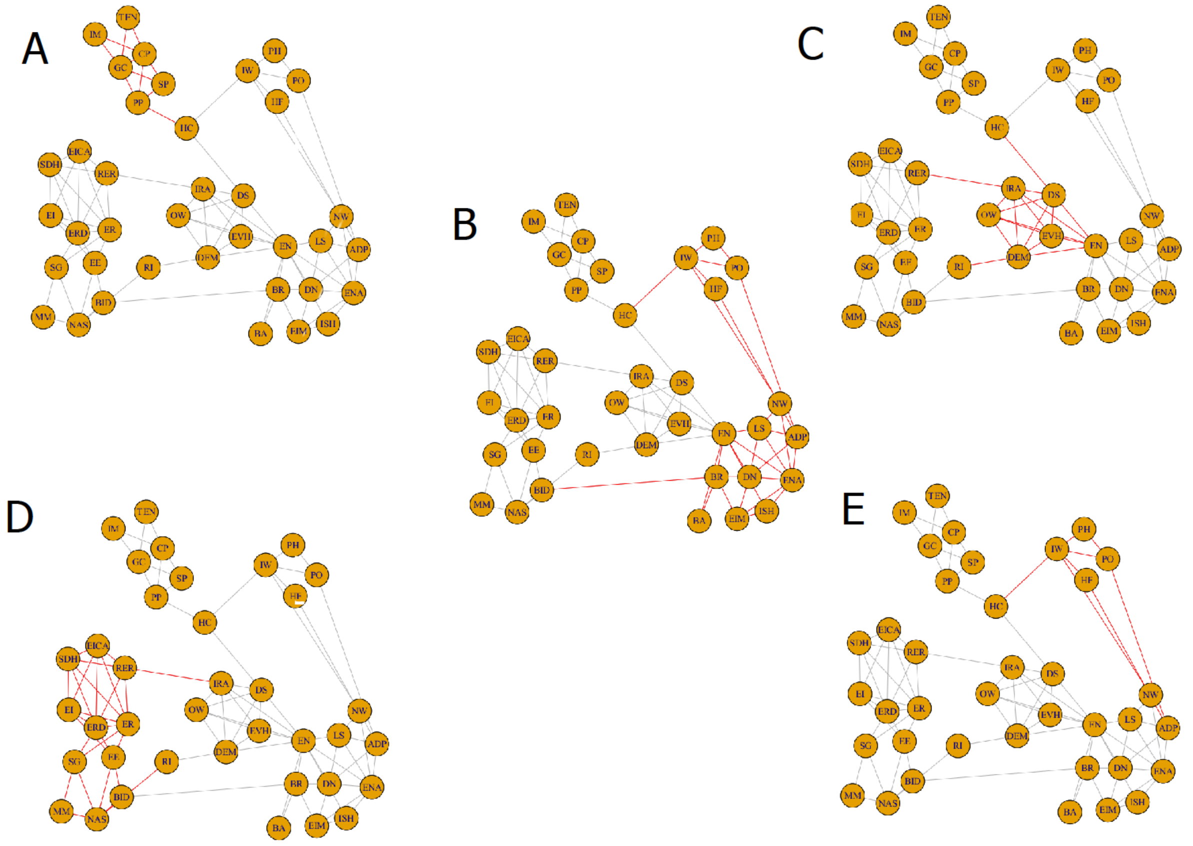

Figure S2. Link clusters of the local link-clustering algorithm. Red lines connect the hypotheses in the following clusters: (A) Propagule cluster, (B) Darwin's cluster and Trait cluster, (C) Resource availability cluster, (D) Biotic interaction cluster and (E) Trait cluster.

6. Discussion

Invasion biology grew hugely over the last three decades. The number of hypotheses and concepts exploded and so did the biases in the field and the problems with these concepts and hypotheses (Pyšek et al. 2008). There is now a lot of confusion over existing concepts in the field, and thus a strong need for a navigation tool. One of the main tasks of this thesis was to find the best-suited network to map a field of science, but it seems there is no easy answer to this question (see chapter 6.1.). Each method has its own benefits and flaws. In a way, one can see every network as a survey, with the surveys having a different number of participants from two (chapter 2, Enders and Jeschke (2018)) to 1518 (chapter 4, Enders et al. (2018)). But network quality does not simply and linearly increase with the number of participants – it is more complicated.

6.1. The problem with maps

When drawing a map of a research field, one is faced with similar problems than when drawing a map of the globe. In both cases, one tries to project a multidimensional original into a two-dimensional map. In the case of a world map, one will face different problems and will distort the projection in at least 2 of 3 ways (Lapaine et al. 2017):

- Sizes of regions appear larger or smaller than on the globe.
- Distances between points are shown as longer or shorter than on the globe.
- Direct routes between points are not shown as straight lines

This also means that every world map is wrong in the sense that it is not an exact representation of the globe; it is a mathematical projection. The same is true for maps of science where a multidimensional vector room is plotted in two dimensions. With this transformation, some information gets lost. But does that mean that every network represented in this work is wrong? Yes and no. Besides the epistemological problems concerning knowledge in general, a network of a field of science is a projection of the field in two dimensions, according to the method that created the network. Every method to create a network has its benefits and flaws. Networks can be right depending on the chosen method and the underlying question. Sometimes this means that it needs additional analyses like in chapter 4 where the resulting survey network did not show specific patterns, but was random and useless as a map of the field. With the additional analyses, the networks Joint-mentions A and B answer a different question. Figure 2 demonstrates this; using this figure 2, one will find different options and depending on your starting point a suggestion for the resulting network. These decisions depend on man- or brainpower, financial possibilities and computing-power.

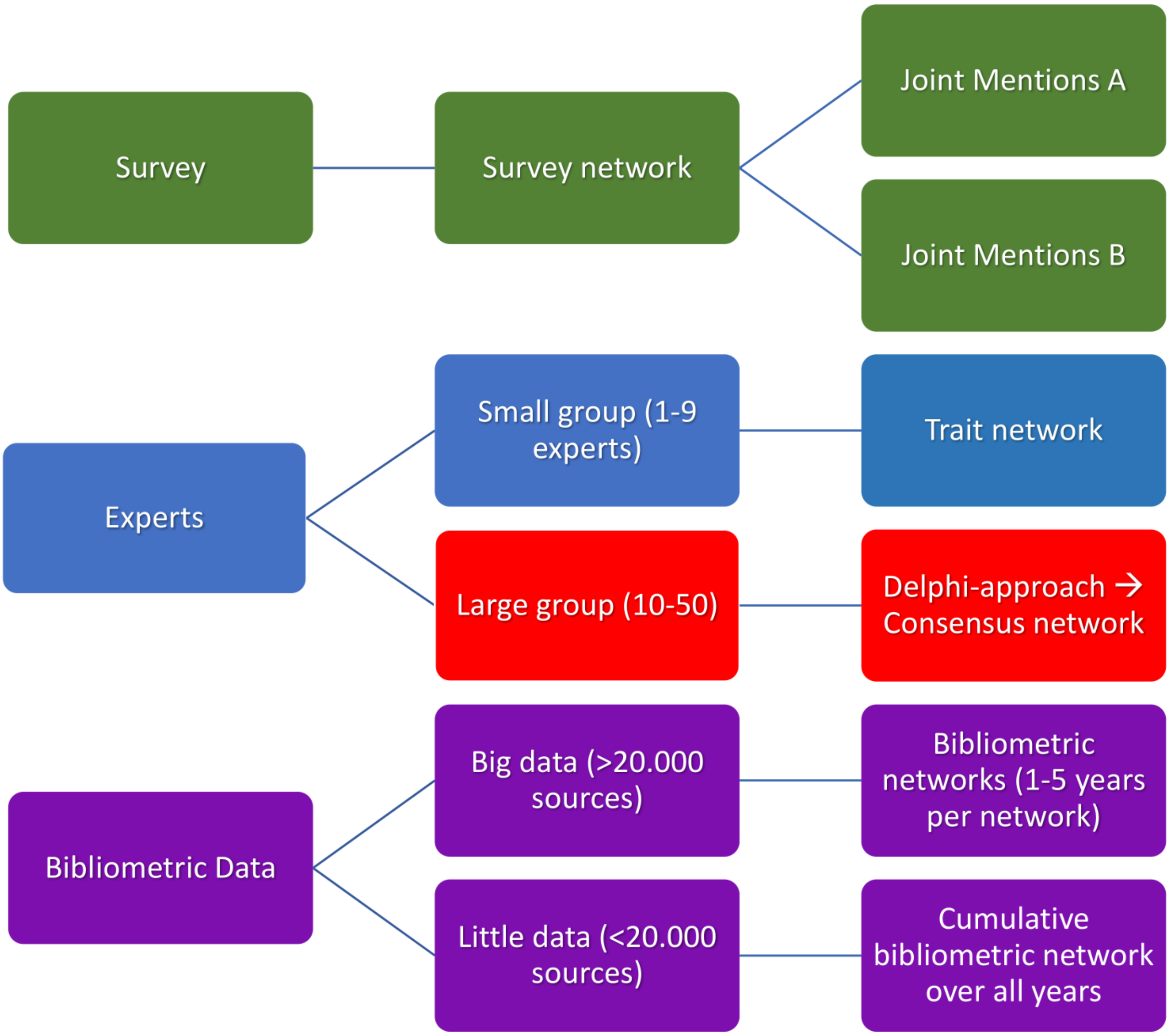

Figure 2 Different methods applied in this thesis to build hypothesis networks, sources of the data and the resulting networks.

6.2. The trait network

The first network that was created for this theses was the trait network in Enders and Jeschke (2018). The network was an important step toward a map of invasion biology, but also shows some flaws. Evidently, it is quite ham-fisted and lacks a deeper insight into the field. With only 3 big clusters, the resolution of the network is very low. With this network, the field is separated in reasonable sub-fields but lacks a clearer separation. On the other hand, it is based on an easily applicable approach to create a network of this research field. It can also be done with a few numbers of scientists and can at least be a stand-in for a more detailed and more sophisticated network.

Despite the flaws of this network, there are also benefits. First, this easily applicable method gives first insights into a field which may not be complete, but still useful. Also, it shows and sharpens the perspective of the experts on their view of the field of science. Third, it can be done easily by a small group of experts. And fourth, it makes transparent why certain hypothesis pairs are connected and others not: this information is explicit in the trait matrix summarizing the characteristics of each hypothesis.

6.3. The survey network

In the survey network (Enders et al. 2018), we could show that there is no internalized map of the field of invasion biology. The study also shows that many scientists have a personal map of hypotheses and concepts they are working with. One can argue that the results could be biased due to intellectual-psychological reasons or since the participants were saturated with questions when being asked to indicate similarities between hypotheses (these questions were asked in the middle of the survey); being saturated or tired of questions can lead to unreliable survey data, which could also explain the range in the answers (Faulbaum et al. 2009). This insight is very interesting for the field, but the resulting networks are useless for the task of building a map for the field. Also, this ‘black box’ approach seems to be useless for a clear network of similarities. There are many factors that cannot be defined and therefore the repeatability could suffer from it. Nevertheless, the results of the Joint-mentions networks give an interesting insight into the work of invasion biology. But also, the survey network still has some benefits. Compared with the other networks (bibliometric and consensus), it also is easier to replicate. The survey could be sent out in an annual rhythm and the changes in the field of science could be seen on a broader time scale. This would have two benefits: First, it would show the influence of the other networks. One could expect that after some years the survey networks would come close to the other networks or show important differences with them. Second, it would show if there is a trend in invasion biology over the years. One concept or hypothesis could raise in popularity and scientists would see more or fewer connections to other hypotheses.

6.4. The bibliometric network

Two networks were produced with the bibliometric approach, the M-network and the S-network (Enders et al. 2019). Both networks were created from the same literature and differ only in the underlying method: The M-network was built after Marshakova (1973) where accepted links (over 95% significant to a null-model) are weighted by co-citation numbers (cf. Havemann 2016). And the S-network following Small and Sweeney (1985) weighted all links with Salton’s cosine of co-citation numbers and omitted links with a cosine below a threshold of 0.1. The best partition of network M has modularity 0.520. The best partition of network S has modularity 0.463. Both networks stick out because they show well separated and distinct clusters. But bibliometrics has some dangers, which should be considered before evaluation of the networks (see below). There is, without a full-text analysis, no way to see why two hypotheses are connected. For example, the hypotheses biotic resistance and biotic acceptance are connected in both networks. The likely reason is that, they contradict each other and are therefore cited together. So, this link probably shows disagreement rather than similarity between the two hypotheses. Another point to be aware of are the clusters presented in the networks. In the M- and S-network, the partitions with the highest modularity where chosen. And after inspection the clusters are useful. This method is recommendable to get an insight into a field of science. The whole analysis depends on the search inquiry, which sets the search-area, and therefore these terms should be rechecked and may be revisited. With a new search term, the analysis could be done in a smaller time range. So, directions in the field of science could be detected.

6.5. Comparing trait and survey networks with the bibliometric network

In comparison to the two networks published by Enders and Jeschke (2018) and Enders et al. (2018), the bibliometric networks of Enders et al. (2019) are way clearer. Compared with the similarity-dissimilarity network in Enders et al. (2018), which was created based on an online survey, the bibliometric network is much clearer with fewer connections and distinct clusters. Apparently, the survey participants had different views on the relationships between invasion hypotheses, possibly because invasion biology has so many hypotheses now that it is hard for researchers to know them all: the similarity-dissimilarity network in Enders et al. (2018) used direct responses given by the survey participants when being asked for hypothesis pairs how similar they are. If participants often simply guessed the similarity of hypothesis pairs, one would expect a random network to emerge from the answers, and this is what Enders et al. (2018) found. This problem was circumvented for two other networks in Enders et al. (2018) – Joint-mentions networks A and B – which are only based on hypotheses that the survey participants indicated to know best. These networks are clearer than the similarity-dissimilarity network, however, they do not seem to be as useful maps as the networks M and S presented in Enders et al. (2019). They are not as clear, their clusters have lower modularity (ca. 0.25 for both networks, cf. Enders et al. 2018), and their clusters are not communities in the strong sense. The strong community definition requires that every node has a stronger internal than external connection.

The network in Enders and Jeschke (2018), which was created by traits of the concepts and hypotheses, has three clusters consisting of concepts with a focus on (i) human interference, (ii) mutualisms and (iii) enemies (predators or parasites). The modularity is relatively high (ca. 0.4) but still lower than for the two networks shown in Enders et al. (2019). Also, the clusters are not communities in the strong sense.

6.6. The consensus network

The consensus (Enders et al. submitted) and bibliometric (Enders et al. 2019) networks are quite similar but still different. First, the consensus network has more nodes (hypotheses) building up the network because each hypothesis was reviewed by its own. In the bibliometric network, the hypotheses EI; enemy inversion, ERD; enemy reduction, IS; increased susceptibility and NAS; new associations were represented by one paper (Colautti et al. 2004) and SG; specialist generalist and BID; biotic indirect effects were represented by one paper (Callaway et al. 2004). Second, there are five new hypotheses considered in the consensus network (PO; polyploidy hypothesis, PH; plasticity hypothesis, CP; colonization pressure, ENA; ecological naivety and EIM; ecological imbalance). The clusters were also renamed to better fit the idea of each cluster. The consensus network also avoids the bibliometric flaws (see below) and with the repetition of the integrated Delphi-process, there should be no strong influence of one person during the process.

The biggest difference between the two networks probably is that there was a new algorithm used to cluster the consensus network. This algorithm clusters links instead of nodes, which leads to nodes that are members of two or more clusters. Due to this algorithm, the network could be clustered finer and the clusters themselves can be more focused. In practice, different aspects of a hypothesis can be used in different fields, and the new algorithm and the resulting clusters represent that way of thinking. Sadly, due to this algorithm there are no advanced ways to measure this network and compare it to the others. Measurements like modularity need strictly distinct clusters.

The consensus process also takes a lot of resources. For two days, a sizable number of academic experts were occupied in the workshop plus they had to travel to and from Berlin, several of them over large distances. The individual work done by each expert beforehand and afterwards was time-consuming, too, and of course, I and other members of the core team of this study had to invest much additional time. Also, the algorithm used for this network designed by Havemann et al. (2019) needed a lot of computing power and time. But nevertheless, the resulting map of invasion biology seems to be the most useful one that currently exists. If there is enough financial and brainpower, this method should always be considered.

6.7. Problems in visualization

Visualization of knowledge brings many benefits, but should also be seen with a grain of salt. There are some problems with the creation of science maps, and these can be categorized into three different groups: bibliometric problems, technical limitations and human flaws.

6.7.1. Bibliometric problems

As outlined above, many large-scale science maps that try to create a picture of connected fields of science are based on bibliometric methods. This leads to two problems: (i) research areas that are logically connected are not always bibliographically connected (Swanson 1986) and (ii) an expert is still needed to interpret the bibliometric results. Because there is no way to see why there is a bibliometric link. So, the reason for a link could not be seen or could have different reasons than a "logical connection".

6.7.2. Technical limitations

The creation of a map out of a large data set still requires a lot of time and computing power. The same is true for the clustering of a big network, even with a simple algorithm it could take many hours to compute. A similar problem emerges in the section of topic finding. The algorithms can only work with a pre-determined set of words. The longer that list is, the longer it takes the computer to calculate it. Also, computers cannot handle mistakes well. If a human had done a mistake in filling a table or form, e.g. mixing up letters, the computer cannot recognize the entries as the same. The same is true for understanding words as synonyms of other words. These tasks, simple for human brains, are still hard for a computer. Maybe with more developed machine-learning, these problems can be solved in the future. Until then, humans will be required to double-check the data that computers and algorithms have produced.

6.7.3. Human flaws

This is a tricky point because of two reasons. First, humans, in general, tend to make mistakes with repetitive tasks. So, misspellings can occur in data-sets and bibliometric data. Second, human brains are made to recognize patterns in everything. That means that many clusters can be seen as valid.

6.8. Conclusions

To evaluate this work, we must have a look at the aims:

(i) Find different ways to create a network to visualize a field of science; in this case, the field of science is invasion biology.

This work presented four different ways to create a network to visualize the scientific field of invasion biology (chapter 2-5). These methods are useful for visualizing a field of science and could be used for many other different fields of science. Depending on the source of data, there are different ways to create a network (see suggestion Figure 2). The previous sub-chapters (see above) also showed that not every network is useful for every aim. So, depending on what the network should represent (e.g. How key papers are connected by citation, how experts see the field or how your workgroup sees the field), different methods are more useful than others.

(ii) Compare the resulting networks.

This was done both in the chapters and here in the Discussion. Measures from the networks were compared (like modularity, degree centrality) and the clusters were visually compared as well. Other comparisons are possible and indeed needed in the future, but the important part here is that the networks are compared as networks, not as strings of numbers. Therefore, mixing up the network would not give different results. The Ipsen-Mikhailov distance seems promising for future quantitative comparisons (cf. Jurman et al. (2011)). This metric compares the networks and gives a distance measure between them. For this task, it would be ideal to have the same number of nodes in a network.

(iii) Evaluate the different networks concerning their overall usefulness, their resolution and the question they address.

As outlined above (chapter 6.1.) the utility of a map or network depends on the question that was asked. Like with maps of the globe, hypothesis networks can be a reasonable representation but not a complete representation of the field. Under the aspect of usefulness for decision makers, students and experts in the field, the bibliometric (chapter 4) and the consensus network (chapter 5) provide good overviews of the field. For a view, how experts see the field and which hypotheses they know best, the survey network and the Joint-mentions networks (chapter 3) are a good way to go. And to get an overview of the field as seen by the own working group, the trait network (chapter 2) is the best and fastest way.

I use the term “resolution” here to describe how easy a global structure can be seen on a map, and how easy it is to get information out of it. This goes with a decrease in the number of links in the network and clustering in well distinct groups. The resolution of the clustering of the maps is increasing from the trait network (chapter 2), over the survey network (chapter 3) to the bibliometric and consensus networks (chapter 4 and 5). An exception is the Joint-mentions networks that have a higher resolution than the survey network itself, but do not show the relations between the hypotheses as seen and reported by the experts in the field.

6.9. Further work

Even though this work is a step forward in visualizing a field of science, there are many more things to do. For example, the survey in chapter 4 should be revisited, maybe shortened and done in regular temporal intervals, and the results should be compared with each other. Also, the consensus network should be done at regular intervals to see shifts in the field and maybe figure out new trends. In addition, there should be more research on comparing the different networks and possibly combining them. Combining the networks could be a way to create a network that shows different benefits of different networks.

Lastly, a combination of empirical studies with a useful network should be done. The website www.hi-knowledge.org (Jeschke et al. 2018) is a good way in this direction. It shows a network of hypotheses (simplified from Enders and Jeschke 2018, i.e. the trait network) and links it with the hierarchy-of-hypotheses approach. Thanks to this linkage, this network also shows how empirically supported these hypotheses are and how they could be separated in different, more precise sub-hypotheses. As a next step, the bibliometric or consensus network should be combined with the data of the HoH approach (Heger et al. 2013; Jeschke and Heger 2018) and shown to a broader audience on the website http://www.hi-knowledge.org (Jeschke et al. 2018). When doing so, the hypotheses should initially be shown as clusters rather than individual hypothesis in order to improve clarity. This thematic map would put an additional layer in the network. After this, connections should be made with other sub-disciplines of biology. In a last step, biology should be connected with other disciplines of science. For this last step, existing maps of science should be evaluated like the map that was done by Klavans and Boyack (2009). After these steps, there would be a complete, multidimensional map of science and for each dimension, another map could be the best fitting one. So, the aim is a zoomable map of science that shows the connections from a paper level, over a hypotheses level, to a clustered concept level, to a sub-discipline level, to finally a complete map of academic knowledge.

Also, a map of topics or ideas should be possible. There are works on this topic to extract topics from the text (e.g. Velden et al. (2017)), but there is still a long way ahead because of the reliability of the algorithms. So, the found topics don’t have to be all actual topics, but the algorithm is not capable of detecting more. Another aspect of this work was that it produced in the table of 39 invasion hypotheses probably the most complete table of its kind. For further work, this table should be revised and updated.

Finally, more work should be put into the comparisons of the network (see above). There are several metrics to compare networks with each other, but not all metrics suit. Also, the networks have to be made equal in size. This means that they need to have the same number of nodes to be compared with currently available methods.

6.10. Coda

Visualization of knowledge or maps of science has proven useful for the corresponding fields of science. The aim of a future map should be that its structure is built in-time by an algorithm and accessible via the internet. For the creation of this web-based map, a bibliometric approach seems to be the best way forward. Maps of science have proven to be very useful, but there are still some alarming problems. The main benefit of computing these maps is to compute large data sets, way too big for human calculations. But nowadays, computers are still too slow and network analysis still needs too much human attention to be seen as useful without an intense check by experts. Therefore, there is still research to do until everyone can use a web-based map.This future advance in technology demands also a self-critical reflection in the work of experts. They have to be aware of the problematic flaws (see above) and should avoid them. As said before, the consensus method (chapter 5) should always be considered as a way to create a map of a research field, but which approach to choose also depends on factors like manpower, brainpower or financial possibilities. The consensus method is the most expensive method of all of them and also needs the most manpower. If one of these or both are not given, the bibliometric method (see chapter 4) is the second-best way to create a map of a field of science. For a “quick & dirty” overview of the field, maybe only for the own working group, the trait method (chapter 2) is useful. If the aim is to see how as many experts as possible see their own field of science, the survey approach (chapter 3) is useful (for a quick overview of the different methods, see Figure 2). As said above, the aim of a map should lead the decision for a method to create it.

7. Publications with author contributions

A Network of Invasion Hypotheses

Published as: Enders, M., and Jeschke, J. M. (2018). A Network of Invasion Hypotheses. Invasion Biology: Hypotheses and Evidence. J. M. Jeschke and T. Heger. Wallingford, CABI**:** 49-59.

ME and JMJ jointly conceived the idea for this chapter. The matrix was created by ME and revised by JMJ. ME wrote the draft. Both authors revised the manuscript.

Drawing a map of invasion biology based on a network of hypotheses

Published as: Enders, M., Hütt, M.-T., Jeschke, J. M. (2018). Drawing a map of invasion biology based on a network of hypotheses. Ecosphere 9: e02146.

ME and JMJ jointly conceived the idea for this publication. ME programmed and analyzed the survey. MTH and ME did the network analyses. ME wrote the draft. All authors revised the manuscript.

A citation-based map of concepts in invasion biology

Published as: Enders M., Havemann F., Jeschke J. M. (2019) A citation-based map of concepts in invasion biology. NeoBiota 47: 23-42.

ME and JMJ jointly conceived the idea for this publication. ME gathered the data. The scripts where programmed by FH and ME. FH and ME analyzed the data. ME wrote the draft. All authors revised the manuscript.

A conceptual map of invasion biology: integrating hypotheses into a consensus network

ME and JMJ jointly conceived the idea for this manuscript. The scripts were programmed by FH and ME. The Delphi process was moderated by ME, FR and JMJ. FH, FR and ME analyzed the data. ME wrote the draft. All authors revised the manuscript.

8. Literature cited

Ahn YY, Bagrow JP, Lehmann S (2010) Link communities reveal multiscale complexity in networks. Nature 466: 761-U711. doi:10.1038/nature09182

Amelio A, Pizzuti C (2014) Overlapping Community Discovery Methods: A Survey. Social Networks: Analysis and Case Studies: 105-125. doi:10.1007/978-3-7091-1797-2__6

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (Eds) The genetics of colonizing species; proceedings. Academic Press, New York, 147–168

Baker HG (1974) The evolution of weeds. Annual Review of Ecology and Systematics 1–24 5: 1–24

Bellard C, Jeschke JM (2016) A spatial mismatch between invader impacts and research publications. Conservation Biology 30: 230-232. doi:10.1111/cobi.12611

Blondel VD, Guillaume JL, Lambiotte R, Lefebvre E (2008) Fast unfolding of communities in large networks. Journal of Statistical Mechanics-Theory and Experiment. doi:Artn P10008 10.1088/1742-5468/2008/10/P10008

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants - a hypothesis. Journal of Ecology 83: 887-889. doi:10.2307/2261425

Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9: 887-895

Bollen J, Van de Sompel H, Hagberg A, Bettencourt L, Chute R, Rodriguez MA, Balakireva L (2009) Clickstream Data Yields High-Resolution Maps of Science. Plos One 4: e4803. doi:ARTN e4803 10.1371/journal.pone.0004803

Börner K (2010) Atlas of science : visualizing what we know. MIT Press, Cambridge, Massachusetts

Börner K (2015) Atlas of knowledge : anyone can map. MIT Press Cambridge, Massachusetts, pp.

Botham N (2006) The book of useless information. Berkeley, London, pp.

Boyack KW, Borner K, Klavans R (2007) Mapping the structure and evolution of chemistry research. Proceedings of Issi 2007: 11th International Conference of the International Society for Scientometrics and Informetrics, Vols I and Ii: 112-+

Boyack KW, Klavans R, Borner K (2005) Mapping the backbone of science. Scientometrics 64: 351-374. doi:10.1007/s11192-005-0255-6

Bradford SC (1934) Sources of information on specic subjects. Engineering 137: 85-86

Brandes U, Delling D, Gaertler M, Gorke R, Hoefer M, Nikoloski Z, Wagner D (2008) On modularity clustering. Ieee Transactions on Knowledge and Data Engineering 20: 172-188. doi:10.1109/Tkde.2007.190689

Brondizio ES, Settele J, Díaz S, Ngo HT (2019) Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. E. S. IPBES, Bonn, Germany, pp.

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2: 436-443. doi:10.2307/3868432

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731-733. doi:10.1038/nature02322

Capellini I, Baker J, Allen WL, Street SE, Venditti C (2015) The role of life history traits in mammalian invasion success. Ecology Letters 18: 1099-1107. doi:10.1111/ele.12493

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15: 22-40. doi:10.1111/j.1472-4642.2008.00521.x

Clauset A, Newman MEJ, Moore C (2004) Finding community structure in very large networks. Physical Review E 70: 066111. doi:10.1103/PhysRevE.70.066111

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: A null model for biological invasions. Biological Invasions 8: 1023-1037. doi:10.1007/s10530-005-3735-y

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733. doi:10.1111/j.1461-0248.2004.00616.x

Collen B., Böhm M., Kemp R., M. BJE (2012) Spineless: status and trends of the world´s invertebrates. . Zoological Society of London, United Kingdom, London, pp.

Crawley MJ, Brown SL, Heard MS, Edwards GR (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters 2: 140-148

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal, pp.

Daehler CC (2001) Darwin's naturalization hypothesis revisited. American Naturalist 158: 324-330. doi:10.1086/321316

Darwin C (1859) On the origin of species by means of natural selection, or, The preservation of favoured races in the struggle for life. J. Murray, London, pp.

De Solla Price DJ (1963) Little Science, Big Science. Columbia University Press, New York, pp.

Diamond J, Case TJ (1986) Overview: introductions, extinctions, exterminations, and invasions. In: Diamond J, Case TJ (Eds) Community Ecology. Harper and Row, New York, 65–79

Divíšek J, Chytry M, Beckage B, Gotelli NJ, Lososova Z, Pysek P, Richardson DM, Molofsky J (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nature Communications 9. doi:ARTN 4631 10.1038/s41467-018-06995-4

Doorduin LJ, Vrieling K (2011) A review of the phytochemical support for the shifting defence hypothesis. Phytochemistry Reviews 10: 99-106. doi:10.1007/s11101-010-9195-8

Duncan RP, Williams PA (2002) Ecology - Darwin's naturalization hypothesis challenged. Nature 417: 608-609. doi:10.1038/417608a

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London, pp.

Enders M, Havemann F, Jeschke JM (2019) A citation-based map of concepts in invasion biology. NeoBiota 47: 23-42

Enders M, Havemann F, Ruland F, Bernard-Verdier M, Catford J, Gomez-Aparicio L, Haider S, Heger T, Kueffer C, Kühn IM, L. A., Musseau C, Novoa A, Ricciardi A, Sagouis A, Schittko C, Strayer DL, Montserrat V, Essel F, Hulme P, van Kleuen M, Kumschick S, Lockwood JL, Mabey AL, McGeoch M, Palma E, Pyšek P, Saul W-C, Yannelli FA, Jeschke JM (submitted) A conceptual map of invasion biology: integrating hypotheses into a consensus network.

Enders M, Hütt M-T, Jeschke JM (2018) Drawing a map of invasion biology based on a network of hypotheses. Ecosphere 9: e02146. doi:10.1002/ecs2.2146

Enders M, Jeschke JM (2018) A Network of Invasion Hypotheses. In: Jeschke JM, Heger T (Eds) Invasion Biology: Hypotheses and Evidence. CABI, Wallingford, 49-59

Eppinga MB, Rietkerk M, Dekker SC, De Ruiter PC, Van der Putten WH (2006) Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114: 168-176. doi:10.1111/j.2006.0030-1299.14625.x

Evans TS, Lambiotte R (2009) Line graphs, link partitions, and overlapping communities. Physical Review E 80. doi:ARTN 016105 10.1103/PhysRevE.80.016105

Faulbaum F, Prüfer P, Rexroth M (2009) Was ist eine gute Frage? Die systematische Evaluation der Fragenqualität. VS, Wiesbaden, pp.

Fortunato S (2010) Community detection in graphs. Physics Reports-Review Section of Physics Letters 486: 75-174. doi:10.1016/j.physrep.2009.11.002

Fridley JD, Sax DF (2014) The imbalance of nature: revisiting a Darwinian framework for invasion biology. Global Ecology and Biogeography 23: 1157-1166. doi:10.1111/geb.12221

Girvan M, Newman MEJ (2002) Community structure in social and biological networks. Proceedings of the National Academy of Sciences of the United States of America 99: 7821-7826. doi:10.1073/pnas.122653799

Gross PL, Gross EM (1927) College Libraries and Chemical Education. Science 66: 385-389. doi:10.1126/science.66.1713.385

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecology Letters 14: 407-418. doi:10.1111/j.1461-0248.2011.01594.x

Häder M, Häder S (2000) Die Delphi-Technik in den Sozialwissenschaften Methodische Forschungen und innovative Anwendungen. VS Verlag für Sozialwissenschaften, Wiesbaden, Germany, pp.

Handcock MS, Hunter DR, Butts CT, Goodreau SM, Morris M (2003) statnet: Software tools for the Statistical Modeling of Network Data., pp.

Havemann F (2016) Einführung in die Bibliometrie. Gesellschaft für Wissenschaftsforschung Berlin, pp.

Havemann F, Gläser J, Heinz M (2017) Memetic search for overlapping topics based on a local evaluation of link communities. Scientometrics 111: 1089-1118

Havemann F, Gläser J, Heinz M (2019) Communities as Well Separated Subgraphs with Cohesive Cores: Identification of Core-Periphery Structures in Link Communities. . In: Aiello LM, Cherifi C, Cherifi H, Lambiotte R, Li P, Rocha LM (Eds) Complex Networks and Their Applications VII, , Studies in Computational Intelligence. Springer International Publishing, 219–230

Heger T, Aguilar C, Bartram I, Braga RR, Dietl GP, Enders M, Gibson DJ, Gómez-Aparicio L, Gras P, Jax K, Lokatis S, Lortie CJ, Mupepele A-C, Schindler S, Starrfelt J, Synodinos A, Jeschke JM (2019) The hierarchy-of-hypotheses approach: A synthesis method for enhancing theory development in ecology and evolution. . EcoEvoRxiv. doi:10.32942/osf.io/6a85f

Heger T, Pahl AT, Botta-Dukat Z, Gherardi F, Hoppe C, Hoste I, Jax K, Lindstrom L, Boets P, Haider S, Kollmann J, Wittmann MJ, Jeschke JM (2013) Conceptual Frameworks and Methods for Advancing Invasion Ecology. Ambio 42: 527-540. doi:10.1007/s13280-012-0379-x

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion - implications for conservations. Conservation Biology 6: 324-337. doi:10.1046/j.1523-1739.1992.06030324.x

Hodges KE (2008) Defining the problem: terminology and progress in ecology. Frontiers in Ecology and the Environment 6: 35-42. doi:10.1890/060108

Huston M (1979) A general hypothesis of species diversity. The American Naturalist 113: 81 - 101

Jeschke JM (2008) Across islands and continents, mammals are more successful invaders than birds. Diversity and Distributions 14: 913-916. doi:10.1111/j.1472-4642.2008.00488.x

Jeschke JM (2014) General hypotheses in invasion ecology. Diversity and Distributions 20: 1229-1234. doi:10.1111/ddi.12258

Hi-Knowledge.org. Hi-Knowledge.org [accessed

Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012a) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14: 1-20. doi:10.3897/neobiota.14.3435

Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012b) Taxonomic bias and lack of cross-taxonomic studies in invasion biology. Frontiers in Ecology and the Environment 10: 349-350. doi:10.1890/12.WB.016

Jeschke JM, Heger T (2018) Invasion biology: hypotheses and evidence. CABI, Wallingford, pp.

Jeschke JM, Keesing F, Ostfeld RS (2013) Novel Organisms: Comparing Invasive Species, GMOs, and Emerging Pathogens. Ambio 42: 541-548. doi:10.1007/s13280-013-0387-5

Jeschke JM, Lokatis S, Bartram I, Tockner K (2019) Knowledge in the dark: scientific challenges and ways forward. Facets 4: 423-441. doi:10.1139/facets-2019-0007

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America (vol 102, pg 7198, 2005). Proceedings of the National Academy of Sciences of the United States of America 102: 9990-9990. doi:10.1073/pnas.0504835102

Jeschke JM, Strayer DL (2006) Determinants of vertebrate invasion success in Europe and North America. Global Change Biology 12: 1608-1619. doi:10.1111/j.1365-2486.2006.01213.x

Johnstone IM (1986) Plant invasion windows - a time-based classification of invasion potential. Biological Reviews of the Cambridge Philosophical Society 61: 369-394. doi:10.1111/j.1469-185X.1986.tb00659.x

Jonas H (1979) <<Das>> Prinzip Verantwortung Versuch einer Ethik für die technologische Zivilisation. Insel Verlag, Frankfurt am Main, 423 S. pp.

Jurman G, Riccadonna S, Visintainer R, Cesare F (2011) Biological network comparison via Ipsen-Mikhailov distance. DOI:

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164-170. doi:10.1016/S0169-5347(02)02499-0

Klavans R, Boyack KW (2009) Toward a Consensus Map of Science. Journal of the American Society for Information Science and Technology 60: 455-476. doi:10.1002/asi.20991

Klavans R, Boyack KW (2014) Mapping altruism. Journal of Informetrics 8: 431-447. doi:10.1016/j.joi.2014.02.002

Kowarik I, Pysek P (2012) The first steps towards unifying concepts in invasion ecology were made one hundred years ago: revisiting the work of the Swiss botanist Albert Thellung. Diversity and Distributions 18: 1243-1252. doi:10.1111/ddi.12009

Lapaine M, Usery EL, Ohio Library and Information Network (2017) Choosing a map projection. 1 online resource pp.

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15-26. doi:10.2307/3546992

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223-228. doi:10.1016/j.tree.2005.02.004

Lockwood JL, Cassey P, Blackburn TM (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. doi:10.1111/j.1472-4642.2009.00594.x

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion ecology. Wiley-Blackwell, Chichester, West Sussex, UK, pp.

Lotka AJ (1926) The frequency distribution of scientic productivity. Journal of the Washington Academy of Sciences 16: 317-323

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature Ecology and Evolution 3: 1835-1835. doi:10.1002/ece3.431

MacArthur R (1970) Species packing and competitive equilibrium for many species. Theoretical Population Biology 1: 1-11

MacArthur R, Levins R (1967) Limiting similarity convergence and divergence of coexisting species. American Naturalist 101: 377-385. doi:10.1086/282505

Mahoney PJ, Beard KH, Durso AM, Tallian AG, Long AL, Kindermann RJ, Nolan NE, Kinka D, Mohn HE (2015) Introduction effort, climate matching and species traits as predictors of global establishment success in non-native reptiles. Diversity and Distributions 21: 64-74. doi:10.1111/ddi.12240

Marshakova IV (1973) System of document connections based on references. Nauchno-Tekhnicheskaya Informatsiya Seriya 2- Informatsionnye Protsessy i Sistemy 6: 5

McGeoch MA, Butchart SHM, Spear D, Marais E, Kleynhans EJ, Symes A, Chanson J, Hoffmann M (2010a) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Diversity and Distributions 16: 95-108. doi:10.1111/j.1472-4642.2009.00633.x

McGeoch R, Watkins S, Berry C, Steedman T, Davie A, Byrne J, Hillis S, Lindsay M, Robb S, Dargie H, Oldroyd K (2010b) The Index of Microcirculatory Resistance Measured Acutely Predicts the Extent and Severity of Myocardial Infarction in Patients With ST-Segment Elevation Myocardial Infarction. Jacc-Cardiovascular Interventions 3: 715-722. doi:10.1016/j.jcin.2010.04.009

Meadows DH, Club of Rome, Project on the Predicament of Mankind (1972) The limits to growth a report for the Club of Rome's Project on the Predicament of Mankind. Universe Books, New York, 205 S. pp.

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, Hastings A, Holland M, Holyoak M, Lambrinos J, Moore K, Yokomizo H (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10: 77-94. doi:10.1111/j.1461-0248.2006.00987.x

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecology Letters 9: 726-740. doi:10.1111/j.1461-0248.2006.00908.x

Nations U (1992) Convention on biological diversity. In: Nations U (Ed), pp.

Nations U (2002) CBD Alien species that threaten ecosystems, habitats or species. In: 6 C (Ed), pp.

Newman MEJ (2006) Modularity and community structure in networks. Proceedings of the National Academy of Sciences of the United States of America 103: 8577-8582. doi:10.1073/pnas.0601602103

Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. Physical Review E 69: 026113. doi:ARTN 026113 10.1103/PhysRevE.69.026113

Pons P, Latapy M (2005) Computing communities in large networks using random walks. Computer and Information Sciences - Iscis 2005, Proceedings 3733: 284-293

Prinzing A, Durka W, Klotz S, Brandl R (2001) The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society B-Biological Sciences 268: 2383-2389. doi:DOI 10.1098/rspb.2001.1801

Pulliam HR (2000) On the relationship between niche and distribution. Ecology Letters 3: 349-361. doi:DOI 10.1046/j.1461-0248.2000.00143.x

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? . In: Nentwig We (Ed) Biological Invasions. Springer-Verlag, Berlin,Germany, 97-125

Pyšek P, Richardson DM, Pergl J, Jarosik V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23: 237-244. doi:10.1016/j.tree.2008.02.002

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655-1661. doi:10.2307/2265768

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7: 781-784. doi:10.1111/j.1461-0248.2004.00642.x

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981-993. doi:10.1111/j.1461-0248.2006.00950.x

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmanek M (2000) Plant invasions - the role of mutualisms. Biological Reviews 75: 65-93. doi:Doi 10.1017/S0006323199005435

Richardson DM, Pyšek P (2008) Fifty years of invasion ecology - the legacy of Charles Elton. Diversity and Distributions 14: 161-168. doi:10.1111/j.1472-4642.2008.00464.x

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - Global biodiversity scenarios for the year 2100. Science 287: 1770-1774. doi:DOI 10.1126/science.287.5459.1770

Schulz AN, Lucardi RD, Marsico TD (2019) Successful invasions and failed biocontrol: The role of antagonistic species Interactions. BioScience: 1-14. doi:10.1093/biosci/biz075

Settele J, Hammen V, Hulme P, Karlson U, Klotz S, Kotarac M, Kunin W, Marion G, O'Connor M, Petanidou T, Peterson K, Potts S, Pritchard H, Pysek P, Rounsevell M, Spangenberg J, Steffan-Dewenter I, Sykes M, Vighi M, Zobel M, Kuhn I (2005) ALARM: Assessing LArge-scale environmental Risks for biodiversity with tested Methods. Gaia-Ecological Perspectives for Science and Society 14: 69-72. doi:10.14512/gaia.14.1.20

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17: 170-176. doi:Doi 10.1016/S0169-5347(02)02495-3

Sher AA, Hyatt LA (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. Biological Invasions 1: 107-114

Simberloff D, Gibbons L (2004) Now you see them, now you don't - population crashes of established introduced species. Biological Invasions 6: 161-172. doi:10.1023/B:Binv.0000022133.49752.46

Simberloff D, Holle BV (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21-32

Small H, Sweeney E (1985) Clustering the Science Citation Index Using Co-Citations .1. A Comparison of Methods. Scientometrics 7: 391-409

Stohlgren TJ, Jarnevitch C, Chong GW (2006) Scale and plant invasions: a therory of biotic acceptance. Preslia 78: 405-426

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21: 645-651. doi:10.1016/j.tree.2006.07.007

Swanson DR (1986) Undiscovered Public Knowledge. Library Quarterly 56: 103-118. doi:Doi 10.1086/601720

te Beest M, Le Roux JJ, Richardson DM, Brysting AK, Suda J, Kubešová M, P. P (2012) The more the better? The role of polyploidy in facilitating plant invasions. Annals of Botany 109:

R core developmet team (2008) R: A language and environment for statistical computing. . R Foundation for Statistical Computing Vienna, Austria

Thuiller W, Gallien L, Boulangeat I, de Bello F, Munkemuller T, Roquet C, Lavergne S (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. Diversity and Distributions 16: 461-475. doi:10.1111/j.1472-4642.2010.00645.x

Trujillo CM, Long TM (2018) Document co-citation analysis to enhance transdisciplinary research. Science Advances 4. doi:ARTN e1701130 10.1126/sciadv.1701130

Tydecks L, Jeschke JM, Wolf M, Singer G, Tockner K (2018) Spatial and topical imbalances in biodiversity research. Plos One 13. doi: 10.1371/journal.pone.0199327

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13: 235-245. doi:10.1111/j.1461-0248.2009.01418.x

Velden T, Boyack KW, Gläser J, Koopman R, Scharnhorst A, Wang SH (2017) Comparison of topic extraction approaches and their results. Scientometrics 111: 1169-1221

Vidal-Garcia M, Keogh JS (2017) Invasive cane toads are unique in shape but overlap in ecological niche compared to Australian native frogs. Ecology and Evolution 7: 7609-7619. doi:10.1002/ece3.3253

Wang T, Hu JT, Wang RQ, Liu CH, Yu D (2018) Tolerance and resistance facilitate the invasion success of Alternanthera philoxeroides in disturbed habitats: A reconsideration of the disturbance hypothesis in the light of phenotypic variation. Environmental and Experimental Botany 153: 135-142. doi:10.1016/j.envexpbot.2018.05.011

Weiher E, Keddy PA (1995) Assembly Rules, Null Models, and Trait Dispersion - New Questions Front Old Patterns. Oikos 74: 159-164. doi:Doi 10.2307/3545686

Wickham H (2007) Reshaping Data with the reshape Package. 12 ed, Journal of Statistical Software, pp.

Williamson MH, Brown KC (1986) The analysis and modeling of British invasions. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 314: 505-522. doi:10.1098/rstb.1986.0070

Xie JR, Kelley S, Szymanski BK (2013) Overlapping Community Detection in Networks: The State-of-the-Art and Comparative Study. Acm Computing Surveys 45. doi:Artn 43 10.1145/2501654.2501657

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.
In der Printversion Ihrer Dissertation muss der vollständige Text des Lebenslaufs vorhanden sein.

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.
In der Printversion Ihrer Dissertation muss der vollständige Text des Lebenslaufs vorhanden sein.