RESEARCH ARTICLE

A citation-based map of concepts in invasion biology

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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

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, Tru-

jillo 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:

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

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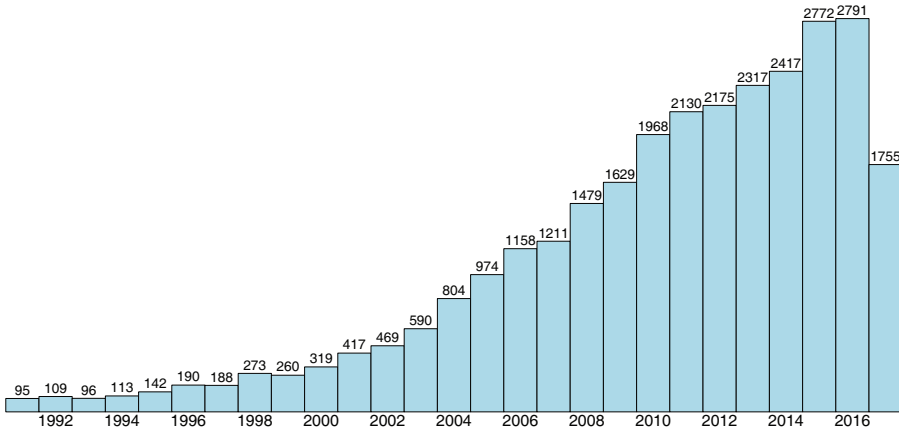
Figure 1. Numbers of publications in invasion biology, using the same search term as Vaz et al. (2017) in the Web of Science. The number of publications in 2017 is relatively low because the search was performed within this year, on 28 August 2017.
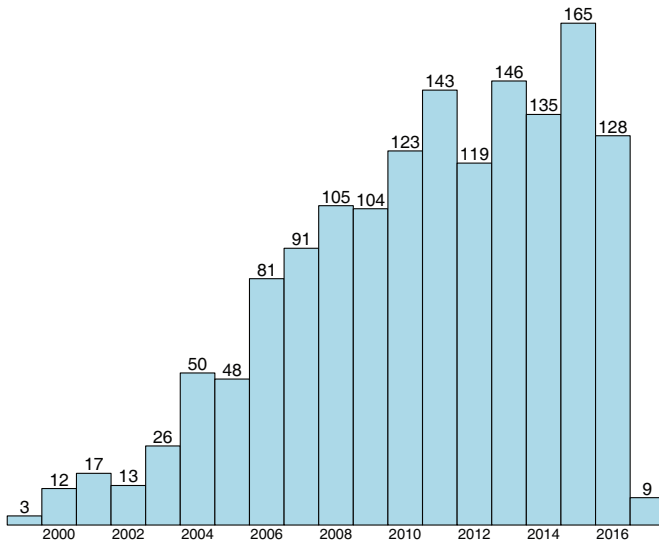

Figure 2. Number of publications per year that cite at least two of the key papers given in Table 1. This sample of 1518 publications was analysed in detail here; it is a subset of the publications shown in Figure 1.

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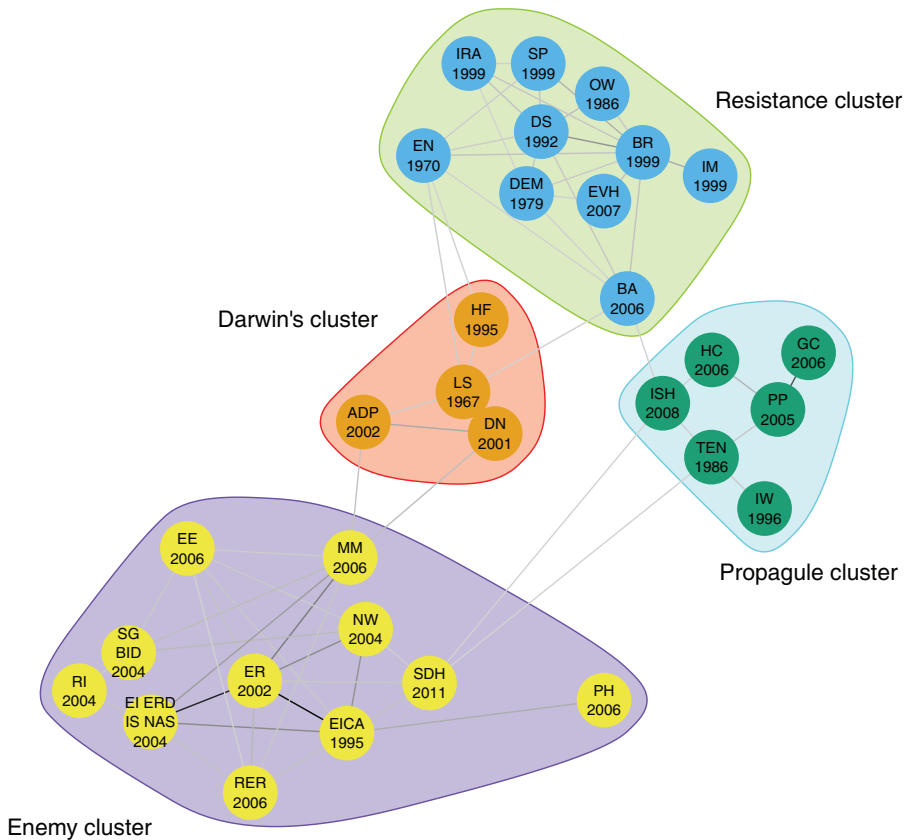
Figure 3. Partition of co-citation network *M* with maximum modularity q = 0.520. Links are weighted with significant co-citation numbers of hypothesis papers (significance level 95%, cf. text). For acronyms of hypotheses see Table 1.

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.

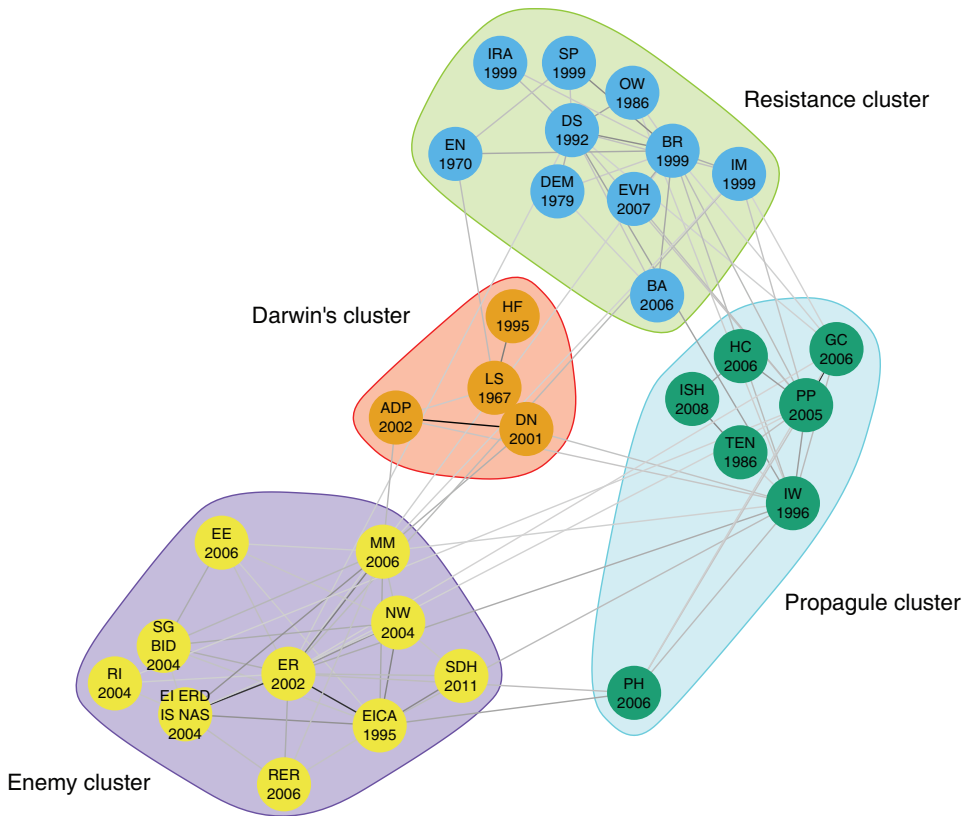| Algorithm	Number of clusters		Modularity	
	M-network	*S*-network	*M*-network	*S*-network
Cluster_optimal	4	4	0.520	0.463
Fast_greedy	4	4	0.520	0.463
Louvain	4	4	0.520	0.463
Leading_eigen	6	4	0.502	0.441
Edge_betweenness	3	5	0.464	0.428
Walktrap	4	5	0.520	0.430

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).

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