

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

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**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.

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## 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. 2012a).

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. (2012a, 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.socisurvey.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; Stohlgren 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:

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

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:

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

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),

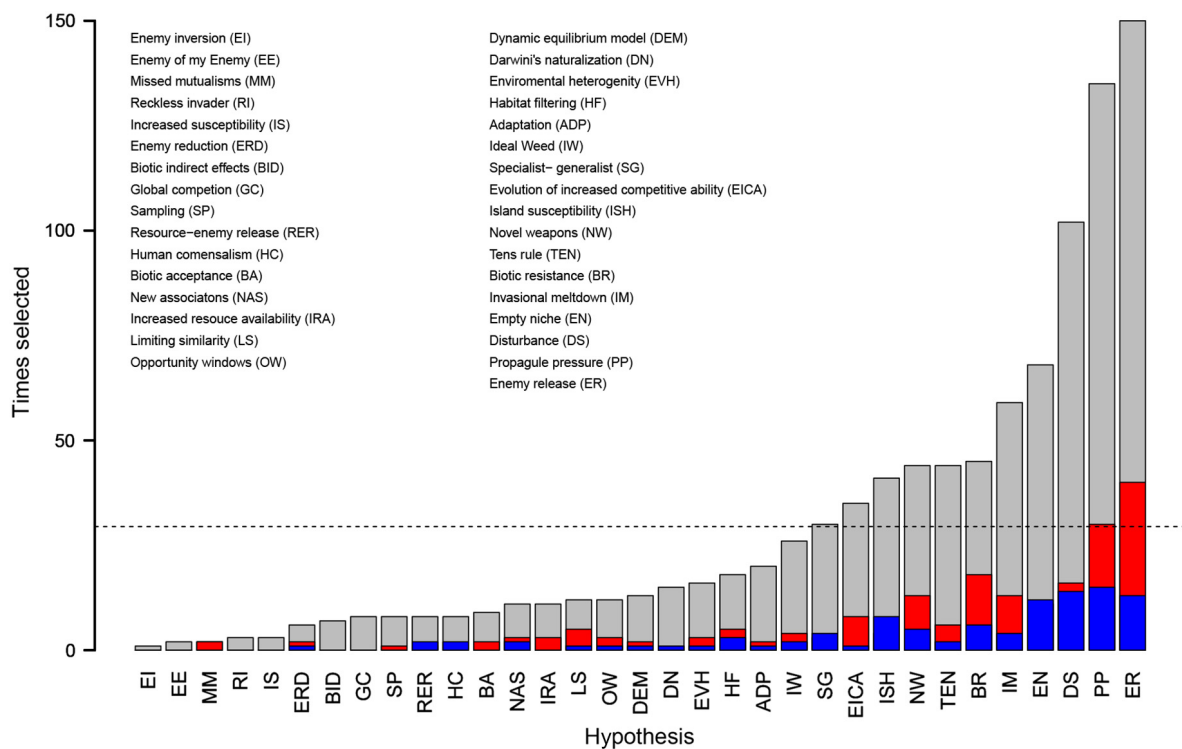


Fig. 1. Number of times each hypothesis was selected by survey participants as those they know best (the dashed line indicates the average across all 33 hypotheses). The red bars indicate the number of times each hypothesis was selected by survey participants who specified their academic position as 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.



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  $8.30 \pm 4.09$  (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  $5.03 \pm 4.95$  (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  $6.45 \pm 2.28$  (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,



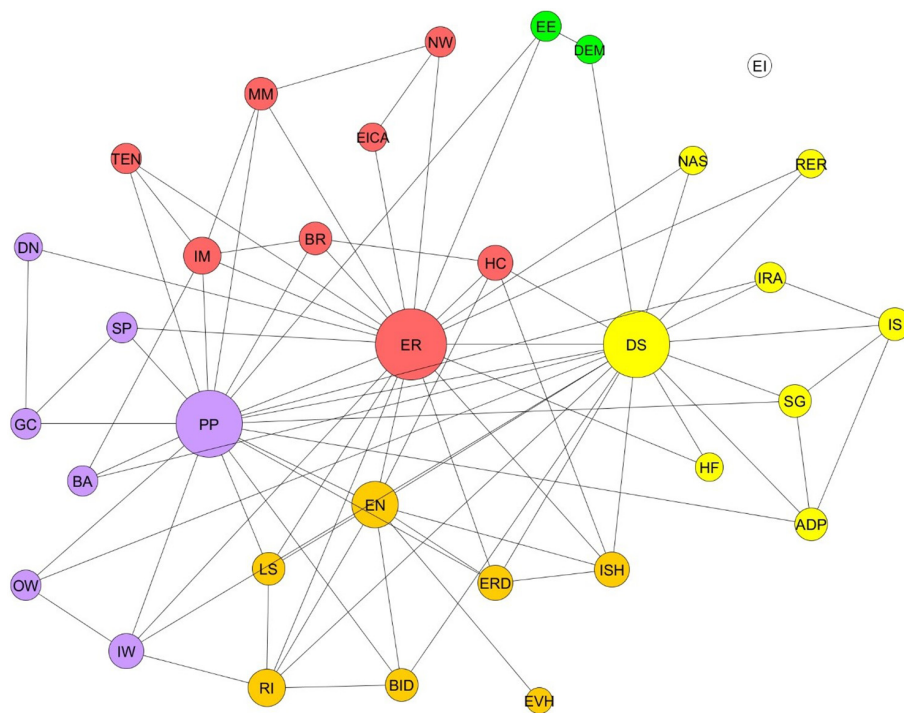


Fig. 3. The joint-mentions network A of invasion hypotheses, based on the participants' responses which hypotheses they know best and standardized by the number of mentions of hypotheses. The degree centrality of a hypothesis is indicated by the size of its circle, and colors indicate different hypothesis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

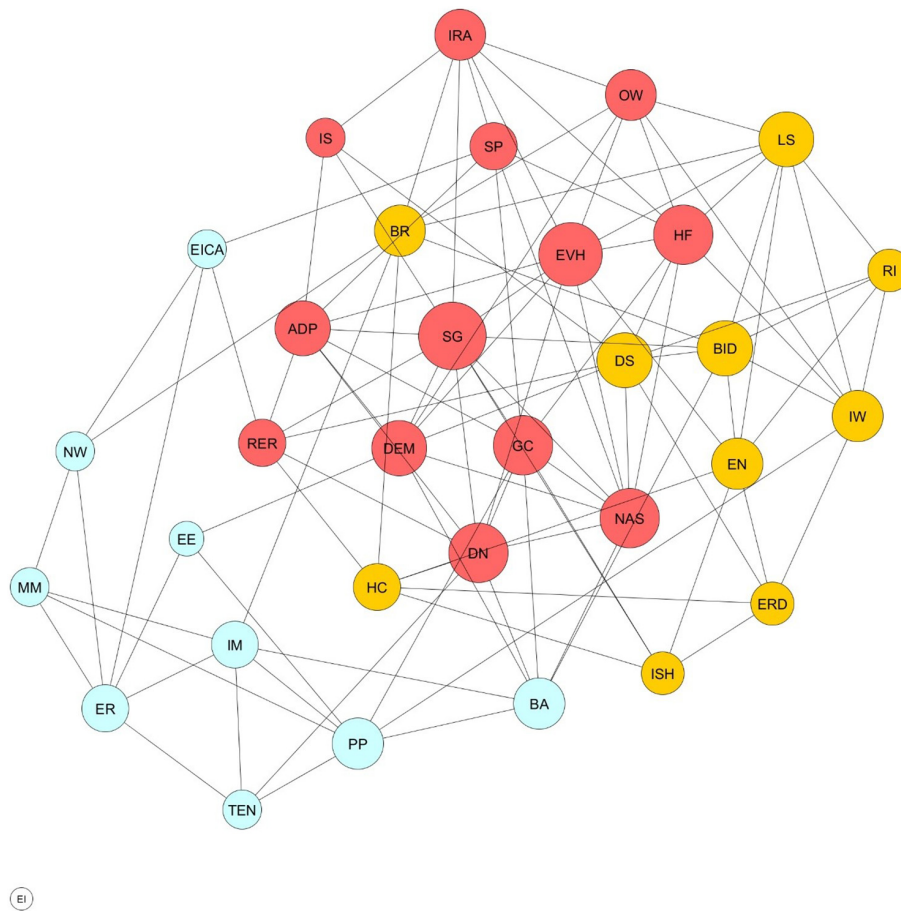


Fig. 4. The joint-mentions network B of invasion hypotheses, based on the participants' responses which hypotheses they know best and standardized by the expected numbers of joint mentions. The degree centrality of a hypothesis is indicated by the size of its circle, and colors indicate different hypothesis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

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### 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>