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Research Idea

Hypothesis Description: Enemy Release Hypothesis

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Abstract

This paper provides a brief overview of a major hypothesis in invasion biology: the enemy release hypothesis. Building on a summary of different previous definitions, we provide the following revised definition: “A reduced pressure by enemies in the non-native range contributes to invasion success.” Further, we suggest formalizing the hypothesis in the basic form ‘subject - relationship - object’ to allow for disambiguating the different existing meanings and enhancing their usability by machines.

Keywords

formalized hypotheses, invasion biology, enemy pressure, non-native range, invasion success

Introduction

This publication is a *Hypothesis Description* paper according to Mietchen et al. (2024) and following the template provided by Heger et al. (2024). It focuses on the enemy release hypothesis (ERH), a major and well-known hypothesis in invasion biology (Enders et al. 2018). The ERH offers a potential explanation for why species are able to establish and spread outside of their native range. To our knowledge, its earliest albeit implicit mention was in a work by the Swiss botanist Albert Thellung (Thellung 1915; see also Kowarik and Pyšek 2012). The publication usually cited as an explicit description is Keane and Crawley (2002), where the hypothesis was formulated specifically for alien plants. Many studies have been designed to study its relevance, for plants as well as other taxonomic groups, and respective reviews as well as meta-analyses abound (Mitchell and Power 2003, Torchin et al. 2003, Colautti et al. 2004, Liu and Stiling 2006, Heger and Jeschke 2014; see also the section 'Reviews and meta-analyses' below).

Along with this widespread use of the ERH came a shift in its definition (see Heger 2022). Jeschke et al. (2012) suggested a very broad definition to capture these different meanings, while Heger and Jeschke 2014 and Heger and Jeschke 2018 suggested several refined versions, which they called ‘sub-hypotheses’.

The previously broad definition suggested by Jeschke et al. (2012), “the absence of enemies in the exotic range is a cause of invasion success”, has some shortcomings that we would like to address here by offering a revised definition. First, the term “absence” does not really capture the intended meaning of this hypothesis, because in the new range, enemies are rarely fully absent. The concept of “enemy release” rather refers to a decrease in enemy numbers and their effects on the non-native organisms. We therefore suggest the formulation “reduced pressure by enemies” instead of “absence of enemies”. “Enemy pressure” is here used to indicate a compound measure of the number of species and individuals of enemies and their individual impacts on invading organisms (see also Heger and Jeschke 2018, Nunes and Kotanen 2018, Najberek et al. 2019, Molleman et al. 2022, Brian and Catford 2023). Second, we suggest replacing “is a cause of invasion success” with “contributes to invasion success”, because this new formulation allows for better alignment with ontologies (e.g. Bucur et al. 2021). The revised definition thus reads as follows: "A reduced pressure by enemies in the non-native range contributes to invasion success."

In the following, we summarize general information about the ERH. We provide a list of definitions or textual descriptions of the ERH and closely related ideas, and a second list with formalized representations of some of the variants of the ERH. These variants include formalized versions of the 'sub-hypotheses' formerly suggested by Heger and Jeschke (2018)Heger and Jeschke 2018. Heger and Jeschke 2018. The aim of this contribution is thus to provide an overview of the various ways the ERH can be interpreted, and deliver citable definitions and formalized versions for them. We hope that this can help disambiguate research around this important hypothesis. The work described here is part

of ongoing efforts to map the landscape of hypotheses in invasion biology (Jeschke et al. 2021) and related fields, such as urban ecology (Lokatis et al. 2023).

General information

Hypothesis name

- Enemy Release Hypothesis

Synonyms

- escape-from-enemy hypothesis
- enemy escape hypothesis
- herbivore escape hypothesis
- predator escape hypothesis
- ecological release hypothesis
- natural enemies hypothesis
- enemy reduction hypothesis

Acronyms

- ERH
- ER

Identifiers

- Wikidata: Q85759287

Domains that make use of this hypothesis

- invasion biology (Wikidata: Q42985020)
- urban ecology (Wikidata: Q1430301)
- restoration ecology (Wikidata: Q2428433)

Reviews and meta-analyses

The following reviews and meta-analyses have been published on the ERH:

Maron and Vilà (2001), Keane and Crawley (2002), Mitchell and Power (2003), Torchin et al. (2003), Colautti et al. (2004), Hinz and Schwarzlaender (2004), Levine et al. (2004), Hierro et al. (2005), Blumenthal (2006), Halpern and Underwood (2006), Liu and Stiling (2006), Mitchell et al. (2006), Reinhart and Callaway (2006), Hänfling (2007), Hawkes (2007), Blakeslee and Byers (2008), Dunn (2009), Ren and Zhang (2009), Chun et al. (2010), Mitchell et al. (2010), Oduor et al. (2010), Lamarque et al. (2011), Roy et al. (2011),

Bezemer et al. (2014), Heger and Jeschke (2014), Blackburn et al. (2015), Prior et al. (2015), Sunny et al. (2015), González-Browne et al. (2016), Meijer et al. (2016), Papacostas et al. (2017), Heger and Jeschke (2018), Zhang et al. (2018), Warren et al. (2021), Chiuffo et al. (2022), Preston et al. (2022), Brian and Catford (2023), Liu et al. (2023).

These studies have been identified via searches in the Web of Science in 2014 and 2016 (Heger and Jeschke 2014, Heger and Jeschke 2018); to find reviews and meta-analyses published after 2016, the search was repeated on 10 January 2024, using the search term "enemy release AND (alien OR exotic OR introduc* OR invas* OR naturali?ed OR nonindigenous OR non-indigenous OR nonnative OR non-native) AND (review OR meta-analyis OR metaanalysis)", and restricting the search to the years 2016-2024.

Related hypotheses

Resource-enemy release hypothesis: “Relative to low-resource plant species, high-resource plant species may be more strongly inhibited by enemies in their native range. [...] Consequently, high-resource species may have greater potential to escape those enemies upon moving to a new range [...] and be more strongly released, relative to native competitors from their new range [...], than are low-resource species.” (Blumenthal 2006, p. 888)

Evolution of increased competitive ability (EICA) hypothesis: "In the absense of herbivores, selection will favor genotypes with improved competitive abilities and reduced resource allocation to herbivore defense." (Blossey and Nötzold 1995, p. 887).

Shifting defense hypothesis: "After having been released from natural specialist enemies, non-native species will allocate more energy to cheap (energy-inexpensive) defences against generalist enemies and less energy to 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" (Enders et al. (2020), p.982, cited after Doorduin and Vrieling (2010)).

Hypothesis definitions

Table 1 provides a list of definitions of the ERH. This list is not a complete list of all definitions that have been used in the literature. It instead focuses on early definitions as well as those that were part of hypothesis compilations.

Table 1.

Different definitions of the ERH, ordered according to the date when they were suggested. The topmost line gives a new suggestion for a revised definition.

Name	Year	Definition	Reference
Enemy release hypothesis	2024	"A reduced pressure by enemies in the non-native range contributes to invasion success"	This publication
Enemy release hypothesis	2023	“Non-native species may rapidly increase in abundance and distribution due to enemy release: the absence, or reduction, of regulation by natural enemies”	Daly et al. (2023), p. 6, based on Keane and Crawley (2002)
Enemy reduction	2020	“The partial release of enemies in the exotic range is a cause of invasion success”	Enders et al. (2018), p. 981, based on Colautti et al. (2004)
Enemy release hypothesis	2012	“The absence of enemies in the exotic range is a cause of invasion success”	Jeschke et al. (2012), p. 3
Enemy release hypothesis	2009	"Upon entry into a new range, invader loses its natural enemies (herbivores, pathogens) that limit its population size in its home (native) range."	Catford et al. (2009)
Enemy release hypothesis	2002	“plant species, on introduction to an exotic region, should experience a decrease in regulation by herbivores and other natural enemies, resulting in an increase in distribution and abundance”	Keane and Crawley (2002), p. 164
Natural enemies hypothesis	2001	"release from specialist natural enemies (herbivores and pathogens) enables exotics to become abundant in their new range. "	Maron and Vilà (2001), p. 362
N/A	1915	Original: “Die starke Ausbreitung neu eingeschleppter Pflanzen hängt meistens damit zusammen, daß nicht nur ihre natürlichen Konkurrenten, die in einer für das Gleichgewicht der Flora und Vegetation sehr förderlichen Weise das starke Überhandnehmen einer einzelnen Art verhindern, in dem neuen Gebiete fehlen, sondern häufig auch gewisse Feinde” Our translation: "The spread of newly introduced plants is usually due to the absence in the new area not only of their natural competitors, which, in a way that is very beneficial for the balance of flora and vegetation, prevents the strong proliferation of a single species, but often also of certain enemies."	Thellung (1915), p. 62

Formalized representation of hypothesis variants

As outlined in the accompanying editorial (Mietchen et al. 2024), expressing hypotheses in a formalized way can have many advantages. In ecology, we are not aware of any existing suggestion for a formalized representation of hypotheses that can be turned into a machine-actionable form. We suggest that representing hypotheses in the form subject - relationship - object can contribute to a clarification of the meaning of textual statements,

and offers the opportunity to highlight the various possible meanings of a hypothesis, thus aiding with disambiguating research on this hypothesis. Here, we made use of a controlled vocabulary for stating the hypothesized relationship, namely the list of relations in the Super Pattern Ontology (Bucur et al. 2021). The use of a controlled vocabulary for expressing hypothesized relationships can contribute to reducing ambiguity, and enhances machine interpretability. This, in turn, can allow the use of AI methodology for processing text and data related to scientific hypotheses.

Table 2 gives suggestions for formalized representations of variants of the enemy release hypothesis. Some of them are based on previous work (see column "Based on"), e.g. also including the sub-hypotheses suggested in Heger and Jeschke (2018), and one that has been developed by the authors for this publication. The first three columns in this table give the respective variant of the ERH in the form 'subject - relationship - object'. Depending on the kind of relationship between subject and object, we suggest classifying the hypotheses as either causal or comparative, which is shown in the fourth column. The rightmost column provides a link to a Wikidata identifier (see Agosti et al. 2022), through which the hypothesis can be further annotated and integrated into the wider linked open data landscape. The entries are ordered according to the date of the associated publication.

Table 2.

Formalized representation of variants of the enemy release hypothesis. For each variant, a Wikidata identifier is given in the table, and a nanopublication is provided in the Nanopublications section and linked from the corresponding Wikidata item. To enable these formalizations, the underlying concepts need to be expressable in some formalized way as well. In most cases, this was done via Wikidata, but this is not necessary; to demonstrate this, the concept "reduced pressure by enemies in the non-native range" was also formalized via a nanopublication (the last one in the Nanopublications section).

Subject	Relationship	Object	Type of hypothesis	Based on	Identifier(s)
reduced pressure by enemies in the non-native range	contributes to	invasion success	causal	This publication	Q122204692
reduced per capita effect of enemies on species in the non-native range	increases	population-level performance of non-native species	causal	Brian and Catford 2023	Q124251906
changed richness and abundance of enemies in the non-native range	increases	population-level performance of non-native species	causal	Brian and Catford 2023	Q124288192
adaptation in response to enemy release in the non-native range	increases	population-level performance of non-native species	causal	Brian and Catford 2023	Q124288203
transport to non-native range	decreases	number of enemies	causal	Heger and Jeschke (2018)	Q124288494

Subject	Relationship	Object	Type of hypothesis	Based on	Identifier(s)
reduced pressure by generalist enemies in the non-native range	contributes to	invasion success	causal	Heger and Jeschke (2018)	Q124288495
reduced pressure by specialist enemies in the non-native range	contributes to	invasion success	causal	Heger and Jeschke (2018)	Q124288498
number of enemies of invasive species	has smaller value than	number of enemies of native species	comparative	Heger and Jeschke (2014)	Q118696022
number of enemies of invasive species in its non-native range	has smaller value than	number of enemies of invasive species in its native range	comparative	Heger and Jeschke (2014)	Q124288505
reduced pressure by enemies in the non-native range	increases	performance of non-native species	causal	Heger and Jeschke (2014)	Q124288510
absence of enemies in the non-native range	contributes to	invasion success	causal	Jeschke et al. (2012)	Q124288516

Outlook

With this hypothesis paper on the enemy release hypothesis, we would like to contribute to a clarification of the meaning of the ERH. For this purpose, we provided a list of existing definitions (Table 1), suggested a revised general definition, introduced formalized representations of different variants (Table 2) and expressed these formalizations as nanopublications (see respective section below).

The overview of the ERH we provide here is to be understood as a first version. Our list of definitions and related meanings of the ERH is most likely incomplete. As emphasized in Mietchen et al. (2024), this newly introduced publication format invites updates. We very much hope that experts working on the ERH or other hypotheses will add content by publishing their own versions and that the approach will be refined over time.

Disclosing the different meanings of hypotheses and formalizing them as suggested in Table 2 can enhance theory development. For example, Heger (2022) suggested representing the ERH as a causal network graph. We presume that future work can build on this and integrate the different causal variants of the ERH into a larger causal network describing hypothesized mechanisms of biological invasions.

Enhancing machine interpretability of statements of the ERH could in the future open up new opportunities for AI applications, including the use of text mining tools for facilitating conceptual synthesis, or data mining tools combined with inductive reasoning for data synthesis (see e.g. Silva et al. 2013). We believe that all of these will be exciting steps forward. We hope that this contribution will therefore be useful for future research on the

ERH as an important mechanism of biological invasions, and that it will also trigger publication of analogous papers on other important hypotheses in ecology and beyond.

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Nanopublications

Nanopublication	Creator	Date
reduced pressure by enemies in the non-native range contributes to invasion success	Tina Heger	01-07-2024 14:41:25
reduced per capita effect of enemies on species in the non-native range increases population-level performance of non-native species	Daniel Mietchen	01-07-2024 14:59:06
changed richness and abundance of enemies in the non-native range increases population-level performance of non-native species	Daniel Mietchen	03-07-2024 06:39:03
adaptation in response to enemy release in the non-native range increases population-level performance of non-native species	Daniel Mietchen	03-07-2024 06:41:09
transport to non-native range decreases number of enemies	Daniel Mietchen	03-07-2024 06:43:29
reduced pressure by generalist enemies in the non-native range contributes to invasion success	Daniel Mietchen	03-07-2024 06:45:51
reduced pressure by specialist enemies in the non-native range contributes to invasion success	Daniel Mietchen	03-07-2024 06:47:57
number of enemies of invasive species has smaller value than number of enemies of native species	Daniel Mietchen	03-07-2024 06:50:55
number of enemies of invasive species in its non-native range has smaller value than number of enemies of invasive species in its native range	Daniel Mietchen	03-07-2024 06:53:18
reduced pressure by enemies in the non-native range increases performance of non-native species	Daniel Mietchen	03-07-2024 07:08:30
absence of enemies in the non-native range contributes to invasion success	Daniel Mietchen	03-07-2024 06:55:58
Class: reduced pressure by enemies in the non-native range	Daniel Mietchen	03-07-2024 07:06:27

Conflicts of interest

The authors have declared that no competing interests exist.
Disclaimer: This article is (co-)authored by any of the Editors-in-Chief, Managing Editors or their deputies in this journal.

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