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Author-formatted, not peer-reviewed document posted on 05/06/2023

DOI: https://doi.org/10.3897/arphapreprints.e107394

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The Enemy Release Hypothesis

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Reviewable v 1

Abstract

The enemy release hypothesis is a major and well-known hypothesis in invasion biology. Building on a summary of different previous definitions, we provide the following revised definition: “A reduced pressure by enemies in the non-native range positively affects 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, nanopublications

Introduction

The enemy release hypothesis (ERH) is a major and well-known hypothesis in invasion biology (Enders et al. 2018). It 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 (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 (e.g. Mitchell and Power 2003, Torchin et al. 2003, Colautti et al. 2004, Liu and Stiling 2006, Heger and Jeschke 2014).

Along with this widespread use came a shift in its definition (see Heger 2022). Jeschke et al. (2012) suggested a very broad definition to capture these different meanings, and

Heger and Jeschke (2018) and Heger and Jeschke (2014) 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 suggestion. First, the term "absence" does not really capture the intended meaning of this hypothesis, because in the new range, enemies are rarely fully absent. We argue that 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, Molleman et al. 2022, Najberek et al. 2019). Second, we suggest exchanging "is a cause of invasion success" with "positively affects invasion success", because this new formulation allows for better alignment with ontologies (e.g. Bucur et al. 2021).

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. The aim of this contribution thus is 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
- herbivore escape hypothesis
- predator escape hypothesis
- ecological release hypothesis

Acronyms

- ERH
- ER

Identifiers

- Wikidata: Q85759287

Domains that make use of this hypothesis

- invasion biology
- urban ecology

Hypothesis definitions

Various definitions have been proposed for the enemy release hypothesis. Even before the name was coined, the general idea had been formulated. Table 1 provides a list of mentions and definitions, including those of closely related ideas.

Formalized representation of hypothesis variants

Representing hypotheses in the form subject - relationship - object provides the opportunity to highlight the various possible meanings of a hypothesis, and thus aids disambiguating research on this hypothesis and assessing its merits in specific contexts. Table 2 gives respective suggestions for formalized representation of the enemy release hypothesis, some of them being based on previous work (see column “Described in”), 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 they have been described.

Outlook

With this contribution, we provide a short summary of existing definitions and meanings of the enemy release hypothesis as one of the most important hypotheses in invasion biology. We suggest that short publications like this one, describing a major hypothesis in greater detail, could be helpful in several respects.

First, 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 enemy release hypothesis as a causal network graph. Future work can build on this and integrate the different causal variants of the ERH in a larger causal network describing hypothesized mechanisms of biological invasions.

Second, linking explicit definitions and formalizations to entries in machine-readable resources like Wikidata will allow for the use of AI-based techniques. As a further step in this direction, we are publishing each formalized hypothesis statement from Table 2 as a separate nanopublication (Groth et al. 2010, Bucur et al. 2023). Nanopublications are assertions of the basic form ‘subject-relationship-object’, with contextual and qualifying information, provenance and publication metadata.

For instance, one of the assertions contained in Rodda and Savidge (2007) could be expressed with "Boiga irregularis" as the subject, "Guam" as the object and "invasive to" as the relationship between subject and object, and to assist disambiguation, each of these three components would be expressed using suitable identifiers (e.g. the Wikidata identifiers Q900781 for "Boiga irregularis", Q16635 for "Guam" and P5588 for "invasive to"). If multiple publications containing this assertion were annotated accordingly, their metadata (e.g. their publication date or language) could then be used in various ways, e.g. for filtering, aggregation or visualization purposes. If multiple publications have more than one formalized assertion each, then it becomes possible to further analyze which assertions - or their components - occur together, as well as how that varies over time or across taxa, locations or languages. Enhancing machine readability of research outputs in these ways can significantly enhance the possibilities for searching, finding, analyzing and summarizing existing knowledge, in invasion biology and beyond.

While the nanopublication approach can be applied to many different kinds of information, our initial focus is on capturing the key components of invasion biology hypotheses. We therefore encourage others to publish similar papers on other hypotheses, in invasion biology and other domains. A respective suggestion for a template can be found in Suppl. material 1, and we welcome comments on it.

Acknowledgments

This research was supported by the VolkswagenStiftung (grant number 97 863; Jeschke et al. 2021) and the Deutsche Forschungsgemeinschaft DFG (HE 5893/8-1; Heger et al. 2022).

Nanopublications

Nanopublication	Creator	Date
URI	Daniel Mietchen	30-05-2023 09:38:58
URI	Daniel Mietchen	30-05-2023 08:34:05
URI	Daniel Mietchen	01-06-2023 06:22:45
URI	Daniel Mietchen	01-06-2023 06:34:08
URI	Daniel Mietchen	30-05-2023 09:03:33
URI	Daniel Mietchen	01-06-2023 06:50:20
URI	Daniel Mietchen	01-06-2023 09:51:30
URI	Daniel Mietchen	01-06-2023 10:01:32
URI	Daniel Mietchen	30-05-2023 09:25:02

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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https://doi.org/10.3897/arphapreprints.e107394

Table 1.

Some variants of the enemy release hypothesis and their definitions, ordered according to the date they have been suggested. The topmost line gives a new suggestion for a revised definition.

Name	Year	Definition	Reference
Enemy release hypothesis	2023	A reduced pressure by enemies in the non-native range positively affects 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 (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
Resource - enemy release hypothesis	2006	“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
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 (2002), p. 164
N/A	1915	“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”	Thellung (1915), p. 62

Table 2.

Formalized representation of different 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 too. In most cases, this was done via Wikidata, but this is not necessary, so to demonstrate this, the concept "reduced pressure by enemies in the non-native range" was instead formalized via a nanopublication (the ninth and last one in the Nanopublications section).

Subject	Relationship	Object	Type of hypothesis	Described in	Identifier(s)
reduced pressure by enemies in the non-native range	positively affects	invasion success	causal	This publication	Q118695994
transport to exotic range	negatively affects	number of enemies	causal	Heger and Jeschke (2018)	Q118610641
reduced pressure by generalist enemies in the non-native range	positively affects	invasion success	causal	Heger and Jeschke (2018)	Q118696014
reduced pressure by specialist enemies in the non-native range	positively affects	invasion success	causal	Heger and Jeschke (2018)	Q118696019
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 the invaded range	has smaller value than	number of enemies of invasive species in the native range	comparative	Heger and Jeschke (2014)	Q118696024
reduced pressure by enemies in the non-native range	positively affects	performance of non-native species	causal	Heger and Jeschke (2014)	Q118696030
absence of enemies in the exotic range	positively affects	invasion success	causal	Jeschke et al. (2012)	Q118696034

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Supplementary material

Suppl. material 1: Draft Template for a Hypothesis Paper

Authors: Tina Heger, Daniel Mietchen, Jonathan M. Jeschke
Data type: Open Document Format file for word processing
Brief description: This template outlines suggested sections for manuscripts describing a formalization of a hypothesis, especially in invasion biology. The format was designed for simplicity to facilitate adoption, and it can be easily extended to capture additional information, e.g. instructions for falsification or generalization, taxonomic or geographic scope, etymology, or relevant information in other languages.
Download file (16.12 kb)