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DOI: https://doi.org/10.3897/arphapreprints.e140550

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Hypothesis Descriptions: Darwin's Naturalization Hypothesis

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Abstract

In this contribution of the *Hypothesis Description* series, we provide an overview of one of the longest-standing hypotheses in invasion science: Darwin's naturalization hypothesis. We present a brief summary of past definitions and propose the revised definition "low phylogenetic similarity between non-native species and the recipient community increases invasion success". This formulation follows the basic form 'subject – relationship – object', enabling clarity for future research and computational applications in invasion biology. We also provide formalized definitions for previous formulations of the hypothesis and identify both related and opposite hypotheses to Darwin's naturalization hypothesis.

Keywords

invasion hypothesis; invasibility; invasiveness; nanopublications; relatedness

1. Introduction

Since the inception of invasion science, numerous hypotheses have been proposed to shed light on why certain communities harbor a greater abundance or richness of invasive species in comparison to others, and why not all non-native species become invasive. In this Hypothesis Description paper, as proposed by Mietchen et al. (2024), we introduce one of the oldest hypotheses in the field, which was posed by Charles Darwin in The Origin of Species (Darwin 1859) and that is now known as "Darwin's naturalization

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hypothesis". In his iconic book, Darwin wrote: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them" (Darwin 1859; p. 60). Since Darwin's first formulation, the hypothesis has been referred to as "Darwin's theory" (Rejmánek 1996) and "Darwin's invasion hypothesis" (Schaefer et al. 2011), while Daehler (2001) was to our knowledge the first publication to refer to it as "Darwin's naturalization hypothesis".

Darwin's naturalization hypothesis offers an explanation as to why some communities are invaded more than others, and thereby provides the basis for predicting biotic resistance, namely a community's ability to reduce or prevent invasions. The hypothesis draws from classical niche theory and poses that non-native species are unable to establish and increase in abundance if the species in the recipient community already have a high niche overlap with the non-native species (MacDougall et al. 2009), resulting in intense competition or shared enemies (Cadotte et al. 2018).

Using observations from the flora of the US, Darwin initially hypothesized that closely related species would compete more intensely than species that are less closely related to each other (Daehler 2001). Daehler (2001) slightly changed Darwin's formulation to a more succinct version, proposing that there will be a reduced probability of naturalization by non-native species with native congeners. Duncan and Williams (2002) added to the definition by mentioning that resistance from the recipient community could result from competition, but also from herbivore pressure and/or pathogen attacks. Jeschke and Erhard (2018) formulated the hypothesis in terms of the richness of closely related species in the recipient community. They posited that invasion success of non-native species would be higher in areas with fewer closely related species than in areas that are rich in closely related species.

Although the formulation of the hypothesis has not changed significantly since then, the emphasis has been set on competitive interactions, and more advanced tools to measure relatedness have led to defining non-native/native species relatedness in terms of phylogenetic distances (e.g. phylogenetic nearest neighbor distance) instead of broad taxonomic classification categories. Park et al. (2020) expanded the definition of Darwin's naturalization hypothesis to incorporate the specific mechanisms facilitating invasion success, stating that lack of competitive exclusion resulting from phylogenetic distinctness would facilitate the establishment of non-native species. Although this formulation is more specific, it only refers to the establishment phase of the invasion process. It also restricts biotic resistance to being the result of competitive interactions, overlooking potential antagonistic effects of preadapted herbivores and pathogens that the non-native species might encounter (Duncan and Williams 2002). Indeed, Schaefer et al. (2011) proposed renaming the hypothesis to "Darwin's hypothesis", arguing that Darwin's focus on competition indicates that he had later stages of the invasion process in mind. Since this suggestion was not widely adopted in the literature, our contribution retains the original name as a reference for future studies testing the hypothesis. However, we also mention this alternative name to help avoid confusion in the literature (section 2.2).

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Following Heger et al. (2024), we propose formalizing the definition of Darwin's naturalization hypothesis in a structured format of 'subject – relation - object' to clarify the various interpretations and facilitate computational applications. Specifically, we propose the following formal definition: "Low phylogenetic similarity between non-native species and the recipient community increases invasion success." Here, we build on the increasingly available and comprehensive phylogenetic data across several taxa, expanding the scope of the hypothesis beyond the establishment phase. With this contribution, we compiled a list of early definitions (Table 1) and proposed citable, formalized versions for clarity and accessibility (Table 2). We also identify related or opposing hypotheses to Darwin's naturalization hypothesis in order to provide an overview of this hypothesis' conceptual context. Therefore, this work builds on current mapping efforts for the landscape of hypotheses in the field of invasion biology (Jeschke et al. 2021).

2. General information

2.1. Hypothesis name

Darwin's naturalization hypothesis

2.2. Synonyms

Darwin's theory (Rejmánek 1996); Darwin's invasion hypothesis (Schaefer et al. 2011)

2.3. Acronym

DNH

2.4. Identifiers

- Wikidata: Q116193385

2.5. Domains that make use of this hypothesis

- invasion biology (Wikidata: Q42985020)
- urban ecology (Wikidata: Q1430301)
- restoration ecology (Wikidata: Q2428433)
- synecology or community ecology (Wikidata: Q4420546)

2.6. Reviews, meta-analyses and large-scale analyses

- Fan, S.-y., Yang, Q., Li, S.-p., Fristoe, T. S., Cadotte, M. W., Essl, F., . . . van Kleunen, M. (2023). A latitudinal gradient in Darwin's naturalization conundrum at

the global scale for flowering plants. Nature Communications, 14(1), 6244. doi: 10.1038/s41467-023-41607-w

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2.7. Related hypotheses

Some other hypotheses in invasion science are based on similar mechanisms, such as the "limiting similarity hypothesis" (Emery 2007; MacArthur and Levins 1967), but there are also seemingly contrasting hypotheses, for example the "preadaptation hypothesis" which also goes back to Darwin (1859). This hypothesis states that being closely related to the native community could provide an advantage to non-native species because of shared adaptations to the environment (Darwin 1859). The diametrically opposed hypotheses regarding the influence of phylogenetic relationship between non-native and resident species on invasion success are jointly referred to as "Darwin's naturalization conundrum" (Diez et al. 2008).

Following findings by Enders et al. (2020), other hypotheses related to Darwin's naturalization hypothesis are:

- Empty niche (MacArthur 1970)
- Ecological naivety (Diamond and Case 1986; Ricciardi and Atkinson 2004)
- sland susceptibility (Jeschke 2008)
- Ecological imbalance (Fridley and Sax 2014)

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3. Hypothesis definitions

Table 1. Selection of definitions for the DNH. The table presents the definition according to this publication and early definitions. It is not an exhaustive list, but highlights key definitions used in the literature

4. Formalized representation of hypothesis variants

Table 2. Formalized representations of the variants of Darwin's naturalization hypothesis provided with corresponding Wikidata identifiers. To support these formalizations, the underlying concepts are expressed in a structured, formalized format

5. Outlook

This contribution proposed a unified and concise definition of Darwin's naturalization hypothesis building on previous formulations (Table 1) and following a structured format that can be replicated for other hypotheses in the field of invasion biology and beyond. We also provide formalized representations of previous formulations of this hypothesis (Table 2). Such an effort is necessary to provide a base map, avoiding contradicting or inaccurate interpretations, thereby guiding the development of future empirical and theoretical studies. For instance, clear formulations can aid applications such as the design of communities resistant to invasions during ecological restoration (e.g., Yannelli 2021). Further and as previously stated by Heger et al. (2024), structuring hypothesis formulations in this way improves machine readability, which is particularly important for AI applications. We also hope that other experts will build on our effort by updating this contribution in the future or following the format used in this series to contribute with descriptions of other hypotheses.

Acknowledgements

This publication was financially supported by the Deutsche Forschungsgemeinschaft (HE 5893/8-1), the VolkswagenStiftung (97 863), and the Alexander von Humboldt Stiftung through the Feodor Lynen Fellowship granted to FAY.

Conflicts of interest

The authors have declared that no competing interests exist.

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Table 1.

Selection of definitions for the DNH. The table presents the definition according to this publication and early definitions. It is not an exhaustive list, but highlights key definitions used in the literature.

Name	Year	Definition	Reference
Darwin's naturalization hypothesis	2024	Low phylogenetic similarity between non-native species and the recipient community increases invasion success	This publication
Darwin's naturalization hypothesis	2023	"Native species in a regional flora could reduce the chances of naturalization for closely related aliens. This is because close relatives should compete more intensely with each other and also because natural enemies of native species might also attack the closely related alien species"	Fan et al. (2023), p. 2
Darwin's naturalization hypothesis	2020	"Lack of competitive exclusion would facilitate the establishment of alien invaders phylogenetically distinct from the native flora"	Park et al. (2020), p. 10904
Darwin's naturalization hypothesis	2018	"Species invade assemblages with distantly related species because they are less likely to overlap in resource requirements; thus, competition will not be as severe."	Cadotte et al. (2018), p. 663
Darwin's naturalization hypothesis	2018	"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."	Jeschke and Erhard (2018), Enders et al. (2020), p. 981
Darwin's naturalization hypothesis	2016	"Alien species more distantly related to native communities are more likely to naturalize" "Alien species more closely related to native communities are less likely to invade, based on the premise that native species more closely related to alien invaders tend to share more similar niches (i.e. phylogenetic niche conservatism) with them, and thus offer stronger biotic resistance"	Ma et al. (2016), p. 1
Darwin's naturalization hypothesis	2010	Immigrant species that are phylogenetically unrelated to the native species will be more likely to naturalize because they may harbor different traits and possibly exploit distinct niches than native species.	Thuiller et al. (2010)
Darwin's naturalization hypothesis	2008	"It has been suggested that alien species with close indigenous relatives in the introduced range may have reduced chances of successful establishment and invasion"	Procheş et al. (2008), p. 5
Darwin's naturalization hypothesis	2002	"Darwin proposed that introduced plant species will be less likely to establish a self-sustaining wild population in places with congeneric native species because the introduced plants have to compete with their close native relatives, or are more likely to be attacked by native herbivores or pathogens"	Duncan and Williams (2002), p. 608
Darwin's naturalization hypothesis	2001	"Competition from species in native genera reduces naturalization by alien congeners" "Reduced probability of naturalization by species with native congeners"	Daehler (2001), p 327-8
Darwin's naturalization hypothesis	1859	"As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them"	Darwin (1859), p. 60

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Table 2.

Formalized representations of the variants of Darwin's naturalization hypothesis provided with corresponding Wikidata identifiers. To support these formalizations, the underlying concepts are expressed in a structured, formalized format

Subject	Relationship	Object	Type of hypothesis	Based on	Identifier(s)
Low phylogenetic similarity between non-native species and the recipient community	increases	invasion success	Causal	This publication	Wikidata: Q130364728
Absence of congeneric species in the non-native range	positively affects	invasion success	Causal	Procheş et al. (2008); Daehler (2001); Duncan and Williams (2002)	Wikidata: Q130364821
Lack of competitive exclusion between phylogenetically dissimilar exotic and native species	positively affects	invasion success	Causal	Park et al. (2020)	Wikidata: Q130364977
Invasion success in ecosystems poor in closely related species	has larger values than	invasion success in ecosystems rich in closely related species	Comparative	Jeschke and Erhard (2018)	Wikidata: Q130364988
Phylogenetic similarity between invading species and the native community	negatively affects	invasion success	Causal	Ma et al. (2016), Fan et al. (2023)	Wikidata: Q130365000