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Hypothesis Description: Darwin's Naturalisation 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 naturalisation hypothesis. We present a brief summary of past definitions and propose the revised definition "high phylogenetic distance 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 formalised definitions for previous formulations of the hypothesis and identify both related and opposite hypotheses to Darwin's naturalisation hypothesis.

Keywords

invasion hypothesis, invasibility, invasiveness, nanopublications, relatedness

Introduction

Since the inception of invasion science, numerous hypotheses have been proposed to shed light on why certain communities harbour 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 naturalisation 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 naturalisation 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 naturalisation hypothesis”. Darwin’s naturalisation 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). Community resistance, as described by these mechanisms, acts as the opposite of invasion success, limiting the establishment and spread of non-native species. Using observations from the flora of the US, Darwin initially hypothesised that closely-related species would compete more intensely than species that are less closely related to each other, based on the assumption that relatedness serves as a proxy for niche overlap (Daehler 2001). Daehler (2001) slightly changed Darwin’s formulation to a more succinct version, proposing that there will be a reduced probability of naturalisation 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. Furthermore, 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 over time, the emphasis has been set on competitive interactions and, recently, more advanced tools to measure relatedness have led to defining non-native/native species relatedness in terms of phylogenetic distances (e.g. phylogenetic nearest neighbour distance) instead of broad taxonomic classification categories. In this line, Park et al. (2020) expanded the definition of Darwin’s naturalisation hypothesis, stating that lack of competitive exclusion resulting from phylogenetic distinctness would facilitate the establishment of non-native species. The mechanism described by Park et al. (2020) builds on previous work exploring the relationship between phylogenetic distances and ecological interactions (e.g. Cavender-Bares et al. (2009)). This formulation is more specific and emphasizes invasion success rather than the resistance of the native community, but 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 pre-

adapted 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 invasion 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 literature, our contribution retains the original name as a reference for future studies testing the hypothesis. This also has the advantage of preventing further confusion with another contrasting hypothesis attributed to Darwin: the pre-adaptation hypothesis. Under this idea, Darwin also suggested that close relatedness to the native community could benefit non-native species through shared adaptations to the environment (Darwin 1859). These opposing hypotheses about the role of phylogenetic distance in invasion success are collectively referred to as “Darwin’s naturalisation conundrum” (Diez et al. 2008). For the sake of completeness and to avoid confusion, we include alternative names (see section 'Synonyms') and identify related or opposing hypotheses to Darwin’s naturalisation hypothesis, thereby also providing an overview of this hypothesis’ conceptual context (see section 'Related hypotheses').

Following Heger et al. (2024), we propose formalising the definition of Darwin’s naturalisation 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: “High phylogenetic distance 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 (section 'Hypothesis definitions') and proposed citable, formalised versions for clarity and accessibility (section 'Formalised representation of hypothesis variants'). Therefore, this work builds on current mapping efforts for the landscape of hypotheses in the field of invasion biology (Jeschke et al. 2021).

General information

Hypothesis name

Darwin’s naturalisation hypothesis

Synonyms

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

Acronym

DNH

Identifiers

- Wikidata: Q116193385

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).

Reviews, meta-analyses and large-scale analyses

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- Procheş Ş, Wilson JRU, Richardson DM, Rejmánek M (2008)Searching for phylogenetic pattern in biological invasions. Global Ecology and Biogeography 17 (1): 5-10. https://doi.org/10.1111/j.1466-8238.2007.00333.x

Related hypotheses

Some other hypotheses in invasion science rely on similar mechanisms, such as the "limiting similarity hypothesis", which posits that that the likelihood of a non-native species successfully invading a community decreases if it closely resembles native species in functional traits (MacArthur and Levins 1967; Emery 2007). There are also seemingly contrasting hypotheses, for example the "pre-adaptation 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 relationships between non-native and resident species on invasion success are jointly referred to as "Darwin's naturalisation conundrum" (Diez et al. 2008).

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

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

Hypothesis definitions

Table 1

Formalised representation of hypothesis variants

Table 2

Outlook

This contribution proposed a unified and concise definition of Darwin's naturalisation 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 formalised 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 using phylogenetic information (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.

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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 literature.

Name	Year	Definition	Reference
Darwin's naturalisation hypothesis	2025	High phylogenetic distance between non-native species and the recipient community increases invasion success	This publication
Darwin's naturalisation hypothesis	2023	"Native species in a regional flora could reduce the chances of naturalisation 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 naturalisation 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 naturalisation 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 naturalisation 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 naturalisation hypothesis	2016	"Alien species more distantly related to native communities are more likely to naturalise". "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 naturalisation hypothesis	2010	(…) "immigrant species that [are] phylogenetic[ally] unrelated to the native species will be more likely to naturalise because they may harbour different traits and possibly exploit distinct niches than native species"	Thuiller et al. (2010)
Darwin's naturalisation 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 naturalisation 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 naturalisation hypothesis	2001	"Competition from species in native genera reduces naturalisation by alien congeners" "Reduced probability of naturalisation by species with native congeners"	Daehler (2001), p 327-8
Darwin's naturalisation 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

Table 2.

Formalised representations of the variants of Darwin's naturalisation hypothesis provided with corresponding Wikidata identifiers. To support these formalisations, the underlying concepts are expressed in a structured, formalised format.

Subject	Relationship	Object	Type of hypothesis	Based on	Identifier(s)
High phylogenetic distance between non-native species and the recipient community	increases	invasion success	Causal	This publication	Wikidata: Q131759376
Absence of congeneric species in the non-native range	increases	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	increases	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