Invasive Species and the Empty Niche Hypothesis – an essay

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Zusammenfassung: Die Ausbreitung von Organismen außerhalb ihres natürlichen Verbreitungsgebiets kann im Zielgebiet zu ökologischen und ökonomischen Problemen führen. Die Wirkmechanismen von Invasivität sind daher von Bedeutung für Grundlagenforschung und für angewandte Wissenschaft. Ob Organismen für „invasiv" gehalten werden, hängt entscheidend von der angelegten Definition ab: Wenn eine Gefährdung bzw. ein Gefährdungspotential Element des Definiens ist, kann eine Art, die im Zielgebiet harmlos ist, nicht „invasiv" sein. Solange die Gefährdung „einheimischer" Organismen in der Definition enthalten ist, können Organismen, die Schäden an Neobiota anrichten, per definitionem nicht „invasiv" sein.
Wiewohl Verbreitung durch menschliche Tätigkeit in allen Definitionen von „invasiv" enthalten ist, kann nicht genug betont werden, dass ohne menschliche Aktivität noch keine Art „invasiv" geworden ist. Tierische oder pflanzliche „Invasionen" zu vermeiden bedeutet also immer, menschliche Tätigkeit verantwortlich zu kontrollieren.
Eine von mehreren Hypothesen zu Mechanismen der Invasivität ist die „Empty Niche Hypothesis". Da verschiedene Definitionen von „ökologische Nische" in Gebrauch sind, stellt sich die Frage, wie eine „leere Nische" entstehen kann. Wenn „ökologische Nische" aufgefasst wird als „Summe aller Interaktionen zwischen einer Art und ihrer Umwelt" oder als „Beruf einer Art", kann es eine leere ökologische Nische nicht geben. Im Konzept der „Günther-Nische" bilden die Anforderungen der Organismen einer Art das System der „autozoischen" Dimensionen und die Gegebenheiten der Umwelt die „ökischen" Dimensionen der ökologischen Nische. Diese ist also ein dynamisches System von Interaktion, sie ist artspezifisch, und sie kann nicht „leer" oder „gefüllt" sein. Das bedeutet notwendiger Weise, dass durch Aussterben einer Art lediglich Umweltgegebenheiten zur Verfügung stehen, die von einer anderen Art genutzt werden können, wodurch aber nicht mehr dieselbe ökologische Nische entsteht.
Organismen werden demnach „invasiv", wenn sie entweder noch nicht genutzte Umweltgegebenheiten erschließen können und sich dadurch die „ökischen Dimensionen ihrer Nische" ändern, oder indem die „autozoischen Dimensionen ihrer Nische" mutieren, oder durch eine Kombination beider Vorgänge. Sie erweitern damit ihre ökologische Nische oder verschieben sie, aber sie „besetzen" keine „leere".

Keywords: ecological niche, Klaus Günther, invasiveness, definitions, empty niche hypothesis

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Introduction

This paper is an essay, not an empirical investigation or a review of the available literature. Species which are alien to a certain area but are nevertheless expanding there, possibly to the detriment of native organisms, are widely regarded as a serious ecological problem. Therefore, the question "what makes a species 'invasive'?" (Rejmánek 1995) has been discussed extensively, and quite a number of hypotheses have been proposed to explain the "invasiveness" of plant and animal species. Kowarik (2010, pp. 138f.) lists five so-called "evolutionary" and 11 "ecological" hypotheses for mechanisms of invasiveness. Among these is the "empty niche hypothesis" (ENH) credited to Elton (1958). Here, I aim at exploring the explanatory value of the ENH and the role of definitions in the discussion on invasiveness.

Invasive Species

Different concepts and definitions of "invasiveness" are in use in the literature, in public discussion, and in legislation. Kowarik (2010 p. 18, tab. 1) gives a detailed definition and a description of the requirements, processes involved, and effects of biological invasions:

> Biological invasion: A process of increase and spread of organisms in areas that they have not reached naturally, but rather by human-facilitated means
>
> Precondition: That dispersal barriers between continents, subcontinents, mainland / islands, biomes, macrochores, or systems of water bodies are overcome by human aid (e.g. by introduction, carry-over, or removal of dispersal barriers)
>
> Processes involved: Transport of organisms or units of dispersal; reproduction, dispersal and establishment of individuals and populations; genetic exchange with other taxa
>
> Effects: Biogeographic, evolutionary, ecological, economic, social (translation: M.S.).

The IUCN provides a different definition:

> An alien species is a species introduced outside its natural past or present distribution; if this species becomes problematic, it is termed an invasive alien species (IAS) (https://www.iucn.org/theme/species/our-work/invasive-species).

The definition by the Convention on Biological Diversity (CBD) is more explicit in stressing the aspect of threat to native organisms:

> An invasive alien species (IAS) is a species that is established outside of its natural past or present distribution, whose introduction and/or spread threaten biological diversity (https://www.cbd.int/invasive/WhatareIAS.shtml).

Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 states:

> "Invasive alien species represent one of the main threats to biodiversity and related ecosystem services …" (para 2), and
>
> "The threat to biodiversity and related ecosystem services that invasive alien species pose takes different forms, including severe impacts on native species …" (para 3)
> (https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32014R1143&from=DE)

Similarly, the Federal Law on the Conservation of Nature (Bundesnaturschutzgesetz – BNatSchG) of 2009 (§7 paragraph 9) defined invasive species as:

> a species whose occurrence outside its natural distribution is a significant potential threat to the native ecosystems, biotopes, and species in those areas (eine Art, deren Vorkommen außerhalb ihres natürlichen Verbreitungsgebiets für die dort natürlich vorkommenden Ökosysteme, Biotope oder Arten ein erhebliches Gefährdungspotenzial darstellt; Translation: M.S.)(https://www.bfn.de/fileadmin/MDB/documents/themen/monitoring/BNatSchG.PDF).

It is obvious that the legal texts stress the threat or negative impacts of aliens on native species; the BNatSchG of 2009 goes further by considering a "significant potential threat". Since there is no scientific criterion of the inception of such a threat, invasion biologists usually prefer the "purely scientific" definition of Kowarik (2010), whereas the legal versions are more in use among experts in nature conservation (Schmidt 2018).

Another aspect of some of the legal definitions is the emphasis on the threat to *native* organisms. One of the paradigmatic invasive species, the Colorado Potato Beetle, *Leptinotarsa decemlineata* (Say, 1824) (Coleoptera: Chrysomelidae), switched hosts in its native range on the eastern slope of the Rocky Mountains from *Solanum rostratum* to *Solanum tuberosum* resulting in it being recorded as a pest in 1859 in Omaha City, Nebraska (Tower 1906, pp. 24f.). Since it was introduced into Europe during the first two decades of the 20th century, it was and still is a pest exclusively on *Solanum tuberosum*, which is native neither to Nebraska nor Europe. The same is also true, e.g., for all invasive pests on *Zea mays* like *Diabrotica virgifera* LeConte, 1858 (Coleoptera: Chrysomelidae). These examples highlight the drawback of legal definitions of invasive species in comparison with the scientific concept.

Ecological Niche

The first to use "niche" in a scientific context was most probably Roswell H. Johnson (1910) who denoted by this term a unit of distribution constrained by food-supply and environmental factors (see Gaffney 1975). Joseph Grinnell (1914, 1917) did not explicitly define the term 'ecological niche' but used it to denote the species-specific food source. In contrast, Charles Sutherland Elton (1927, p. 64) wrote that "the 'niche' of an animal means its place in the biotic environment, its relations to food and enemies", but also "... we may take as a niche all the carnivores which prey upon small mammals ...". This means that Elton left a certain ambiguity as to the species-specificity of the term 'ecological niche'. In 1933, he coined the handy metaphor of the niche as the 'profession' of a species, whereas the habitat is its 'address', which Eugene P. Odum adopted in his 1953 text book (p. 15).

George Evelyn Hutchinson's concept of 'ecological niche' (1958) was and is the most widely accepted in ecology. He described the niche as "an n-dimensional hypervolume ..., every point in which corresponds to a state of the environment which would permit the species ... to exist indefinitely". J. Roughgarden (1972) favoured a non-spatial concept of 'ecological niche', the width of which is defined by "the variety of resources a population exploits". Putman & Wratten (1984) summarised their concept of 'ecological niche' by stating (p. 105) that it is "the sum of all interactions of an organism and its (abiotic and biotic) environment" (see also Schmitt 1991).

Depending on the applied definition of 'ecological niche', an "empty" niche is logically impossible. A "place" can be empty, but neither a "profession", "resources", nor "relationships" can be. Additionally, the species-specificity of the opportunities that could be exploited by an invasive species is not clear from several of the above listed concepts. A little known concept of 'ecological niche' was outlined by Klaus Günther in 1950 that, together with the concept of 'ecological license' by Günther Osche (1966) could provide a terminological framework for scientific explanations (Schmitt 1987). According to Günther, the ecological niche is formed or constituted by two sets of dimensions that overlap to a certain degree. These two sets are (1) the "autozoic" dimensions, i.e. the "features of organisation and behaviour of the respective animal species", and (2) the "oecic", i.e. "the corresponding environmental factors, ….. e.g. ranges of temperature and humidity, the extent of the presence of trees, sand, herbs, elephants, knot-holes, lime, dung, grasshoppers, big stones, pools, bears etc. etc." … "insofar as these two systems of dimensions coincide, the "ecological niche" of any animal species results" (die "ökologische Nische" als die Gesamtheit der besonderen Bedingungen, die einer Tierart das Leben ermöglichen, ist definiert einmal durch die Organisationseigentümlichkeiten eines Tieres und seine Verhaltensweise gegenüber der Umwelt, zum anderen durch die Umweltgegebenheiten, die auf Grund von Organisation und Verhaltensweise des Tieres für dessen Leben unentbehrlich oder günstig oder allenfalls normalerweise belanglos sind …. Die „ökischen" Dimensionen, d.h. die zur Umwelt gehörigen Dimensionen …. z.B. die Schwankungsbereiche von Temperatur und Feuchtigkeit, das Ausmaß des Vorhandenseins von Bäumen, Sand, Kräutern, Elefanten, Astlöchern, Kalk, Dung, Heuschrecken, großen Steinen, Tümpeln, Bären usw. usw. … insoweit diese beiden Dimensionssysteme zur Deckung gelangen, entsteht die „ökologische Nische" jeder Tierart").

In this text, Günther referred to animals throughout, but his concept of "niche" applies to other organisms as well. The "Günther-niche" is non-spatial and can, consequently, be neither "empty" nor "occupied", but is formed or constituted by the individuals of a species interacting with their environment (or rather "umwelt", see Bock & von Wahlert 1965). If a species goes extinct, its ecological niche vanishes necessarily. Only the oecic dimensions formerly constituting part of the niche will then be available and provide "ecological licences" (Osche 1966) for another species to widen or to shift its ecological niche. To summarise: the "Günther-niche" is species-specific, dynamic, and unique.

Non-invasive species can become invasive either by a change of "autozoic" dimensions of their niche, e.g. in reproductive biology, metabolism, morphological features, behavioural abilities etc., or by a change in "oecic" dimensions of their niche, e.g. being transferred to a new environment by human activities, change in temperature or precipitations, or arrival of new possible prey, predators, parasitoids, or vectors.

Discussion

When searching for an answer to the question "what makes a species invasive" (Rejmánek 1995), it is clear that a trivial answer (albeit necessarily true, due to the definition) is "human activity". I am not aware of any case of a species that became spontaneously invasive. Consequently, all attempts to prevent organisms from becoming invasive have to focus on the "human factor". This makes responsible control of human impact on nature imperative. But it is also important to see that different definitions of 'invasiveness' lead to different and possibly unexpected consequences. Under the definitions of the IUCN, CBD, and EU (see above), the Harlequin Ladybird (*Harmonia axyridis*) can be regarded 'invasive' only if its potential to threaten biodiversity is demonstrated. The Colorado Potato Beetle (*Leptinotarsa decemlineata*) or the Western Corn Rootworm (*Diabrotica virgifera*) are not invasive (against common usage) under the BNatSchG 2009 definition because their host plants do not occur naturally in their target areas. Such inconsistencies will not arise under the 'scientific' definition of Kowarik (2010).

Günther's concept of 'ecological niche' provides a clear terminology that points to the fact that each species is unique and its disappearance will not leave an "empty niche" that can be filled by another – e.g. invasive – species. The available "ecological licences" (Osche) can be exploited by another species and get incorporated in its "Günther-niche", but the ecological role of the replacing species will inevitably differ from that of the replaced one. Günther's concept cannot offer direct advice for practical measures against invasive organisms, and it is not the intention of this essay to discuss applied aspects of invasion biology. Applying Günther's approach provides a conceptual framework to understand that in some cases, e.g. in the Colorado Potato Beetle, changes of the oecic niche dimensions are crucial for making a species invasive, whereas in others, e.g. the Harlequin Ladybird, autozoic factors might play an important part (Verheggen & al. 2017), as they acquired semiochemicals that promote their invasive success. The latter case is especially interesting since here symbiotic microorganisms – the microbiome – mediate between organism and umwelt (Vilcinskas 2015), so that the autozoic niche dimensions are composed of the organism's proper requirements plus those of their microbiome. Another example for the impact of autozoic factors in whether a species may become invasive and thus a pest is the potential of *Leptinotarsa* beetles to adapt to potato as host plants within five generations (Aloykhin & al. 2013). At any rate, contrary to what the ENH suggests, an "empty niche" is not a precondition for a species to become invasive. According to the "Günther-niche" concept, it is also possible that a change in the "autozoic" component of the niche allows the organisms of a species to outcompete native competitors and expand their range so that they become "invasive" under any of the above listed definitions.

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