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Constraints and release at different scales – The role of adaptation in biological invasions

Alexandra Erfmeier[a,b,*]

[a]*Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle Wittenberg, Am Kirchtor 1, D-06108 Halle, Germany*
[b]*German Institute for Integrative Biodiversity Research (iDiv), Bio City, Leipzig, Germany*

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Abstract

Attempts to find a consensus on traits promoting the invasiveness of exotic species have agreed on the idiosyncrasy of successful invasions. Despite considerable efforts to integrate aspects of context-dependency into theories of invasions, none of them has provided an evolutionary perspective taking consistently into account the direction of environmental changes in terms of 'constraint' *vs*. 'release'. Applying the filter theory of species sorting, I consider different filters at different scales explaining evolutionary changes during invasions. Within this hierarchical approach, the focus is on the factorial filters climate, abiotic environment and biotic environment, distinguishing trophic interactions and plant-plant interactions. This review summarizes the evidence of adaptive shifts from native to exotic ranges, thereby differentiating the direction of shifts with regard to either constrained or released situations. Following this systematic approach, the present paper identifies further trade-offs within hierarchical levels complementing already existing hypotheses such as those for biotic interactions. In particular, the role of climatic changes should more explicitly be linked with evolutionary responses during invasions. Studying exotic species successfully invading several regions with different environmental conditions will be a promising starting point to enlarge the understanding of context-dependency of invasions.

Zusammenfassung

Auf der Suche nach Merkmalen, welche die Invasivität exotischer Arten fördern, hat sich vor allem herausgestellt, dass erfolgreiche Invasionen sich in ihren spezifischen Eigenheiten unterscheiden. Trotz zahlreicher Bemühungen, die Bedeutung der Kontext-Abhängigkeit in Theorien zu Invasionen zu integrieren, hat bislang kein solcher Ansatz eine evolutionäre Perspektive unter Berücksichtigung der Richtung von Umweltveränderungen im Sinne von Verknappung *vs*. Erleichterung geboten. Unter Anwendung der Filter-Theorie des '*species sorting'* betrachte ich hier Filter, die auf verschiedenen Skalenebenen als

*Correspondence address: Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle Wittenberg, Am Kirchtor 1, D-06108 Halle, Germany. Tel.: +49 345 5526230; fax: +49 345 27228.
E-mail address: alexandra.erfmeier@botanik.uni-halle.de

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Selektionsfaktoren wirken, um evolutionäre Veränderungen im Verlauf von Invasionen zu erklären. Bei dieser hierarchischen Herangehensweise liegt der Fokus auf den faktoriellen Filtern Klima, abiotische Umwelt und biotische Umwelt, letztere getrennt nach Interaktionen zwischen und innerhalb trophischer Ebenen. Das vorliegende Review fasst Beispiele adaptiver Verschiebungen vom Heimatareal zum Invasionsgebiet zusammen und unterscheidet die Richtung der Verschiebung hinsichtlich entweder erschwerter oder erleichterter Bedingungen. Mit Hilfe dieser systematischen Herangehensweise identifiziert die vorliegende Arbeit weitere *trade-offs* innerhalb hierarchischer Levels, welche bereits bestehende Hypothesen zu biotischen Interaktionen, wie beispielsweise EICA, ergänzen. Insbesondere die Rolle von klimatischen Verschiebungen sollte ausdrücklicher mit der Suche nach evolutionären Antworten im Verlauf von Invasionen verbunden werden. Die Untersuchung solcher exotischer Arten, die in mehreren Regionen mit unterschiedlichen Umweltbedingungen expandieren, ist ein vielversprechender Ansatz, das Verständnis der Kontext-Abhängigkeit von Invasionen zu erweitern.

Keywords: Adaptation; Biotic context; Climatic context; Covariates; Environmental context; Hierarchical levels; Species sorting

Introduction

"Nothing in biology makes sense except in light of evolution (Dobzhansky 1973)." This paradigm has guided researchers in invasion biology during the last decades. A large body of studies on invasive plants and animals has suggested that invading populations have experienced evolutionary shifts to cope with environmental changes in the new environments (Lee 2002; Lambrinos 2004; Maron, Vilà, Bommarco, Elmendorf, & Beardsley 2004). Alternative explanations suggest phenotypic plasticity to play an important role in invasions, in particular, in the initial establishment and persistence of a population following introduction. This applies most notably when levels of genotypic diversity, a precondition for selection, are low (Drenovsky et al. 2012). While plasticity can buffer against environmental hazards, it can also be adaptive itself and assist rapid adaptation to new conditions (Nicotra et al. 2010). The most explicit link to evolution in invasion is provided by studying native and invasive populations in a common environment approach, which helps to identify genetic shifts in traits during range expansions. During the last decade, comparisons of native and invasive origins have developed from single case studies (Siemann & Rogers 2001; Leger & Rice 2003), experimental multispecies approaches (Blumenthal & Hufbauer 2007) towards summarizing reviews and meta-analyses (Bossdorf et al. 2005; Colautti, Maron, & Barrett 2009), and some of them have consistently identified increased plant size in invasive populations. However, the attempt to find general patterns with regard to the role of evolutionary shifts during invasions has not been satisfactorily rewarded, yet, and this might be attributable to the fact that different drivers of selection may produce different patterns.

Adaptation is influenced by the strength of local selection, the amount of genetic variance, the demographic cost of maladaptation, but also by the spatial scale of gene flow and the amount of habitat heterogeneity (Hanski, Mononen, & Ovaskainen 2011). However, the strength of local adaptation is also related to geographical distance, which depends on its association with environmental differences and, accordingly, acts as an additional selective agent (Joshi et al. 2001). In consequence, abiotic and biotic factors considerably affect the degree of adaptations encountered during plant invasions. Several attempts have been made to grasp such context-dependency in invasions, including process-oriented ecological frameworks that identified geographic, abiotic, biotic and landscape filters to act subsequently during stages of invasions (Eppstein & Molofsky 2007; Theoharides & Dukes 2007). However, these hierarchical filters can also act as agents of selection. Thus, while awareness is rising for the need to quantify the complexity of co-varying conditions in hierarchical factors across scales (Milbau, Stout, Graae, & Nijs 2009), there is also the need to consider invasions from an evolutionary-explicit perspective to uncover mechanistic relationships.

'Constraint' *vs*. 'release' across hierarchical main factors

Exotic species can encounter more stressful or more beneficial conditions relative to their habitat of origin (Fig. 1). Accordingly, along an environmental gradient, as depicted by the horizontal axis in Fig. 1, the change from native to exotic situations can occur in opposite directions and, thus, be associated with different selection pressures that differentially affect the extent of phenotypic adjustments. While the upper part of the figure represents situations of increasing constraints (transitions (a) and (b) in Fig. 1), the lower part describes the inverse scenario of increasing release, where the relative comparison of native to exotic populations implies changes towards more favourable situations with regard to the focal environmental factor (transitions (c) and (d) in Fig. 1). Conditions of constraints (a, b) imply shifts in functional traits leading to specialization with respect to factors of constraints following mechanisms of classical positive selection, where natural selection is acting to eliminate deleterious variants (Kimura & Ohta 1974). Conversely, under conditions of release (c, d), adaptations in these traits include the abandonment of specialization normally involving costs of construction, which may be allocated elsewhere, *e.g.*, in