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Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis

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Abstract

Biotic resistance is an important component to limiting the spread of invasive plants into native communities. However, under certain conditions native plants may also facilitate invasion, a process identified as biotic assistance. Identifying the conditions that associate with resistance and assistance is needed to better understand the factors driving species invasion.

Substantial theory and empirical work suggests net effects of neighbors may be dependent upon habitat productivity and environmental conditions. How that applies to the interaction among the resident community and the invaders is largely untested. Here we compiled data from 23 articles, which had experimentally determined the strength of biotic resistance and/or assistance. We then combined these data with remote-sensing estimates of productivity, precipitation and temperature at each study site. Using standard meta-analytical techniques we determined the overall effect resident communities had on the emergence, growth, reproduction and survival of non-native invaders. Further, we tested whether the interaction between resident communities and invasive species was influenced by primary productivity, temperature and precipitation.

Across all sites, we found broad support for biotic resistance, while evidence for biotic assistance was rare. However, we found the relative magnitude of biotic resistance on invaders increased with temperature or precipitation; a pattern consistent with the stress gradient hypothesis. In contrast we found no evidence that the strength of biotic resistance varied as a function of primary productivity. Further evaluation of the relationship between productivity and environmental conditions on the direction and strength of the effect of resident species on invaders may help predict invasion establishment and success. Understanding or predicting the susceptibility of communities to invasion may help prioritize management efforts.

Zusammenfassung

Biotische Resistenz ist eine wichtige Komponente für die Begrenzung des Eindringens von invasiven Pflanzen in einheimische Gemeinschaften. Indessen können einheimische Pflanzen unter bestimmten Bedingungen die Invasion begünstigen, ein Prozess, der hier als “biotische Assistenz” (‘biotic assistance’) bezeichnet wird. Die Bedingungen herauszufinden, die mit Resistenz und Assistenz verbunden sind, ist notwendig, um die Faktoren, die die Invasion von Arten steuern, besser zu verstehen. Umfangreiche theoretische und empirische Forschungen legen nahe, dass der Nettoeffekt von Nachbarn von der Produktivität des Lebensraums und den Umweltbedingungen abhängen könnte. Wie dies auf die Interaktion zwischen der vorhandenen Gemeinschaft und den Neuankömmlingen zutrifft, blieb weitgehend ungeprüft. Wir stellten Daten aus 23 Artikeln zusammen, die die Stärke von

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biotischer Resistenz und/oder Assistenz experimentell bestimmt hatten. Für jeden Untersuchungsstandort kombinierten wir diese Daten mit Schätzungen der Produktivität, Niederschlagsmenge und Temperatur aus der Fernerkundung. Mit normalen Techniken der Metaanalyse bestimmten wir den Gesamteinfluss, den die vorhandenen Gemeinschaften auf Keimungserfolg, Wachstum, Reproduktion und Überleben der invasiven Arten ausübten. Wir testeten ebenfalls, ob die Interaktionen zwischen vorhandenen Gemeinschaften und invasiven Arten von Primärproduktion, Temperatur oder Niederschlag beeinflusst wurden. Über alle Standorte hinweg fanden wir breite Unterstützung für biotische Resistenz, während Belege für biotische Assistenz selten waren. Allerdings fanden wir, dass die relative Größe der biotischen Resistenz gegen Invasoren mit der Temperatur oder der Niederschlagsmenge zunahm, ein Muster, welches mit der Stressgradienten-Hypothese übereinstimmt. Dagegen fanden wir keine Belege dafür, dass die Stärke der biotischen Resistenz als Funktion der Primärproduktion variierte. Weitere Untersuchungen zur Beziehung zwischen Produktivität und Umweltbedingungen und der Richtung und Stärke des Einflusses der vorhandenen Artengemeinschaft auf die Invasoren könnten dazu beitragen, Besiedlung und Erfolg von Invasoren vorherzusagen. Die Anfälligkeit von Gemeinschaften gegen Invasionen zu verstehen oder vorherzusagen, könnte helfen, Managementbemühungen zu priorisieren.

Keywords: Abiotic conditions; Biotic assistance; Context-dependence; Competition; Facilitation; Stress gradient hypothesis

Introduction

Biotic resistance is the ability of a resident community to limit recruitment and growth of invasive species (Levine, Adler, & Yelenik 2004). As such, when looking at biotic resistance we tend to assume that the resident community will have a negative effect on invasive species (i.e. competition) (Levine et al. 2004). However, resident communities may also facilitate invasive species establishment, growth and spread (Badano, Villarroel, Bustamante, Marquet, & Cavieres 2007). The processes where native species facilitate exotic species have been termed biotic assistance (Inderjit & Cahill 2015). Biotic resistance or assistance may result from both direct as well as indirect interactions (Bever 2003; Levine et al. 2004; Inderjit & Cahill 2015). Consequently, the outcome of the interaction between native communities and invasive species may range from biotic resistance to assistance (Fig. 1).

The effectiveness of native communities at limiting invasion varies (Lonsdale 1999), and this variation has been partly explained through changes in species richness and phylogenetic diversity within the native community (Dukes 2001; Kennedy et al. 2002; Strauss, Webb, & Salamin 2006; Gerhold et al. 2011). Absent, however, is a broad analysis across species and systems, investigating how habitat productivity and environmental conditions influence the ability of the resident communities to resist, or potentially facilitate invasion (Fig. 1). This is particularly surprising as substantial theory suggests that the intensity and outcomes of plant–plant interactions are dependent upon primary productivity and environmental stress (Grime 1973; Bertness & Callaway 1994). The same may be true for invasive species' effect on the resident community with the strength and direction of this effect varying depending on the habitat's productivity and/or environmental conditions (Fig. 1) (e.g. MacDougall, Boucher, Turkington, & Bradfield 2006).

Plant ecologists have long focused on the relationship between competition and productivity. It has been proposed that competition becomes stronger and influences community assembly as productivity increases, while stressful conditions are more important for assembly at low productivity (Grime 1973). A slightly different model, the stress gradient hypothesis (Bertness & Callaway 1994) proposes that competition is predominant in environments of intermediate productivity, while facilitation occurs more frequently in both highly stressful and highly productive environments. In contrast, an alternative theory proposes that competition is important across a productivity gradient, with different resources being limiting at both ends of this gradient (Tilman 1988). Further, two meta-analyses suggest a general decline in competition with increased productivity and decreased stress (Goldberg, Rajaniemi, Gurevitch, & Stewart-Oaten 1999; Maestre, Valladares, & Reynolds 2005). However, these theories have rarely been tested in the context of invasion and biotic resistance (von Holle 2005, 2013; Chambers, Roundy, Blank, Meyer, & Whittaker 2007; Lortie & Cushman 2007; Harrison, Cornell, & Grace 2015; Reisner, Doescher, & Pyke 2015).

Evidence suggests that environmental conditions and productivity may be important in determining invasion success. For example, invasive species are commonly found invading productive environments with greater resource availability (Stohlgren et al. 1999; Foster, Smith, Dickson, & Hildebrand 2002), however, this is not always the case, as invasive species can also be found invading stressful habitats (Badano et al. 2007; Lortie & Cushman 2007). Although invasive species performance tends to increase under benign, fertile conditions (Dukes & Mooney 1999; Chambers et al. 2007; Gerhardt & Collinge 2007; Goldstein & Suding 2014; Harrison et al. 2015), this advantage can be offset or decreased by the presence of a more resistant community in those areas (Chambers et al. 2007; Eskelinen & Harrison