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BIOTIC RESISTANCE AND FLUCTUATING RESOURCES: KEY FACTORS FOR INVASION SUCCESS?

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ABSTRACT

To explain the process of biological invasion, several hypotheses have been put forward e.g. enemy release hypothesis, invasional meltdown hypothesis, novel weapon hypothesis, fluctuation resources hypothesis, biotic resistant hypothesis, etc. I collected the abstracts from search engines on the internet. I searched for biotic resistance and fluctuation resources hypotheses, collected 25 research papers, and reviewed them. Out of nine studies written for the biotic resistance hypothesis, five were in support and the other five were against the hypothesis. However, there seems only evidence against the fluctuation resources hypothesis. For it, I found four articles in support of this hypothesis. Any hypothesis alone cannot explain the causes behind the invasion's success. Therefore, I have an opinion to establish a combined theory for it.

Key Words: *Biological invasion, Biotic resistance hypothesis, Fluctuation resources hypothesis*

Introduction

Introduction and subsequent establishment of exotic plants in a new region replacing native plant species called biological invasion by plants (Hoffmann & Courchamp 2016). These species that cause biological invasion are of two different types. They are invasive and non-invasive plants. Exotic plants that produce reproductive offspring often in huge numbers far from parent plants and thus have the potential to invade over a large area called invasive species (Pysek et al 2004). Invasive plants cause substantial economic and ecological harm to native ecosystems (Dogra et al 2010).

Loss of native biodiversity, change in structure and functions of ecosystems, reduction in crop production, and domination over native aquatic biota are some negative impacts of biological invasion. Native biodiversity, nutrients, dispersal of propagules, and other anthropogenic activities are the major factors among others that cause the process of biological invasion (Tilman & Lehman 2001).

Hypotheses in Biological Invasion

Several major hypotheses have been put forward to understand biological invasion, but the general applicability of these hypotheses is largely unknown. Out of major hypotheses e.g. invasional meltdown, novel weapons, enemy release, etc are better supported by evidence than other hypotheses e.g. biotic resistance, tens rule, etc. It is shown that experimental support for these hypotheses has declined over time (Jeschke et al 2012). These results have applications for basic and applied research, policy making, and invasive species management, as their effectiveness depends on better hypotheses.

In particular, mutualisms between plants and the animals that disperse, and pollinate them and modification of habitat by both animals and plants seem common and often important in enhancing invasions. Mutual interactions among invaders may well lead to accelerated impacts on native ecosystems and an invasional 'meltdown' process (Simberlof & Holle 1999). Invasional meltdown hypothesis states that the presence of non-native species facilitates the establishment and spread of other non-native species, leading to a positive feedback loop and a cascade of invasions.

One commonly accepted mechanism for alien plant invasions is the enemy release hypothesis, which states that plant species, on introduction to a non-native region, experience a decrease in regulation by herbivores and other natural enemies, resulting in a rapid increase in distribution and abundance (Kaene & Crawley 2002).

Based on native biodiversity and nutrients, there is formulation of two hypotheses i.e. biotic resistance hypothesis (Elton 1958) and fluctuation resources hypothesis (Davis et al 2000) respectively. The biotic resistance hypothesis states that native plants in an area create biological resistance to invasion by processes like herbivory, competition, predation, fungal biota, etc (Levine et al 2004).

The "novel weapons hypothesis" proposes that some invaders transform because they possess novel biochemical weapons that function as powerful allelopathic agents of new plant-soil microbial interactions. Root exudates produced by exotic plants that are usually ineffective against their natural neighbors in their natural range may be highly inhibitory to the native plants in invaded communities. In other words, the novel weapons of some plant invaders provide them with an advantage. The non-palatability of exotic plants to native herbivores is another example. The selective advantage of possessing a novel weapon may result in the rapid evolution of that weapon (Callaway & Ridenour 2004).

The fluctuation resources hypothesis states that the nutrient content in a habitat determines the invasion success. The increase in eutrophication level, mostly the increase in nutrients and very rarely decrease of nutrients invites biological invasion i.e. fluctuation in nutrient resources (Davis et al 2000). The remaining hypotheses proposed so far to explain the invasion success (Jeschke & Heger 2018) are as follows.

The island susceptibility hypothesis states that Islands are more vulnerable to invasion than mainland areas because they have lower species diversity, fewer natural enemies, and more vacant niches.

Disturbance hypothesis: Disturbance, such as fire, flood, or other human activities, creates opportunities for invasion by reducing the abundance and diversity of native species and increasing the availability of resources.

Evolution of increased competitive ability hypothesis: Non-native plants allocate more resources to growth and reproduction than to defense against enemies in the introduced range, resulting in increased competitive ability and invasiveness.

Shifting defense hypothesis: Non-native animals shift their defense strategies from chemical or physical defense against enemies to behavioral or morphological defense against novel predators in the introduced range, resulting in increased survival and invasiveness.

Ten's rule: Only about 10% of non-native species in the introduced range become established and only about 10% of those become invasive.

Phenotypic plasticity hypothesis: Non-native species have higher phenotypic plasticity (the ability to change their traits in response to environmental conditions) than native species, allowing them to adapt to novel environments and cope with environmental heterogeneity.

Darwin's naturalization hypothesis: Non-native species that are phylogenetically distant from native species are more likely to naturalize and become invasive than those that are closely related because they have less competition and more novel traits.

Limiting similarity hypothesis: Non-native species that are functionally similar to native species are less likely to naturalize and become invasive than those that are functionally different because they have more competition and less niche availability

Propagule pressure hypothesis: The number and frequency of individuals introduced to a new region determine the likelihood of establishment and invasion because they increase the genetic diversity and demographic viability of the introduced population.

Biotic resistant hypothesis

In 1958, Charles Elton hypothesized that more diverse communities should be less susceptible to invasion by exotic species. The biotic resistant hypothesis postulates that species-diverged communities are less effective to invasion because food and mates are less common and the intensity of competition within them is high.

Biotic resistance is the ability of native species in a community to limit the invasion of exotic species (Byun & Lee 2007). However, biotic resistance is not widely used to manage invasive plants. An experiment was carried out to find the processes of invasion by *Ageratina altissima* a model invasive species in South Korea. A competition experiment was conducted based on a competition design with *A. altissima* and monocultures or mixtures of resident plants. As an indicator of biotic resistance, a relative competition index was calculated (RCIavg) based on the average performance of *A. altissima* in a competition treatment compared with that of the control; seeds of *A. altissima* were sown. To explain the effect of diversity, several diversity–interaction models were tested. In monoculture treatments, the RCIavg of resident plants was significantly different. Fast-growing annuals had the highest. RCIavg of resident plants was significantly greater in a mixture than in a monoculture. Group identity and diversity of native plant communities were good indicators of biotic resistance to invasion by introduced *A. altissima*. Thus, it can be concluded that the monoculture of natives is less resistant than varieties of natives to exotic aliens.

Biotic resistance is an important factor in limiting the spread of invasive plants into resident communities. However, under certain conditions, native plants may also facilitate invasion. Identifying the conditions that are associated with resistance and assistance is to understand better the factors driving species invasion. Sufficient theory and experimental work suggest net effects of neighbors may be dependent upon habitat productivity and environmental conditions (Stotz et al 2016). But these factors are untested. These data were combined with remote sensing to estimate productivity, precipitation, and temperature at each study site. Using standard meta-analytical techniques, the overall effect resident communities had on the emergence, growth, reproduction, and survival of non-native invaders was determined. Further, it was tested whether the interaction between resident communities and invasive species was affected by primary productivity, temperature, and precipitation. Across all sites, broad support was found for biotic resistance, while evidence for biotic assistance was rare.

Analyses of three terrestrial data sets showed similar patterns, with native herbivores generally preferring exotic plants, while exotic herbivores rarely exhibited a preference. Thus, exotic plants may escape their coevolved herbivores only to be preferentially consumed by the native generalist herbivores in their new ranges, suggesting that native herbivores may provide biotic resistance to plant invasions (Parker & Hay 2005).

Evidence against Biotic resistant hypotheses

The study of soil biota in the context of exotic plants has been the emergence of two biogeographic patterns involving invasive plants and soil microbes. Once, in their non-native ranges invasive plants commonly interact differently with the same soil microbes than resident plants (Rout & Callaway 2012). Next, invasive plants interact with soil microbes differently in their home ranges than they do in their non-native ranges. It is found that these interactions can be described at multiple scales: from individual plants to continents. The microbes support invasive plants than the natives after modifications of their role by aliens.

Imperata cylindrica (invasive to America) grown in logged and unlogged pine forests in an experiment site with high species richness and less species richness showed no significant relationship between the rate of *Imperata* spread (Collins et al 2007).

Biotic resistance, the ability of communities to resist aliens, has become an interest in the research and management communities. It is about the current status and knowledge gaps of biotic resistance in forest ecosystems (Nunez-Mir et al 2017). The biotic resistant hypothesis, which predicts that species-rich communities should be better at resisting invasions than species-poor communities, has been experimentally tested many times and is often poorly supported. In this study, Nunez-Mir contrasted this hypothesis with some alternative hypotheses to find better descriptors of invasion resistance. These alternative hypotheses state that resistance to invasions is determined by abiotic factors, community saturation (i.e., the number of resident species relative to the maximum number of species that can be supported), presence/absence of key species, or weighted species richness. (Weighted species richness is a weighted sum of the number of species, where each species' weight describes its contribution to resistance). It was found that weighted species richness best-predicted invasion success.

Charles Elton (1958) proposed that high species diversity and low disturbance provide biotic resistance against invasions by exotic species. While there is some evidence for this hypothesis, there are numerous other factors associated with invasive species richness, and the strength of those relationships is often scale-dependent. Among oceanic island groups, habitat diversity, human population size, and economic activity have been identified as among the significant drivers of invasive species richness (Ackerman et al 2016).

The understory community was sampled in an old-growth, temperate forest to test alternative hypotheses explaining the establishment of exotic plants. The individual and net importance of distance from areas of human disturbance, native plant diversity, and environmental gradients were measured in determining exotic plant establishment (Gilbert & Lechowicz 2005)**.** Distance from disturbed areas, both within and around the reserve, was not correlated to exotic species richness. Numbers of native and exotic species were positively correlated at large (50 m^2) and small (10 m^2) plot sizes.

Both native and exotic species richness increased with soil pH and decreased along a gradient of increasing nitrate availability. Exotic species were restricted to the upper portion of the pH gradient and had individual responses to the availability of soil resources. These results are inconsistent with both the biotic-resistance and fluctuation resources hypotheses for invasibility. Environmental conditions favoring native species richness also favor exotic species richness, and competitive interactions with the native flora do not appear to limit the entry of additional species into the understory community. It appears that exotic species with niche (function/position) requirements poorly represented in the regional flora of native species may establish with relatively little resistance or consequence for native species richness

Biological invasions are a pervasive and costly environmental problem that is needed to understand intense management and research activities over the past fifty years. Yet accurate predictions of community susceptibility to invasion remain mysterious. The biotic resistance hypothesis, which argues that diverse communities are highly competitive and readily resist invasion, is supported by both theory and experimental studies conducted at small spatial scales. However, there is also convincing evidence that the relationship between the diversity of native and invading species is positive when measured at regional scales (Kennedy et al 2002). Although this latter relationship may arise from external factors, such as resource heterogeneity, that varies with the diversity of native and invading species at large scales

Fluctuation resources hypothesis

The invasion of habitats by non-native plant and animal species is a global phenomenon with potentially negative consequences for ecological, economic, and social systems (Davis et al 2000). Here, it was used insights from experiments and long-term monitoring studies of vegetation. This theory explains that fluctuation in resource availability is identified as the key factor controlling invasibility, the susceptibility of an environment to invasion by non-resident species. The theory is mechanistic and quantitative leading to a variety of testable predictions. It was concluded that the mysterious nature of the invasion process arises from the fact that it depends upon conditions of resource enrichment or release.

An increase in the number of available resources (nutrients) is known to affect the temporal variability of community properties (Li et al 2017). Here an experiment was conducted with a laboratory protist community subjected to selected resources that vary in intensity, duration, and time of supply, and examined the impact of fluctuating resource availability on the temporal variability of the recipient community. The results showed that the temporal variation of total protist abundance increased with the magnitude of resources to native and recipient communities, although the same total amounts of nutrients were added to each community. Meanwhile, the timing effect of fluctuating resources did not significantly alter community variability. Further analysis showed that fluctuating resource availability increased community temporal variability by increasing the degree of community-wide species synchrony and decreasing the stable effects of dominant species. Hence, the importance of fluctuating resource availability is influencing community stability especially when global ecosystems are experiencing high rates of anthropogenic nutrient inputs.

Two common hypotheses, increased resource availability and enemy release, may explain invasion if they favor the same species (Blumenthal et al 2009). This would be expected if plant species adapted to high levels of available resources in their native range are particularly susceptible to enemies, and benefit most from a lack of enemies in their new range. Thus enemy release and increases in resource availability may act in cooperation to favor exotic over native species

Recent theory has suggested a mechanistic relationship between resource availability, competition, and invasibility. A field experiment, in which resources were manipulated with competition, confirmed that changes in resource availability affected competition intensity, which in turn affected invasibility (Davis & Pelsor 2001). It was found that fluctuations in resource availability of as short as a few weeks had a large impact on plant invasion success (survival and percentage cover), including up to 1 year following the fluctuations. If resource availability is a primary mechanism controlling invasibility, it may serve as a unifying concept that can integrate earlier ideas regarding invasibility. The results emphasize the important role of history in the invasion process, particularly the occurrence of random, short-lived events that temporarily reduce or suspend competition and increase invasibility. Therefore, it may be very difficult, or even impossible, to reconstruct the ecology of particular invasions after the fact.

Evidence against fluctuation resources hypothesis

The fluctuating resource hypothesis (FRH) proposes that fluctuations in resource supply can temporally reduce competition from native species, thereby providing temporary opportunities for invading species. Although FRH has the potential to integrate many existing hypotheses regarding mechanisms of community invasibility, previous tests and evaluations of FRH were based on a single trophic level, did not take the timing effect into account, and had difficulties in distinguishing the effects of resource pulses (reserve supply) from other similar processes (Li and Stevens 2012). FRH was tested here in multi-trophic aquatic microcosms by creating resource pulses, controlling resource quantity, propagule supply, and pulse repetition frequency, and manipulating the timing of pulses relative to the timing of the arrival of new invasive species to local communities.

Thus invasion success was positively related to resource pulses, and invaders had strong performance in treatments receiving coincident pulses, although not all invaders gained more benefit when resources were supplied at large magnitude than supplied at continuous rates. Therefore not only fluctuations in resources but also reserve supply rate (pulse rate), timing propagule supply, etc also influence the invasion success (Li and Stevens 2012).

Conclusion

The review of biotic resources and the fluctuation resources hypothesis reveals that there are both supportive and non-supportive views of the biologists. Out of 10 hypotheses for biotic resistance, Elton 1958, Byun & Lee 2007, Levine et al 2004, Stotz et al 2016, Parker & Hay 2005 are in support but Rout and Callaway 2005, Nunez-Mir 2017, Ackerman et al 2016, Gilbert & Lichowicz 2005 and Kennedy et al 2002 are opposing the view of biotic resistant that diverged native communities repel the invasion process. Similarly, out of five articles found in the literature review, four are in support. They are Davis et al 2000 who proposed this hypothesis, Li et al 2017, Bluementhal et al 2009 and, Davis & Pelsor 2001. The only article; Li & Stevens 2012, is against the fluctuation resources hypothesis. It seems that the fluctuation resources hypothesis stands better even today to be approved as a theory. However, the biotic resistant hypothesis has equal criticisms and support. The combined hypothesis may work for biological invasion management.

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