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DR DANIEL MONTESINOS (Orcid ID : 0000-0003-2893-0878)

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Mini-review

Fast invasives fastly become faster: invasive plants align largely with the fast side of the plant economics spectrum

Daniel Montesinos^{1,2*}

¹Australian Tropical Herbarium, James Cook University, McGregor Road, Smithfield, 4878, Queensland, Australia

²Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000, Coimbra, Portugal

*Corresponding author: daniel.montesinos@jcu.edu.au

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Abstract

1. Invasive plants generally align with the *fast* side of the plant's trait economics spectrum, characterised by fast nutrient acquisition, growth, and reproduction. However, there are numerous and notable exceptions, including woody invasives.
2. The generalization that invasives are *fast* is driven by the high occurrence of invasive ruderal species colonising nutrient-rich disturbed habitats, a consequence of anthropogenic disturbance usually going hand-in-hand with biological introductions.
3. Successful invasive plants have shown a remarkable ability to rapidly adapt to the new regions where they are introduced. These changes predominantly involve increased resource acquisition, growth, and reproduction, aligning them even further with the fast side of the plant economics spectrum.
4. Common garden experiments with invasive model systems provide valuable insights about the speed and direction of adaptive responses to different climates, helping us to predict general plant responses to global change.
5. *Synthesis*: Invasive plant species commonly present fast nutrient acquisition, growth, and reproduction, but this general pattern is mostly driven by ruderal species. Still, common garden experiments comparing populations from distant world regions show a clear trend for already "fast" invasive plants to rapidly adapt towards even "faster" traits in their non-native regions.

Key words: alien, biogeography, common garden, disturbance, climate change, plant physiology, ruderal, trade-offs.

Spanish Abstract

1. Las plantas invasoras se encuentran generalmente alineadas en el lado *rápido* del espectro económico de rasgos de las plantas, caracterizado por una adquisición de nutrientes, crecimiento, y reproducción rápido. Sin embargo, existen numerosas y notables excepciones, incluyendo las plantas leñosas invasoras.
2. La generalización de que las plantas invasoras son *rápidas* se debe principalmente a la alta incidencia de plantas invasoras ruderales, que habitualmente invaden hábitats perturbados y ricos en nutrientes. Esto es un resultado lógico del hecho de que las perturbaciones antropogénicas y las introducciones biológicas a menudo se acompañan las unas a las otras.

- Accepted Article
3. Las plantas invasoras exitosas muestran una habilidad notable para adaptarse a las condiciones ambientales con las que se encuentran en las nuevas regiones en las que son introducidas. Estos cambios incluyen, predominantemente, aumentos en la capacidad de adquirir recursos, crecer, y reproducirse, alineándolas aún más en el lado *rápido* del espectro económico de rasgos de las plantas.
 4. Experimentos desarrollados en condiciones de jardín común con plantas invasoras modelo nos desvelan información importante sobre cómo, y a qué velocidad, las plantas pueden adaptarse a climas diferentes. Esto nos permite usar a las plantas invasoras como modelos con los que predecir como las plantas en general pueden responder al cambio climático.
 5. *Síntesis*: Las plantas invasoras a menudo presentan características que les permiten adquirir nutrientes, reproducirse, y crecer rápidamente, aunque este patrón general se encuentra muy influenciado por la alta frecuencia de especies invasoras ruderales. Aún así, experimentos en condiciones de jardín común, comparando poblaciones de regiones distantes del mundo, muestran una clara tendencia en la que plantas invasoras *rápidas* adaptan rápidamente sus rasgos para ser aún más *rápidas* en las regiones no nativas que invaden.

Palabras clave: biogeografía, jardín común, perturbación, cambio climático, fisiología de plantas, ruderal.

The “world-wide fast-slow plant economics spectrum” (Reich, 2014) is a particularly suitable framework for the study of the physiological and life-history trade-offs involved in plant adaptation. Somewhat surprisingly, its explicit use in the field of invasive ecology is rare, even though invasive studies are frequently based on experiments assessing adaptive trade-offs across native and non-native regions. This mini-review aims to bridge this conceptual gap by contextualising invasion research within the framework of the fast-slow plant economics spectrum.

Invasives plants are over-represented at the fast side of the plant economics spectrum

Invasive plants generally grow faster and larger than native species, allocating more resources to leaf-area and shoot growth, and possessing advantageous physiological traits (Dawson et al., 2011; van Kleunen et al., 2010). Invasives tend to have short-lived N-rich leaves that result in faster N cycling and more available N on the invaded communities when compared with uninvaded communities (Castro-Díez et al., 2014; Lee et al., 2017; Liao et al., 2008; Vilà et al., 2011). Invasives also tend to have lower leaf mass per area, and enhanced photosynthetic capacity and nutrient capture (Lake & Leishman, 2004; Peñuelas et al., 2009). Interestingly, while growth rates are significantly higher for invasives than for natives overall, the magnitude of that difference is even larger in the tropics and subtropics than in temperate climates, suggesting that fast growth rates are a requirement for successful invasions in tropical environments (van Kleunen et al., 2010). Plant invasions tend to increase N cycling and pools in the habitats they occupy, mainly via increased N-fixation, but also via a host of other traits associated with fast N turnover, such as low leaf costs, high leaf N content, and short leaf lifespan (Castro-Díez et al., 2014; Pyšek & Richardson, 2007). However, we cannot discard that increased levels of N could be at least partially a consequence of disturbance (Castro-Díez et al., 2014). Regardless, one study estimated that the increase of N cycling and availability as a result of biological invasions can be two to three times more important in tropical forests than in temperate or Mediterranean habitats (Castro-Díez et al., 2014). This might be explained by higher chemical processing at higher temperatures, which suggests that global warming will increase invasive impacts on nutrient cycling in these regions, as long as enough water is available.

Overall, we can generalize that invasive species tend to be located predominantly at the fast side of the plant economics spectrum. Notable exceptions include woody invasives, which were not found to have higher SLA, N content, or photosynthetic rates than other woody natives, or other natives in general (Guo et al., 2018; Ordonez & Olff, 2013). As a result of this difficulty in defining universal invasive profiles,

recent attempts propose that realistic predictive generalisations can only be made within relatively narrow combinations of pathways, habitats, and traits - e.g. “cacti with clonal fragmentation in arid ecosystems” (Novoa et al., 2020).

Ruderal invasives drive overall trends, but invasives are everywhere

Disturbance is generally beneficial for invasive plants (Guo et al., 2018; Jauni et al., 2015; Xiao et al., 2016), and disturbed, nutrient rich habitats are more prone to be invaded by exotics from the fast side of the plant economic spectrum (Davis et al., 2000; Leishman et al., 2010). However, generalizations about specific traits responsible for invasive success are far from universal. For instance, invasive plants tend to be highly efficient in N allocation, but the specific mechanisms used to achieve higher N fixation while incurring in lower metabolic costs than natives are broad ranging (Funk et al., 2013). Both native and invasive plants align with a common axes of leaf carbon strategies, with invasives predominantly occupying the higher end of that spectrum. However, this is mostly driven by the over-abundance of ruderal invasives, and turns out to be independent of whether the species is invasive or native, but rather on the presence of disturbance in the habitats they occupy (Leishman et al., 2010; Xiao et al., 2016). Not only are habitats subjected to high levels of disturbance more prone to be invaded, but they are also the native source of numerous species which are invasive world-wide (Kalusová et al., 2013). In other words, invasive plants tend to predominate in highly disturbed habitats with high resource availability, but increased anthropogenic disturbance goes hand-in-hand with increased alien propagule pressure (Kalusová et al., 2017; Perrings, 2010; Pyšek et al., 2010, 2020) in a reinforcing cycle which explains both the predominance of invasives in ruderal habitats, and the importance of disturbance for successful biological invasions. This does not mean that non-ruderal habitats are impervious to invasion, but rather that disturbance is an important gateway for invasives which are usually introduced first into ruderal habitats, from where they spread to other habitats, most frequently via disturbance (Catford et al., 2012).
impervious

Fast becomes faster

Invasive plants have shown a remarkable ability to rapidly adapt to different conditions across the native and non-native ranges that they occupy (Callaway & Ridenour, 2004; Colautti & Lau, 2015; Hierro et al., 2009, 2020; Maron et al., 2004), frequently presenting distinct genotypes locally adapted to different

climatic niches across biogeographic region (Atwater et al., 2018). Local adaptation can occur so frequently and so rapidly that incipient degrees of reproductive isolation have arisen between populations separated for less than 200 generations, which might be seen as the preliminary stages of allopatric speciation (Irimia et al., unpublished manuscript; Montesinos et al., 2012). Even non-invasive naturalised exotics have been found to develop the same kind of adaptive trait changes (increased growth, size, etc.) as their invasive congeners (García et al., 2013). It is, thus, unsurprising that non-native plant species expand their distribution ranges in several major world regions, in response to climate changes that broaden the availability of feasible environmental envelopes (Pyšek et al., 2020; Seebens et al., 2017).

Two main hypotheses are popular when it comes to explaining how introduction into new locations triggers rapid evolutionary change: The Enemy Release Hypothesis (ERH) and the related Evolution of Increased Competitive Ability (EICA) hypothesis. The ERH states that plants introduced into new non-native regions escape from pathogens and herbivores from the native range that are not present in the non-native range. EICA states that this can improve the fitness of non-native plants via selective changes to resource allocation trade-offs. These changes involve reduced investments into defences -which become unnecessary in the absence of pathogens and herbivores- and increased investments in growth and reproduction (Callaway & Ridenour, 2004; Correia et al., 2016; Hierro et al., 2020; Liu & Stiling, 2006; Maron et al., 2004). Interestingly, biogeographic comparisons of native and introduced populations of invasive plants consistently show species, which already aligned with the fast side of the plant economics spectrum in their native range, adapting in their non-native range towards traits even further along the fast side of the plant economics spectrum (Rotter & Holeski, 2018; Whitney & Gabler, 2008). Non-native species with larger relative growth rates (RGR) have also been found to be more likely to become successful invasives (Grotkopp et al., 2010). However, this trend is not exclusive to ruderal invasives, and non-ruderal woody invasives have also been found to present larger SLA in populations in their non-native range when compared with populations in their native range (Leishman et al., 2014).

Invasives show what is possible for natives

We define alien exotic species as those organisms inhabiting new environments but, as it turns out, many native plants are now experiencing new environments too, as a consequence of global change. Regardless of their relative position on the plant economics spectrum, invasive plants can still thrive under climate niches different from the ones in their sites of origin (Atwater et al., 2018). In fact, all plants experience

selection on resource allocation trade-offs across the plant economics spectrum (Ackerly et al., 2004; Reich, 2014), and we are learning that native species might be able to develop local adaptations just as frequently and rapidly as invasive species (Oduor et al., 2016). The climate-based physiological mechanisms involved in plant invasions have been found to be similar to those involved in range-expanding native species in terms of carbon acquisition, changes in phenology, or biotic interactions (Essl et al., 2019; Leishman et al., 2007; Van der Putten et al., 2010). For instance, enemy release can be an important factor for native plants expanding their distribution ranges in response to climate change (Engelkes et al., 2008; Lakeman-Fraser & Ewers, 2013; Van der Putten et al., 2010). Thus, a better understanding of how climate change affects plant enemies and mutualists can help predictions of plant species range shifts (Heleno et al., 2020; Pugnaire et al., 2019; Rosche et al., 2019; Van der Putten et al., 2010). Interestingly, range expansions can be seen as a double-edged sword which can help to preserve some native species in the face of global change, but can also disrupt the communities being occupied by these range expanding *neo-natives* (Essl et al., 2019; Wallingford et al., 2020). Much like invasive plants, range-expanding natives could impact above- and below-ground communities and alter nutrient cycling and biotic interactions (Pugnaire et al., 2019; Wallingford et al., 2020). Whether native plants experience more beneficial or more detrimental plant-soil feedbacks as a result of global change will be key to understand and predict plant responses to climate change (Pugnaire et al., 2019).

Biogeographical comparisons of native and non-native genotypes developed in common garden experiments are increasingly available, and provide with a unique opportunity to test adaptation across the expanded breadth of the plant fast-slow economic spectrum that individual invasive species show across their native and non-native ranges (Hierro et al., 2005). The focus on invasives sometimes comes with the added benefit of knowing approximate introduction dates, which can be used to infer the speed of local adaptation (Leger & Rice, 2007). Successful invasive plant species present an idiosyncratic array of traits and processes with varying relative importance, conferring them significant advantages under specific conditions (Novoa et al., 2020). Consequently, only a fraction of the numerous exotic species being introduced across the world is able to become highly successful in their new non-native regions (Theoharides & Dukes, 2007). If invasives are to provide insight about the responses of native plants to climate change, we should expect a similarly idiosyncratic divide between successful and unsuccessful natives (Kleunen et al., 2011).

Conclusions

An increasing body of evidence, largely supported by common garden experiments, highlights the importance of fast plant economics for biological invasions, a pattern which is only reinforced by the evidence for natural selection in the non-native range for even faster economics. However, this generalization has numerous and important exceptions, like woody species, and varying degrees of relative importance, such as the difference between tropical vs. temperate habitats. This brief review highlights the importance of ruderal habitats as a gateway for plant invasions, and thus the importance of limiting disturbance to prevent biological invasions, particularly in tropical areas threatened by increasing human encroachment (Laurance et al., 2009). The study of invasion ecology is also highly informative to make general predictions about native plant responses to climate change, and might prove valuable in mitigating the consequences of global change for native plant communities, for instance, by highlighting the importance of preserving above- and below-ground mutualisms, and the importance of the potential loss of natural enemies for resource allocation trade-offs (Pugnaire et al., 2019; Rosche et al., 2019; Van der Putten et al., 2010).

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Data Availability

This review does not use any data.

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