Functional niche differences between native and invasive tree species from the southern Brazilian mixed forest

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Abstract: Biological invasion is a major threat to global biodiversity and ecosystem services. We examined the functional traits similarity between a set of native and non-native invasive tree species from the Southern Brazilian subtropical mixed forest, part of an important global hotspot for biodiversity conservation. We hypothesized that invasive species occupy marginal niche spaces. We ordered the species using the Principal Component Analysis based on their wood density, leaf area, and specific leaf area. These are all important traits that summarize essential ecological strategies associated with resource acquisition and conservation. Functional overlaps between non-native and native species were analyzed through kernel density estimation of continuous traits data. While native and non-native invasive species were distributed along the same functional gradients, the position of non-native species in the functional space is species and traits specific. We concluded that within Brazilian subtropical mixed forests, the functional dissimilarity as a key factor in invasion success could not be generalized for all species and traits.

Key words: alien species, araucaria forest, biological invasion, functional niche space.

INTRODUCTION

Biological invasion is a pervasive expression of the Anthropocene (Kueffer 2017) and a major threat to global biodiversity (Mack et al. 2000, Vilà et al. 2011, Bellard et al. 2016). This is a complex process that is influenced by biotic and abiotic factors (Richardson et al. 2000, Shea & Chesson 2002, MacDougall et al. 2009, Blackburn et al. 2015). Because of its adverse impacts on natural habitats, such as changes in biochemical and hydrological cycles and extinction of native species (Vilà & Hulme 2017), the understanding of invasion drivers has become a significant challenge for conservation biology (van Kleunen et al. 2010, 2015, Frehse et al. 2016, Dechoum et al. 2018).

In general, species may expand its occurrence into regions with environmental conditions similar to or distinct from those found in its natural range (Datta et al. 2019). After taking place in a novel area, interspecific interactions play an essential role in invasiveness (Richardson et al. 2000). For example, release from negative biotic interactions, such as herbivores (Williams & Sahli 2016) and positives feedback (e.g., mycorrhizal fungi fostering invasive species in novel areas) (Urcelay et al. 2019) may favor non-natives to outperform local species (Mitchell et al. 2006, Blumenthal et al. 2009).
Given the importance of interspecific interactions in biological assemblies, the understanding of the invasion process has been based on the ecological niche theories (Levine & D’Antonio 1999, Drenovsky et al. 2012). According to the hutchinsonian concept, the coexistence of species that share similar environmental requirements is limited by competition (i.e., limiting similarity) (Blonder 2018). Following the eltonian niche definition, each species may have a “place” in nature where it can exist (Gibson-Reinemer 2015) and play a functional role (Dehling & Stouffer 2018). Considering that both niche theories take into account ecological dimensions linked to biotic interactions and the use of resources (Miller & Holloway 2017), functional rich biological communities, by showing fewer unused niche spaces, are considered more resistant to invasion (Ricciardi & MacIsaac 2008). In this context, a non-native species may invade a natural community by exploring the same ecological niche of local species through superior fitness or by occupying marginal niche space, i.e., a subset of the hypervolume populated by few native species (Shea & Chesson 2002, Byers 2002, Kueffer et al. 2010). Whether escaping competition by populating marginal niches or displacing other resident species, identifying invasion paths is a fundamental step towards the definition of management strategies (Byun et al. 2018).

In recent years, many ecological studies have focused on the functional traits of invasive species (Lai et al. 2015, Carmona et al. 2016, Funk et al. 2016, Cadotte et al. 2018). By investigating patterns of functional similarities, these researches have enlightened the knowledge about the paths by which non-native species may become invasive (Cadotte et al. 2018, Hulme & Bernard-Verdier 2018). While low functional overlap suggests that invasion occurs in vacant niches (Lambdon et al. 2008), a high overlap indicates that species are influenced by the same environmental filters (Carboni et al. 2016). This pattern is in line with limiting similarity hypothesis, which states that non-native species that are functionally similar to native ones in the resident community are less prone to turn into a successful invader (Bennett 2019).

We examined the functional traits similarity between a set of native and non-native invasive tree species from the Southern Brazilian subtropical mixed forest, part of an important global hotspot for biodiversity conservation. We expect that non-native invasive species occupy marginal functional spaces populated by a few native ones.

**MATERIALS AND METHODS**

**Invasive tree species selection**

Based on the literature (Zenni & Ziller 2011, Guidini et al. 2014, Lazzarin et al. 2015, Nunes et al. 2018), we selected the most conspicuous invasive tree species of the subtropical mixed forest in Southern Brazil, namely *Hovenia dulcis* Thunb (Rhamnaceae), *Ligustrum lucidum* W.T.Aiton (Oleaceae), *Morus nigra* L., *Pinus elliottii* L. and *Pinus taeda* L. (Pinaceae). *L. lucidum* and *H. dulcis* are both native to temperate Asia, being introduced in Brazil as an ornamental urban tree (Ayup et al. 2014) and in small agricultural settlements (Padilha et al. 2015). *Morus nigra* (Moraceae) is native to the mountains of south-west Asia (Whittemore 2006), introduced as domestic orchards. Both *Pinus* are North American species introduced as commercial plantations (Simberloff et al. 2010).

**Functional trait characterization**

We analyzed the following functional traits for both native and invasive species: wood density (g/cm³), leaf area (cm²), and specific leaf area (cm²/g). These traits summarize essential
ecological strategies associated with resource acquisition and conservation (Wright et al. 2004, Chave et al. 2009) that have been described as influential on species invasiveness (Crous et al. 2012, Drenovsky et al. 2012). The wood density, leaf area, and specific leaf area were extracted from the “Banco de Dados de Atributos Funcionais para a Floresta com Araucárias”, available at https://github.com/higuchip/FT_database. This database represents an ongoing effort, carried out since 2013, to characterize the functional traits of tree species (gymnosperms and angiosperms) in the Mixed Subtropical Forest of Southern Brazil. From trees occurring in areas of mixed subtropical forest, functional traits have been characterized by the Pérez-Harguindeguy protocol (Pérez-Harguindeguy et al. 2013). In its current version, the database is composed of 83 species, 1,342 wood samples, and 22,416 scanned leaves. For this study, we filtered the database, extracting only tree species that had at least five functionally characterized individuals.

**Data analysis**

We ordered native and non-native species using a Principal Component Analysis (PCA). For this, all variables were standardized (i.e., values scaled to zero mean and unit variance). By overlapping the convex hulls of native and non-native species in the ordination, we evaluated how each group shares the functional gradients summarized by the PCA axis. Also, we determined the kernel density estimation for each functional trait to find the relative position of non-native invasive species within each specific functional niche. All the analyses were implemented using R (R Core Team 2019), along with ade4 (Dray & Dufour 2007), FactoMiner (Lê et al. 2008), factoextra (Kasambara & Mundt 2017) and ggExtra (Attali & Baker 2018) packages.

**RESULTS**

Among the invasive species, *Morus nigra* presented the largest leaf area (LA=75.0 cm²) and specific leaf area (SLA=319.0 cm² g⁻¹); and *Ligustrum lucidum* showed the highest wood density (WD=0.68 g.cm⁻³) (Table 1). In contrast, *Pinus taeda* had the lowest leaf area (LA=2.6 cm²) and wood density (WD=0.38 g.cm⁻³); and *Pinus elliottii* had the smallest specific leaf area (SLA=42.3 cm² g⁻¹).

The first two axes of the functional ordination explained 38.2 and 33.9% of the total inertia (Fig. 1). While Axis 1 summarized ecological strategies related to leaf area (contribution = 52.06%) and specific leaf area (contribution = 44.73%), Axis 2 was associated with wood density (contribution = 84.80%). Thus, Axis 1 shows a gradient of leaf

<table>
<thead>
<tr>
<th>Species</th>
<th>LA</th>
<th>SLA</th>
<th>WD</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hovenia dulcis</em></td>
<td>58.7</td>
<td>233.9</td>
<td>0.60</td>
</tr>
<tr>
<td><em>Ligustrum lucidum</em></td>
<td>32.6</td>
<td>68.4</td>
<td>0.68</td>
</tr>
<tr>
<td><em>Morus nigra</em></td>
<td>75.0</td>
<td>319.0</td>
<td>0.47</td>
</tr>
<tr>
<td><em>Pinus elliottii</em></td>
<td>3.9</td>
<td>42.3</td>
<td>0.41</td>
</tr>
<tr>
<td><em>Pinus taeda</em></td>
<td>2.6</td>
<td>87.6</td>
<td>0.38</td>
</tr>
</tbody>
</table>

LA: leaf area (cm²); SLA: specific leaf area (cm² g⁻¹); WD: wood density (g.cm⁻³).
traits, with more membranous and larger leaves on the right and more coriaceous and smaller leaves on the left. Axis 2 shows species with higher wood density in the upper part and with lower wood density and larger leaves in the lower part. As suggested by a high convex hull overlapping, both native and invasive species occur along the same functional gradients summarized by the PCA axes.

Although not differing in the distribution along PCA axes, when each trait is considered separated, we observed that results are idiosyncratic, meaning that the occurrence of invasive species along the kernel density estimation of the native's traits values is species and traits specific (Fig. 2). We observe that Hovenia dulcis and Morus nigra have relatively larger and more membranous leaves when compared to the most native species, then occupying marginal leaf functional niches (Fig 2a, b). In the same way, Pinus elliotti, with the smallest SLA, occupies a functional leaf niche with few species (Fig. 2b). For wood density, all exotic species have similar values to most native species (Fig. 2c).

DISCUSSION

Our results suggest that non-native and native species share the same functional gradient (i.e., distribution along both axes of PCA ordination). However, the position of non-native species in the functional space is species and traits specific. For wood density, most invasive and native species shared similar functional space. On the other hand, for leaf traits, some species (e.g., Morus nigra and Hovenia dulcis) occupy marginal spaces. Overall, these results suggest that non-natives may become invasive by exploring different strategies, such as occurring in marginal functional niches or competing in spaces with a higher number of species.

According to the PCA ordination, the most explanatory axis summarized ecological strategies related to leaf traits, which was also

![Figure 1. Functional ordination by the Principal Component Analysis (PCA) for a set of native and non-native invasive tree species from the subtropical mixed forest in southern Brazil. Vectors represent continuous functional traits (mean.la= mean leaf area; mean.sla= mean specific leaf area; mean.wd= mean wood density). Species ordinations delimited by the convex hull according to the origin groups (non-native – blue; native – yellow).](image)
highlighted by an earlier study investigating forests along an altitudinal gradient in the same region (Soboleski et al. 2017). Species frequently observed at higher elevations forests, with perennial and more coriaceous leaves, such as *Pinus* spp. and *Ligustrum lucidum*, were ordered on the left of Axis 1. Conversely, deciduous species with more membranous leaves, such as *Hovenia dulcis*, observed at the lower altitudes, were arranged on the right of Axis 1. In fact, while *Pinus* spp. and *Ligustrum lucidum* are reported as invasive at higher altitudes (Guidini et al. 2014), *Hovenia dulcis* is observed at lower altitudes (Lazzarin et al. 2015) in the region. On a regional scale, the thickness of leaves is often related to temperature gradients (Rosbakh et al. 2015). Therefore, our findings can be associated with adaptations to frosts in higher altitude areas (Soboleski et al. 2017).

Axis 2 is associated with the wood economy spectrum (Chave et al. 2009), summarizing important ecological strategies such as those related to resource acquisition and conservation. Trees with softer wood at the bottom of the ordination, such as *Pinus* spp., are usually pioneers and fast-growing species, specialists of disturbed areas. Otherwise, harder wood species, including *Hovenia dulcis* and *Ligustrum lucidum*, at the top of the ordination, usually, are slow-growing shade-tolerant species. These results suggest that functional traits are a suitable predictor of where a non-native species is likely to invade (van Kleunen et al. 2010).

For the studied tree species, the expectation of functional dissimilarities between non-native and native species (van Kleunen et al. 2010, Lai et al. 2015, Moodley et al. 2013, Tecco et al. 2013, Bezeng et al. 2015) was not confirmed. Although some species occupy marginal leaf functional space, the results are idiosyncratic. This pattern is an indicative that even tree communities with a high intensity of interspecific competition

![Figure 2. Traits Probability Density (TPD) of (a) leaf area (cm²), (b) specific leaf area (cm².g⁻¹) and (c) wood density (g.cm⁻³) for a set of native tree species (black line) from the subtropical mixed forest in southern Brazil. Vertical dashed lines indicate mean traits values for the non-native invasive tree species (red = *Hovenia dulcis*; orange = *Ligustrum lucidum*; green = *Morus nigra*; yellow = *Pinus elliotti*; blue = *Pinus taeda*).](image-url)
may also be susceptible to invasion. When a community is invaded, non-native species may become dominant by replacing native ones through limiting similarity process (MacDougall et al. 2009), then causing biodiversity loss (Bellard et al. 2016) and functional composition changes (Villà et al. 2011, Sodhi et al. 2019).

In summary, our results indicate that exotic tree species may become invasive through different ecological strategies. This pattern reinforces the idea of the complexity of the invasion process, which means that control strategies cannot be generalized to all species.

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