



AGRARIAN SCIENCES

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 positive 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 & Maclsaac 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/cm^3), leaf area (cm^2), and specific leaf area (cm^2/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 influent 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 1. Mean values and standard deviation (between parentheses) of functional traits of invasive tree species in the southern Brazilian subtropical mixed forests (number of trees = 10, number of leaves/tree = 10).

Species	LA	SLA	WD
<i>Hovenia dulcis</i>	58.7 (12.7)	233.9 (9.9)	0.60 (0.05)
<i>Ligustrum lucidum</i>	32.6 (4.7)	68.4 (21.0)	0.68 (0.12)
<i>Morus nigra</i>	75.0 (16.1)	319.0 (162.0)	0.47 (0.03)
<i>Pinus elliottii</i>	3.9 (0.6)	42.3 (3.61)	0.41 (0.02)
<i>Pinus taeda</i>	2.6 (0.4)	87.6 (10.2)	0.38 (0.04)

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

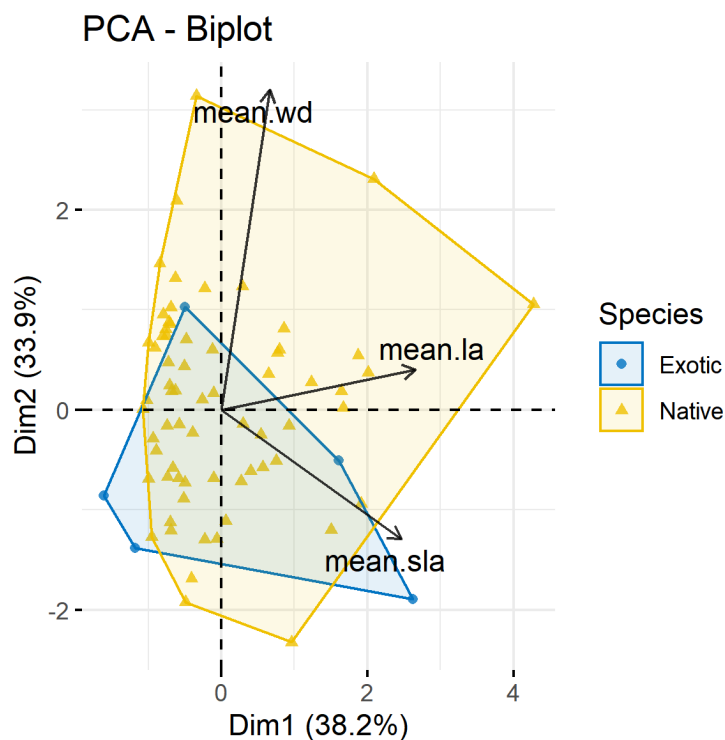


Figure 1. Functional ordination by the Principal Component Analysis (PCA) for a set of native and non-native invasive tree species from the subtropical mixed forest in southern Brazil. Vectors represent continuous functional traits (mean.la= mean leaf area; mean.sla= mean specific leaf area; mean.wd= mean wood density). Species ordinations delimited by the convex hull according to the origin groups (non-native – blue; native – yellow).

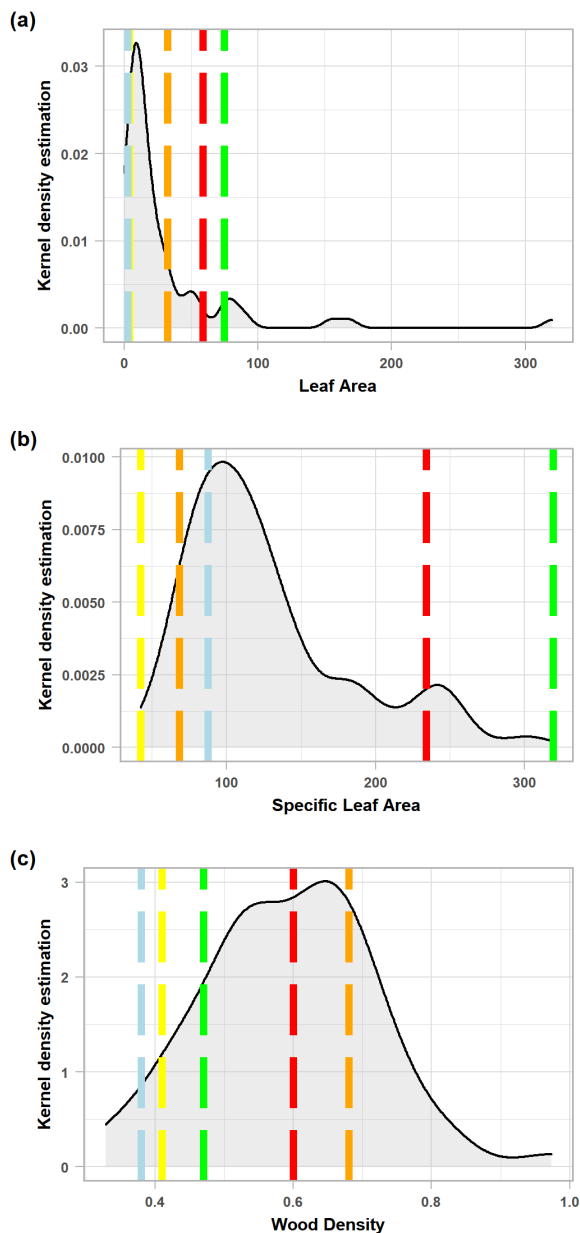


Figure 2. Traits Probability Density (TPD) of (a) leaf area (cm²), (b) specific leaf area (cm² g⁻¹) and (c) wood density (g cm⁻³) for a set of native tree species (black line) from the subtropical mixed forest in southern Brazil. Vertical dashed lines indicate mean traits values for the non-native invasive tree species (red = *Hovenia dulcis*; orange = *Ligustrum lucidum*; green = *Morus nigra*; yellow = *Pinus elliotti*; blue = *Pinus taeda*).

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

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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REFERENCES

- ATTALI D & BAKER C. 2018. ggExtra: Add Marginal Histograms to 'ggplot2', and More 'ggplot2' Enhancements. R package version 0.8. Available at <https://CRAN.R-project.org/package=ggExtra>. Accessed on August 21 2019.
- AYUP MM, MONTTI L, ARAGÓN R & GRAU HR. 2014. Invasion of *Ligustrum lucidum* (Oleaceae) in the southern Yungas: Changes in habitat properties and decline in bird diversity. *Acta Oeco* 54: 72-81.
- BELLARD C, CASSEY P & BLACKBURN TM. 2016. Alien species as a driver of recent extinctions. *Biol Lett* 12(2): 20150623.
- BENNETT JA. 2019. Similarities between invaders and native species: Moving past Darwin's naturalization conundrum. *J Veg Sci* 30(5): 1027-1034.
- BEZENG SB, DAVIES JT, YESSOUFOU K, MAURIN O & BANK MV. 2015. Revisiting Darwin's naturalization conundrum: explaining invasion success of non-native trees and shrubs in southern Africa. *J Ecol* 103(4): 871-879.
- BLACKBURN TM, LOCKWOOD JL & CASSEY P. 2015. The influence of numbers on invasion success. *Mol Ecol* 24(9): 1942-1953.
- BLONDER B. 2018. Hypervolume concepts in niche- and trait-based ecology. *Ecogr* 41(9): 1441-1455.
- BLUMENTHAL D, MITCHELL CE, PYŠEK P & JAROŠÍK V. 2009. Synergy between pathogen release and resource availability in plant invasion. *PNAS* 106(19): 7899-7904.
- BYERS JE. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97(3): 449-458.
- BYUN C, DE BLOIS S & BRISSON J. 2018. Management of invasive plants through ecological resistance. *Biol Invasions* 20: 13-27.
- CADOTTE MW, CAMPBELL SE, LI S-P, SODHI DS & MANDRAK NE. 2018. Preadaptation and naturalization of non-native species: Darwin's two fundamental insights into species invasion. *Annu Rev Plant Biol* 69: 661-84.
- CARBONI M ET AL. 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. *Ecol Lett* 19(3): 219-229.
- CARMONA CP, BELLO F DE, MASON NWH & LEPŠ J. 2016. Traits without borders: Integrating functional diversity across scales. *Trends Ecol Evol* 31(5): 382-394.
- CHAVE J, COOMES D, JANSEN S, LEWIS SL, SWENSON NG & ZANNE AE. 2009. Towards a worldwide wood economics spectrum. *Ecol Lett* 12(4): 351-366.
- CROUS CJ, JACOBS SM & ESLER KJ. 2012. Wood anatomical traits as a measure of plant responses to water availability: invasive *Acacia mearnsii* De Wild. compared with native tree species in fynbos riparian ecotones, South Africa. *Trees* 26(5): 1527-1536.
- DATTA A, SCHWEIGER O & KÜHN I. 2019. Niche expansion of the invasive plant species *Ageratina adenophora* despite evolutionary constraints. *J Biogeogr* 46(7): 1306-1315.
- DECHOUM M DE S, SAMPAIO AB, ZILLER SR & ZENNI RD. 2018. Invasive species and the global strategy for plant conservation: How close has Brazil come to achieving Target 10? *Rodriguésia* 69(4): 1567-1576.
- DEHLING DM & STOUFFER DB. 2018. Bringing the Eltonian niche into functional diversity. *Oikos* 127(12): 1711-1723.
- DRAYS & DUFOURAB. 2007. The ade4 package: Implementing the duality diagram for ecologists. *J Stat Softw* 22(4): 1-20.
- DRENOVSKY RE, GREWELL BJ, D'ANTONIO CM, FUNK JL, JAMES JJ, MOLINARI N, PARKER IM & RICHARDS CL. 2012. A functional trait perspective on plant invasion. *Ann Bot* 110(1): 141-153.

- FREHSE F DE A, BRAGA RR, NOCERA GA & VITULE JRS. 2016. Non-native species and invasion biology in a megadiverse country: scientometric analysis and ecological interactions in Brazil. *Biol Invasions* 18: 3713-3725.
- FUNK JL, STANDISH RJ, STOCK WD & VALLADARES F. 2016. Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology* 97(1): 75-83.
- GIBSON-REINEMER DK. 2015. A vacant niche: how a central ecological concept emerged in the 19th century. *Bull Ecol Soc Am* 96(2): 324-335.
- GUIDINI AL, SILVA AC, HIGUCHI P, ROSA AD, SPIAZZI FR, NEGRINI M, FERREIRA TS, SALAMI B, MARCON AK & BUZZI JUNIOR F. 2014. Invasão por espécies arbóreas exóticas em remanescentes florestais no Planalto Sul Catarinense. *Rev Árvore* 38(3): 469-478.
- HULME PE & BERNARD-VERDIER M. 2018. Evaluating differences in the shape of native and alien plant trait distributions will bring new insights into invasions of plant communities. *J Veg Sci* 29(2): 348-355.
- KASAMBARA A & MUNDT F. 2017. Factoextra: Extract and visualize the results of multivariate data analyses. R package version 1.0.5. Available at <https://CRAN.R-project.org/package=factoextra>. Accessed on Aug 21 2019.
- KUEFFER C. 2017. Plant invasions in the Anthropocene. *Science* 358(6364): 724-725.
- KUEFFER C, DAEHLER CC, TORRES-SANTANA CW, LAVERGNE C, MEYER JY, OTTO R & SILVA L. 2010. A global comparison of plant invasions on oceanic islands. *Persp Plant Ecol* 12(2): 145-161.
- LAI HR, MAYFIELD MM, GAY-DES-COMBES JM, SPIEGELBERGER T & DWYER JM. 2015. Distinct invasion strategies operating within a natural annual plant system. *Ecol Lett* 18(4): 336-346.
- LAMBON PW, LLORET F & HULME PE. 2008. Do alien plants on Mediterranean islands tend to invade different niches from native species? *Biol Invasions* 10: 703-716.
- LAZZARIN LC, SILVA AC DA, HIGUCHI P, SOUZA K, PERIN JE & CRUZ AP. 2015. Invasão biológica por *Hovenia dulcis* Thunb. em fragmentos florestais na região do Alto Uruguai, Brasil. *Rev Árvore* 39(6): 1007-1017.
- LÊ S, JOSSE J & HUSSON F. 2008. FactoMineR: An R Package for Multivariate Analysis. *J Stat Softw* 25(1): 1-18.
- LEVINE JM & D'ANTONIO CM. 1999. Elton Revisited: A Review of evidence linking diversity and invasibility. *Oikos* 87(1): 15-26.
- MACDOUGALL AS, GILBERT B & LEVINE JM. 2009. Plant invasions and the niche. *J Ecol* 97(4): 609-615.
- MACK RN, SIMBERLOFF D, LONSDALE WM, EVANS H, CLOUT M & BAZZAZ FA. 2000. Biotic Invasions: Causes, Epidemiology, Global Consequences, and Control. *Ecol Appl* 10(3): 689-710.
- MILLER JA & HOLLOWAY P. 2017. Niche theory and models. In: Richardson D et al (Eds), *International Encyclopedia of Geography: People, the Earth, Environment and Technology*, New York: J Wiley & Sons, New York, USA, p. 1-10.
- MITCHELL CE ET AL. 2006. Biotic interactions and plant invasions. *Ecol Lett* 9(6): 726-740.
- MOODLEY D, GEERTS S, RICHARDSON DM & WILSON JR. 2013. Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. *Plos ONE* 8: e75078.
- NUNES A DA S ET AL. 2018. *Ligustrum lucidum* como uma espécie invasora oportunista em uma Floresta com Araucária no sul do Brasil. *Rodriguésia* 69(2): 351-362.
- PADILHA DL, LOREGIAN AC & BUDKE JC. 2015. Forest fragmentation does not matter to invasions by *Hovenia dulcis*. *Biodivers Conserv* 24: 2293-2304.
- PÉREZ-HARGUINDEGUY N ET AL. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust J Bot* 61: 167-234.
- R CORE TEAM. 2019. R: A Language and environment for statistical computing [Internet]. Vienna, Austria; Available at <https://www.r-project.org/>. Accessed on Aug 21 2019.
- RICHARDSON DM, PYŠEK P, REJMÁNEK M, BARBOUR MG, PANETTA FD & WEST CJ. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib* 6: 93-107.
- RICCIARDI A & MACISAAC HJ. 2008. The book that began invasion ecology. *Nature* 452(7183): 34.
- ROSBAKH S, RÖMERMANN C & POSCHLOD P. 2015. Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. *Alp Bot* 125: 79-86.
- SHEA K & CHESSON P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17(4): 170-176.
- SIMBERLOFF D ET AL. 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecol* 35(5): 489-504.

SOBOLESKI VF ET AL. 2017. Floristic-functional variation of tree component along an altitudinal gradient in araucaria forest areas, in Southern Brazil. *An Acad Bras Cienc* 89: 2219-2228.

SODHI DS, LIVINGSTONE SW, CARBONI M & CADOTTE MW. 2019. Plant invasion alters trait composition and diversity across habitats. *Ecol Evol* 9(11): 6199-6210.

TECCO PA, URCELAY C, DÍAZ S, CABIDO M & PÉREZ-HARGUINDEGUY N. Contrasting functional trait syndromes underlay woody alien success in the same ecosystem. *Austral Ecol* 38(4): 443-451.

URCELAY C, LONGO S, GEML J & TECCO PA. 2019. Can arbuscular mycorrhizal fungi from non-invaded montane ecosystems facilitate the growth of alien trees? *Mycorrhiza* 29(1): 39-49.

VAN KLEUNEN M ET AL. 2015. Global exchange and accumulation of non-native plants. *Nature* 525: 100-103.

VAN KLEUNEN M, WEBER E & FISCHER M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol Lett* 13(2): 235-245.

VILÀ M ET AL. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14(7): 702-708.

VILÀ M & HULME PE. 2017. Impact of biological invasions on ecosystem services, 1st ed., Cham: Springer, 378 p.

WILLIAMS VJ & SAHLI HF. 2016. A comparison of herbivore damage on three invasive plants and their native congeners: Implications for the enemy release hypothesis. *Castanea* 81(2): 128-137.

WHITTEMORE AT. 2006. Notes on southwestern Moraceae. *SIDA* 22(1): 769-775.

WRIGHT IJ ET AL. 2004. The worldwide leaf economics spectrum. *Nature* 428(6985): 821-827.

ZENNI RD & ZILLER SR. 2011. An overview of invasive plants in Brazil. *Brazilian J Bot* 34(3): 431-446.

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