Increases in local richness (α-diversity) following invasion are offset by biotic homogenization in a biodiversity hotspot

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Abstract

The world's ecosystems are experiencing unparalleled rates of biodiversity change with invasive species implicated as one of the drivers that restructure local assemblages. Here we focus on the processes leading to biodiversity change in a biodiversity hotspot, the Brazilian Cerrado. The null expectation that invasion leads to increase in local species richness is supported by our investigation of the grass layer in two key habitats (campo sujo and campo úmido). Our analysis uncovered a linear relationship between total richness and invasive richness at the plot level. However, because the invasive species – even though few in number - are widespread, their contribution to local richness (α-diversity) is offset by their homogenizing influence on composition (β-diversity). We thus identify a mechanism that can help explain the paradox that species richness is not declining in many local assemblages, yet compositional change is exceeding the predictions of ecological theory. As such, our results emphasize the importance of quantifying both α-diversity and β-diversity in assessments of biodiversity change in the contemporary world.

Keywords: Biodiversity change; invasion impact; β-diversity; Cerrado; species richness

1. Introduction

The world's ecosystems are under unprecedented pressure. Although species richness (α-diversity) is being eroded at the global level [1,2] the pattern of change at local and regional scales is more mixed with evidence of increases, of decreases and of no net shift in species richness over time (e.g. [3–7]). The absence of a trend in species richness in local assemblages should not, however, be used to conclude that these systems are unresponsive to anthropogenic drivers. There is growing evidence that compositional change (temporal turnover, also referred to as temporal β-diversity) is occurring at rates that exceed baseline levels and is in excess of the predictions of ecological theory [3,8]. Reconciling these shifts in temporal β-diversity with apparent stasis in assemblage α-diversity is thus an important challenge since it will influence policy for the protection of biodiversity in a rapidly changing world. Understanding whether compositional change is dominated by species replacement or species loss will guide conservation efforts [9].

Invasive species are drivers of species extinctions [10] and ecosystem change. The role they play in reshaping native assemblages may contribute to these apparently contradictory biodiversity trends. Indeed, as Buckley and Catford [11] argue, the null expectation of biodiversity change in assemblages experiencing invasions should be an increase in local species richness. In addition, if the richness of invasive species in an area is markedly lower than native richness (as is typically the case in highly diverse areas, crucially in the Southern Hemisphere [12]), the net effect should be that sites that contain exotic species will be more similar to one another, than equivalent sites supporting only native species. Here we test this expectation by focussing on the Cerrado (Brazilian savanna) (Figure S1), a tropical

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biodiversity hotspot [13]. Specifically, we argue that sites where invasive plants are present will be more botanically similar, i.e. exhibit reduced β-diversity, than sites without invasives, and that their compositional similarity will increase as invasive richness increases.

The Cerrado is the savanna with the highest plant diversity in the world [14], but is increasingly threatened by habitat transformation and fragmentation due to agribusiness expansion [15], and by biological invasions (e.g. [16,17]). As a result, the Cerrado has been reduced to approximately 34% of its original distribution [18]. Remaining Cerrado fragments are being progressively colonized by invasive pines (*Pinus* spp.) [16,19] and African grasses (e.g. [17]).

2. Material and methods

Data collection

Our paper analyses data [20] collected in the Itirapina Ecological Station, a Protected Area located in the Cerrado domain, in the Southeast of Brazil (22°11′–22°15′S, 47°51′–47°57′W). Itirapina Cerrado is a mosaic of habitat types, distinct regarding vegetation structure, species composition, and dominant lifeform; habitat type is related to abiotic conditions such as hydric regime, topography and soil type [21]. The main habitat types present are campo sujo (shrub-dominated habitat) and campo úmido (grass-dominated habitat) [21]; these are the focus of our study.

Our survey was in a 7 km^2 portion of the Protected Area, some parts of which have been invaded by isolated pine individuals (*Pinus elliottii*). We surveyed plots that contained single pine individuals, and matched these with control plots with no pine trees present. In each plot, we recorded all plant species present in the grass layer (graminoids – grasses (Poaceae family), sedges (Cyperaceae family) and rushes (Juncaceae family) - and lianas (several botanic families) (see Electronic Supplementary Materials and [22] for more detailed sampling methods). Because only the grass layer contains more than one invasive species we focussed on it in this study. In total, 300 plots were sampled, 114 in campo sujo and 186 in campo úmido. Each recorded plant was identified to species (or the lowest taxonomic level possible) and categorized as native or invasive.

Invasive species

Overall, we recorded 80 plant taxa, belonging to 17 botanical families, of which 76 species are native. The four species invasive to Brazil - the pine *P. elliottii* (slash pine) and three grass species: *Urochloa decumbens* (signal grass, previously named as *Brachiaria decumbens*), *Melinis repens* (natal grass) and *Melinis minutiflora* (molasses grass) are established in the Cerrado [19]. *P. elliottii* is native to the southeast USA [23], and the first record of a *P. elliottii* plantation in Brazil is 1948 [24]. *U. decumbes*, *M. minutiflora* and *M. repens* are grasses native to Africa that were intensively introduced in Brazil as forage grasses and are now widespread in most of the phytogeographical domains of Brazil [19]. Invasive species are defined as non-native species that have become established and can impact on native biodiversity [25].

Data analysis

To understand the relationship between invasive richness and total richness, we first modelled the number of invasive species per plot (0 (native species only), 1, 2, 3 or 4) as a predictor of the total number of species per plot, using a linear model; the graphs were plotted using the R plotly package [26,27]. To provide an indication of how widespread the invasive species are, we also plotted their frequency of occurrence, relative to the other species present.

Second, we computed pairwise species dissimilarity between plots (Jaccard dissimilarity) in areas with 1, 2, 3 or 4 invasives versus areas with natives only (because only 4/300 plots contained all four invasive species, these were grouped together with plots containing three invasive species in each habitat in these analyses). The Jaccard dissimilarity index [28] is based on the proportion of species exclusive to each site in relation to total species richness of both sites being compared. Jaccard dissimilarity ranges from 0 (assemblages with identical species composition) to 1 (assemblages completely distinct in species composition). To calculate pairwise between-site values of total Jaccard amongst all sampled plots, we used the beta.pair function in the R betapart package [29]. Dissimilarity combines two effects (a shift in richness, known as nestedness, and substitution of species, known as turnover) - in which: β_{jac} (total Jaccard) = β_{jtu} (turnover) + β_{jne} (nestedness). To compute nestedness and turnover components of the total multi-site Jaccard dissimilarity across all plots we used the beta.multi function in the betapart package, which computes a single value for each component. To test for compositional

differences between groups with different numbers of invasive species we used Kruskal-Wallis tests (with Bonferroni correction), implemented using the R ggpubr package [30].

3. Results

Our results show a positive linear relationship between total number of species per plot and the number of invasive species per plot. In other words, areas with more species have more invasive species (Figure 1, Table S1 in the Supplementary Materials). Sites with progressively more invasive species are compositionally more similar to one another than sites that have native species only (Figure 2). β-diversity change is dominated by turnover in all cases, ranging from 77.4 to 98.3% of total Jaccard dissimilarity (see Table S2). Invasive species are widespread in the sampled area (Figure S2).
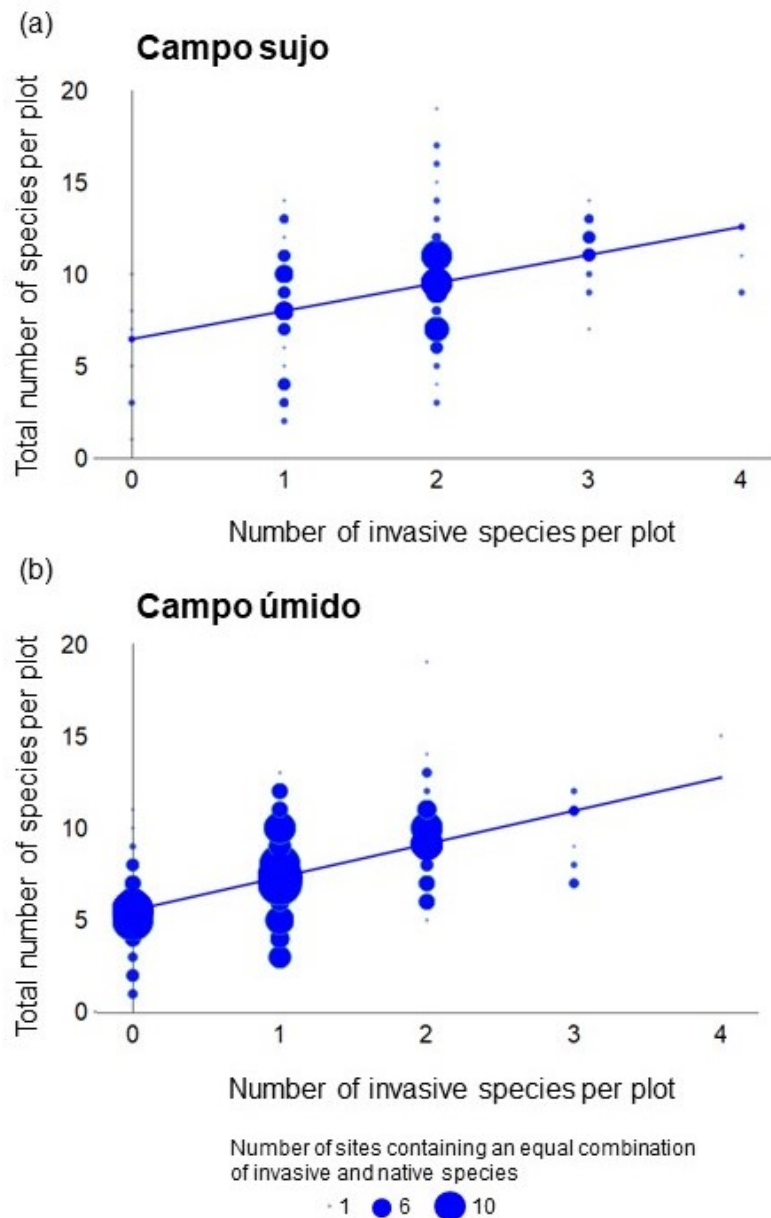
Figure 1. Linear models showing the relationship of total number of species per plot as a function of number of invasive species per plot of campo sujo (a) and campo úmido (b) Cerrado habitats visualized using the plotly package from R [27]. Size of circle represents the number of sites for which there is the same combination of native and invasive species. In total, 300 5x5m plots were sampled, 114 in campo sujo and 183 in campo úmido. Linear regression for campo sujo: y = 6.4604 + 1.5282x and for campo úmido: 5.5327 + 1.7996x. Plots with more species have more invasive species in both campo sujo and campo úmido habitats (p-values <0.001, see Table S1).
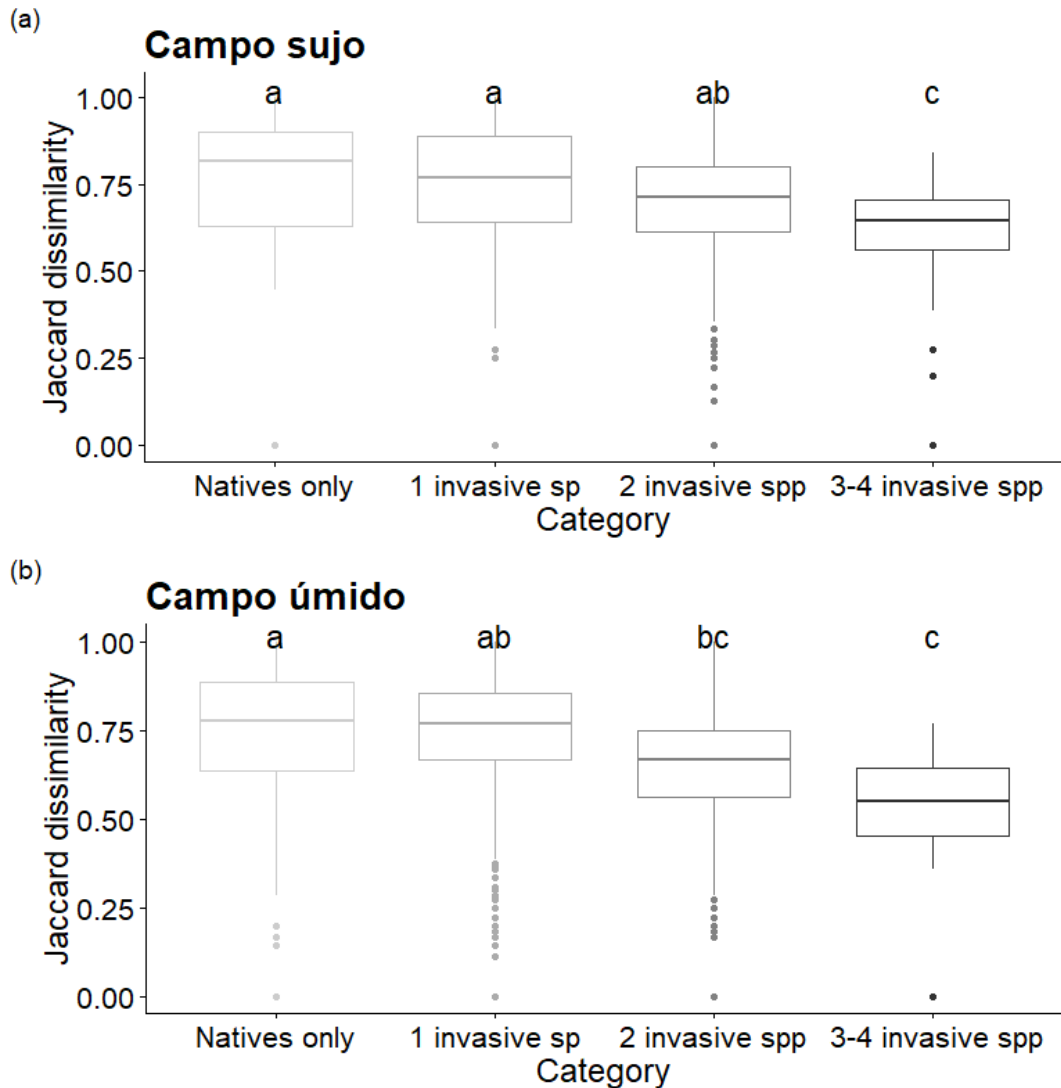
Figure 2. Total Jaccard dissimilarity (β_{jac}) between plots with native species only (lighter colour), and plots with 1, 2 or 3 to 4 invasive species in both campo sujo (a) and campo úmido (b) habitats. This analysis considers incidence data in a pairwise analysis calculated using 'beta.pair' function in the R betapart package [29]. Sites that progressively contain more invasive species are more similar (less dissimilar) in species composition to one another compared to sites that contain native species only. Multiple comparisons with Bonferroni correction, Kruskal-Wallis $p < 2.2e\text{-}16$ for both habitats. Different letters represent significant differences amongst groups (see Table S3).

4. Discussion

The world's ecosystems are experiencing unparalleled rates of biodiversity change [1,3]. Scientists, however, have disagreed about the nature of such changes [2]. Here we identify a mechanism that can help explain the paradox that species richness in many local assemblages is apparently untrending at a time when natural systems are exposed to a range of anthropogenic drivers, including species invasions. We show, for two Cerrado habitats, that – as predicted by Buckley & Catford [11] - local richness is correlated with invasive richness (Figure 1). In other words, sites that contain more invasive species also tend to have higher overall richness. However, at the same time, sites with more invasive species are less different from one another in terms of their composition than they would be if only native species were present (Figure 2). The reason for this is quite straightforward. Although there are few invasive species relative to the native species (4/76), these taxa are widespread (Figure S2) and occur in more localities than many native species. Thus, invasive species, even if relatively few in number, can reduce β-diversity and consequently homogenize biodiversity at regional (γ- diversity)

scales. This influence, which is far in excess of what would be expected on the basis of their richness alone, highlights how even a few invasive species can restructure vulnerable ecosystems [17,31,32], and underlines the importance of understanding biodiversity change across the organizational and spatial scales [33,34] at which the consequences of anthropogenic impacts emerge [1].

As we have shown, any increase (or stasis) in species richness cannot be viewed as a benign unless accompanying changes in composition (and potential shifts in ecosystem function [11,35]) are considered. Our finding thus supports the assertion that changes in species richness (α-diversity) alone may not be a good predictor of invasive species impacts and that β-diversity metrics should be included to assess effects of invasion on native biodiversity [36]. It also helps explain the very mixed sets of outcomes in analyses of the impacts of invasive species on native assemblages (e.g. [32,37,38]). To date, most of the literature on the impacts of invasive species has focused on α-diversity [37], particularly on observed species richness (e.g. [39]) or the Shannon index (e.g. [40]). This suggests that biodiversity change arising from compositional rearrangements may be under reported in the literature on invasive species.

Invasive species are only one of several explanations for marked shifts in β-diversity that can occur in the absence of a clear trend in α-diversity. For example, climate change could lead to replacements of species by taxa more suited to the new conditions while land transformations may favour suites of taxa able to thrive in modified landscapes [41]. Similarly, the turnover component of β-diversity change could dominate in some assemblages (as here) and the nestedness component in others. Biotic homogenization or differentiation may result from such compositional rearrangements [42]. A variety of mechanisms, therefore, could account for the elevated rates of β-diversity reported by [3,7,8]. By focusing on changes in β-diversity in a known local system we detected a key mechanism of β-diversity change which would have been missed at the macroecological scale. The take-home message is that we should not focus on richness alone (or on other metrics of α-diversity) as our indicator of healthy ecosystems, but must also consider how assemblage composition is changing in the contemporary world. To do this we need to understand why biodiversity change is happening, and what the consequences of this change are for the functioning of the systems involved.

References

1.   McGill BJ, Dornelas M, Gotelli NJ, Magurran AE. 2015 Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* **30**, 104–113. (doi:10.1016/j.tree.2014.11.006)

2.   Primack RB, Miller-Rushing AJ, Corlett RT, Devictor V, Johns DM, Loyola R, Maas B, Pakeman RJ, Pejchar L. 2018 Biodiversity gains? The debate on changes in local- vs global-scale species richness. *Biol. Conserv.* **219**, A1–A3. (doi:10.1016/j.biocon.2017.12.023)

3.   Dornelas M, Gotelli NJ, McGill B, Shimadzu H, Moyes F, Sievers C, Magurran AE. 2014 Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science (80-.).* **344**, 296–299. (doi:10.1126/science.1248484)

4.   Elahi R, O'Connor MI, Byrnes JEK, Dunic J, Eriksson BK, Hensel MJS, Kearns PJ. 2015 Recent Trends in Local-Scale Marine Biodiversity Reflect Community Structure and Human Impacts. *Curr. Biol.* **25**, 1938–1943. (doi:10.1016/j.cub.2015.05.030)

5.   Sax DF, Gaines SD. 2003 Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* **18**, 561–566. (doi:10.1016/S0169-5347(03)00224-6)

6.   Supp SR, Ernest SKM. 2014 Species-level and community-level responses to disturbance: A cross-community analysis. *Ecology* **95**, 1717–1723. (doi:10.1890/13-2250.1)

7.   Vellend M, Baeten L, Myers-Smith IH, Elmendorf SC, Beausejour R, Brown CD, De Frenne P, Verheyen K, Wipf S. 2013 Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci.* **110**, 19456–19459. (doi:10.1073/pnas.1312779110)

8.   Magurran AE, Dornelas M, Moyes F, Gotelli NJ, McGill B. 2015 Rapid biotic homogenization of marine fish assemblages. *Nat. Commun.* **6**, 8405. (doi:10.1038/ncomms9405)

9.   Wiersma YF, Urban DL. 2005 Beta diversity and nature reserve system design in the Yukon, Canada. *Conserv. Biol.* **19**, 1262–1272. (doi:10.1111/j.1523-1739.2005.00099.x)

10. Bellard C, Cassey P, Blackburn TM. 2016 Alien species as a driver of recent extinctions. *Biol. Lett.* **12**, 20150623. (doi:10.1098/rsbl.2015.0623)

11. Buckley YM, Catford J. 2016 Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *J. Ecol.* **104**, 4–17. (doi:10.1111/1365-2745.12501)

12. van Kleunen M *et al.* 2015 Global exchange and accumulation of non-native plants. *Nature* **525**, 100–103. (doi:10.1038/nature14910)

13. Mittermeier RAA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CGG, Lamoreux J, Da Fonseca GABAB, Robles Gil P. 2004 *Hotspots Revisited : Earth's biologically richest and most endangered ecoregions*. CEMEX, Conservation International and Agrupacion Sierra Madre.

14. Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 20359–20364. (doi:10.1073/pnas.0903410106)

15. Strassburg BBN *et al.* 2017 Moment of truth for the Cerrado hotspot. *Nat. Ecol. Evol.* **1**. (doi:10.1038/s41559-017-0099)

16. Abreu RCR, Durigan G. 2011 Changes in the plant community of a Brazilian grassland savannah after 22 years of invasion by Pinus elliottii Engelm. *Plant Ecol. Divers.* **4**, 269–278. (doi:10.1080/17550874.2011.594101)

17.   Pivello VR, Shida CN, Meirelles ST. 1999 Alien grasses in Brazilian savannas: a threat to the biodiversity. *Biodivers. Conserv.* **8**, 1281–1294. (doi:10.1023/A:1008933305857)

18.   Machado RB, Ramos Neto MB, Pereira PGP, Caldas EF, Gonçalves DA, Santos NS, Tabor K, Steininger M. 2004 *Estimativas de perda da área do Cerrado Brasileiro*. Brasília: Conservação Internacional.

19.   Zenni RD, Ziller SR. 2011 An overview of invasive plants in Brazil. *Rev. Bras. Botânica* **34**, 431–446. (doi:10.1590/S0100-84042011000300016)

20.   Kortz AR, Magurran AE. 2019 Data from: Increases in local richness (alpha-diversity) following invasion are offset by biotic homogenization in a biodiversity hotspot. *Dryad Digit. Repos.* (doi:doi.org/10.5061/dryad.298pr5b)

21.   Zanchetta D, Delgado JM, Silva CEF, Reis CM. 2006 *Plano de Manejo Integrado das Unidades de Conservação de Itirapina-SP*. Instituto Florestal.

22.   Kortz AR, Silva Matos DM, Magurran AE. 2018 From individuals to communities: how singleton invasive pine saplings lead to biodiversity change in the Brazilian Cerrado hotspot. *J. Veg. Sci.* **00**, 1–11. (doi:https://doi.org/10.1111/jvs.12668)

23.   McGregor KF, Watt MS, Hulme PE, Duncan RP. 2012 What determines pine naturalization: species traits, climate suitability or forestry use? *Divers. Distrib.* **18**, 1013–1023. (doi:10.1111/j.1472-4642.2012.00942.x)

24.   Simberloff D *et al.* 2010 Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecol.* **35**, 489–504. (doi:10.1111/j.1442-9993.2009.02058.x)

25.   Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL. 2013 Progress toward understanding the ecological impacts of nonnative species. *Ecol. Monogr.* **83**, 263–282. (doi:10.1890/13-0183.1)

26.   RCoreTeam. 2014 R: A Language and Environment for Statistical Computing Foundation for Statistical Computing, Vienna).

27.   Sievert C. 2018 Plotly for R.

28.   Jaccard P. 1900 Contribution au problème de l'immigration post-glaciare de la flore alpine. *Bull. la Société Vaudoise des Sci. Nat.* **36**, 87–130.

29.   Baselga A, Orme CDL. 2012 Betapart: An R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–812. (doi:10.1111/j.2041-210X.2012.00224.x)

30.   Kassambara A. 2018 Package 'ggpubr': 'ggplot2' Based Publication Ready Plots. , 120.

31.   Ensino C De *et al.* 2011 Plantas da Serra Negra. , 1–26.

32.   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**, 702–708. (doi:10.1111/j.1461-0248.2011.01628.x)

33.   Stohlgren TJ, Rejmanek M. 2014 No universal scale-dependent impacts of invasive species on native plant species richness. *Biol. Lett.* **10**, 20130939–20130939. (doi:10.1098/rsbl.2013.0939)

34.   Powell KI, Chase JM, Knight TM. 2013 Invasive plants have scale-dependent effects on diversity by altering species-area relationships. *Science (80-.).* **339**, 316–318. (doi:10.1126/science.1226817)

35.   Hobbs RJ *et al.* 2006 Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob. Ecol. Biogeogr.* **15**, 1–7. (doi:10.1111/j.1466-822X.2006.00212.x)

36.   Yurkonis KA, Meiners SJ, Wachholder BE. 2005 Invasion impacts diversity through altered community dynamics. *J. Ecol.* **93**, 1053–1061. (doi:10.1111/j.1365-2745.2005.01029.x)

37. Levine JM, Vila M, Antonio CMD, Dukes JS, Grigulis K, Lavorel S. 2003 Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. B Biol. Sci.* **270**, 775–781. (doi:10.1098/rspb.2003.2327)

38. Simberloff D *et al.* 2013 Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* **28**, 58–66. (doi:10.1016/j.tree.2012.07.013)

39. Cleland EE *et al.* 2004 Invasion in space and time: Non-native species richness and relative abundance respond to interannual variation in productivity and diversity. *Ecol. Lett.* **7**, 947–957. (doi:10.1111/j.1461-0248.2004.00655.x)

40. Firn J, House APN, Buckley YM. 2010 Alternative states models provide an effective framework for invasive species control and restoration of native communities. *J. Appl. Ecol.* **47**, 96–105. (doi:10.1111/j.1365-2664.2009.01741.x)

41. Bellard C, Jeschke JM, Leroy B, Mace GM. 2018 Insights from modeling studies on how climate change affects invasive alien species geography. *Ecol. Evol.* **8**, 5688–5700. (doi:10.1002/ece3.4098)

42. Socolar JB, Gilroy JJ, Kunin WE, Edwards DP. 2016 How Should Beta-Diversity Inform Biodiversity Conservation? *Trends Ecol. Evol.* **31**, 67–80. (doi:10.1016/j.tree.2015.11.005)