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Non-interactive effects of plant invasion and landscape modification on native communities

Ben Gooden

University of Wollongong, bgooden@uow.edu.au

Kris French

University of Wollongong, kris@uow.edu.au

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Non-interactive effects of plant invasion and landscape modification on native communities

Abstract

Aim Biological invasions and anthropogenic habitat modification are considered to be the leading drivers of global environmental change, yet their synergistic impacts on native communities remain poorly understood. We tested the effects of an invasive grass, *Stenotaphrum secundatum*, on an endangered coastal swamp forest community across an anthropogenic land use gradient. We also investigated the relative importance of landscape versus local community attributes in mediating the effects of *S. secundatum* invasion on the community. **Location** Four hundred kilometres of the coastline of south-eastern Australia. **Methods** We compared the diversity, composition and recruitment of resident vegetation in 32 invaded and 32 non-invaded forest stands across an anthropogenic land use gradient. Local disturbance and environmental attributes of the forest (e.g. fire severity, litter abundance, canopy openness, vegetation structure) and adjacent landscape matrix (e.g. cover of forest, urban and agricultural land) were measured in detail at each site. **Results** Invasion was associated with substantial local extinctions of native plant species (i.e. 83% fewer species in invaded sites), altered community compositions and an 85% reduction in rates of woody plant recruitment. Local disturbances and environmental attributes of forest stands and adjacent landscape matrix were similar between invaded and native sites. Invasion caused a twofold increase in litter biomass, which we hypothesize is the primary mechanism by which the invader excludes native species. Landscape modification had no effect on the diversity of adjacent swamp forest. There was no interactive effect of landscape modification and invasion on the native community; species losses in response to invasion were high regardless of the condition of the adjacent matrix. **Main conclusions** We show that impacts of non-native species are not dependent on landscape context and, unexpectedly, that invasion by an alien plant poses a greater threat to diversity of endangered swamp forests than modification of the adjacent matrix.

Keywords

Alien species, anthropogenic disturbance gradient, biological invasions, endangered ecological community, St. Augustine Grass, *Stenotaphrum secundatum*

Disciplines

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Title:

Non-interactive effects of plant invasion and landscape modification on native communities

Authors:

Ben Gooden* and Kris French

Institutional details: Institute for Conservation Biology and Environmental Management,
School of Biological Sciences, University of Wollongong.

Address: University of Wollongong, Northfields Avenue, Wollongong, NSW, 2522,
Australia.

* Author for correspondence: Ben Gooden; phone: +61242528993; email:

bengooden@gmail.com, bg662@uowmail.edu.au

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17 **Abstract**

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21 *Stenotaphrum secundatum*, on an endangered coastal swamp forest community across an
22 anthropogenic land-use gradient. We also investigated the relative importance of landscape
23 versus local community attributes in mediating the effects of *S. secundatum* invasion on the
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25 **Location:** 500 km of the coastline of south eastern Australia.

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38 interactive effect of landscape modification and invasion on the native community; species
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43 **Abstract word count: 297**

44 **Key-words:** Alien species, anthropogenic disturbance gradient, endangered ecological
45 community, global environmental change, habitat modification, St. Augustine Grass, species
46 richness, *Stenotaphrum secundatum*

47

48

49 (A) Introduction

50 Biotic invasions and anthropogenic habitat modification are considered to be the leading
51 drivers of global environmental change and reductions in the diversity of indigenous species
52 (Vitousek *et al.*, 1996; Wilcove *et al.*, 1998; Mack, 2003; Lockwood *et al.*, 2007). Whilst
53 information on invasive species' impacts has increased dramatically in recent decades (Vilà
54 *et al.*, 2011), there is very little evidence for how invasion and habitat modification interact to
55 drive community change. Indeed, in a review of 11588 studies on landscape change (i.e.
56 habitat loss, fragmentation and altered land use) and 3528 studies on species invasion by
57 Didham *et al.* (2007), only 1.2% of studies investigated the simultaneous effects of invasion
58 and habitat modification on native communities, and only 0.03% sought to determine how the
59 two processes interact to impact resident communities. An understanding of how such
60 threatening processes interact to structure indigenous communities is necessary in order to
61 prioritise areas most at risk of species extinctions (Williams *et al.*, 2005).

62

63 There are several major pathways by which non-native species invasion and habitat
64 modification could interact to drive community change. First, local and landscape
65 disturbances of natural areas, such as livestock grazing, fire, deforestation, urbanisation and
66 nutrient addition, can directly facilitate non-native species invasion and the concomitant
67 losses of native species through increases to available resources and non-native propagules
68 (Dukes & Mooney, 1999; Davis *et al.*, 2000; Davis & Pelsor, 2001). Since invasion is
69 coincident with habitat modification in these cases, it is very difficult to discern whether
70 invasion is the driver of community change or a coincidental symptom of habitat
71 modification (MacDougall & Turkington, 2005). For example, Silliman and Bertness (2004a)
72 found that urban development along the border of marshes was associated with reduced soil
73 salinities, increased nitrogen availability and invasion of the marsh by the non-native reed

74 *Phragmites australis*, which in turn was associated with substantial local extinctions of native
75 marsh species. It is uncertain, however, whether native species were directly excluded by *P.*
76 *australis* under these changed abiotic conditions, or whether the invader was simply
77 occupying vacant disturbed spaces no longer suitable for natives.

78

79 Second, invasion and habitat modification can act synergistically on native communities,
80 whereby the emergent effect of their interaction is greater than the ‘simple additive effects of
81 either of these processes operating independently’ (Didham *et al.*, 2007). In this case, the
82 initial spread and establishment of the non-native invader may or may not be dependent upon
83 habitat modification, yet the resultant impacts of invasion on the community are enhanced by
84 the habitat disturbance. For example, Green and Galatowitsch (2002) found that invasion of
85 experimental wetlands by the non-native grass *Phalaris arundinacea* reduced the abundance
86 of native plants under both low and high nitrogen availabilities, yet the magnitude of the
87 invader’s impacts on native abundances was greater when resource levels were high.

88

89 The spatial context of habitat modification can also influence changes to native communities
90 (Suarez *et al.*, 1998; Collinge *et al.*, 2003; Steffan-Dewenter, 2003). For example, Williams
91 *et al.* (2006) found that local extinction of native grassland plants was primarily driven by
92 changes to the condition of the landscape matrix (i.e. extent of adjacent urbanisation and fire
93 regime) more so than changes to local attributes of the patch itself, such as its size. What
94 remains unknown is which, if any, of these contrasting scales of habitat modification interact
95 with non-native species invasion to drive community change. For instance, if native diversity
96 within the community is constrained primarily by pollinator availability or long-distance
97 dispersal of propagules across sites, then the condition of the landscape matrix might be more
98 important than local site attributes in driving community responses to invasive species

99 (Bullock *et al.*, 2002; Kupfer *et al.*, 2006; Bartomeus *et al.*, 2010; Herrera & Garcia, 2010;
100 Schmucki *et al.*, 2012). On the other hand, if diversity is driven by the availability of suitable
101 microsites for propagule settlement and germination, or competition with resident species,
102 then modification to local site attributes might be more important in modulating the invader's
103 effects (Collins *et al.*, 2002).

104

105 We used a broad scale multi-site comparison procedure (Adair & Groves, 1998) to examine
106 the interactive effects of a non-native plant invader (*Stenotaphrum secundatum* (Walter
107 Kuntze) and anthropogenic habitat modification on an endangered coastal swamp forest
108 community of southeastern Australia. *S. secundatum* is a perennial, C₄, stoloniferous, clonal
109 grass (Poaceae) originating from the tropical and subtropical Atlantic coastlines of Africa and
110 the Americas (Sauer, 1972). It has become invasive in coastal forest of Australia, although its
111 impacts on resident communities is unknown (Daehler *et al.*, 2004; Pacific Islands
112 Ecosystems at Risk, 2005). Specifically, we asked:

- 113 1. Is *S. secundatum* invasion into swamp forest associated with changes to the
114 understorey plant community?
- 115 2. How do impacts of *S. secundatum* invasion on the native forest vary across a gradient
116 of anthropogenic land use in the adjacent landscape matrix?
- 117 3. Is landscape context (i.e. extent of anthropogenic modification, latitudinal position,
118 etc.) or the local attributes of the forest (e.g. fire severity, canopy structure and
119 openness, litter biomass, ~~etc.~~) the more important driver of community change?

120

(A) Methods

(B) Study area and habitat

The study was located in remnant stands of Swamp Oak Floodplain Forest (sensu Tozer *et al.* (2010), and hereafter termed swamp forest) along approximately 500 km of the southern coastline of New South Wales (NSW), south eastern Australia, between Sydney (33° 51' 54" S; 151° 12' 20" E) and Eden (37° 03' 55" S; 149° 54' 04" E). The study region has a warm temperate climate (Bureau of Meteorology, 2013) with mean annual rainfall of between 700 and 1000 mm at Eden and Sydney, respectively, and mean annual temperatures ranging from 16°C in winter to 25°C in summer (Bureau of Meteorology, 2012). The swamp forest occurs on marine-derived, saline, waterlogged or periodically inundated sandy loams along the edges of coastal embayments, estuaries and brackish floodplains below 10m ASL (Tozer *et al.*, 2010). It is dominated by the nitrogen-fixing tree *Casuarina glauca* Sieber ex Spreng. and a dense groundcover of swamp forbs and graminoids (Tozer *et al.*, 2010). The community is listed as endangered in NSW (NSW Office of Environment & Heritage 2013), since as little as five to 20 percent of the original (pre-European) swamp forest remains and only less than five percent of extant stands are located within conservation reserves (Tozer *et al.*, 2010).

(B) Sampling procedures

(C) Site selection

We used a correlative, multi-site comparison procedure (Adair & Groves, 1998) to assess the potential effects of *S. secundatum* invasion on the understorey vascular plant assemblage of the swamp forest, whereby patches of invaded forest were surveyed and compared with native reference/control forest sites. All known remnant stands of swamp forest occurring in the study area (based on Tozer *et al.*, 2010) were visited in June 2010 and inspected for the presence of *S. secundatum*. We haphazardly selected a subset of 32 invaded (defined as forest

with an understorey consisting of $\geq 80\%$ projected foliage cover of *S. secundatum*) and 32 native reference (defined as forest understorey with $< 5\%$ projected foliage cover of *S. secundatum*) sites, which were surveyed between September 2010 and March 2011.

Sites were separated by at least 100 m, and the mean ($\pm$ SE) distance from one site to its nearest neighbour was 5.5 ($\pm$ 1.3) km. Given that the diversity of coastal swamp vegetation along eastern Australia is known to increase with latitude (Saintilan, 2009), and the extensive duration of the survey period (approximately seven months), we included latitude and survey date as covariates in statistical models to account for sampling effects. Furthermore, to account for the potential confounding effects of anthropogenic disturbances, such as urbanisation and deforestation, of the landscape matrix surrounding each forest site on *S. secundatum* invasion and its potential community impacts, we ensured that invaded and native sites were evenly distributed across a continuum of landscape disturbance intensities, from relatively intact, pristine coastal landscapes with no history of anthropogenic land use to sites embedded within intensively urbanised stretches of coast (see related discussion by Brooks *et al.*, 2010; see Appendix S1 in Supporting Information).

(C) Vegetation surveys

Each of the 64 sites consisted of a 2×2 m (i.e. 4 m²) quadrat (hereafter referred to as the ‘plot’) randomly positioned in either the centre of a patch of *S. secundatum* (with > 1 m separating the edge of the quadrat from the edge of the infestation) or a patch of non-invaded vegetation. This size of quadrat was chosen as it is known to be appropriate for sampling fine-scale patterns of understorey plant communities associated with dense infestations of invasive grasses (Brewer, 2008; Cushman & Gaffney, 2010). In each 4 m² plot we measured the number (i.e. richness) and abundance of native and other non-native understorey vascular

plant species, and the number of native tree and shrub recruits (see Table 1 for details). Understorey vegetation was considered to comprise any species growing below 2 m in height (Brewer, 2008; Brooks *et al.*, 2010). We did not survey forest vegetation in the middle and upper canopies in these plots because *S. secundatum* grows exclusively along the forest floor, has a shallow root system, and is thus unlikely to directly compete with and displace mature trees and shrubs (Brewer, 2008; Brooks *et al.*, 2010; Spyreas *et al.*, 2010). Non-native species were defined as those introduced from other regions within Australia or other countries (Mason & French, 2007). Species nomenclature followed Harden (1990, 1992, 1993, 2002). Species abundance was estimated by dividing the plot into a 5 cm grid of 1600 intersecting points, and then calculating the percentage of points under which each species occurred. Recruits were defined as non-reproductive, juvenile seedlings or saplings of native trees and shrubs less than 2 m in height.

We measured the percentage cover, depth and volume of leaf litter in each plot, as these are known to be key regulators of plant communities (Facelli & Pickett, 1991), particularly in association with non-native grasses, which can extensively modify the litter dynamics of forest ecosystems (Allison & Vitousek, 2004; Wolkovich *et al.*, 2009). Litter cover was estimated using the grid-intercept method as described above for species abundance, then converted from percentage to cm²; depth was measured as the mean vertical distance (cm) between the soil surface and the top of the litter layer at five points positioned randomly across the plot; volume was calculated by multiplying mean litter depth by litter cover. In a separate study, we measured litter biomass (kg. m⁻²) in three invaded and three native 1 × 1 m plots nested within four invaded forest stands (see Appendix S2 for details of biomass sampling).

(C) Community-scale sampling

To test the assumption that invaded and native sites were similar prior to invasion by *S. secundatum* (see related discussion by Adair & Groves, 1998; Lambrinos, 2000; Brooks *et al.*, 2010), and to test for the local effects of biotic, environmental and disturbance characteristics of the forest on the understorey plant assemblage, the following community-scale predictor variables were measured in a 20 × 20 m quadrat centred on the 4 m² plot (see Table 1 for details): total native and non-native vascular plant species richness (including mature tree and shrub species ≥ 2 m in height), the number of dead and living tree and shrubs individuals ≥ 2 m in height, percentage cover of four vegetation layers characteristic of the swamp forest, and fire severity. Fire severity was assessed by applying a four-point scale to every tree and shrub individual greater than 2 m in height ('1' = fire not evident; '2' = charcoal on bark only; '3' = charcoal penetrated to wood; '4' = tree death apparently caused by fire), then calculating an overall fire damage score per site using the formula developed by Fensham *et al.* (1994): [Sum of fire damage scores/4 × (no. standing living trees + no. standing dead trees)].

(C) Landscape-scale sampling

Within the landscape matrix surrounding each forest site we estimated the percentage cover abundance of three dominant land-use types: urban, agriculture and native vegetation. This was done remotely using Google Earth (2012) satellite imagery and following Ives *et al.* (2011): at an 'eye' altitude of 2.19 km, a 78 ha circular quadrat (with radius of 500 m) was centred upon each 20 x 20 m forest site; this circular quadrat was then divided into a 20 m-square grid of 1200 intersecting points, and the abundance of each land use type was calculated as the percentage of points under which each occurred. Urban land was defined as deforested land dominated by residential or industrial buildings, hard, impermeable surfaces

(e.g. roads, pathways) and peri-urban vegetation intensively managed by humans, such as parks, gardens, cemeteries, recreation reserves (McDonnell & Pickett, 1990). Agricultural land was defined as deforested land actively used for livestock grazing or food crops. Urban and agricultural covers were added to give an overall cover of anthropogenic land use. Native vegetation included forest, shrubland and marsh, with no history of intensive logging or human management.

(B) Data analysis

General linear models were constructed to assess the effects of *S. secundatum* invasion and the environmental, physical, disturbance and biotic characteristics of the plot, community and surrounding landscape (i.e. predictor variables; Table 1) on native and non-native species richness and abundance (i.e. response variables). All analyses were done using the statistical package JMP[®] 9 (SAS Institute Inc. 2010). Minimal best-fit models were constructed using a backwards step-wise elimination procedure (following Field, 2010), whereby non-significant predictors ($P > 0.05$) were successively removed from a complete model (i.e. all predictors included). Model fit was verified at each stage of variable elimination by calculating Akaike's Information Criterion (Akaike, 1974). Poisson regression (Coxe *et al.*, 2009) was used to model the number of native tree and shrub seedlings, as these were found at low densities and transformations were unable to improve normality of the data.

Multicollinearity amongst predictor variables was assessed by generating a matrix of Pearson correlation coefficients and calculating variance inflation factors for those predictors included in the reduced best-fit model (Quinn & Keough, 2002). Normality of the data was assessed by inspecting plots of studentised residuals and performing the Shapiro-Wilk test (Miller, 1997). Variation in community and landscape predictors between invaded and native sites

was examined using t-tests, in order to detect potential confounding effects of these site attributes on community responses to invasion. For further details of assessment of multicollinearity and construction of best-fit models, see Appendix S3.

Differences in native and non-native communities between invaded and native sites were analysed using distance-based permutational multivariate analyses of variance (PERMANOVAs) (Anderson, 2001; McArdle & Anderson, 2001), performed with the statistical packages PRIMER 6 (Clarke & Gorley, 2006) and PERMANOVA+ B version (Anderson & Gorley, 2007). PERMANOVAs were done using Bray-Curtis similarity indices, which were calculated using species cover abundance and presence/absence data for all possible combinations of site pairs (McArdle & Anderson, 2001). Presence/absence transformations allowed us to detect contributions of rare and less abundant species to community change.

Similarity percentage (SIMPER) analysis was used to identify the species contributing most strongly to the compositional differences between native and invaded sites (Clarke, 1993). Differences in the abundance and frequency of occurrence between native and invaded sites for those species identified by SIMPER were verified using non-parametric Kruskal-Wallis tests (Zar, 1999).

(A) Results

A total of 111 understorey vascular plant species from 44 families were recorded, 86 being native and 25 alien to the community (see Appendix S4). Native and invaded sites had a total of 86 and 15 native species, and 18 and 17 non-native species, respectively. Strikingly, 83% of native species were not recorded from sites invaded by *S. secundatum*.

(B) General linear models of species richness and abundance

Six variables were chosen for inclusion as predictor variables in models (i.e. community native richness, upper-canopy cover, density of living trees, matrix vegetation cover and latitude; Appendix S3). T-tests revealed that none of the predictor variables (except litter volume and biomass, see below) varied between invaded and native sites (Table 2).

(C) Litter volume and biomass

Leaf litter volume of invaded sites was more than twice that of native forest sites (Fig. 1(a); Table 2). Furthermore, invaded sites had a significantly greater total (i.e. native and *S. secundatum* combined) biomass of litter than native sites (ANOVA: $F_{1,16} = 11.020$, $P = 0.004$; Fig. 1(b); Appendix S2); however, there was no difference in the biomass of native litter between invaded and native sites (ANOVA: $F_{1,16} = 4.240$, $P = 0.1316$; Appendix S2), indicating that increased litter biomass in invaded sites was driven by the addition of *S. secundatum* litter.

(C) Native species

The final model of native species richness included three predictor variables (i.e. invasion category, number of native species in the surrounding forest community, and anthropogenic land use in the surrounding landscape matrix), which together explained 71% of the variation in native species richness (Table 3). Invaded sites had more than four-times fewer native species than native reference sites (Fig. 2(a)). There was a significant interactive effect

between invasion and anthropogenic landscape modification: post-hoc linear regressions revealed that native richness and anthropogenic land use cover were unrelated across native sites ($R^2 = 0.028$; $P = 0.3616$; Fig. 3), but were positively associated across invaded sites ($R^2 = 0.150$; $P = 0.0314$; Fig. 3). However, this interactive effect was weak, and the positive relationship between native richness and anthropogenic landscape modification across invaded sites was likely driven by an unusually high number of native species located at one invaded site at the northern boundary of the study region (Site code: 'Corrimal invaded'; native richness: 6; matrix anthropogenic cover: 66.83%; Fig. 3). We found that anthropogenic landscape modification no longer had any effect (either alone or in interaction with invasion) on native species richness when data from this site were excluded from the GLM, although the significant negative effect of invasion was retained (Table 3). In addition, the number of native understorey species in the patch-scale plot (4 m²) was significantly and positively related to the total number of native plant species in the surrounding community-scale quadrat (400 m²). Native species richness was unaffected by survey date, latitudinal position of the survey site, vegetation abundance in the surrounding community (i.e. % ground and upper canopy cover, and tree density) or density of dead trees.

There was a significant reduction in the cover abundance of native vegetation associated with *S. secundatum* invasion (Table 3, Fig. 2(b)): invaded sites were covered with less than 10% of native vegetation, yet native sites typically had greater than 70% native vegetation cover. The abundance of native vegetation was not influenced by any other environmental or disturbance characteristics of the surrounding community or landscape.

(C) Tree and shrub recruitment

Native sites were 7-times more likely to be occupied by tree and shrub recruits than invaded sites (Table 4, Fig. 4). There was also a trend ($P = 0.052$) towards an increased likelihood of detecting recruits with increasing latitude, but only across native sites; the presence of *S. secundatum* was associated with reduced recruit density regardless of the site's latitudinal position.

(C) Other non-native species

Non-native species richness was positively associated with the number of non-native species present in the surrounding forest community (Table 3). In contrast to models of native species, non-native species richness was not affected by *S. secundatum* invasion or anthropogenic landscape modification. There was also no effect of any other environmental or disturbance characteristics of the surrounding community or landscape on non-native richness.

(B) Models of community compositions

The composition of native communities based on the identity and frequency of occurrence of species (i.e. presence/absence data) varied significantly between invaded and native sites (average of Bray-Curtis dissimilarity of 87.91 %; Table 5). Compositions also differed significantly when species abundances were considered, yet this only increased the magnitude of site dissimilarities by about 9 % (average dissimilarity of 97.10 %), indicating that the main driver of community differentiation was a change to the identity and/or frequency of occurrence of species in response to *S. secundatum*. Invasion had no effect on the composition of non-native species (Table 5).

339 Nineteen native species (i.e. less than 25% of the total number of native species recorded
340 from all sites) contributed up to 90% of the total variation in community compositions
341 between invaded and native sites (SIMPER analysis on abundance data; Table 6). All species
342 showed a pattern of reduced cover abundance associated with *S. secundatum* invasion,
343 although this trend was only significant for two species (*C. dactylon* and *V. hederacea*; Table
344 6). Strikingly, 11 of the 19 species contributors were completely absent from forest invaded
345 by *S. secundatum*, highlighting that community change was driven primarily by local species
346 extinctions.

347

348

(A) Discussion

(B) Invasion and community change

Invasion by *S. secundatum* into an endangered swamp forest community was strongly associated with reduced abundance of resident vegetation and altered community compositions, mainly through considerable local extinctions of native species. Indeed, *S. secundatum* invasion was associated with a four-fold decline in native species richness, with more than 80% of species being completely absent from invaded forest. In contrast, *S. secundatum* invasion had no effect on other non-native flora. A comparison with similar studies indicates that the magnitude of species decline associated with *S. secundatum* invasion is at least twice as great as for other non-native grasses invading similar habitats: for example, invasion by *Urochloa mutica* in tropical wetlands (Ferdinands *et al.*, 2005; Michelan *et al.*, 2009); *Phragmites australis* in freshwater wetlands (Farnsworth & Meyerson, 1999) and saltmarsh (Silliman & Bertness, 2004a); and *Hymenachne amplexicaulis* in freshwater swamps (Houston & Duivenvoorden, 2002), all of which show only a two-fold reduction in resident species in association with invasion. There was a substantial reduction in tree and shrub recruitment associated with invasion, signalling a potential long-term structural shift from tree- to grass-dominated swamp. Forest conversion to grassland, typically through recruitment limitation of woody vegetation, has been documented elsewhere in response to non-native grass invasion (e.g. Eliason & Allen, 1997; Lambrinos, 2000; Davis *et al.*, 2005; Litton *et al.*, 2006).

(C) Is *S. secundatum* the driver or passenger of community change?

Due to the correlative nature of multi-site comparative procedures commonly used to detect invader impacts, especially over large spatial scales, it is inherently difficult to establish a

causal link between invasion and community change. Indeed, there is a substantial body of evidence that invasion is contingent upon increases in resource availability, such as light and nutrients, caused by habitat disturbances that disrupt or remove indigenous vegetation (Davis *et al.*, 2000; Davis & Pelsor, 2001; Theoharides & Dukes, 2007). Thus, an important question that must first be addressed is whether invasion by *S. secundatum* was the likely driver of community change or simply established in disturbance-generated gaps in the understorey vegetation. However, we measured many key habitat and disturbance characteristics of the forest and surrounding landscape (such as fire severity, canopy openness, tree density and extent of urban development), which have been shown elsewhere to facilitate non-native grass invasion (e.g. D'Antonio *et al.*, 2001; Veldman *et al.*, 2009; Warren II *et al.*, 2011), and found that none covaried with invasion, or had any effect on the number or abundance of native species. Indeed, *S. secundatum* was as likely to occur within geographically remote, 'pristine' forest with a high density of trees, very low light and fire levels, and no recent history of disturbance as within forest embedded in an extensively urbanised matrix. The clear predictor of local species extinction in our models was invasion by *S. secundatum*.

It is possible, though, that there were other intrinsic, yet unconsidered, historical differences between native and invaded sites that had coincidentally driven reductions in community diversity and *S. secundatum* invasion. The majority of surveyed forest patches are remote and have very poor, if any, record of historical vegetation changes (Tozer *et al.*, 2010; Atlas of Living Australia, 2013b). Also, *S. secundatum* was first introduced to the study region as early as 1882 (Atlas of Living Australia, 2013a) and its invasion may have been facilitated by disturbances occurring very many decades ago (e.g. sand mining, logging, agistment of cattle into the swamp forest from adjacent agricultural land), the physical effects of which are no longer evident. However, within the vast majority of the remnant forest patches we surveyed

both invaded and native sites (Appendix S1), and the scale of disturbances, such as logging and grazing, are likely to have been greater than the distances between these neighbouring sites (see Adams & Engelhardt, 2009 for a similar discussion); thus, most sites probably shared similar disturbance histories. There may have been small-scale differences, though, between invaded and native patches of forest in soil pH, nutrient availability, depth, salinity and hydrology, none of which were examined in our study, but are known to vary over small scales (Grant *et al.*, 2003) and are important regulators of invasion and community dynamics in coastal plant communities (Guntenspergen & Levenson, 1997; Green & Galatowitsch, 2001). These conflicting models of impact could be reconciled through invader addition (e.g. Lee *et al.*, 2006; Flory & Clay, 2010) and removal (e.g. D'Antonio *et al.*, 1998) experiments, and continued monitoring of spreading *S. secundatum* populations (Maestas *et al.*, 2003).

Further evidence that *S. secundatum* displaced rather than replaced native vegetation is its ability to establish and proliferate within non-disturbed, deeply shaded forest habitats. Unlike other non-native grass species, *S. secundatum* maintains high yield and reproductive vigour under low light conditions (Mullen & Shelton, 1996; Genovesi *et al.*, 2009), and its competitive performance increases with shade (Smith & Whiteman, 1983; Samarakoon *et al.*, 1990). Long-term monitoring plots have shown that adventitious *S. secundatum* stolons can spread from established patches into abutting non-invaded forest without any precursory disturbance to the native vegetation, where it is able to reach covers of more than 50 % within two years (Gooden unpublished data; available on request). Indeed, Mullen and Shelton (1996) have shown that the main mechanism of spread and establishment is via adventitious stolons, which when planted at a rate of one stolon per 1 m² can cover a 1 ha field in four months. In addition, Gooden and French (currently in review; data available on request) found that native and invaded soil seed banks located at the same sites investigated here had similar densities of propagules of woody species, despite invaded sites having substantially

fewer seedlings within the standing vegetation. This indicates that even if *S. secundatum* was not the primary or original cause of native species loss, it certainly has led to the suppression of native species over time.

(C) Litter: a mechanism by which invasion drives community change?

Forest invaded by *S. secundatum* had twice the amount of litter (by volume and mass) compared with native forest, indicating that changes to litter accumulation rates may be one of the mechanisms by which *S. secundatum* excludes native species. Increased litter accumulation is frequently associated with non-native grass invasion (Evans *et al.*, 2001; Mack *et al.*, 2001; Lenz *et al.*, 2003). Increased *S. secundatum* litter might reduce the germination and establishment of native plants through shading and changes to the microclimate experienced by recruits (Lenz *et al.*, 2003; Farrer & Goldberg, 2009); modify rates of litter decomposition and subsequent nutrient availabilities to natives (Evans *et al.*, 2001; Ehrenfeld, 2003; Ogle *et al.*, 2003); or intercept native propagules, preventing them from becoming incorporated into the soil seed bank. It is uncertain which, if any, of these processes are operating in forest invaded by *S. secundatum*, but this warrants further investigation.

(B) Non-interactive effects of invasion and anthropogenic landscape modification

Contrary to our expectations, we found no evidence for interactive effects of invasion and landscape modification on the forest community; the rate of species decline in response to *S. secundatum* invasion was high irrespective of the condition of the adjacent matrix. These results are directly opposite to most studies, which typically find that interactive effects of invasion and landscape modification on native communities are negatively synergistic, whereby the adverse effects of both are greater than the simple additive effects of each (e.g.

Green & Galatowitsch, 2002; Winsome *et al.*, 2006; Didham *et al.*, 2007). Our results indicate that the impacts of *S. secundatum* invasion are not enhanced within modified landscapes, but also that invaded forest sites are not buffered against species losses in areas where adjacent terrestrial habitats are relatively intact, with a high cover and diversity of vegetation communities. Furthermore (and also unexpectedly), we found that anthropogenic landscape modification had no independent effect on the diversity of adjacent swamp forest patches. We had expected the richness of resident vegetation to decline with increasing cover of anthropogenic land in the adjacent matrix as a result of reduced vegetation abundance and associated disruptions to the abiotic (e.g. increased nutrient deposition, altered hydrology and soil chemistry) and biotic (productivity, seed dispersal and pollinator mutualisms) processes required for the maintenance of biodiversity in the coastal swamp forest (e.g. Faulkner, 2004; Silliman & Bertness, 2004b; Lee *et al.*, 2006; McKinney, 2006, 2008). This could be because the majority of resident plants of the swamp forest have the capacity for long distance dispersal, usually via wind and water (Benson & McDougall, 1993-2005; Thorsen *et al.*, 2009), and populations within isolated forest patches may receive sufficient supplies of propagules from neighbouring sites to buffer against local population declines.

In terms of management, our results suggest that there is no particular spatial context in which the community is most at risk of invasion and that requires more urgent management intervention to arrest local species extinctions. However, rates of community recovery following removal of *S. secundatum* are unlikely to be similar across all landscape contexts (Bell *et al.*, 1997). Patches of forest in heavily modified landscapes may have disrupted networks of pollinators and seed dispersers (Williams *et al.*, 2005; Bartomeus *et al.*, 2010), as well as altered abiotic conditions (particularly hydrology and nutrient regimes) that are required for the recruitment and establishment of many swamp species within this region

(Clarke & Hannon, 1970; Clarke, 1983). Thus, many species may require assisted recovery to gain representation in the standing vegetation upon *S. secundatum* removal from modified landscapes.

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References

- Adair, R.J. & Groves, R.H. (1998) *Impact of environmental weeds on biodiversity: a review and development of a methodology*. Biodiversity Group, Environment Australia., Canberra.
- Adams, S.N. & Engelhardt, K.A.M. (2009) Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches. *Biological Conservation*, **142**, 1003-1010.
- Akaike, H. (1974) A new look at the statistical model identification. *Automatic Control, IEEE Transactions on*, **19**, 716-723.
- Allison, S. & Vitousek, P. (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia*, **141**, 612-619.
- Anderson, M.J. (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 626-639.
- Anderson, M.J. & Gorley, R.N. (2007) *PERMANOVA+ for primer: guide to statistical methods*. PRIMER-E, Plymouth.
- Atlas of Living Australia (2013a) Accessed October 2013, http://biocache.ala.org.au/occurrences/search?q=lsid:urn:lsid:biodiversity.org.au:apni.taxon:414915&sort=occurrence_date#tab_recordsView.
- Atlas of Living Australia (2013b). Accessed 11 October 2013, <http://biocache.ala.org.au/explore/your-area>.
- Bartomeus, I., Vila, M. & Steffan-Dewenter, I. (2010) Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *Journal of Ecology*, **98**, 440-450.
- Bell, S.S., Fonseca, M.S. & Motten, L.B. (1997) Linking restoration and landscape ecology. *Restoration Ecology*, **5**, 318-323.
- Benson, D.H. & McDougall, L. (1993-2005) Ecology of Sydney plant species Parts 1-10. *Cunninghamia*, **3-9**
- Brewer, S. (2008) Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. *Biological Invasions*, **10**, 1257-1264.
- Brooks, K.J., Setterfield, S.A. & Douglas, M.M. (2010) Exotic Grass Invasions: Applying a Conceptual Framework to the Dynamics of Degradation and Restoration in Australia's Tropical Savannas. *Restoration Ecology*, **18**, 188-197.
- Bullock, J.M., Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002) Plant dispersal and colonization processes at local and landscape scales. *Dispersal ecology*, 279-302.
- Bureau of Meteorology (2012) *Climate Data Online*. Bureau of Meteorology. Accessed November 2012, <<http://www.bom.gov.au/climate/data/?ref=fr>>.
- Bureau of Meteorology (2013) *Temperate Zone (warm summer, cool winter)*. Bureau of Meteorology. Accessed October 2012, <<http://www.bom.gov.au/climate/environ/travel/tempzone.shtml>>.
- Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117-143.
- Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth.
- Clarke, L.D. & Hannon, N.J. (1970) The mangrove swamp and salt marsh communities of the Sydney district: III. Plant growth in relation to salinity and waterlogging. *Journal of Ecology*, **58**, 351-369.
- Clarke, P.J. (1983) Nitrogen pools in a mangrove - saltmarsh system. *Wetlands (Australia)*, **3**, 85-93.
- Collinge, S.K., Prudic, K.L. & Oliver, J.C. (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology*, **17**, 178-187.
- Collins, S.L., Glenn, S.M. & Briggs, J.M. (2002) Effect of local and regional processes on plant species richness in tallgrass prairie. *Oikos*, **99**, 571-579.
- Coxe, S., West, S.G. & Aiken, L.S. (2009) The analysis of count data: A gentle introduction to Poisson regression and its alternatives. *Journal of Personality Assessment*, **91**, 121-136.
- Cushman, J.H. & Gaffney, K. (2010) Community-level consequences of invasion: impacts of exotic clonal plants on riparian vegetation. *Biological Invasions*, **12**, 2765-2776.

- D'Antonio, C.M., Hughes, R.F. & Vitousek, P.M. (2001) Factors influencing dynamics of two invasive C-4 grasses in seasonally dry Hawaiian woodlands. *Ecology*, **82**, 89-104.
- D'Antonio, C.M., Hughes, R.F., Mack, M., Hitchcock, D. & Vitousek, P.M. (1998) The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *Journal of Vegetation Science*, **9**, 699-712.
- Daehler, C.C., Denslow, J.S., Ansari, S. & Kuo, H.-C. (2004) A Risk-Assessment System for Screening Out Invasive Pest Plants from Hawaii and Other Pacific Islands. *Conservation Biology*, **18**, 360-368.
- Davis, M.A. & Pelsor, M. (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters*, **4**, 421-428.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528-534.
- Davis, M.A., Bier, L., Bushelle, E., Diegel, C., Johnson, A. & Kujala, B. (2005) Non-indigenous grasses impede woody succession. *Plant Ecology*, **178**, 249-264.
- Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A. & Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, **22**, 489-496.
- Dukes, J.S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, **14**, 135-139.
- Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503-523.
- Eliason, S.A. & Allen, E.B. (1997) Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology*, **5**, 245-255.
- Evans, R.D., Rimer, R., Sperry, L. & Belnap, J. (2001) Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications*, **11**, 1301-1310.
- Facelli, J.M. & Pickett, S.T. (1991) Plant litter: its dynamics and effects on plant community structure. *The Botanical Review*, **57**, 1-32.
- Farnsworth, E. & Meyerson, L. (1999) Species Composition and Inter-annual Dynamics of a Freshwater Tidal Plant Community Following Removal of the Invasive Grass, *Phragmites australis*. *Biological Invasions*, **1**, 115-127.
- Farrer, E.C. & Goldberg, D.E. (2009) Litter Drives Ecosystem and Plant Community Changes in Cattail Invasion. *Ecological Applications*, **19**, 398-412.
- Faulkner, S. (2004) Urbanization impacts on the structure and function of forested wetlands. *Urban Ecosystems*, **7**, 89-106.
- Fensham, R., Fairfax, R. & Cannell, R. (1994) The invasion of *Lantana camara* L. in Forty Mile Scrub National Park, north Queensland. *Australian Journal of Ecology*, **19**.
- Ferdinands, K., Beggs, K. & Whitehead, P. (2005) Biodiversity and invasive grass species: multiple-use or monoculture? *Wildlife Research*, **32**, 447-457.
- Field, A. (2010) *Discovering Statistics Using SPSS*, 3 edn. SAGE Publications Ltd.
- Flory, S.L. & Clay, K. (2010) Non-native grass invasion alters native plant composition in experimental communities. *Biological Invasions*, **12**, 1285-1294.
- Genovesi, A., Jessup, R., Engelke, M. & Burson, B. (2009) Interploid St. Augustinegrass [*Stenotaphrum secundatum* (Walt.) Kuntze] hybrids recovered by embryo rescue. *In Vitro Cellular & Developmental Biology - Plant*, **45**, 659-666.
- Google Earth 7.0 (2012). Accessed 2012, <<http://www.google.com/earth/index.html>>.
- Grant, D.W., Peters, D.P., Beck, G.K. & Fraleigh, H.D. (2003) Influence of an exotic species, *Acroptilon repens* (L.) DC. on seedling emergence and growth of native grasses. *Plant Ecology*, **166**, 157-166.
- Green, E.K. & Galatowitsch, S.M. (2001) Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha x glauca*). *Canadian Journal of Botany-Revue Canadienne De Botanique*, **79**, 170-178.

- Green, E.K. & Galatowitsch, S.M. (2002) Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. *Journal of Applied Ecology*, **39**, 134-144.
- Guntenspergen, G.R. & Levenson, J. (1997) Understory plant species composition in remnant stands along an urban-to-rural land-use gradient. *Urban Ecosystems*, **1**, 155-169.
- Harden, G.J. (1990) *Flora of New South Wales*. University of New South Wales Press Ltd., Sydney.
- Harden, G.J. (1992) *Flora of New South Wales*. University of New South Wales Press Ltd., Sydney.
- Harden, G.J. (1993) *Flora of New South Wales*. University of New South Wales Press Ltd., Sydney.
- Harden, G.J. (2002) *Flora of New South Wales*. University of New South Wales Press Ltd., Sydney.
- Heritage, N.O.o.E.a. (2013) *Swamp Oak Floodplain Forest of the New South Wales North Coast, Sydney Basin and South East Corner Bioregions - profile*. Available at: <http://www.environment.nsw.gov.au/threatenedSpeciesApp/profile.aspx?id=10945> (accessed October 2012).
- Herrera, J.M. & Garcia, D. (2010) Effects of Forest Fragmentation on Seed Dispersal and Seedling Establishment in Ornithochorous Trees. *Conservation Biology*, **24**, 1089-1098.
- Houston, W.A. & Duivenvoorden, L.J. (2002) Replacement of littoral native vegetation with the ponded pasture grass *Hymenachne amplexicaulis*: effects on plant, macroinvertebrate and fish biodiversity of backwaters in the Fitzroy River, Central Queensland, Australia. *Marine and Freshwater Research*, **53**, 1235-1244.
- Ives, C.D., Hose, G.C., Nipperess, D.A. & Taylor, M.P. (2011) Environmental and landscape factors influencing ant and plant diversity in suburban riparian corridors. *Landscape and Urban Planning*, **103**, 372-382.
- Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global ecology and biogeography*, **15**, 8-20.
- Lambrinos, J.G. (2000) The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered mediterranean-type shrubland in California. *Diversity and Distributions*, **6**, 217-231.
- Lee, S.Y., Dunn, R.J.K., Young, R.A., Connolly, R.M., Dale, P.E.R., Dehayr, R., Lemckert, C.J., McKinnon, S., Powell, B., Teasdale, P.R. & Welsh, D.T. (2006) Impact of urbanization on coastal wetland structure and function. *Austral Ecology*, **31**, 149-163.
- Lenz, T.I., Moyle-Croft, J.L. & Facelli, J.M. (2003) Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. *Austral Ecology*, **28**, 23-32.
- Litton, C.M., Sandquist, D.R. & Cordell, S. (2006) Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *Forest Ecology and Management*, **231**, 105-113.
- Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2007) *Invasion Ecology*. Blackwell Publishing Ltd.
- MacDougall, A.S. & Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42-55.
- Mack, M.C., D'Antonio, C.M. & Ley, R.E. (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: A case study of C-4 grasses in Hawaii. *Ecological Applications*, **11**, 1323-1335.
- Mack, R.N. (2003) Global plant dispersal, naturalization, and invasion: Pathways, models and circumstances. *Invasive Species- Vectors and Management Strategies* (ed. by G.M. Ruiz and J.T. Carlton). Island Press, Washington, DC.
- Maestas, J.D., Knight, R.L. & Gilgert, W.C. (2003) Biodiversity across a Rural Land-Use Gradient
- Biodiversidad a lo largo de un Gradiente de Uso de Suelo Rural. *Conservation Biology*, **17**, 1425-1434.
- Mason, T.J. & French, K. (2007) Management regimes for a plant invader differentially impact resident communities. *Biological Conservation*, **136**, 246-259.
- McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, **82**, 290-297.
- McDonnell, M.J. & Pickett, S.T. (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*, **71**, 1232-1237.

- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247-260.
- McKinney, M.L. (2008) Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, **11**, 161-176.
- Michelan, T.S., Thomaz, S.M., Mormul, R.P. & Carvalho, P. (2009) Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity. *Freshwater Biology*, **55**, 1315-1326.
- Miller, R.G. (1997) *Beyond ANOVA : basics of applied statistics*. Chapman & Hall, London.
- Mullen, B.F. & Shelton, H.M. (1996) *Stenotaphrum secundatum*: a valuable forage species for shaded environments *Tropical Grasslands*, **30**, 289-297.
- Ogle, S.M., Reiners, W.A. & Gerow, K.G. (2003) Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *American Midland Naturalist*, **149**, 46-58.
- Pacific Islands Ecosystems at Risk (2005) *Pacific Islands Ecosystems at Risk - Stenotaphrum secundatum*. Institute of Pacific Islands Forestry, USDA Forest Service International Program. Accessed October 2012, <http://www.hear.org/pier/wra/pacific/stenotaphrum_secundatum_htmlwra.htm>.
- Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Saintilan, N. (2009) Biogeography of Australian saltmarsh plants. *Austral Ecology*, **34**, 929-937.
- Samarakoon, J.R., Wilson, J.R. & Shelton, H.M. (1990) Growth, morphology and nutritive quality of shaded *Stenotaphrum secundatum*, *Axonopus compressus* and *Pennisetum clandestinum*. *Journal of Agricultural Science, Cambridge*, **114**, 161-169.
- SAS Institute Inc. (2010) *Using JMP 9*. SAS Institute Inc, Cary, NC.
- Sauer, J. (1972) Revision of *Stenotaphrum* (Gramineae: Paniceae) with attention to its historical geography. *Brittonia*, **24**, 202-222.
- Schmucki, R., Reimark, J., Lindborg, R. & Cousins, S.A.O. (2012) Landscape context and management regime structure plant diversity in grassland communities. *Journal of Ecology*, **100**, 1164-1173.
- Silliman, B.R. & Bertness, M.D. (2004a) Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. *Conservation Biology*, **18**, 1424-1434.
- Silliman, B.R. & Bertness, M.D. (2004b) Shoreline Development Drives Invasion of *Phragmites australis* and the Loss of Plant Diversity on New England Salt Marshes
- El Desarrollo Costero Impulsa la Invasión de *Phragmites australis* y la Pérdida de Diversidad de Plantas en Marismas de Nueva Inglaterra. *Conservation Biology*, **18**, 1424-1434.
- Smith, M.A. & Whiteman, P.C. (1983) Evaluation of tropical grasses in increasing shade under coconut canopies. *Experimental Agriculture*, **19**, 153-161.
- Spyreas, G., Wilm, B.W., Plocher, A.E., Ketzner, D.M., Matthews, J.W., Ellis, J.L. & Heske, E.J. (2010) Biological consequences of invasion by reed canary grass (*Phalaris arundinacea*). *Biological Invasions*, **12**, 1253-1267.
- Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, **17**, 1036-1044.
- Suarez, A.V., Bolger, D.T. & Case, T.J. (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology*, **79**, 2041-2056.
- Theoharides, K.A. & Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256-273.
- Thorsen, M.J., Dickinson, K.J. & Seddon, P.J. (2009) Seed dispersal systems in the New Zealand flora. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 285-309.

- Tozer, M.G., Turner, K., Keith, D.A., Tindall, D., Pennay, C., Simpson, C., MacKenzie, B., Beukers, P. & Cox, S. (2010) Native vegetation of southeast NSW: a revised classification and map for the coast and eastern tablelands. *Cunninghamia*, **11**, 359-406.
- Veldman, J.W., Mostacedo, B., Pena-Claros, M. & Putz, F.E. (2009) Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. *Forest Ecology and Management*, **258**, 1643-1649.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702-708.
- Vitousek, P.M., Dantonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468-478.
- Warren II, R.J., Wright, J.P. & Bradford, M.A. (2011) The putative niche requirements and landscape dynamics of *Microstegium vimineum*: an invasive Asian grass. *Biological Invasions*, **13**, 471-483.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *Bioscience*, **48**, 607-615.
- Williams, N., Morgan, J., McCarthy, M. & McDonnell, M. (2006) Local extinction of grassland plants: the landscape matrix is more important than patch attributes. *Ecology*, **87**, 3000.
- Williams, N.S., Morgan, J.W., McDonnell, M.J. & McCarthy, M.A. (2005) Plant traits and local extinctions in natural grasslands along an urban-rural gradient. *Journal of Ecology*, **93**, 1203-1213.
- Winsome, T., Epstein, L., Hendrix, P.F. & Horwath, W.R. (2006) Competitive interactions between native and exotic earthworm species as influenced by habitat quality in a California grassland. *Applied Soil Ecology*, **32**, 38-53.
- Wolkovich, E.M., Bolger, D.T. & Cottingham, K.L. (2009) Invasive grass litter facilitates native shrubs through abiotic effects. *Journal of Vegetation Science*, **20**, 1121-1132.
- Zar, J.E. (1999) *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey.

Supporting Information

Appendix S1. Schematic diagram depicting the allocation of *Stenotaphrum secundatum*-invaded sites across a gradient of anthropogenic landscape modification (i.e. urbanisation and agriculture). Percentages are the cover abundances of anthropogenic land in a circular plot (500 m radius) surrounding each 20 × 20 m invaded site. Geographic positions of sites are given as latitudes and longitudes beside each plot.

Appendix S2. Contribution of *Stenotaphrum secundatum* to leaf litter biomass in invaded swamp forest.

Aim: The primary vegetation surveys revealed that sites invaded by *S. secundatum* had about twice the volume of litter than native reference sites. It remained unclear, however, whether this increase in the volume of space occupied by litter was due to an increase in the mass of litter or, rather, changes to the architecture of the litter layer (i.e. had the mass of litter remained constant, but had the litter layer become less dense?). Furthermore, if indeed invasion was associated with an increase in the litter mass, it was unknown whether this extra litter was derived from *S. secundatum* or an increase in the supply of native litter.

We asked:

1. Do *S. secundatum*-invaded sites have a greater biomass (kg.m^{-2}) of leaf litter than native reference sites?
2. If so, is this extra litter derived from *S. secundatum* or additional native litter?

Litter sampling: We sampled leaf litter from four extensively invaded swamp forest locations, where the size of *S. secundatum* patches exceeded 1 ha and the foliage cover of *S. secundatum* within each patch was $\geq 80\%$ (Puckeys: $34^{\circ}24'25.10''\text{S}$, $150^{\circ}53'50.90''\text{E}$; Kioloa: $35^{\circ}32'46.50''\text{S}$, $150^{\circ}22'56.50''\text{E}$; Nangudga: $36^{\circ}14'48.21''\text{S}$, $150^{\circ}8'15.45''\text{E}$ and Wallaga Lake: $36^{\circ}21'56.10''\text{S}$, $150^{\circ}4'7.80''\text{E}$). Litter was defined as dead leaf and stem (diameter ≤ 20 mm) material that is detached from living vegetation. Litter was sampled from within six 1×1 m plots at each location – three plots within *S. secundatum* infestations and three plots within adjacent non-invaded vegetation. Invaded plots were located in the centre of infestations (at least 5 m from the edge of each *S. secundatum* patch), native plots were located at least 10 m from the edge of infestations, and all plots were separated by at least 20 m. Litter was separated into litter derived from native vegetation (the bulk of which was derived from the dominant canopy tree *Casuarina glauca*) and *S. secundatum*, oven dried at 60°C for one week and then weighed (± 0.01 g). Biomass was expressed as kg.m^{-2} .

Data analysis: We used two-way analyses of variance (ANOVAs) to detect the variation in (1) native litter biomass and (2) total (native + *S. secundatum*) litter biomass between native and invaded plots (fixed factor) and amongst the four locations (random factor).

Results: The biomass of native litter varied significantly amongst locations, but not between invaded and native plots (Table 1). The total biomass of litter (i.e. native and *S. secundatum* litter combined) was significantly greater in invaded than native plots, and also varied amongst locations. However, the effects of invasion on total litter biomass did not vary across locations (as indicated by the non-significant interaction term in the model).

Conclusion: Invasion by *S. secundatum* is associated with increased accumulation of leaf litter. Since the mass of native litter remained constant between invaded and native plots, we conclude that the additional litter was derived from *S. secundatum*. Thus, *S. secundatum* invasion modifies litter regimes of the swamp forest by directly increasing rates of litter accumulation.

Table 1. Results of two-way ANOVA for native and total (native + *S. secundatum*) litter biomass (kg.m⁻²) in response to *S. secundatum* invasion (fixed factor) and location (random factor).

Model source Predictor variable	DF	SS	F	P*	r ²	Direction of response
Native litter						
Model	7	0.0686	2.9308	0.0355	0.4529	
Invasion	1	0.0128	4.2398	0.1316		
Location	3	0.0468	4.6666	0.0158		(Nangudga = Wallaga = Puckeys) > Kioloa
Invasion*Location	3	0.0090	0.9000	0.4628		
Error	16	0.0535				
Total litter						
Model	7	0.2743	11.2813	<0.0001	0.8315	
Invasion	1	0.0383	11.0197	0.0043		Invaded > Native
Location	3	0.2041	3.5925	0.0371		(Nangudga = Wallaga) > (Puckeys = Kioloa)
Invasion*Location	3	0.0320	3.0674	0.0580		
Error	16					

* Values in bold indicate statistical significance

Appendix S3. Details of data analysis (multicollinearity and construction of general linear models).

Assessment of multicollinearity: The assessment of multicollinearity amongst predictor variables consisted of three stages: first, prior to the construction of GLMs, multicollinearity amongst the continuous predictor variables (not including invasion category) was assessed by constructing a matrix of Pearson correlation coefficients. Second, t-tests were performed to determine whether any of these continuous predictors varied significantly between invaded and native sites. This was an important step in determining whether the effects of *S. secundatum* invasion on the native community were confounded by any of the environmental and disturbance characteristics of the swamp forest and surrounding landscape. Third, variance inflation factors (VIFs) were calculated for those predictors (both main effects and interaction terms) included in the reduced best-fit model. Predictors with VIF values less than “10” were considered to provide strong and independent estimates of the response variable, and were thus retained in the final reduced model.

Model assumptions: Normality of the data was assessed by inspecting plots of studentised residuals and performing the Shapiro-Wilk test. Homogeneity of variance amongst means was tested using Cochran’s C test. Data were square root or $\log(x + 1)$ transformed as necessary to conform to these assumptions. Influential data points and outliers were identified by calculating Cook’s distances and inspecting plots of studentised residuals, respectively. Only one influential data point was detected: the number of dead trees and shrubs in a native site located at the northern section of the study region (site code: Bellambi #1), which generally had greater than 10 times the number of dead trees and shrubs than other sites. Removal of this site from the model resulted in an improvement of the fit, which was confirmed by an inspection of R^2 and AIC values.

Construction of general linear models: Pearson correlation coefficients revealed that six variables (i.e. community native richness, upper-canopy cover, density of living trees, matrix anthropogenic cover and latitude) were strongly correlated with most other environmental and disturbance covariates but, importantly, not amongst one another (Table 1). These six variables were thus considered to provide independent estimates within the GLMs and good surrogates for all other predictors in the models. Likewise, the other predictors were considered to be redundant and not included in the models. A further three variables (i.e. survey date, ground-layer cover and dead tree density) were included in the models as these were uncorrelated with any other predictors. Furthermore, t-tests showed that none of the predictors, with the exception of leaf litter volume and biomass, varied significantly between invaded and native sites.

Table 1. Correlation matrix of continuous predictor variables used to construct general linear models of alien and native species richness and abundance in coastal swamp forest invaded by the alien turf grass, *S. secundatum*. Values are Pearson correlation coefficients (n = 63). Values in bold indicate significant correlations between pairs of predictors

Predictor variable code	LIT	NC	AC	% GC	% S	% MC	% UC	# LT	# DT	F	% MV	% MU	% MAG	% MAN	LAT
# NAT_COMM	-0.36														
# ALIEN_COMM	-0.14	0.18													
% GROUND_COVER	0.21	-0.05	0.04												
% SHRUB	0.04	0.30	-0.12	0.05											
% MID_CANOPY	0.20	-0.10	-0.02	0.09	-0.02										
% UPPER_CANOPY	-0.10	0.13	0.22	-0.10	-0.15	-0.39									
# LIVE_TREE	-0.04	-0.21	-0.18	-0.02	-0.21	0.44	-0.23								
# DEAD_TREE	-0.15	-0.20	-0.15	-0.21	-0.06	-0.07	-0.09	0.05							
FIRE	-0.01	0.05	-0.20	-0.05	0.10	-0.23	0.00	-0.30	0.14						
% MAT_VEG	-0.14	0.20	-0.46	-0.17	0.27	-0.09	-0.17	-0.11	-0.02	0.47					
% MAT_URBAN	-0.06	-0.10	0.53	-0.06	-0.03	-0.21	0.16	-0.03	0.07	-0.29	-0.54				
% MAT_AGRI	-0.17	-0.02	0.01	-0.05	-0.16	-0.30	0.17	-0.24	0.08	0.13	0.17	-0.35			
% MAT_ANTHROP	-0.13	-0.12	0.57	-0.09	-0.11	-0.35	0.25	-0.13	0.12	-0.25	-0.49	0.90	0.08		
LATITUDE	0.21	0.03	-0.43	0.04	-0.01	0.11	0.15	0.04	0.10	0.07	0.17	-0.53	0.15	-0.50	
COLLECTION	0.20	0.01	-0.03	0.01	0.23	0.08	0.13	-0.10	-0.17	-0.08	-0.06	-0.07	-0.10	-0.14	0.07

LIT = LITTER VOLUME; # NC = # NAT_COMM; # AC = # ALIEN_COMM; % GC = % GROUND_COVER; % S = % SHRUB; % MC = % MID_CANOPY; % UC = % UPPER_CANOPY;
LT = # LIVE_TREE; # DT = # DEAD_TREE; F = FIRE; % MV = % MAT_VEG; % MU = % MAT_URBAN; % MAG = % MAT_AGRI; % MAN = % MAT_ANTHROP; LAT = LATITUDE

Appendix S4. List of native and alien vascular plant species recorded from *S. secundatum*-invaded and native reference sites (i.e. 2 × 2 m plot). Mean foliage cover abundance (%) and percentage of sites occupied are provided for each species

Species origin Family Species	Native sites (n = 31)		Invaded sites (n = 32)	
	Mean cover (%)	Sites occupied (%)	Mean cover (%)	Sites occupied (%)
Alien				
Apiaceae				
<i>Hydrocotyle bonariensis</i> Lam.	0.10	9.38	0.22	9.38
Apocynaceae				
<i>Araujia sericifera</i> Brot.	0.00	0.00	0.07	3.13
Asparagaceae				
<i>Asparagus aethiopicus</i> L.	1.03	21.88	0.80	18.75
<i>Asparagus asparagoides</i> (L.) Druce	0.11	12.50	0.63	12.50
Asteraceae				
<i>Aster subulatus</i> Michx.	0.01	6.25	0.00	0.00
<i>Bidens pilosa</i> L.	0.01	3.13	0.01	3.13
<i>Chrysanthemoides monilifera</i> subsp. <i>rotundata</i> (DC.) Norl.	0.11	3.13	0.00	0.00
<i>Cirsium vulgare</i> (Savi) Ten.	0.07	6.25	0.00	0.00
<i>Conyza bonariensis</i> (L.) Cronquist	0.04	3.13	0.00	0.00
<i>Delairea odorata</i> Lem.	0.00	0.00	0.23	6.25
Commelinaceae				
<i>Tradescantia fluminensis</i> Vell.	0.00	0.00	1.12	15.63
Convolvulaceae				
<i>Ipomoea indica</i> (Burm.f.) Merr.	0.12	3.13	0.04	6.25
Crassulaceae				
<i>Crassula multicava</i> Lem.	0.01	3.13	0.00	0.00
<i>Crassula sarmentosa</i> var. <i>sarmentosa</i> Harv.	0.07	3.13	0.03	3.13
Iridaceae				
<i>Watsonia meriana</i> (L.) Mill.	0.00	0.00	0.01	3.13
Juncaceae				
<i>Juncus acutus</i> L.	0.11	3.13	0.04	3.13
Myrsinaceae				
<i>Anagallis arvensis</i> L.	0.00	3.13	0.00	0.00
Poaceae				
<i>Ehrharta erecta</i> Lam.	0.42	12.50	0.09	9.38
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	0.16	6.25	0.17	6.25
<i>Setaria pumila</i> (Poir.) Roem. & Schult.	0.02	3.13	0.00	0.00
Rosaceae				
<i>Rubus fruticosus</i> L. species aggregate	0.00	0.00	0.08	3.13
Rubiaceae				
<i>Coprosma repens</i> A.Rich.	0.03	3.13	0.00	0.00
Solanaceae				

<i>Solanum nigrum</i> L.	0.00	6.25	0.00	0.00
<i>Solanum pseudocapsicum</i> L.	0.04	3.13	0.00	0.00
Verbenaceae				
<i>Lantana camara</i> L.	0.03	6.25	0.02	3.13
Native				
Acanthaceae				
<i>Pseuderanthemum variabile</i> (R.Br.) Radlk.	0.00	3.13	0.00	0.00
Aizoaceae				
<i>Tetragonia tetragonioides</i> (Pall.) Kuntze	0.24	15.63	0.16	6.25
Apiaceae				
<i>Apium prostratum</i> Labill. ex Vent.	2.28	18.75	0.04	3.13
<i>Centella asiatica</i> (L.) Urb.	0.05	3.13	0.00	3.13
<i>Hydrocotyle peduncularis</i> R.Br. ex A.Rich.	0.11	9.38	0.00	0.00
<i>Trachymene incisa</i> Rudge	0.00	3.13	0.00	0.00
Apocynaceae				
<i>Marsdenia rostrata</i> R.Br.	0.08	3.13	0.00	0.00
<i>Parsonsia straminea</i> var. <i>glabrata</i> Pichon	1.78	40.63	1.00	12.50
<i>Tylophora barbata</i> R.Br.	0.00	0.00	0.00	3.13
Asteraceae				
<i>Centipeda minima</i> subsp. <i>minima</i> (L.) A.Braun & Asch.	0.05	3.13	0.00	0.00
<i>Lagenophora gracilis</i> Steetz	0.02	9.38	0.00	0.00
<i>Leptinella longipes</i> Hook.f.	0.29	6.25	0.00	0.00
<i>Senecio linearifolius</i> A.Rich.	0.01	3.13	0.00	0.00
<i>Senecio</i> spp.	0.02	3.13	0.00	0.00
Brassicaceae				
<i>Cardamine microthrix</i> I.Thomps.	0.01	3.13	0.00	0.00
Caryophyllaceae				
<i>Stellaria flaccida</i> Hook.	0.01	6.25	0.00	0.00
Casuarinaceae				
<i>Casuarina glauca</i> Sieber ex Spreng.	0.31	18.75	0.07	6.25
Chenopodiaceae				
<i>Enchylaena tomentosa</i> R.Br.	0.00	3.13	0.00	0.00
<i>Rhagodia candolleana</i> subsp. <i>candolleana</i> Moq.	1.66	3.13	0.00	0.00
<i>Sarcocornia quinqueflora</i> subsp. <i>quinqueflora</i> (Bunge ex Ung.-Sternb.) A.J.Scott	0.46	6.25	0.00	0.00
Commelinaceae				
<i>Commelina cyanea</i> R.Br.	0.13	15.63	0.06	15.63
Convolvulaceae				
<i>Calystegia marginata</i> R.Br.	0.22	6.25	0.00	0.00
<i>Dichondra repens</i> J.R.Forst. & G.Forst.	1.52	21.88	0.00	0.00
Cyperaceae				
<i>Baumea juncea</i> (R.Br.) Palla	21.05	37.50	2.22	12.50
<i>Carex appressa</i> R.Br.	0.96	12.50	0.00	0.00
<i>Carex longibrachiata</i> Boeck.	1.49	6.25	0.00	0.00
<i>Ficinia nodosa</i> (Rottb.) Goetgh. et al.	0.03	3.13	0.00	0.00
<i>Gahnia clarkei</i> Benl	1.18	9.38	0.00	0.00

<i>Gahnia melanocarpa</i> R.Br.	0.27	3.13	0.00	0.00
<i>Isolepis inundata</i> R.Br.	0.00	3.13	0.00	0.00
<i>Lepidosperma laterale</i> R.Br.	0.10	3.13	0.00	0.00
<i>Schoenoplectus validus</i> (Vahl) A.Löve & D.Löve	0.07	3.13	0.00	0.00
Dennstaedtiaceae				
<i>Hypolepis muelleri</i> N.A.Wakef.	2.45	9.38	0.00	0.00
Dennstaedtiaceae				
<i>Pteridium esculentum</i> (G.Forst.) Cockayne	0.32	6.25	0.00	0.00
Dilleniaceae				
<i>Hibbertia scandens</i> (Willd.) Gilg	0.02	3.13	0.00	0.00
Euphorbiaceae				
<i>Chamaesyce dallachyana</i> (Baill.) D.C.Hassall	0.01	3.13	0.00	0.00
Fabaceae				
<i>Acacia longifolia</i> subsp. <i>sophorae</i> (Labill.) Court	0.03	3.13	0.00	0.00
<i>Desmodium gunnii</i> Benth. ex Hook.f.	0.09	9.38	0.00	0.00
<i>Desmodium varians</i> (Labill.) G.Don	0.03	3.13	0.00	0.00
<i>Glycine clandestina</i> J.C.Wendl.	0.01	3.13	0.00	0.00
<i>Glycine microphylla</i> (Benth.) Tindale	0.09	3.13	0.00	0.00
Geraniaceae				
<i>Geranium homeanum</i> Turcz.	0.04	6.25	0.00	0.00
Goodeniaceae				
<i>Goodenia ovata</i> Sm.	0.23	3.13	0.00	0.00
<i>Selliera radicans</i> Cav.	10.34	28.13	0.88	9.38
Haloragaceae				
<i>Gonocarpus teucrioides</i> DC.	0.04	3.13	0.00	0.00
Juncaceae				
<i>Juncus kraussii</i> subsp. <i>australiensis</i> (Buchenau) Snogerup	4.59	25.00	1.94	28.13
<i>Juncus usitatus</i> L.A.S.Johnson	0.26	3.13	0.00	0.00
Juncaginaceae				
<i>Triglochin microtuberosa</i> Aston	0.05	3.13	0.00	0.00
<i>Triglochin procera</i> R.Br.	0.01	3.13	0.00	0.00
<i>Triglochin striata</i> Ruiz & Pav.	3.02	12.50	0.00	0.00
Lamiaceae				
<i>Clerodendrum tomentosum</i> R.Br.	0.01	3.13	0.00	0.00
<i>Plectranthus parviflorus</i> Willd.	0.00	0.00	0.00	3.13
Lauraceae				
<i>Cassytha pubescens</i> R.Br.	0.02	3.13	0.00	0.00
Lobeliaceae				
<i>Lobelia anceps</i> L.f.	0.11	9.38	0.00	0.00
<i>Pratia purpurascens</i> (R.Br.) E.Wimm.	0.13	21.88	0.00	0.00
Lomandraceae				
<i>Lomandra longifolia</i> Labill.	1.13	9.38	0.00	0.00
Luzuriagaceae				
<i>Eustrephus latifolius</i> R.Br. ex Ker Gawl.	0.04	3.13	0.00	0.00

<i>Geitonoplesium cymosum</i> (R.Br.) A.Cunn. ex Hook.	0.19	3.13	0.00	0.00
Menispermaceae				
<i>Stephania japonica</i> var. <i>discolor</i> (Blume) Forman	0.06	6.25	0.00	0.00
Myrtaceae				
<i>Eucalyptus robusta</i> Sm.	0.02	3.13	0.00	0.00
<i>Melaleuca ericifolia</i> Sm.	0.05	6.25	0.00	0.00
Oleaceae				
<i>Notelaea longifolia</i> Vent.	0.03	3.13	0.00	0.00
Oxalidaceae				
<i>Oxalis perennans</i> Haw.	0.01	3.13	0.00	0.00
<i>Oxalis rubens</i> Haw.	0.01	6.25	0.00	0.00
Phyllanthaceae				
<i>Breynia oblongifolia</i> Muell.Arg.	0.01	3.13	0.00	0.00
Pittosporaceae				
<i>Pittosporum undulatum</i> Vent.	0.02	6.25	0.00	0.00
Poaceae				
<i>Cynodon dactylon</i> (L.) Pers.	12.58	53.13	0.32	18.75
<i>Echinopogon ovatus</i> (G.Forst.) P.Beauv.	0.01	3.13	0.00	0.00
<i>Entolasia marginata</i> (R.Br.) Hughes	0.37	15.63	0.00	0.00
<i>Entolasia stricta</i> (R.Br.) Hughes	0.16	6.25	0.00	0.00
<i>Imperata cylindrica</i> P.Beauv.	0.01	6.25	0.00	0.00
<i>Microlaena stipoides</i> (Labill.) R.Br.	1.89	25.00	0.00	0.00
<i>Oplismenus aemulus</i> (R.Br.) Roem. & Schult.	1.48	28.13	0.01	3.13
<i>Oplismenus imbecillis</i> (R.Br.) Roem. & Schult.	0.53	15.63	0.00	0.00
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	0.73	18.75	0.30	25.00
<i>Poa labillardierei</i> Steud.	0.38	3.13	0.00	0.00
Pteridaceae				
<i>Adiantum aethiopicum</i> L.	0.50	3.13	0.00	0.00
Ranunculaceae				
<i>Clematis aristata</i> Ker Gawl.	0.12	6.25	0.00	0.00
<i>Ranunculus plebeius</i> R.Br. ex DC.	0.01	3.13	0.00	0.00
Rosaceae				
<i>Rubus parvifolius</i> L.	0.08	9.38	0.00	0.00
Rubiaceae				
<i>Galium propinquum</i> A.Cunn.	0.04	9.38	0.00	0.00
<i>Morinda jasminoides</i> A.Cunn.	0.04	6.25	0.00	0.00
Solanaceae				
<i>Solanum prinophyllum</i> Dunal	0.01	3.13	0.00	0.00
<i>Solanum stelligerum</i> Sm.	0.08	6.25	0.00	0.00
Theophrastaceae				
<i>Samolus repens</i> (J.R.Forst. & G.Forst.) Pers.	1.09	28.13	0.14	9.38
Violaceae				
<i>Viola hederacea</i> Labill.	4.88	34.38	0.00	0.00

Tables

Table 1. Description of disturbance, environmental and spatial predictor variables used to construct general linear models of alien and native species richness and cover abundance in coastal swamp forest invaded by the alien turf grass *Stenotaphrum secundatum*

Variable type <i>Scale of parameter*</i>	Code	Variable definitions	Units
Response variable			
Native groundcover species richness		Species growing < 2 m height	Number/4 m ²
Native vegetation abundance			% planar cover
Native woody recruit density		Juvenile woody tree and shrub individuals < 2 m height	Number/4 m ²
Alien species richness		Species growing < 2 m height	Number/4 m ²
Predictor variable			
<i>Patch</i>			
Invasion category	INVASION	(0) Native (<i>S. secundatum</i> cover < 5%) (1) Invaded (<i>S. secundatum</i> cover ≥ 80%)	% planar cover
Litter volume	LITTER_VOL	Continuous variable	m ³
<i>Community</i>			
Community alien plant richness	# ALIEN_COMM	Continuous variable	Number species/400 m ²
Number of dead trees	# DEAD_TREE	Continuous variable (individuals ≥ 2 m height)	Number/400 m ²
Fire damage score	FIRE	Continuous variable	n/a
Community native plant richness	# NAT_COMM	Continuous variable	Number species/400 m ²
Ground-layer foliage cover	% GROUND_COVER	Continuous variable (canopy stratum: < 0.5 m)	% planar cover
Shrub-layer foliage cover	% SHRUB	Continuous variable (canopy stratum : 0.5 ≤ x < 2 m)	% planar cover
Mid-canopy foliage cover	% MID_CANOPY	Continuous variable (canopy stratum : 2 ≤ x < 10 m)	% planar cover
Upper-canopy foliage cover	% UPPER_CANOPY	Continuous variable (canopy stratum : ≥ 10 m)	% planar cover
Number of living trees	# LIVE_TREE	Continuous variable (individuals ≥ 2 m height)	Number/400 m ²
<i>Landscape</i>			
Matrix urban land cover	% MAT_URBAN	Continuous variable	% planar cover
Matrix agricultural land cover	% MAT_AGRI	Continuous variable	% planar cover
Matrix anthropogenic land cover	% MAT_ANTHROP	Continuous variable	% URBAN + % AGRI
Matrix natural vegetation cover	% MAT_VEG	Continuous variable	% planar cover
<i>Covariate (sampling effect)</i>			
Latitude	LATITUDE	Continuous variable	Decimal degrees south
Collection date	COLLECTION	Continuous variable	Number of days since first survey

* Patch: 2 × 2 m (4 m²) quadrat; Community: 20 × 20 m (400 m²) quadrat; Landscape: circular quadrat with radius of 500 m (area approx. 80 ha) encompassing the patch- and community-scale quadrats.

Table 2. Results of t-tests showing the variation in disturbance, environmental and spatial variables between native (n = 31) and invaded (n = 32) swamp forest sites

<i>Environmental parameter</i>	Units	Mean ($\pm$ SE)		<i>t</i> _{1,62}	<i>P</i>
Response variable		Native sites	Invaded sites		
<i>Disturbance</i>					
Community alien plant richness	Number species/400 m ²	6.42 ($\pm$ 0.96)	6.50 ($\pm$ 0.95)	0.06	0.9526
Number of dead trees	Number/400 m ²	3.94 ($\pm$ 0.61)	3.44 ($\pm$ 0.60)	0.59	0.5601
Fire damage score	n/a	0.27 ($\pm$ 0.01)	0.28 ($\pm$ 0.01)	1.24	0.2204
Matrix urban land cover	% planar cover	24.83 ($\pm$ 3.63)	25.89 ($\pm$ 3.90)	0.20	0.8430
Matrix agricultural land cover	% planar cover	4.06 ($\pm$ 1.85)	3.01 ($\pm$ 1.35)	0.46	0.6467
Matrix anthropogenic land cover	% planar cover	28.90 ($\pm$ 3.45)	28.63 ($\pm$ 3.67)	0.05	0.9272
<i>Environmental</i>					
Litter volume	m ³	0.22 ($\pm$ 0.02)	0.53 ($\pm$ 0.04)	6.31	<0.0001; Fig. 1(a)
Ground-layer foliage cover	% planar cover	68.55 ($\pm$ 4.28)	78.16 ($\pm$ 3.59)	1.72	0.0905
Shrub-layer foliage cover	% planar cover	26.77 ($\pm$ 2.97)	19.94 ($\pm$ 3.16)	1.58	0.1199
Mid-canopy foliage cover	% planar cover	26.45 ($\pm$ 2.87)	25.47 ($\pm$ 2.67)	0.25	0.5986
Upper-canopy foliage cover	% planar cover	36.94 ($\pm$ 2.21)	37.41 ($\pm$ 2.17)	0.15	0.8796
Number of living trees	Number/400 m ²	75.10 ($\pm$ 6.67)	71.94 ($\pm$ 6.45)	0.34	0.7346
Matrix natural vegetation cover	% planar cover	38.01 ($\pm$ 3.17)	33.63 ($\pm$ 2.89)	1.02	0.3144
<i>Covariate (sampling effect)</i>					
Latitude	Decimal degrees south	35.21 ($\pm$ 0.12)	35.25 ($\pm$ 0.12)	0.27	0.7849
Collection date	Number of days since first survey	146.16 ($\pm$ 39.65)	165.25 ($\pm$ 43.35)	0.32	0.7463

Table 3. Results of general linear models for native species richness (both full model and with the outlier site ‘Corrimal invaded’ removed) and percentage vegetation cover abundance, and alien species richness in coastal swamp forest invaded by the alien turf grass *S. secundatum*. Values in bold indicate statistical significance. Models presented provide the ‘best fit’ for each response variable based on the backwards step-wise elimination procedure, where the elimination of predictors at each step was verified using the Akaike Information Criterion (AIC)

<i>Response variable</i>	Predictor variable	DF	SS	F	P	r²	AIC	Direction of response
<i>Patch native species richness</i>								
	Model	4	28.870	35.632	<0.0001	0.711	86.48	
	INVASION	1	11.182	55.204	<0.0001			Native richness more than four-times lower in invaded than native plots; Fig. 2(a).
	# NAT_COMM	1	5.255	25.945	<0.0001			Positive association between plot (4 m ²) and community (400 m ²) scale native species richness.
	% MAT_ANTHROP	1	0.438	2.160	0.1470			See interaction.
	INVASION*% MAT_ANTHROP	1	1.046	5.164	0.0268			Positive association between plot native richness and matrix anthropogenic land cover across invaded sites only; plot native richness and matrix anthropogenic land cover unrelated across native sites; Fig.3.
	Error	58	11.748					
<i>Patch native species richness (Corrimal removed)</i>								
	Model	3	28.121	44.592	<0.0001	0.70	86.19	
	INVASION	1	11.634	55.343	<0.0001			See above
	# NAT_COMM	1	4.915	23.382	<0.0001			See above
	% MAT_ANTHROP	1	0.286	1.360	0.248			
	Error	58						
<i>Patch native vegetation cover (%)</i>								
	Model	1	705.806	234.447	<0.0001	0.794	252.59	
	INVASION	1	705.806	234.447	<0.0001			Native cover more than 10-times lower in invaded than native plots; Fig. 2(b).
	Error	61	166.410					
<i>Patch alien species richness</i>								
	Model	1	12.197	80.204	<0.0001	0.568	64.51	
	# ALIEN_COMM	1	12.197	80.204	<0.0001			Positive association between plot (4 m ²) and community (400 m ²) scale alien species richness.
	Error	61	9.277					

Table 4. Results of Poisson regression for seedling density of native ~~woody~~ tree and shrub species in coastal swamp forest invaded by the alien turf grass *S. secundatum*. Values in bold indicate statistical significance. The model presented provides the ‘best fit’ for the response variable based on the backwards step-wise elimination procedure, where the elimination of predictors at each step was verified using the Akaike Information Criterion (AIC)

Predictor variable	DF	χ^2	<i>P</i>	AIC	Direction of response
Model	3	24.013	<0.0001	98.069	
INVASION	1	12.174	0.0005		Native woody tree and shrub seedling density more than seven-times lower in invaded than native plots; Fig. 4.
LATITUDE	1	0.002	0.9665		
INVASION*LATITUDE	1	3.776	0.0520		Trend ($P < 0.1$) towards increased likelihood of seedling occurrence with increasing latitude across native sites only.
Error	59				

Table 5. Results of one-way permutational multivariate analyses of variance (PERMANOVA) testing the effects of *S. secundatum* invasion on the composition of (a) native and (b) alien plant species assemblages in coastal swamp forest. Analyses used cover abundance and presence/absence data for both native and alien assemblages

Source of variation	DF	MS	Pseudo- <i>F</i>	<i>P</i>
(a) Native species composition				
Cover abundance				
INVASION	1	13222	2.988	0.001
Error	54	4424.7		
Model	55			
Presence/Absence				
INVASION	1	11218	3.019	0.002
Error	54	3716.3		
Model	52			
(b) Alien species composition				
Cover abundance				
INVASION	1	4669.6	1.012	0.425
Error	32	4615.2		
Model	33			
Presence/Absence				
INVASION	1	3733.5	0.913	0.491
Error	24	4090.8		
Model	29			

Table 6. Summary of similarity percentage analyses (SIMPER) showing cumulative contributions (up to 90%) of different native species to compositional dissimilarities between native and invaded swamp forest sites. Data are the (a) average percentage foliage cover and (b) average number of sites occupied (i.e. presence/absence) per species amongst replicate 4 m² sites within each invasion category. Summaries of Kruskal-Wallis tests are presented for those species contributing $\geq 5\%$ to compositional differences

Data source <i>Species</i>	Invasion category ^a		Av. Dissimilarity	Diss/SD	Contribution (%)	Cumulative (%)	Kruskal-Wallis test	
	Native	Invaded					χ^2	<i>P</i> [*]
(a) Species abundance (mean percentage foliage cover)								
Average Bray-Curtis dissimilarity between native and invaded sites = 97.10%								
<i>Baumea juncea</i>	14.7825	2.8375	15.91	0.58	16.38	16.38	3.268	0.0706
<i>Cynodon dactylon</i>	13.76188	0.4125	14.75	0.53	15.19	31.57	8.414	0.0037
<i>Selliera radicans</i>	8.514375	1.13	8.9	0.4	9.16	40.73	3.120	0.0773
<i>Juncus kraussii</i> subsp. <i>australiensis</i>	5.179375	2.4775	8.12	0.42	8.37	49.1	0.171	0.6793
<i>Viola hederacea</i>	5.50375	0	8.05	0.41	8.29	57.39	13.376	0.0003
<i>Hypolepis muelleri</i>	2.764375	0	4.07	0.3	4.19	61.58		
<i>Parsonsia straminea</i> var. <i>glabrata</i>	2.01	1.285	3.59	0.42	3.69	65.27		
<i>Triglochin striata</i>	3.4075	0	2.96	0.24	3.05	68.32		
<i>Apium prostratum</i>	2.576875	0.0575	2.57	0.32	2.65	70.97		
<i>Dichondra repens</i>	1.715625	0	2.44	0.32	2.51	73.48		
<i>Microlaena stipoides</i>	2.135	0	2.19	0.38	2.25	75.74		
<i>Rhagodia candolleana</i>	1.875	0	2.17	0.18	2.24	77.97		
<i>Oplismenus aemulus</i>	1.665625	0.0075	1.92	0.39	1.98	79.95		
<i>Gahnia clarkei</i>	1.32875	0	1.81	0.19	1.86	81.81		
<i>Carex longibrachiata</i>	1.68125	0	1.64	0.2	1.69	83.5		
<i>Carex appressa</i>	1.0825	0	1.52	0.27	1.56	85.06		
<i>Lomandra longifolia</i>	1.28	0	1.52	0.28	1.56	86.62		
<i>Leptinella longipes</i>	0.3225	0	1.41	0.18	1.46	88.08		
<i>Phragmites australis</i>	0.774375	0.3825	1.37	0.35	1.41	89.49		
(b) Species presence/absence (mean percentage of sites occupied)								
Average Bray-Curtis dissimilarity between native and invaded sites = 87.61%								

<i>Cynodon dactylon</i>	48	24	6.41	0.83	7.32	7.32	6.125	0.0133
<i>Juncus kraussii</i> subsp. <i>australiensis</i>	23	36	5.93	0.73	6.77	14.09	0.2514	0.6161
<i>Parsonsia straminea</i> var. <i>glabrata</i>	42	16	5.29	0.75	6.04	20.13	6.815	0.0090
<i>Phragmites australis</i>	16	32	4.89	0.67	5.59	25.71	0.745	0.3882
<i>Baumea juncea</i>	29	16	4.78	0.66	5.45	31.16	2.586	0.1078
<i>Selliera radicans</i>	26	12	4.16	0.61	4.75	35.92		
<i>Samolus repens</i>	23	12	4.02	0.56	4.59	40.51		
<i>Commelina cyanea</i>	16	2	3.45	0.57	3.94	44.45		
<i>Apium prostratum</i>	19	4	3.14	0.48	3.59	48.03		

* Values in bold indicate statistical significance for Kruskal-Wallis tests

Figures

Fig.1.

Fig. 2

Fig. 3.

Fig.4.

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Fig. 1. Average ($\pm$ SE) (a) leaf litter volume (m^3) and (b) total (native + *S. secundatum*) litter biomass (kg.m^{-2}) in native ($n = 31$) and invaded ($n = 32$) coastal swamp forest patches. Note the differences in y-axis units between figure plates.

Fig. 2. Average ($\pm$ SE) native (a) species richness and (b) vegetation cover in native ($n = 31$) and invaded ($n = 32$) coastal swamp forest patches. Note the differences in y-axis units between figure plates.

Fig. 3. Relationship between native species richness in coastal swamp forest patches (number of species/ 4 m^2) and anthropogenic land use cover (%) of the surrounding landscape matrix across ~~(a)~~-native ($n = 31$) and ~~(b)~~-invaded ($n = 32$) sites. Solid and dotted trend lines indicate relationships between native richness and anthropogenic landscape modification with ($n = 32$) and without ($n = 31$) the outlier site ‘Corrimal invaded’ (circled), respectively. ~~Note the different in range between y axes.~~

Fig. 4. Average ($\pm$ SE) density of native ~~woody~~-tree and shrub seedlings in native ($n = 31$) and invaded ($n = 32$) coastal swamp forest patches.