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Acacia longifolia invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests

Katherine G. Rascher · André Große-Stoltenberg · Cristina Máguas · João Augusto Alves Meira-Neto · Christiane Werner

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Abstract *Acacia* spp. are among the most serious plant invaders worldwide, and *Acacia longifolia* specifically causes problems in Portugal. In this study, we evaluated the impacts of *A. longifolia* invasion on community structure, light climate, plant diversity and regeneration in pine forests and open stabilized dunes in northern and southern Portugal. Having the growth form of a small tree or shrub, between 1 and 8 m tall, *A. longifolia* tended to dominate the middle stratum of forests and to share dominance in the upper stratum of open dunes. The presence of *A. longifolia* was associated with a decreased canopy cover in the lower stratum of all studied habitats, and at some sites with a significantly increased leaf area index and reduced light intensity in the understory. Species number and diversity were reduced in some habitats by up to 50% in invaded compared to non-invaded areas. Furthermore, in forest habitats, *A. longifolia* seedlings were facilitated by proximity to an adult *A. longifolia* while the establishment and growth of native seedlings was negatively impacted. The replacement of drought tolerant native species by the water spending invader, *A. longifolia*, may have serious implications for ecosystem functioning, especially during the prolonged drought periods predicted to occur in Portugal in the future.

Keywords *Acacia* · Community structure · Plant diversity · Plant invasion · Mediterranean dune ecosystem

Introduction

The Mediterranean basin is particularly susceptible to plant invasions (Gritti et al. 2006; Thuiller et al. 2005) especially along the coastline (Chytrý et al. 2009, Gasso et al. 2009). Invasions in this region have potentially severe conservation consequences because of the high degree of endemism and the presence of numerous biodiversity hotspots (Médail and Quézel 1997). In Portugal, the number of non-indigenous plant taxa has been increasing and *Acacia* spp. are among the most problematic invaders (Almeida and Freitas 2001, 2006). Specifically, the introduced leguminous shrub or small tree *Acacia longifolia* (Andrews) Willd., which was initially introduced to

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The authors Katherine G. Rascher and André Große-Stoltenberg contributed equally to the manuscript.

K. G. Rascher (✉) · C. Werner
Experimental and Systems Ecology, University
of Bielefeld, Universitätstr. 25, 33615 Bielefeld, Germany
e-mail: katherine.grieve@uni-bielefeld.de

A. Große-Stoltenberg
Institute of Landscape Ecology, University of Münster,
Robert-Koch-Str. 28, 48149 Münster, Germany

C. Máguas · J. A. A. Meira-Neto
Environmental Biology Research Center (CBA),
University of Lisbon, Campo Grande, C2 Building,
1749-016 Lisbon, Portugal

stabilize dunes and control erosion, causes ecological problems in Portugal. *Acacia longifolia* decreases native plant diversity (Marchante et al. 2003), significantly alters soil properties (e.g. Marchante et al. 2008a, b, 2009) and impacts water cycling (Rascher et al. 2009) in Portuguese coastal dune ecosystems. Leguminous trees are overrepresented among invasive plant species worldwide (Haysom and Murphy 2003), but are seldom found in undisturbed Mediterranean systems, and their ability to fix atmospheric nitrogen may significantly impact ecosystem functioning (Ehrenfeld 2003; Lambdon et al. 2008).

Compared with native species, *A. longifolia* has an advantage in light interception due to its rapid growth rate (Peperkorn et al. 2005) and small tree life form, which differs from that of most native species (Marchante et al. 2003). Furthermore, the ability of *A. longifolia* to fix atmospheric N_2 may be especially advantageous in the nutrient-poor sand dune ecosystems along the Portuguese coast (Peperkorn et al. 2005). In South Africa, *Acacia* spp. have been shown to have long lasting effects on soil nitrogen pools due to their litter having low quality carbon which binds organic nitrogen in microbial pools (Yelenik et al. 2007). Controlled studies have demonstrated that *A. longifolia* exhibits low plasticity by using resources at high rates even under limiting conditions (e.g. drought stress), in contrast to native species which decrease resource extraction rates under stressful conditions (Werner et al. 2010). There is also evidence that *A. longifolia* invasion disrupts the competitive balance between native species (Werner et al. 2010) and alters ecosystem functioning (e.g. nutrient and water cycles) in invaded areas (Hellmann et al. 2011; Rascher et al. 2009).

In Portugal, the impact of *A. longifolia* invasion on biodiversity (Marchante et al. 2003), soil characteristics (Marchante et al. 2008a, b, 2009), water cycling (Rascher et al. 2009), and nitrogen availability (Hellmann et al. 2011) have been studied. Controlled experiments have lent further insight into competition dynamics between *A. longifolia* and native species (Peperkorn et al. 2005; Werner et al. 2010). However, there is a lack of understanding of how intact plant communities respond to invasion, and predicting how different habitats will respond, even to the same plant invader, remains a challenge (Rejmanek et al. 2005). In this paper, we quantify the consequences of *A. longifolia* invasion in two contrasting habitats (open dunes and pine forests) at two sites varying in precipitation regime along the Atlantic coast of Portugal.

We document the effect of *A. longifolia* invasion on plant species diversity, vertical vegetation structure and light climate (using hemispherical photographs) and further evaluate regeneration dynamics by documenting seedling number and size in invaded and non-invaded habitats. We hypothesized that the presence of *A. longifolia* would (1) decrease native species diversity, (2) decrease light penetration to the forest understory, and (3) adversely impact the regeneration of native species. We further hypothesized that invasion dynamics would differ between forest and open dunes sites.

Materials and methods

Site description

Field sites were established along the Atlantic coast in the north (Praia de Mira, N40°25.7′ W8°48.0′) and south (Pinheiro da Cruz, N38°15.2′ W8°45.8′) of Portugal. The natural vegetation at both field sites is west Iberian Mediterranean sand-dune complexes on poor sandy soils (dystric regosols in the open dunes and orthic podzols in the dune forests). The most interior dunes are typically occupied by xerophytic scrub and pine plantation (Honrado et al. 2002). These dune complexes are rich in endemic species (Bohn et al. 2003). All field sites consist of habitat types protected by the NATURA 2000 habitat directive (ICN 2006). The dune sites consist of grey dune formations dominated by psammophile chamaephytes and dunes with sclerophyllic shrub vegetation (*Cisto-Lavanduletalia*). The *Pinus pinaster* Aiton forests in the coastal dunes are semi-natural or planted. For further phytosociological classification of the studied areas see Costa et al. (1998) and Rivas-Martínez et al. (2002).

Experimental design

To analyze the impact of *A. longifolia* with high detail at a local scale we established two 1,000 m^2 plots (20 m × 50 m) at each site in areas representative of the surrounding landscape; one in open stabilized dunes and one in dune pine forest dominated by *Pinus*

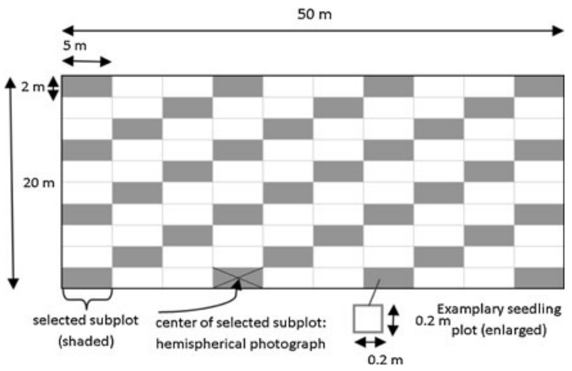


Fig. 1 Illustration detailing the experimental design implemented in each of the four habitats

pinaster Aiton. At each location the forest and open dune sites were located less than 2 km apart (along an east to west transect at Praia de Mira and a southeast to northwest transect at Pinheiro da Cruz). The plots were divided into 100 subplots (2 m × 5 m = 10 m^2) and measurements made in every 3rd subplot (Fig. 1); 34 subplots per site for a total of 136 subplots analyzed in this study. This small scale guaranteed homogenous environmental conditions while being large enough to encompass subplots with and without *A. longifolia*. Each studied subplot was characterized as invaded or non-invaded according to presence or absence of *A. longifolia*. Throughout this paper the study plots are termed north forest (NF), north dunes (ND), south forest (SF) and south dunes (SD).

Climate conditions

The climate at both study locations can be classified as Mediterranean-type with an oceanic influence due to the proximity of the Atlantic Ocean. Climate data was obtained from stations nearby to the study sites at São Jacinto (N40°39.7′, W8°44.1′; 30 km north from Praia de Mira) and Alcácer do Sal in the south (N38°22.3′, W08°31.3′; 25 km northeast from Pinheiro da Cruz). Average (30 year average 1961–1991) annual precipitation in the north is 841 mm with 50 mm occurring during the summer months (June to August). The south is drier having average annual rainfall of 573 mm and only 26 mm of rain during the summer. Furthermore, the north is cooler (mean annual temperature 14.4°C, mean maximum temperature for the hottest month 22.3°C) than the south (mean annual temperature 16.3°C, mean maximum temperature for the hottest month 30.8°C).

Vegetation structure

Vegetation structure was characterized for every third 10 m^2 subplot (Fig. 1). Vegetation was first subdivided into three height strata: (1) adult plants taller than 1.5 m, (2) plants shorter than 1.5 m (which encompassed adult shrubs and juveniles of woody species) and (3) seedlings. Woody, herbaceous and annual species (see "Appendix" for a full species list) were covered in this study although the only seedlings encountered were those of woody species. All sampling was conducted between August and December 2007; accordingly any species only present during spring would have been missed. For the adult and juvenile plants height, crown diameter, and stem diameter at ground level (only plants >1.5 m tall) were measured. Height to the nearest 0.5 m was measured for plants >1.5 m (using geometric principles—e.g. 'the stick method' Kramer and Akca 2002) and plants <1.5 m were classified into height classes: 0–10, 11–25, 26–50, 51–100 and 101–150 cm. Crown diameter was calculated as the arithmetic mean of the north–south and east–west diameters (measured to the nearest 5 cm) even if crowns were deformed or asymmetric. Stem diameter was calculated from measurements of stem circumference at ground level.

From these measurements basal area, canopy cover and plant density were calculated. For each species, basal area was calculated as the sum of the cross-sectional area (calculated using diameter at ground level) of all individuals greater than 1.5 m tall. In a similar manner, canopy cover for each species was calculated as the sum of the projected crown area (calculated from crown diameter) of all individuals. Crown area was regarded as a closed area without gaps which we acknowledge most likely resulted in an overestimation of total canopy cover. However, this overestimation should be felt equally across all species thus not impacting relative comparisons. Both basal area and canopy cover were scaled to a hectare basis (m^2 ha^{-1}). Plant density for each species was simply the count of individuals of that species found and is reported per subplot.

0.2 m × 0.2 m plots were established for the study of seedlings within the studied 10 m^2 subplots. The seedling plots were established subjectively to incorporate the maximum density of healthy seedlings. In invaded subplots, a seedling plot was always placed underneath an adult *A. longifolia* (if seedlings were present in that location) and a second plot was established if seedlings were identified growing inside the subplot but not directly underneath an *Acacia* crown. One seedling plot was established in non-invaded subplots. The location of each seedling plot was classified into one of three groups depending on its proximity to an adult *A. longifolia*: under, near (<5 m), or distant (>5 m) from an adult *A. longifolia*. Seedlings were classified into the same height classes as used for the adult plants: 0–10, 11–25, 26–50, 51–100 and 101–150 cm.

Calculation of diversity indices

Shannon's Index, Simpson's Diversity and Pielou's Evenness were calculated based on total canopy cover of each species (calculated from measurements of crown diameter, see previous section) for each of the 34 studied subplots in each habitat (Kent and Coker 1992). We combined canopy cover of adult plants >1.5 m and adult/juvenile plants <1.5 m. Shannon's Index (H′) was calculated as:

$$H' = -\sum_{i=1}^{N} p_i \ln p_i \tag{1}$$

and Simpson's Diversity, using the reciprocal index (1/D) formulation, was calculated as:

$$\frac{1}{D} = \sum_{i=1}^{N} \left(p_i^2\right)^{-1} \tag{2}$$

where p_i is the proportion of canopy cover from species i and N is the total cover of all species. Pielou's Evenness J' was calculated from Shannon's Index as

$$J' = \frac{H'}{\ln N} \tag{3}$$

where H' is the Shannon Index and N the total cover of all species.

Hemispherical photographs

Hemispherical photographs using three different exposures (−1.3, 0, 1.3) were taken with a Nikon Coolpix 950 camera with a Nikon FC-E8 fish-eye lens attached to a tripod fixed at 1.3 m above ground level. The camera was placed in the center of each 10 m^2 subplot used for vegetation structure measurements and oriented towards north. Photographs were taken at either dusk or dawn (to ensure homogenous sky conditions) during September 2007 in the south and during November and December 2007 in the north. The photographs at both sites were taken after the vegetation had a chance to recover from summer droughts (>1 month in the south and >3 months in the north). Since the upper story species are largely evergreen we do not expect that the differences in timing impacted our results. Leaf area index (LAI) and transmitted gap light were calculated from the photograph with the best contrast using Gap Light Analyzer 2.0 software (Frazer et al. 1999).

Statistical analyses

The 10 m^2 subplots were used as the statistical unit in all analyses of adult\juvenile plants, diversity indices, and LAI and transmitted gap light calculated from hemispherical photographs. For seedlings the 0.04 m^2 seedling plots were the statistical unit. T-tests were used to compare LAI, canopy openness, transmitted gap light, species richness, Shannon's Index, Simpson's Diversity and Pielou's Evenness between invaded and non-invaded areas in each habitat. Poisson generalized linear models followed by a Tukey test for multiple comparisons were used to compare density between species within each habitat and seedling density as a function of distance from adult *A. longifolia*. All analyses were conducted in R version 2.6.2 using the base, lmtest, and multcomp packages (R Development Core Team 2008).

Results

Impacts of *A. longifolia* invasion: heterogeneity across habitats

Increases in basal area as a result of *A. longifolia* invasion were much more pronounced for the dune than the forest sites (Table 1). Furthermore, increases in upper stratum canopy cover were greater in dune as compared to forest habitats (Table 1). Across all four habitats, total canopy cover was increased in invaded habitat (Fig. 2). *Acacia longifolia* invasion had differential impacts on vegetation structure in the two strata. At all sites, the presence of *A. longifolia* resulted in increased canopy cover in the upper stratum (Table 1). *A. longifolia* presence was associated with both decreased (ND, SF) and increased (NF, SD) canopy cover in the lower stratum (Table 1). Furthermore, the extent of invasion was generally greater in the north than in the south (Table 1). In the NF, 88% of the studied subplots were invaded and *A. longifolia*'s contribution to canopy cover in invaded subplots was 57.0% in the upper stratum and 64.7% in the lower stratum (Table 1) yielding a 57.4% contribution to total canopy cover (Fig. 2). In the ND, fewer subplots were invaded (29%) but *A. longifolia* accounted for 87.5% of the total canopy cover (Fig. 2) largely driven by its extreme dominance (95.6%) in the upper stratum (Table 1). The contribution of *A. longifolia* to total canopy cover of invaded subplots in the south was smaller (45.7% in the SD and 52.3% in the SF; Fig. 2).

Invasion effects on vegetation structure and understory light climate

Acacia longifolia tended to be taller than the native understory shrubs and reached a similar height or was shorter than the overstory pine trees. Accordingly, *A. longifolia* filled a largely unexploited height class niche (small tree/large shrub) at both sites in the south (Fig. 3c, d). In the north there was greater overlap between the height distributions of *A. longifolia* and other native species; but, *A. longifolia* mean height still fell between that of *P. pinaster* and the other native species (Fig. 3a, b). Furthermore, *A. longifolia* density was generally greater than that of native species in the upper stratum (Fig. 4). This tendency of *A. longifolia* to dominate the upper stratum coincided with a decreased native species density in the lower stratum of invaded subplots compared to non-invaded subplots (Fig. 4). This effect was significant at all sites except the NF (where the % of non-invaded habitat was extremely low resulting in a small sample size for non-invaded habitat; Table 1). The effect of invasion was also apparent in changes to the canopy cover of both strata. In invaded areas, *A. longifolia* made up between 42.6 and 95.6% of the canopy cover in the upper stratum and there was an associated decrease in canopy cover of native understory shrubs in the lower stratum (Table 1). Native species completely dominated the lower stratum (100% cover) of non-invaded subplots but their contribution decreased substantially

Table 1 Stand characteristics of invaded and non-invaded areas in the four studied habitats

	North Dunes (ND)		North Forest (NF)		South Dunes (SD)		South Forest (SF)	
	Inv	Non	Inv	Non	Inv	Non	Inv	Non
Habitat breakdown (%)	29	71	88	12	32	68	50	50
Basal area (m^2/ha)	18	1	54	51	27	3	30	46
Canopy cover								
Upper stratum (m^2/ha)	3,757	158	26,437	16,783	20,293	1,877	13,563	11,075
Acacia (%)	95.6	0	57.0	0	42.6	0	58.3	0
Pinus (%)	4.4	100	40.2	62.7	57.4	100	30.2	99.7
Other (%)	0	0	2.7	37.3	0	0	11.5	0.3
Lower stratum (m^2/ha)	1,058	3,073	1,313	697	3,933	2,541	2,044	3,090
Acacia (%)	58.5	0	64.7	0	62.2	0	2.4	0
Pinus (%)	0	0	0.2	0	0	4.1	0	0
Other (%)	41.5	100	35.0	100	37.8	95.9	97.6	100

Habitat breakdown (% of studied subplots which were invaded and non-invaded), total basal area of plants growing in the upper stratum (>1.5 m in height) and canopy cover of plants in the upper and lower strata. For canopy cover the total (m^2 ha^{-1}) and percent contribution of *Acacia longifolia*, *Pinus pinaster* and all other species are also given. The lower stratum does not include plants considered as seedlings. Data are totals for each habitat type and invasion status and are scaled up and expressed on a per hectare basis

Inv invaded subplots, *Non* non-invaded subplots

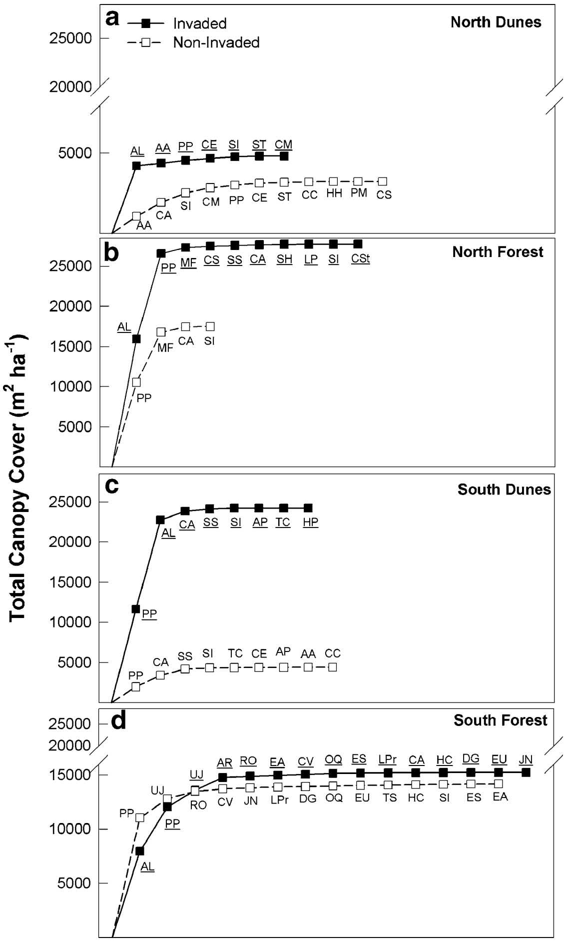


Fig. 2 Cumulative total canopy cover (*upper* and *lower* strata combined) for invaded subplots (*black squares*) and non-invaded subplots (*white squares*) in the four habitats: **a** north dunes, **b** north forest, **c** south dunes and **d** south forest. *Each point* represents the contribution of one species. *Two* or *three letter* abbreviations identify the species with *underlined letters* corresponding to invaded habitat (see "Appendix" for a full species list). These curves reflect the dominance structure with species arranged according to their relative contribution to total canopy cover

to less than 50% when *A. longifolia* was present in both habitat types in the north and in the SD (Table 1). In the SF *A. longifolia* contributed very little to the cover of the lower strata (<3%; Table 1) This dominance of the middle stratum (between ~ 1.5 and 8 m) by *A. longifolia* in invaded areas had a large impact on the leaf area index (LAI) and transmitted gap light to the understory. At all sites LAI tended to be greater and transmitted gap light to be lower in invaded compared to non-invaded subplots (Table 2).

Invasion effects on plant diversity

In the ND and SF, *A. longifolia* invasion was associated with a significant decrease in the species number and diversity as estimated by both Shannon's Index and Simpson's Dominance (Table 3). This impact was especially large in the ND where a 50% reduction in species number and plant diversity in invaded relative to non-invaded subplots was found. The ND was the only habitat where Pielou's Evenness was also significantly reduced by invasion (Table 3). Furthermore, the ND exhibited the largest reduction (40%) in the number of native species in invaded vs. non-invaded subplots (Fig. 2a). Impacts on average species number per subplot and diversity indices were smaller but still substantial (~ 25%) in the SF. In the ND this resulted from a large decrease in the overall number of native species found in invaded subplots (Fig. 2a). In contrast, the number of native species in the SF was the same in invaded and non-invaded areas. In the NF and SD there were no significant changes in average number of species per subplot, diversity or evenness. Both of these habitats had very low average numbers of species and plant diversity even in non-invaded subplots (Table 3) as well as a lower total species number compared to the ND and SF sites (Fig. 2). Overall, native species numbers tended to be reduced in invaded habitat in the dune sites but to remain constant or even increase in the forest sites (Fig. 2).

Invasion effects on plant regeneration

Presence of *A. longifolia* was associated with a change in crown diameter distributions of the native species. In the NF, where extremely high recruitment of young *A. longifolia* individuals was seen, there were very few native species present and no clear pattern in the crown diameter distribution of native species (Fig. 5b). In all other habitats, the crown size distributions of native species in non-invaded subplots followed an exponential decay shaped distribution due to the dominance of smaller size class (i.e. younger) individuals (Fig. 5a, c, d). In contrast, in invaded subplots, the native species crown diameter distributions had no clear maximum density at low size classes (e.g. in the SF and SD; Fig. 5c, d) or a significantly reduced number of individuals in the smallest size class (e.g. in the ND; Fig. 5a).

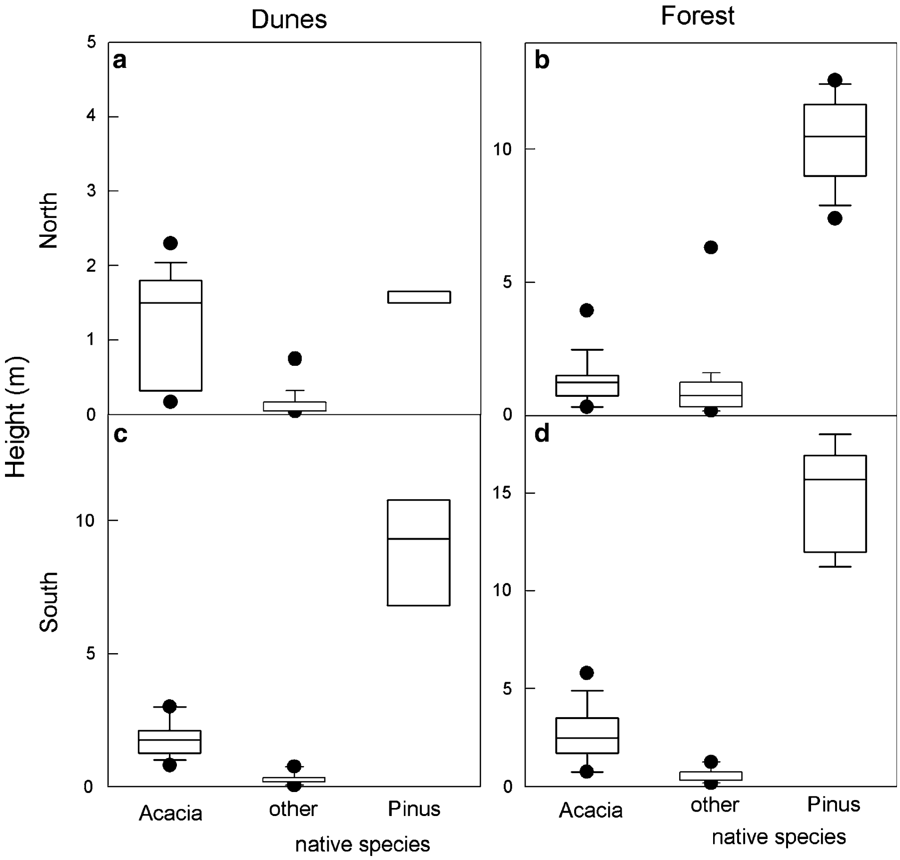


Fig. 3 Plant height distributions for *Acacia longifolia* (Acacia), *Pinus pinaster* (Pinus) and other native species in the four habitats: **a** north dunes, **b** north forest, **c** south dunes and **d** south forest. *Boxes* depict the 25th, 50th and 75th percentiles, *whiskers* the 10th and 90th and *dots* the 5th and 95th. Not all percentiles could be computed for all species in every habitat. For illustration purposes, *P. pinaster* saplings in the lower stratum (<1.5 m in height) were grouped with other species. Note that for individuals in the lower stratum the mean value of each height class was used and that there are different scales on the y-axis for the different habitats

Acacia longifolia itself similarly exhibited exponential decay shaped distributions in both forest sites (Fig. 5b, d) while in both dunes sites the distributions were more normally distributed. This indicates that *A. longifolia* populations in the forest sites are actively recruiting younger individuals (Fig. 5b, d) while the populations in the dunes are not (Fig. 5a, c). Furthermore, *A. longifolia* seems to expand through vegetative reproduction in the open stabilized dunes while reproducing sexually in the forest sites.

In accordance, there were very few seedlings present in the open stabilized dunes, and no clear influence of adult *A. longifolia* presence in this habitat could be ascertained (Fig. 6a, c). In the forest sites seedling numbers were still quite low; but nevertheless, a clear effect of *Acacia* invasion on seedling density was found (Fig. 6b, d). Native seedling presence was highest in plots distant to adult *A. longifolia*, with native seedling density being significantly reduced in plots underneath adult *A. longifolia* at both forest sites (Fig. 6b, d). In the SF, native seedling density was also significantly lower in plots nearby to adult *A. longifolia* relative to the density of distant plots (Fig. 6d). In contrast, *A. longifolia* seedling presence was greatest under adult *A. longifolia* and decreased with increasing distance from adult *A. longifolia* (Fig. 6b, d). Furthermore, in the forest sites, close proximity to adult *A. longifolia* corresponded to a broader range of seedling height classes for the invader (Fig. 7a, b, d, e). In contrast, only the smallest size classes of native seedlings were found underneath adult *A. longifolia* (Fig. 7a, d). This indicates that *A. longifolia* self-facilitates its own offspring while inhibiting the regeneration and growth of native seedlings.

Discussion

Impact of *A. longifolia* invasion on vegetation structure, composition and dynamics

Here we have shown that, among other previously documented novel traits of *A. longifolia* in Portugal

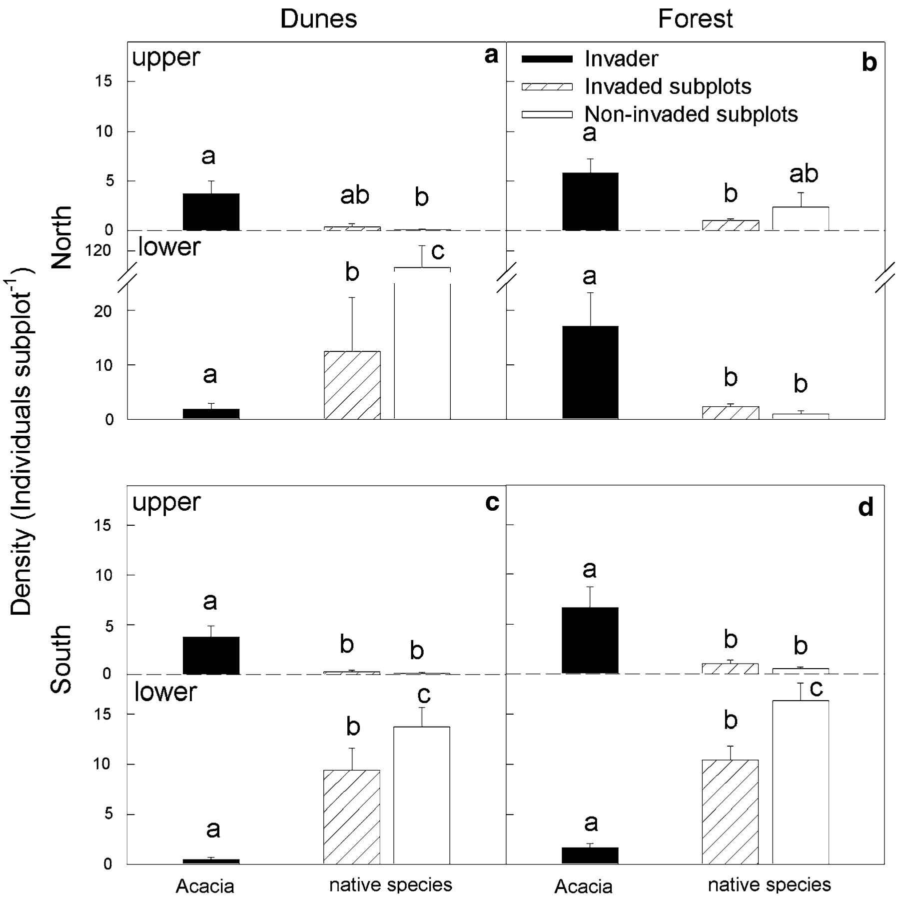


Fig. 4 Plant density (individuals per 10 m^2 subplot) in the upper (>1.5 m) and lower strata (<1.5 m) for *Acacia longifolia* (*black bars*) and other species in invaded (*hashed bars*) and non-invaded subplots (*solid bars*) in the four habitats: **a** north dunes, **b** north forest, **c** south dunes and **d** south forest. *Different letters* above *bars* within a habitat and stratum indicate significant density difference ($P < 0.05$). Data are means with standard errors. Note the different scales on the y-axis for the different habitats

Table 2 Leaf area index (LAI) and transmitted gap light calculated from hemispherical photos for invaded and non-invaded areas of the four studied habitats

	North Dunes (ND)		North Forest (NF)		South Dunes (SD)		South Forest (SF)	
	Inv	Non	Inv	Non	Inv	Non	Inv	Non
LAI (m^2 m^{-2})	0.29 ± 0.24	0 ± 0	1.73 ± 0.05	1.60 ± 0.20	0.88 ± 0.20	0.25 ± 0.04 *	1.13 ± 0.08	0.86 ± 0.04 *
Transmitted gap Light (%)	85 ± 8	99 ± 0 *	28 ± 1	29 ± 4	62 ± 8	82 ± 5 *	43 ± 3	53 ± 3 *

Data are means ± SE

Inv invaded subplots, *Non* non-invaded subplots

* Significant difference between invaded and non-invaded subplots within a habitat (n = 3–19); $P < 0.05$

such as nitrogen fixation (Hellmann et al. 2011; Marchante et al. 2008a, b, 2009), high water use rates (Rascher et al. 2009), and production of a thick litter layer (Marchante et al. 2008b), *A. longifolia* added a vegetation layer of tall shrubs and small trees which was a relatively empty stratum in non-invaded areas (Fig. 3). In agreement with previous studies of *A. longifolia* in northern Portugal (Marchante et al. 2003), we document here that *Acacia longifolia* invasion changed community structure dramatically in all studied habitats. Especially in the open dune sites, *A. longifolia*'s growth form differed substantially from that of the native species, which, except for *P. pinaster*, tend to have very low stature (Fig. 3a, c). These pristine dune communities, which are typically characterized by an open structure and low plant

Table 3 Number of species, Shannon's index, Simpson's dominance and Pielou's evenness for invaded and non-invaded subplots at the four study sites

	Number of Species		Shannon's index (H')		Simpson's dominance (1/D)		Pielou's evenness (J)	
	Invaded	Non-invaded	Invaded	Non-invaded	Invaded	Non-invaded	Invaded	Non-invaded
ND	2.9 ± 0.53	6.0 ± 0.25 *	0.6 ± 0.16	1.3 ± 0.07 *	1.8 ± 0.27	3.4 ± 0.23 *	0.5 ± 0.12	0.7 ± 0.03 *
NF	2.5 ± 2.0	2.0 ± 0.0	0.6 ± 0.07	0.6 ± 0.06	1.7 ± 0.11	1.7 ± 0.16	0.6 ± 0.06	0.8 ± 0.09
SD	3.0 ± 0.35	3.0 ± 0.32	0.7 ± 0.11	0.8 ± 0.08	2.0 ± 0.18	2.1 ± 0.19	0.7 ± 0.08	0.8 ± 0.06
SF	4.5 ± 0.37	5.8 ± 0.44 *	1.1 ± 0.09	1.4 ± 0.07 *	2.8 ± 0.24	3.5 ± 0.22 *	0.8 ± 0.04	0.8 ± 0.02

Data are subplot means ± SE

* Significant difference between invaded and non-invaded subplots within a habitat (n = 3–19); $P < 0.05$

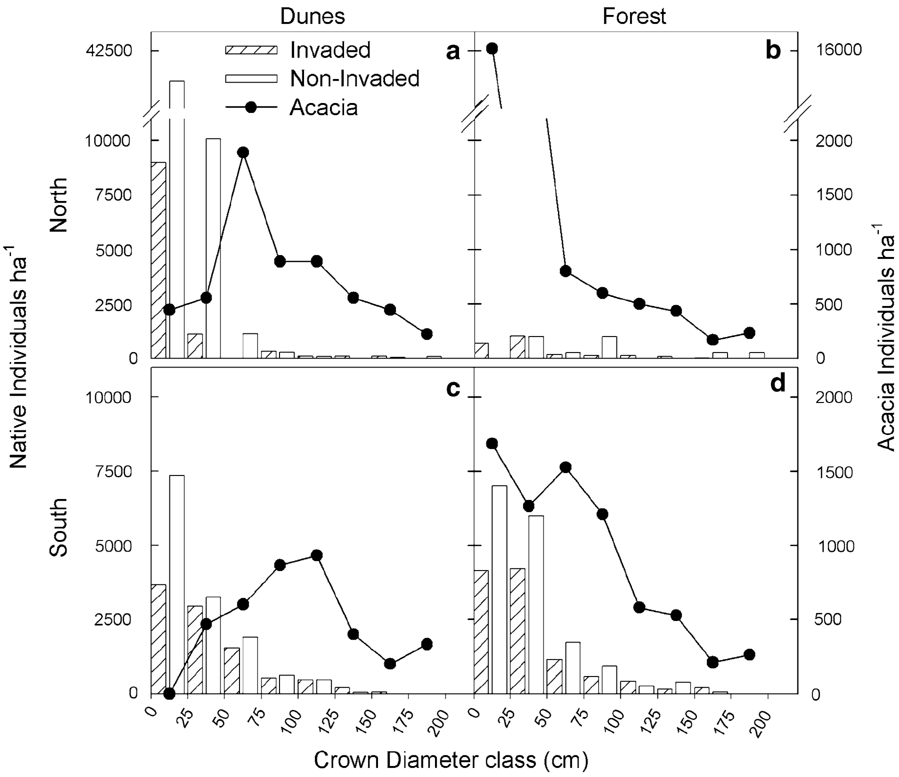


Fig. 5 Distribution of crown diameter (individuals per hectare) for *Acacia longifolia* (*black circles*) and native species in invaded (*hashed bars*) and non-invaded subplots (*solid bars*) in the four habitats: **a** north dunes, **b** north forest, **c** south dunes and **d** south forest. Note the different scales used for the northern and southern sites and for *Acacia longifolia* versus the native species

cover, are being transformed into scrublands by *A. longifolia*. Even in forest habitats the invader dominated a stratum of the forest that was occupied by very few other species (e.g. *Myrica faya* in the north; Fig. 2b; Fig. 3b, d). This strategy of dominating the middle stratum of forests is also typical of *A. longifolia* in invaded areas in Australia (Emms et al. 2005) where it shades out herb and shrub species (Costello et al. 2000) and negatively impacts overstory regeneration (Muyt 2001). Furthermore, the domination of the middle stratum allowed *A. longifolia* to intercept light (Table 2), which would have previously reached the understory, thus suppressing native understory species. Dune plant communities are typically comprised of species with low stature, slow growth rates and low canopy cover (Fig. 2a, c; "Appendix") allowing for high light intensities at ground level (Table 2). Accordingly, species adapted to these conditions typically do not tolerate low light intensities (Smith and Huston 1989).

Regeneration of both the invader and native species were also impacted by *A. longifolia* invasion. In

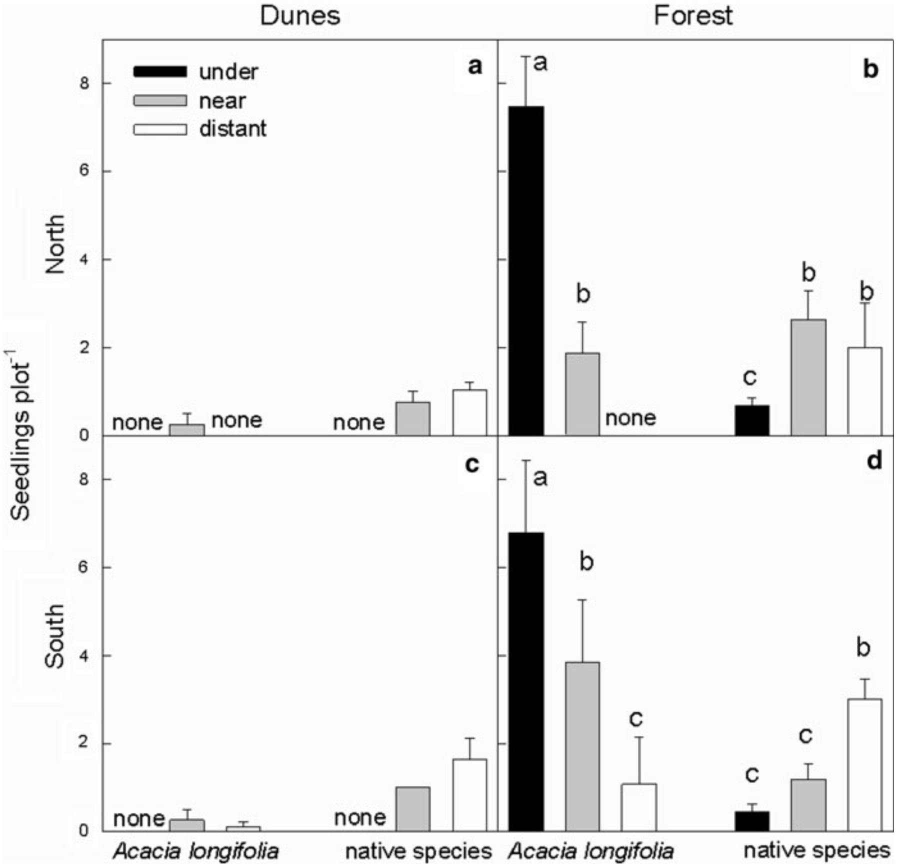
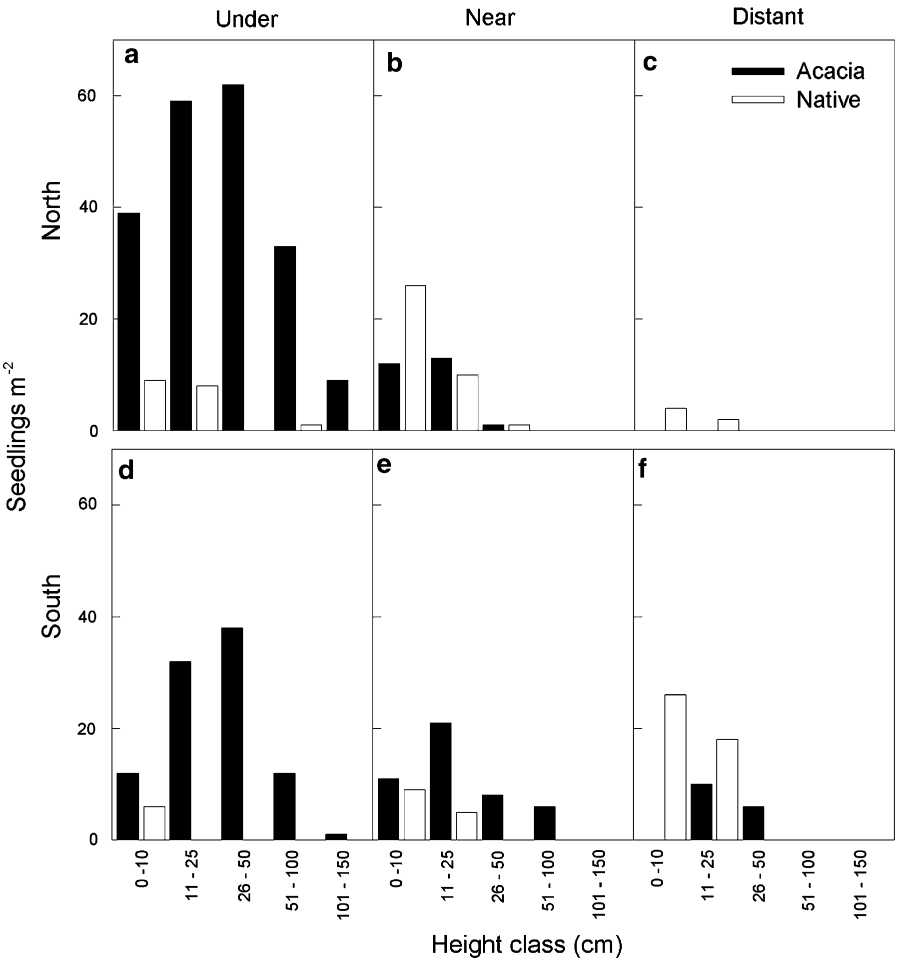


Fig. 6 Counts of native species and *Acacia longifolia* seedlings (individuals per 0.04 m^2 plot) in the four habitats: **a** north dunes, **b** north forest, **c** south dunes and **d** south forest. Each seedling plot was either located under (*black bars*), near (*gray bars*) or distant (*white bars*) from an adult *A. longifolia* individual. Due to the low number of seedlings in the dune habitats no statistical analysis was done. For the forest sites, *different letters* above *bars* within a habitat indicate significant difference in seedling density ($P < 0.05$)

general, few seedlings were found in this study which may be partially attributed to the timing of sampling (September to December). Nevertheless, in the forest sites, we found that native species regeneration was negatively affected by the presence of *A. longifolia* (Figs. 6, 7). This may have resulted from altered soil chemistry and nutrient cycling in invaded areas (e.g. Marchante et al. 2008a, b, 2009), or from the altered aboveground vegetation structure leading to microclimatic differences e.g. light intensity (Table 2), underneath and distant from *Acacia* stands. Previously, *A. longifolia* has been shown to grow better in its own soils (with higher C and N contents) than soils collected from underneath other N-fixing plant species (Rodríguez-Echeverría et al. 2009), and also to benefit more from increased soil nitrogen than native Mediterranean species (Peperkorn et al. 2005). In agreement, this study demonstrates that, at least in forest sites, *A. longifolia* self-facilitates its own offspring as indicated by the increased seedling density (Fig. 6) and broader seedling age class distribution (Fig. 7) of invasive seedlings underneath or nearby to adult *A. longifolia* (<5 m distant). The ability of invasive species to ameliorate their own growth conditions thus resulting in a positive feedback is theorized to be an important mechanism supporting plant invasions (Corbin and D'Antonio 2004; Ehrenfeld 2003). Furthermore, other studies have documented that invasiveness of *Acacia* spp. can be attributed in part to the production of very large seed banks (Pieterse and Cairns 1986; Zenni et al. 2009) and that the presence of *A. longifolia* inhibits the germination and sprouting of native species (Marchante et al. 2003) and depresses the abundance of native species (Richardson et al. 1992). Similar impacts on regeneration of native species have also been found for the invasive *Prosopis juliflora*. Growth of both native seedlings and annual species were inhibited under the *P. juliflora* canopy while establishment of its own seedlings was facilitated (El-Keblawy and Al-Rawai 2007).

Acacia spp. invasions have been associated with decreases in plant diversity in a range of open dune

Fig. 7 Height class distribution of *Acacia longifolia* (*black bars*) and native (*open bars*) seedlings in plots (**a**, **d**) underneath, (**b**, **e**) near (<5 m) or (**c**, **f**) distant (>5 m) from an adult *A. longifolia* in the two forest sites: **a**–**c** north forest, **d**–**f** south forest. Due to the extremely low seedling density in the dune sites (Fig. 4a, c) height class distributions were not examined in those sites



sites in northern Portugal (e.g. Marchante et al. 2003), species abundance in the South African fynbos (e.g. Holmes and Cowling 1997; Richardson et al. 1992) and species richness in Australian coastal grasslands (Costello et al. 2000). Here we similarly document a tendency toward greater plant diversity (e.g. increased Shannon's index, Simpson's Dominance and Pielou's Evenness) in non-invaded compared to invaded habitats, although differences were not always statistically significant (Table 3). In the most affected sites (ND and SF), there was a significant decrease of average species number per subplot and plant diversity indices (Table 3). Interestingly, it was at the extremes of the moisture gradient (e.g. the most humid site, NF, and the driest site, SD) that no significant changes in diversity indices or average species number per subplot were found (Table 3). In the SD there was indeed a reduction in the total number of native species found in invaded vs. non-invaded habitat (7 vs. 9; Fig. 2c). For the NF there was a greater total number of native species found in invaded than non-invaded habitat (Fig. 2b). This contradictory result may be at least partially an artifact of the small proportion of non-invaded plots which may have resulted in sampling bias (Table 1). Furthermore, the number of native species tended to be lower in invaded relative to non-invaded habitat in the dune sites but to remain constant or even increase in the forest sites (Fig. 2), indicating that *A. longifolia* impacts the native vegetation differently in these contrasting habitat types.

Consequences of *A. longifolia* invasion for ecosystem functioning

This substantial alteration to vegetation structure has potentially profound implications for above- and below-ground carbon storage in these ecosystems.

We have demonstrated here that *A. longifolia* presence is associated with an increase in total canopy cover, basal area (Table 1) and plant density in the upper stratum (Fig. 4). Similarly, Van Wilgen et al. (2001) noted that since total above ground biomass tends to increase due to invasion by *Acacia* spp. there is potential for increased ecosystem carbon storage. However, since flammability and fire severity are also elevated due to invasion by *Acacia* spp. (Osunkoya et al. 2005; Van Wilgen and Richardson 1985), ecosystem carbon storage could actually decrease. Asner et al. (2009) recently illustrated in Hawaii that, even though the invasive *Morella faya* (a.k.a *Myrica faya*) increased aboveground biomass by up to 350%, ecosystem carbon storage did not increase because the added biomass of the invader was offset by a decreased biomass of the native understory species. We have similarly shown here that *A. longifolia* presence significantly increased above ground basal area as well as total and upper stratum canopy cover in invaded areas (Table 1; Fig. 2). However, at some sites (ND, SF), there was a concomitant decrease in density and canopy cover particularly of native species, in the lower stratum (Table 1; Fig. 4). Accordingly, it appears that the effect of *A. longifolia* invasion on ecosystem carbon storage is difficult to generalize and strongly dependent on site specific characteristics.

Changes to above ground vegetation structure due to *A. longifolia* invasion will also impact below ground processes. At other sites along Portugal's northern coast, *A. longifolia* invasion was shown to decrease the soil C:N ratio leading to increased rates of potential nitrification (Marchante et al. 2008b) and to alter the microbial catabolic diversity of soils (Marchante et al. 2008a). Similarly, in the South African fynbos, *Acacia saligna* increased both total and available nitrogen and impacted ecosystem nutrient cycling more severely than *Lupinus luteus*, an invasive annual in the same system (Yelenik et al. 2007). Also documented in many studies of *Acacia* spp. invasions is the presence of a thick litter layer (e.g. Marchante et al. 2004; Marchante et al. 2008a, b; Osunkoya et al. 2005; Yelenik et al. 2004), which has been shown to contain low-quality carbon thus immobilizing nitrogen in the microbial community (Marchante et al. 2008b; Yelenik et al. 2007).

Alterations to vegetation composition brought about by *A. longifolia* invasion may have further impacts on ecosystem functioning, such as water and carbon cycling, since *A. longifolia* and native species differ markedly in their functional traits and resource use strategies (Peperkorn et al. 2005; Rascher et al. 2009, 2010; Werner et al. 2010). Native Mediterranean species typically have characteristic traits (e.g. strong stomatal control, sclerophyllous leaves and/or seasonal changes in root/shoot ratio) for minimizing water loss, thereby allowing them to survive summer drought periods (Werner and Correia 1996; Werner et al. 1999, 2001, 2002). These adaptations result in decreased resource extraction and down-regulation by native species during times when resources are scarce (Peperkorn et al. 2005; Werner et al. 2010). In contrast, controlled studies have shown that *A. longifolia* exhibits a constant allocation pattern (i.e. no change in root/shoot ratio), low plasticity and high growth rates allowing it to accumulate high biomass and outcompete native species under drought and well-watered conditions (Peperkorn et al. 2005; Werner et al. 2010) which has profound implications for the integrity and functioning of these invaded habitats. Furthermore, Rascher et al. (2009) documented that the water status of *P. pinaster* in the SF was negatively impacted by the presence of *A. longifolia* with the largest reduction in *P. pinaster* water use occurring when *A. longifolia* sap flow was highest. Accordingly, given the future climate scenarios predicted for the Mediterranean (i.e. increased drought severity and duration; IPCC 2007), the impact of *A. longifolia* on the water status of co-occurring species may be more severe in the future. The marked decrease in density and canopy cover of drought resilient native understory species (Table 1; Fig. 2; Fig. 4) combined with the large contribution of the drought susceptible invader to basal area, canopy cover, and plant density in invaded habitat (Table 1; Figs. 2, 4, 5) indicate that ecosystem vulnerability to drought may be substantially greater in invaded habitats.

However, it must also be acknowledged that *A. longifolia* has been shown to be more susceptible to severe drought than native species (as measured by relative reduction in biomass in drought vs. well-watered conditions; Werner et al. 2010). Nevertheless, under drought conditions, *A. longifolia* still laid down more biomass than native competitors did under well-watered conditions (Werner et al. 2010). Even though *A. longifolia* may be highly susceptible to drought on the individual level, on a population level it has enormous resources to recover due in part to its enormous seed bank (Pieterse and Cairns 1986; Zenni et al. 2009). Accordingly, even during the extended droughts predicted for the studied sites in the future, it is not clear that native species will be able to regain their competitive advantage. Overall, there is increasing evidence that invasion by the resource demanding *A. longifolia* significantly modifies the native habitat to an extent that greatly hinders restoration attempts (e.g. Marchante et al. 2008b, 2009; Rodríguez-Echeverría et al. 2009).

Conclusions

We have documented here, for two sites along the Portuguese coast, that *A. longifolia* significantly changed vegetation structure and filled a nearly unexploited height class niche (small tree/large shrub) in open stabilized dunes and pine forests. The most pronounced effects of *A. longifolia* invasion were an increase in density, basal area and plant cover in the upper stratum and a tendency for decreased transmission of light to the understory and decreased plant diversity. Furthermore, in forest sites, there was a significant inhibition of native species regeneration. These effects, combined with pronounced differences in ecological strategy (Rascher et al. 2010) and the lower drought tolerance of the invader (e.g. Peperkorn et al. 2005; Werner et al. 2010), indicate that invaded habitats may have increased drought vulnerability. Furthermore, in terms of restoration prospects, even after the removal of *A. longifolia*, regeneration of the native plant community will continue to be impacted by lingering effects from the altered seedling age class structure documented here.

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Appendix

See Table 4.

Table 4 Full species list

Species Name	ID	North Dunes	North Forest	South Dunes	South Forest	Growth Form
Acacia longifolia (Andrews) Willd.	AL	x	x	x	x	T/S
Acacia retinodes Schltdl.	AR				x	T/S
Ammophila arenaria (L.) Link	AA	x		x		G
Armeria pungens (Link) Hoffanns & Link	AP			x		dS
Calluna vulgaris (L.) Hull	CV				x	S
Calystegia soldanella (L.) R. Br.	CS	x				F
Carpobrotus edulis (L.) N.E. Br.	CE	x		x		dS
Cistus salviifolius (L.)	CS		x			dS
Corema album (L.) D. Don	CA	x	x	x	x	S
Corynephorus canescens (L.) P. Beauv.	CC	x		x		G
Crucianella maritima (L.)	CM	x				H
Cytisus striatus (Hill) Rothm.	CSt		x			S
Daphne gnidium D.	DG				x	S
Erica australis L.	EA				x	S
Erica scoparia L.	EL				x	S
Erica umbellata L.	EU				x	dS
Halimium commutatum Pau.	HC				x	dS
Halimium halimifolium (L.) Willk.	HH	x				dS
Helichrysum picardii Boiss & Reuter	HP			x		dS

Table 4 continued

Species Name	ID	North Dunes	North Forest	South Dunes	South Forest	Growth Form
Juniperus navicularis Gand.	JN				x	S
Lavandula pedunculata (Mill.) Cav.	LP		x			dS
Lithodora prostrata (Loisel.) Griseb.	LPr				x	dS
Myrica faya Aiton	MF		x			T/S
Osyris quadripartita Hochst. & Steud.	OQ				x	S
Pancratium maritimum L.	PM	x				F
Pinus pinaster Aiton	PP	x	x	x	x	T
Rosmarinus officinalis L.	RO				x	S
Santolina impressa Hofmanns & Link	SI	x	x	x	x	dS
Scirpus holoschoenus (L.) Soják	SH		x			G
Sedum sediforme (Jacq.) Pau	SS	x				F/H
Seseli tortuosum (L.)	ST	x				F/H
Stauracanthus sp.	SS		x	x		S
Thymus camosus Boiss	TC			x		dS
Thymus sp.	TS				x	dS
Ulex jussiaei Webb	UJ				x	S

T tree, *(d)S* (Dwarf) shrub, *F* forb, *H* herb, *G* graminoid

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