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# Pronounced difference in community structure between the edge and the interior: analysing small-scale variability of a maritime woodland

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## Abstract

While changes in plant community structure have often been documented along large-scale environmental gradients, there is a paucity of information on small-scale community variability, particularly in coastal tree assemblages. This study focused on the small-scale, edge to interior, variation in the community structure of subtropical maritime woodland in Amakusa, south-western Japan. Comparison was made between the edge and the interior habitats within this maritime woodland bordering the intertidal shore and receiving the full impact of sea wind. Although the two habitats were separated by only 10-20m, there was a significant change in tree assemblage structure in terms of relative abundance patterns, density, and morphology including tree sizes and branching tendency. While *Quercus glauca* was predominant in both the interior and the edge, its dominance was less pronounced in the edge with a more equitable pattern of relative abundances of tree species. Comparing shade-tolerant versus shade-intolerant species, density of the latter was higher in the edge than in the interior, while a similar but non-significant trend was shown by the former. In addition, shade-tolerant species (including *Q. glauca*) showed that tree size was smaller in the edge than in the interior, while shade-intolerant species showed an opposite (but non-significant) tendency. Further, while both shade-tolerant and intolerant species showed greater tendencies of multiple-trunk structure in the edge than in the interior, this difference was more marked in shade-intolerant species. Overall, the study draws attention to the potential importance of small-scale variation in community structure of non-mangrove maritime tree assemblages.

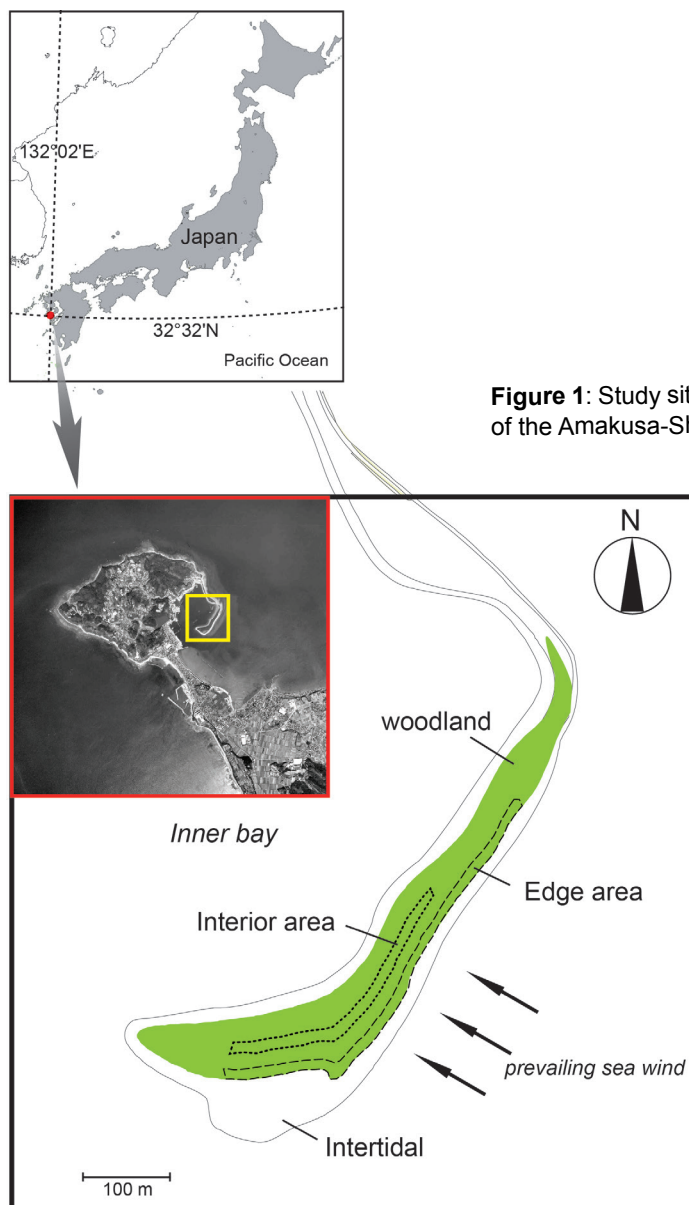
**Keywords:** relative abundance patterns; density; morphology; coexistence; *Quercus glauca*

## Introduction

Edges in forests and woodlands constitute an interface to the outer environment with a suite of environmental conditions often different from internal sites, which are thought to affect plant/animal communities in different ways (Williams-Linera 1990; Chen *et al.* 1999; Mourelle *et al.* 2001; Dignan & Bren 2003; Rheault *et al.* 2003; Harper *et al.* 2004; Ries & Sisk 2004; Shirley 2004). However, relatively little is known in detail about the responses of different assemblages to environmental variation associated with edges (Williams-Linera 1990; McDonald & Urban 2004; Baldwin & Bradfield 2005; Asquith & Mejia-Chang 2005; Dickie & Reich 2005). In particular, edge-related variation in community structure of tree assemblages on a small spatial scale has rarely been explored.

Coastal woodlands exist in an interface between

terrestrial and marine environments with marked changes in environmental conditions and experience pronounced physical disturbances in the form of storms (cf. Bellingham *et al.* 1996; Masaka & Sato 2002) the magnitudes of which are generally greater than those experienced by inland forests. In addition to physical disturbances, the sea wind causes a stress in the form of salt spray (Zhu *et al.* 2002) which is detrimental to most terrestrial plants, the effect of which is ameliorated towards the woodland interior by trees in the edge working as a windbreak (Asquith & Mejia-Chang 2005). Thus, coastal woodland is considered to be exposed to environmental stresses of greater magnitudes than in inland forests facing grassland or old-fields (Ries & Sisk 2004), pointing to a possibility of notable small-scale variation in community structure along the edge-interior gradient. While mangrove assemblages have received some attention in this respect (Hogarth 1999; Lovelock & Feller 2003), there



**Figure 1:** Study site (“Magarizaki” sand spit) on the Tomioka Peninsula of the Amakusa-Shimoshima Island, western Kyushu.



**Figure 2:** (a) Overview of the apical part of “Magarizaki” sand spit, looking towards east; (b) land-intertidal interface (the ‘edge’) of the Magarizaki woodland.

is a dearth of detailed analysis of changes in community structure of coastal or maritime assemblages, particularly of non-mangrove trees.

The present study deals with variation in community structure of a subtropical maritime woodland in Amakusa, south-western Japan. The woodland occurs on a narrow sand spit surrounded by the sea and receives the full impact

of sea wind particularly from the eastern side (see below). The specific objectives of the study are to elucidate whether and how variation in community structure occurs between the edge and the interior of this woodland, with particular reference to relative abundances, density and morphology of trees.

## Materials and Methods

The study site was located on the north-western corner of the Amakusa-Shimoshima Island in Kyushu, south-western Japan (32°32'N, 130°02'E) (Fig. 1). The woodland occurred in a narrow sand spit called 'Magarizaki' (Fig. 2) projecting into the Ariake Sea, part of the East China Sea, covering a total of 2.33 ha. The apical area (500m long) of this spit, 0-3.8m above sea level, was chosen as study site (see also Yoko-o & Tokeshi 2011, 2012). This site was partially isolated from the basal part of the spit by a narrow (c.10m), barren gap where the seawater breached the land in the past and its eastern side was exposed to the effect of sea wind while the western side was more protected by steep coastal hills across a small enclosed bay. This region has been described as sub-tropical with summer surface water temperatures constantly reaching above 28°C (Kawai & Tokeshi 2004) and the maximum momentary wind velocity of > 20 m s<sup>-1</sup> occurs 7-10 times per year.

Data were collected in 2004-2005 from the middle section of the study site designated as the 'edge' (0-10m zone from the woodland border) and the 'interior' (20-30m zone from the border) of the woodland (Fig. 1). Seven reference points were randomly chosen along the shore and a pair of edge and interior quadrats (10 x 10m) were established at each point. Trees inside the quadrats were marked with numbered tags on the trunk at the time of the first survey; all trees > 4cm diameter at breast height (dbh at 1.3m) were identified and measured for dbh. Trees with multiple trunks at breast height with an equivalent of > 12cm<sup>2</sup> total cross sectional areas were also included. In the case of multiple trunks, the circumference of each trunk was measured. Size (*S*) of each tree was represented as a sum of cross-sectional area based on dbh, thus,

$$S = \sum_{i=1}^{N} (d_i / 2)^2 \pi$$

Where  $d_i$  is diameter at breast height of the  $i$ th trunk of a tree



**Figure 3:** Example photographs of canopy openness in June 2005. (a) edge site, (b) interior site. (c) *Quercus glauca* with fruits.

and  $n$  is the number of trunks. The abundance of a species was represented as the sum of cross sectional areas (at breast height) of all individuals belonging to that species. Hence the relative abundance of the  $x$ th species ( $P_x$ ) among a total of  $N$  species (for the combined data) is,

$$P_x = A_x / \sum_{j=1}^N A_j$$

( $A_x = \sum S$ , i.e. the sum of  $S$  of all individuals of species  $x$ )

As this abundance measure was used for the analysis of species abundance patterns, models such as the zero-sum multinomial model (Hubbell 2001) and the lognormal model which are based on numbers of individuals are not applicable. Instead, we employed the Power Fraction model (Tokeshi 1996, 1999), a flexible and parsimonious model of niche apportionment previously used for species-rich animal assemblages (Gaston & Blackburn 2003; Marquet *et al.* 2003), was fitted. This model has parameter  $k$  relating to the probability of abundance-related selection in a sequential niche fragmentation process where  $k = 0$  represents no selection or random selection with respect to abundance (equivalent to the Random Fraction model, Tokeshi 1993) and  $k = 1.0$  represents a strong selection of more abundant species for subsequent niche division (MacArthur Fraction model, Tokeshi 1993). In other words, positive value of  $k$  ( $k > 0$ )

represent the progressive decaying of dominant status and negative values ( $k < 0$ ) represent the opposite, i.e. the reinforcement of dominant status. For estimating the  $k$  values of observed data, Monte Carlo simulations were conducted with 1000 replications for each value of  $k$  to minimise the residual sums of squares on rank-abundance plots.

Morphological variation of trees in the edge and the interior was examined by calculating the branching index ( $BI$ ) expressed as the ratio of trunk numbers to cross-sectional area, thus,

$$BI = (\text{the number of trunks at breast height}) / S$$

For data analysis, tree species were classified as either shade-tolerant or shade-intolerant according to an online database (<http://www.pfaf.org/database>); in the present study, shade-tolerant species included *Quercus glauca*, *Ligustrum japonicum*, *Myrsine seguinii*, *Prunus zippeliana*, *Gardenia jasminoides*, *Euonymus japonicus* and *Elaeagnus macrophylla*.

Canopy openness was assessed by taking photographs at 3-4 points in each quadrat with a fish-eye lens attached to a digital camera (Englund *et al.* 2000) at 1m height in December 2004 and June 2005 (Fig. 3). Photographs were analysed using the Canopon2 program (<http://takenaka-akio.cool.ne.jp/etc/canopon2/index.html>).

**Table 1.** Tree species recorded within the study site in the Magarizaki sand spit, Amakusa-Shimoshima Island, Japan. Summed values of total cross-sectional area ( $S$ ) are shown.

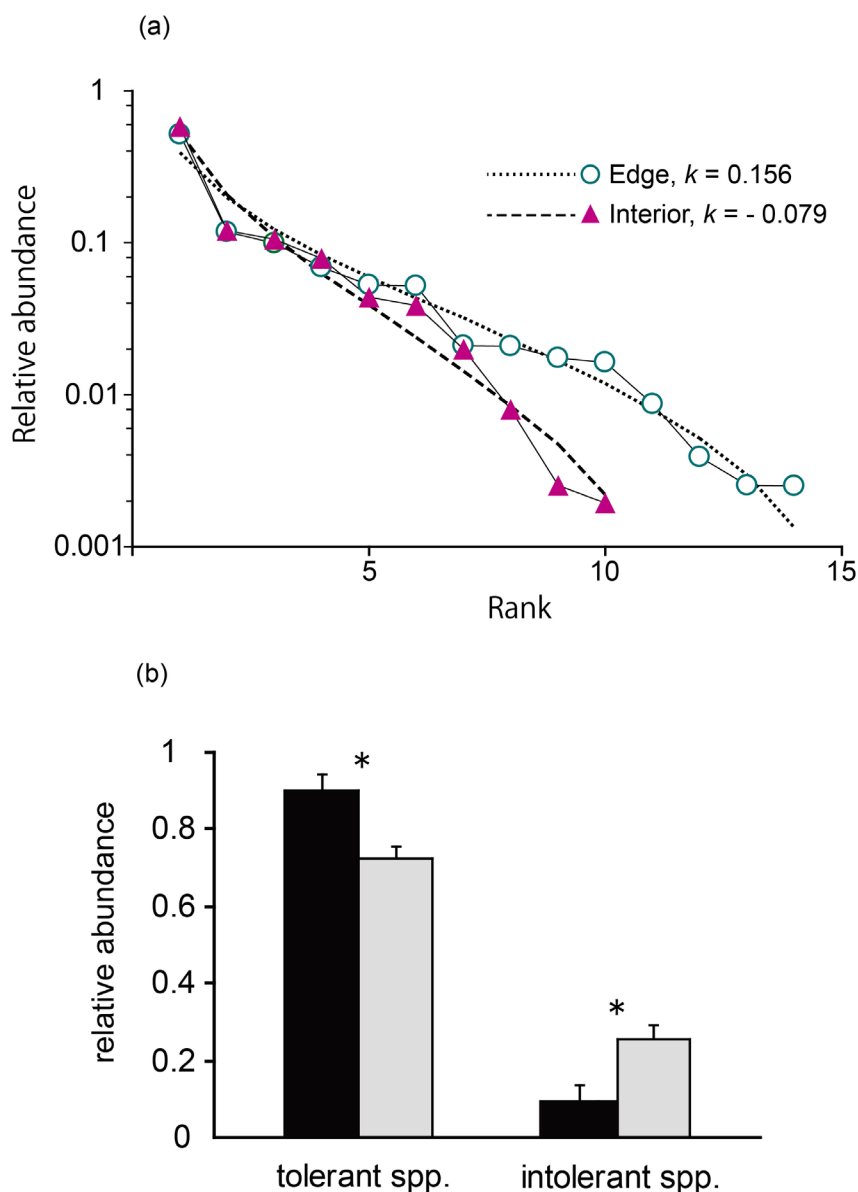
species	total cross-sectional area ( $S$ cm <sup>2</sup> )	relative abundance ( $P_x$ )
<i>Quercus glauca</i> (Thunberg)	33659.9	0.479
<i>Rhus succedanea</i> (Linnaeus)	13216.9	0.188
<i>Ligustrum japonicum</i> (Thunberg)	7046.6	0.101
<i>Pittosporum tobira</i> (Thunberg) Aiton	5029.3	$7.15 \times 10^2$
<i>Prunus zippeliana</i> (Miquel)	3090.2	$4.39 \times 10^2$
<i>Myrsine seguinii</i> (Léveillé)	2824.9	$4.02 \times 10^2$
<i>Hibiscus hamabo</i> (Siebold et Zuccarini)	1644.6	$2.34 \times 10^2$
<i>Ilex integra</i> (Thunberg)	1253.5	$1.78 \times 10^2$
<i>Gardenia jasminoides</i> (Ellis)	720.8	$1.02 \times 10^2$
<i>Litsea coreana</i> (Léveillé)	616.5	$8.76 \times 10^3$
<i>Rhaphiolepis umbellata</i> (Thunberg) Makino	444.1	$6.31 \times 10^3$
<i>Euonymus japonicus</i> (Thunberg)	335.1	$4.76 \times 10^3$
<i>Lyonia ovalifolia</i> (Wallich) Drude	251.5	$3.58 \times 10^3$
<i>Litsea japonica</i> (Thunberg) Jussieu	65.0	$9.24 \times 10^4$
<i>Elaeocarpus sylvestris</i> (Loureiro) Poiret	60.9	$8.65 \times 10^4$
<i>Elaeagnus pungens</i> (Thunberg)	50.8	$7.22 \times 10^4$
<i>Xylosma congestum</i> (Loureiro) Merrill	20.4	$2.90 \times 10^4$
<i>Cerasus speciosa</i> (Koidzumi) Ohba	12.2	$1.74 \times 10^4$

## Results

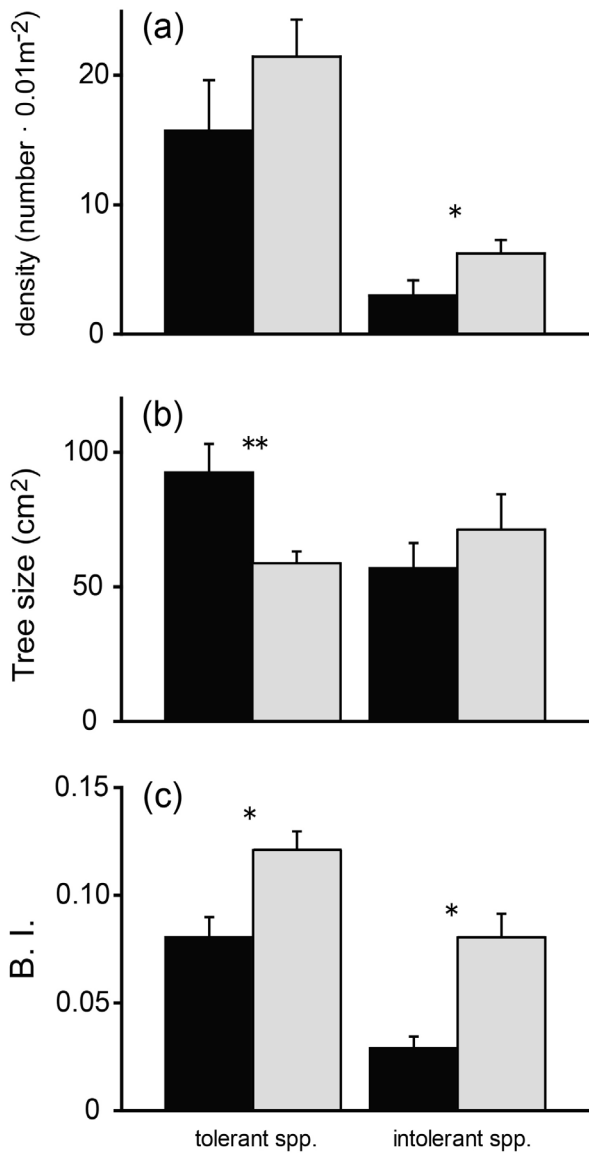
Table 1 gives the list of woodland tree species recorded in the Magarizaki spit, Amakusa-Shimoshima Island. In this study site, *Quercus glauca* (Fig. 3c) was the most dominant species with a higher relative abundance in the interior ( $59.6 \pm 3.1\%$ ) (mean  $\pm$  SE) than in the edge ( $48.1 \pm 3.1\%$ ) (Mann-Whitney U test,  $P < 0.05$ ). Species abundance patterns were different between the edge and the interior with more equitable abundances of species in the edge as indicated by a larger value of parameter  $k = 0.156$  of the Power Fraction model than in the interior ( $k = -0.079$ ,

Fig. 4a). Shade-tolerant species had a higher relative abundance in the interior while shade-intolerant species showed an opposite pattern (Mann-Whitney U test,  $P < 0.05$ , Fig. 4b).

The density of shade-tolerant species was not significantly different between the interior and the edge, while that of shade-intolerant species was significantly higher in the edge (Mann-Whitney U test,  $P < 0.05$ , Fig. 5a). The size of shade-tolerant species was significantly reduced in the edge compared with the interior ( $P < 0.01$ ), but no such trend was observed for shade-intolerant species (Fig. 5b). Both shade-tolerant and intolerant species showed



**Figure 4.** (a) Rank abundance patterns of trees in the edge (circles) and the interior (triangles) of a small maritime woodland, Amakusa, Kyushu. Values of the fitted Power Fraction model are superimposed: the edge, dotted line; the interior, broken line. (b) Relative abundances of shade-tolerant and shade-intolerant species in the interior (black bars) and the edge (grey bars). Means + 1SE. \* $P < 0.05$



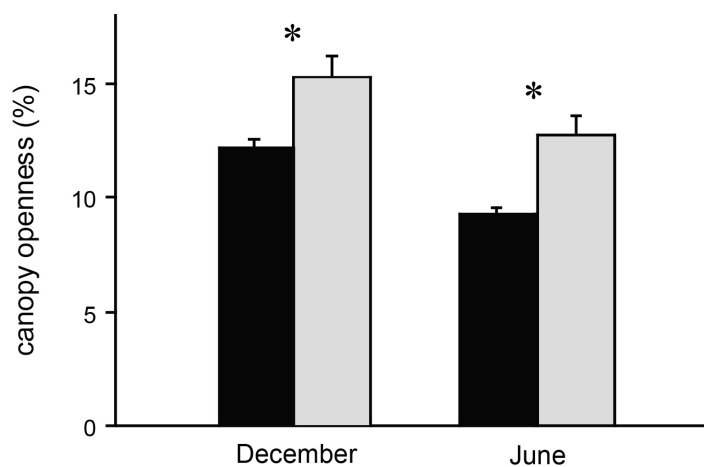
**Figure 5:** (a) density, (b) tree size, and (c) branching index (*BI*) of shade-tolerant and shade-intolerant species in the interior (black bars) and the edge (grey bars). Mean +1SE. \**P* < 0.05, \*\**P* < 0.01.

a greater branching tendency in the edge as indicated by higher values of *BI* (*P* < 0.05, Fig. 5c).

The edge had greater canopy openness than the interior in both December and June (*P* < 0.05), with a similar magnitude of reduction in canopy openness from winter to summer (Fig. 6).

### Discussion

The present study investigated the nature of small-scale variation in species abundance patterns alongside variation in morphological characteristics of a non-mangrove maritime tree assemblage. It is notable that significant variation in community structure was observed between the edge and the interior of this maritime woodland, even



**Figure 6:** Canopy openness in the interior (black bars) and in the edge (grey bars) in December 2004 and June 2005.



though the distance involved was less than 20m. More equitable relative abundances occurred in the edge than in the interior as indicated by a larger value of  $k$  in the former, pointing to small-scale variation in assemblage patterns. In terms of niche apportionment, positive values of  $k$  would indicate higher probabilities for more abundant species to be subjected to niche division, while negative values would indicate an opposite trend (Tokeshi 1996). Therefore, the species abundance pattern in the interior suggests the dominance of more abundant species in the niche apportionment process while that in edge suggests a reduction in such dominance.

Reduced dominance of abundant species was apparently linked to morphological variation of trees, particularly two shade-tolerant species *Q. glauca* and *L. japonicum* which together constituted well over 60 % of abundance, from the interior to the edge. It is interesting to note that, while shade-tolerant species showed no significant difference in density between the interior and the edge, they had significantly reduced sizes in the edge. This contrasts with shade-intolerant species that showed no significant difference in size between the habitats (or even a weak tendency of larger sizes in the edge, Fig. 5). These observations suggest that the reduced dominance of abundant species in the edge was due mainly to their

reduced sizes, but not to reduced density. This points to the importance of using abundance measures based on area (cover) or body sizes of organisms rather than numbers of individuals in the analyses of species abundance pattern (Tokeshi 1993, 1999).

Previous studies on *Q. glauca* revealed its morphological and physiological plasticity under variable environmental conditions (Sumida *et al.* 1997; Miyazawa *et al.* 2003, 2004; Yoko-o & Tokeshi 2011), which must at least partially explain why they could maintain dominance in both the interior and the edge. On the other hand, the observed morphological changes of trees in the study site are considered to be mainly due to the effects of sea wind. Trees often show wind-induced changes in morphology: in mountain ridges, tree trunks were thinner with elfin structure (Lawton 1982; Foster 1988). As wind velocity is generally higher in the edge than in the interior sites (Asquith and Mejia-Chang 2005), trees in the edge experience greater physical disturbances which would cause more frequent damages to trunks and branches. This would result in multi-trunk structures (i.e. higher values of  $BI$ ). In addition, irradiance is known to induce branching due to self-shade avoidance under better light conditions (Henry & Aarssen 1997). Thus, it is likely that wind-induced disturbances and light availability combine to generate morphological variation along the edge-interior gradient.

Apart from morphological changes, wind/typhoon-induced disturbances are considered to result in higher mortality and more frequent gap formation in edge areas (Lovejoy *et al.* 1984; Williams-Linera 1990; Tanner *et al.* 1991; Kapos *et al.* 1993; Laurance 1997). This concurs with our observation that canopy openness was greater in the edge (Fig. 6), as documented for neotropical forest edges (Williams-Linera 1990). Wind with salt spray would cause partial mortality of leaves and branches or complete death of a tree individual. Thus, greater canopy openness in the edge maintained by wind disturbances coupled with smaller sizes of shade-tolerant species would facilitate shade-intolerant species to coexist in this maritime woodland. In a similar vein, Gutiérrez *et al.* (2005) suggested that the coexistence of shade-tolerant and shade-intolerant tree species in a Patagonian forest can be explained by the frequency of disturbances.

While it is well known that shade-intolerant species are less abundant in the forest interior as darker conditions suppress their growth (Wales 1972; McDonald & Urban 2004), their morphological variation between the interior and the edge areas, particularly in comparison with shade-tolerant species, has been less recognised. Given the fact that the sizes of shade-intolerant species tended to be slightly larger in the edge than in the interior (Fig. 5), though

not statistically significant, larger values of  $BI$  observed in the edge indicate that shade-intolerant species had more marked local-scale variation in branching morphology than shade-tolerant ones. A highly branched structure allows a greater amount of foliage to be borne without increasing height, which would be more advantageous in the edges where wind impact is more pronounced. Thus, shade-intolerant species appear to be morphologically well adapted to edge environments.

In sum, the present study has demonstrated that significant variation can occur even on a small spatial scale in the community structure of maritime tree assemblages. More research is necessary for a better understanding of the spatial variability of coastal vegetation systems.

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••• Editor's note •••

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