

Marginal populations under pressure: spatial and temporal heterogeneity of *Ascophyllum nodosum* and associated assemblages affected by human trampling in Portugal

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ABSTRACT: Anthropogenic disturbances are major threats to coastal biodiversity and may exert drastic effects on natural populations occurring at the borders of the geographical distribution of species, which are thus already experiencing sub-optimal environmental conditions. In this paper, we examined the effects of experimental intensities of human trampling on temporal and spatial variance of the brown seaweed *Ascophyllum nodosum* and associated organisms in north Portugal. This is the southernmost population of *A. nodosum* in Europe and shows morphological and demographic traits that are different from those of populations from more central locations within its range of distribution. Results indicated that high trampling intensity reduced the small-scale spatial heterogeneity in the abundance of *A. nodosum*, whose cover was stabilized around relatively low values, and of the associated red algae *Polysiphonia lanosa* and *Rhodothamniella floridula*; however, it increased the spatial variance of limpets and green foliose macroalgae of the genus *Ulva*. Idiosyncratic responses in temporal patterns were also documented, with high trampling intensity causing relatively larger fluctuations in the structure of whole *A. nodosum* associated assemblages and in the abundance of *Ulva* spp., and smaller fluctuations in the cover of *Fucus vesiculosus*. The present findings are key to predicting the relatively unstudied responses of coastal populations of *A. nodosum* to increasing anthropogenic disturbance and have important implications for the management and conservation of the examined population, which represents a relevant component of the biodiversity of European rocky shores.

KEY WORDS: *Ascophyllum nodosum* · Trampling disturbance · Marginal populations · Spatial heterogeneity · Temporal heterogeneity · Rocky intertidal

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INTRODUCTION

Examining the factors responsible for patterns of distribution, abundance and diversity of organisms is a key issue in ecology (Menge & Sutherland 1987, Danielson 1991). This is of great concern under current increasing rates of direct and indirect anthropogenic perturbations over terrestrial and marine

systems, which are known to drastically affect the geographic limits and range shifts of species (Parmesan et al. 2005, Gaston 2009).

Natural and anthropogenic disturbances are among the main drivers of the structure of natural assemblages through direct and indirect mechanisms (Sousa 1984, Petraitis et al. 1989). Disturbance can directly eliminate some species, but can also release

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new resources that can increase the local abundance of other species (Connell 1978, Huston 1994). Consequently, the ability of assemblages to resist or recover from disturbance depends largely on the particular life traits of each species (Keough & Quinn 1998, Schiel & Taylor 1999, Bertocci et al. 2005).

A large number of conceptual and empirical studies have examined the effects of disturbance on the diversity of populations and assemblages, usually focusing on average response variables (McCabe & Gotelli 2000, Mackey & Currie 2001, Molinos & Donohue 2010). In contrast, relatively fewer studies have experimentally investigated the relationships between traits of disturbance and spatial and temporal patterns of distribution, abundance and diversity of organisms (Collins 2000, Benedetti-Cecchi et al. 2005, Bertocci et al. 2005). Nevertheless, there is mounting evidence of their ecological importance. Temporal fluctuations of species, for instance, may cause drastic changes in functional traits of natural systems, including productivity and stability (Johnson et al. 1996), and may be related directly to the risk of extinction (Inchausti & Halley 2003) and inversely to overall biodiversity (Lande 1993, Vucetich et al. 2000). Spatial variability of key organisms (e.g. grazers and predators) may be responsible for patchy distributions of consumed resources (Fairweather 1988, Navarrete 1996, Benedetti-Cecchi et al. 2005). Spatial heterogeneity of abiotic factors (e.g. the availability of nutrients) may drastically affect the outcome of biological interactions, and spatially heterogeneous habitats may support assemblages significantly different to those found in more homogenous habitats (Day et al. 2003).

Recreational uses and commercial harvesting are major anthropogenic sources of disturbance in intertidal habitats (Keough & Quinn 1998, Brown & Taylor 1999, Schiel & Taylor 1999). Intense trampling associated with such activities can drastically affect patterns of distribution, abundance and diversity of macroalgal assemblages on rocky shores (Keough & Quinn 1998, Araújo et al. 2009).

There is increasing evidence that canopy-forming macroalgae are particularly sensitive to anthropogenic disturbance (Benedetti-Cecchi et al. 2001, Milazzo et al. 2004, Airoidi & Beck 2007, Connell et al. 2008, Mangialajo et al. 2008). As foundation species, they provide a specific habitat for diversified associated organisms and contribute to the high biodiversity of rocky shores (Pavia et al. 1999, Lilley & Schiel 2006, Schiel & Foster 2006). Their reduced abundance may cause drastic changes in associated assemblages through modifications of light condi-

tions, temperature, hydrodynamics, sedimentation and habitat preemption (Reed & Foster 1984, McCook & Chapman 1991) that may exert positive (e.g. by ameliorating physical conditions), or negative (e.g. by monopolizing the substratum) effects (Bertness et al. 1999, Bulleri et al. 2002). Under current and predicted scenarios of increasing anthropogenic threats to the persistence of canopy-forming macroalgae (e.g. Lilley & Schiel 2006), investigating their responses and those of associated assemblages is of overwhelming conservation importance.

On temperate rocky shores, common habitat formers are large furoid algae, such as *Ascophyllum nodosum* (L.) Le Jol., which are typically dominant in the intertidal habitat on sheltered rocky shores of the North Atlantic (Pavia et al. 1999). The European distribution of *A. nodosum* ranges between the Arctic circle and North Portugal, where a single population occurs in a rocky intertidal area ~3 km long, and 10s of km from the nearest northern populations (Lima et al. 2007). Previous studies have indicated a variety of abiotic and biological factors and processes as responsible for variations in the patterns of *A. nodosum* and associated assemblages at several locations within its geographical range (Jenkins et al. 1999, Cervin et al. 2005, Svensson et al. 2009). In contrast, experimental studies on the effects of disturbance on marginal populations are rare (but see Araújo et al. 2009).

Marginal populations (i.e. those occurring at peripheral locations corresponding to the limits of their geographical distribution) are assumed to live in a sub-optimal environment (Bridle & Vines 2007) and thus represent target systems for investigating the consequences of natural and anthropogenic stressors. Such populations often occur in small sizes which, combined with the harshness of local conditions, may reduce their resistance and resilience to further disturbances (Guo et al. 2005). Edge populations may also show distinctive ecological adaptations that confer upon them an important conservation value under scenarios of environmental modifications, such as those predicted by climate models (Hampe & Petit 2005).

The population of *Ascophyllum nodosum* on the north Portuguese coast is an excellent system for addressing these issues for several reasons. Firstly, the general life traits of this species, including low recruitment and dispersal ability (Åberg & Pavia 1997, Dudgeon & Petraitis 2005) and slow growth (Åberg & Pavia 1997, Cervin et al. 2005), make it highly sensitive to disturbance (Olsen et al. 2010). Secondly, as a marginal population, it might be ex-

posed to an increased extinction risk compared to centrally located populations due to its relatively small size and isolation (Guo et al. 2005). Thirdly, this population has a relevant conservation value as it shows distinguishing morphological and demographic traits, including higher reproductive output, higher density and smaller size of individuals compared to central populations located in northwest France (Araújo et al. 2011).

A previous experimental study on the Portuguese population of *Ascophyllum nodosum* showed that high intensities of human trampling can negatively affect the mean abundance of this species, the co-occurring furoid *Fucus vesiculosus* and understory species, while enhancing the cover of ephemeral green algae (Araújo et al. 2009). However, how changes in the intensity of disturbance affect spatial and temporal patterns of the same population and associated organisms has never been experimentally investigated. The present study was aimed at filling this gap, by experimentally testing hypotheses on the effects of a range of trampling intensities on measures of temporal and spatial variance of *A. nodosum* and associated algal and invertebrate taxa in North Portugal. Theoretical (Benedetti-Cecchi 2003), modelling (Benedetti-Cecchi 2000) and empirical (Berlow 1999, Benedetti-Cecchi et al. 2005, Bertocci et al. 2005) studies suggested that large spatial and temporal variability of response variables may be associated with mild disturbances (low intensity), while reduced fluctuations in space and/or time may be caused by severe (high intensity) disturbance. Such predictions are mostly the consequence of the scaling relationship between the mean and the variance (Taylor 1961), which should apply in all cases where a response variable is drastically reduced, such as the cover of benthic organisms exposed to extreme events of disturbance. Therefore, we specifically tested the hypotheses that (1) for species, such as *A. nodosum* and other associated furoid algae, that are directly affected negatively by trampling, increasing intensity of experimental events of human trampling would be inversely related to measures of the temporal and spatial heterogeneity of abundance, while (2) the opposite would occur for species, such as ephemeral green algae, that could indirectly benefit from disturbance. Effects of experimental trampling on (1) the temporal and spatial variation of the total number of taxa (a surrogate for species richness) and (2) the structure of whole assemblages associated with *A. nodosum* resulting from such changes in individual abundances were also examined.

MATERIALS AND METHODS

Study site and experimental procedures

This study was carried out between December 2005 and April 2006 on the rocky shore of Praia Norte in Viana do Castelo, NW Portugal (41° 41' N, 8° 51' W), on intertidal assemblages dominated by *Ascophyllum nodosum*, representing the southernmost population in Europe. Abiotic and biological characteristics of the study site have been previously described in detail (Araújo et al. 2009). The shore is subject to intense and frequent human recreational and harvesting activities, particularly during summer (Araújo et al. 2009). Therefore, to experimentally test the effects of trampling on *A. nodosum* assemblages, a manipulative experiment was performed during winter and early spring months and at the less frequented parts of the shore, as indicated in Araújo et al. (2009).

Unmanipulated control and 3 levels of experimental intensity (low, medium and high: LI, MI and HI, corresponding to 5, 15 and 30 tramples, respectively) of trampling were chosen, based on preliminary estimations of the number of people visiting the shore during 1 yr and applied in the field following procedures described in detail in Araújo et al. (2009). Briefly, it was assumed that the trampling disturbance experienced by each experimental patch (2.5 × 2.5 m) was directly related to the number of people visiting the shore at low tide, as estimated according to a preliminary survey carried out for a period of 1 yr on 4 stretches of shore (~100 m long) interspersed throughout the study site. The LI treatment was then selected as corresponding to the observed annual intensity of trampling averaged across all stretches, MI as corresponding to the average of the 5 highest values of observed frequencies of human presence, and HI as simulating a further increase (2 × MI) in the human frequency of human visits to the shore. Experimental disturbance was performed by dividing each experimental patch into 4 rows that were trampled by 2 persons weighing ~70 kg each and wearing gumboots, with the number of tramples for LI, MI and HI corresponding to the number of times each row was trampled. Two trampling events were carried out each month during each week of spring tides.

The abundance of *Ascophyllum nodosum* and associated organisms was visually estimated in terms of percentage cover (sessile organisms) or number of individuals (mobile animals) in each of three 50 × 50 cm quadrats randomly established in each of three 2.5 × 2.5 m patches assigned to control and trampling

intensity treatments (see Araújo et al. 2009 for details) at 5 dates over the experimental period.

Data analysis

To examine the effects of experimental trampling on the temporal and spatial heterogeneity of the structure of whole assemblages and the abundance of individual taxa, multivariate and univariate measures of variance over the 5 dates of sampling and over replicate quadrats (data from the 3 replicate quadrats per patch per sampling time were first averaged) were calculated separately for each patch assigned to each treatment. Measures of temporal variance of the abundance of the most numerous taxa and of the total number of taxa were calculated by estimating variance components using a 1-way ANOVA with time as a factor, performed separately for each response variable in each patch. This procedure produced replicate estimates of temporal variance independent of sampling error (Searle et al. 1992). Negative values were interpreted as underestimates of null variances and were set to zero. Analogous estimates were calculated for multivariate responses to experimental treatments. Multivariate pseudo-variance components were estimated from Bray-Curtis dissimilarities (Bray & Curtis 1957), which were calculated on untransformed data separately for each patch, using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) with time as a factor. Variance and pseudo-variance components were then analyzed using a 1-way ANOVA with Intensity as a fixed factor that included 4 levels (unmanipulated control, low, medium and high intensity of trampling) and 3 replicates (the 3 patches assigned to each treatment).

Analogous procedures were used to estimate variance and pseudo-variance components of univariate and multivariate response variables, respectively, among the 3 replicate quadrats sampled per patch per sampling time. These produced independent estimates of spatial variance that were analyzed with a 2-way ANOVA, including the crossed factors Time (random, 5 levels) and Intensity (fixed, 4 levels as in the previous analysis), with 3 replicates.

Before each ANOVA, Cochran's *C* tests were done to check for homogeneity of variances. When necessary, data were log-transformed. Student-Newman-Keuls (SNK) tests were used for post-hoc comparisons of significant means.

Changes in the structure of whole assemblages in each treatment were graphically compared by calcu-

lating centroids of 'average' assemblages per patch per sampling date. First, principal coordinates (Gower 1966) were calculated from the Bray-Curtis dissimilarity matrix of the whole data set. Then, centroids were obtained separately for each treatment and sampling time by averaging the principal coordinates over the 3 replicates per patch (McArdle & Anderson 2001). Finally, multivariate patterns were displayed using a non-metric multidimensional scaling (nMDS) plot based on Euclidean distances.

RESULTS

Temporal heterogeneity

Assemblages exposed to the highest intensity of experimental trampling showed temporal fluctuations that are significantly larger than those occurring in unmanipulated patches and under the 2 lower intensities (Fig. 1; ANOVA: $MS_{Intensity} = 89\,169.9$, $F_{3,8} = 7.61$, $p < 0.01$; SNK: $HI > MI = Control = LI$, $SE = 62.496$). The only univariate response variables that were significantly affected by trampling were the brown furoid alga *Fucus vesiculosus* ($MS_{Intensity} = 94667.7$, $F_{3,8} = 5.18$, $p < 0.05$) and green foliose algae of the genus *Ulva* ($MS_{Intensity} = 21.1$, $F_{3,8} = 23.28$, $p < 0.001$), but with clearly different pat-

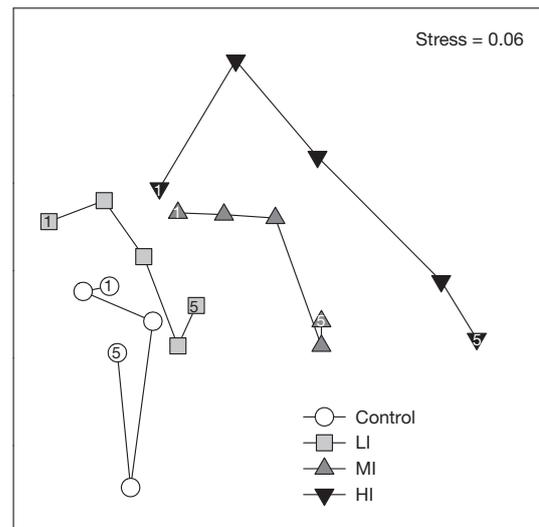


Fig. 1. *Ascophyllum nodosum*. Non-metric multidimensional scaling (nMDS) of the temporal trajectories of assemblages in the unmanipulated treatment (control) and under different trampling levels (LI, MI and HI: low, medium and high intensity, respectively). Symbols: centroids of assemblages ('averaged' across quadrats and patches) subject to each treatment at each sampling time (1 to 5), and calculated from principal coordinates

terns. Each trampled treatment caused reduced fluctuations in the abundance of *F. vesiculosus* compared to the control (Fig. 2B; SNK: Control > MI = LI = HI, SE = 78.054), while the abundance of *Ulva* spp. was more variable during the study under the 2 highest intensities of experimental disturbance than under the low intensity and in unmanipulated patches (Fig. 2G; SNK: HI = MI > LI = Control). All other individual taxa examined, including *Ascophyllum nodosum*, and the total number of taxa did not respond significantly to trampling, and showed temporal variations over the course of the study that are comparable among treatments despite large differences in abundances (Fig. 2A,C–F,H–J).

canopy-forming species. Effects of treatments did not vary with time of sampling for all multivariate and univariate response variables (Tables 1 & 2). The spatial heterogeneity of *A. nodosum* was larger in the control than under medium and high trampling intensity, with low intensity being inconsistently ranked between these 2 treatments (Table 2, Fig. 4A). Similar patterns were displayed by the turf-forming red algae *Polysiphonia lanosa*, with consistently lower values for all manipulated treatments compared to the control (Table 2, Fig. 4F), and by *Rhodothamniella floridula*, whose spatial heterogeneity was larger in unmanipulated patches and under low disturbance than under both more severely trampled treatments

Spatial heterogeneity

Trampling did not affect the spatial variability of the structure of assemblages at the scale of quadrats (Table 1, Fig. 3) and the total number of taxa (Table 2, Fig. 4J), while it exerted significant effects on *Ascophyllum nodosum* and a number of individual taxa associated with this

Table 1. ANOVA examining the effects of time and intensity of trampling on spatial variance of the structure of assemblages. ns: not significant ($p > 0.05$)

| Source of variation | df | MS | F | Denominator for F |
|---------------------|---------------|------|------|-------------------|
| Time, T | 4 | 0.26 | 0.65 | Residual |
| Intensity, I | 3 | 0.87 | 2.51 | T × I |
| T × I | 12 | 0.35 | 0.87 | Residual |
| Residual | 40 | 0.40 | | |
| Cochran's C test | C = 0.136, ns | | | |
| Transformation | Ln(x+1) | | | |

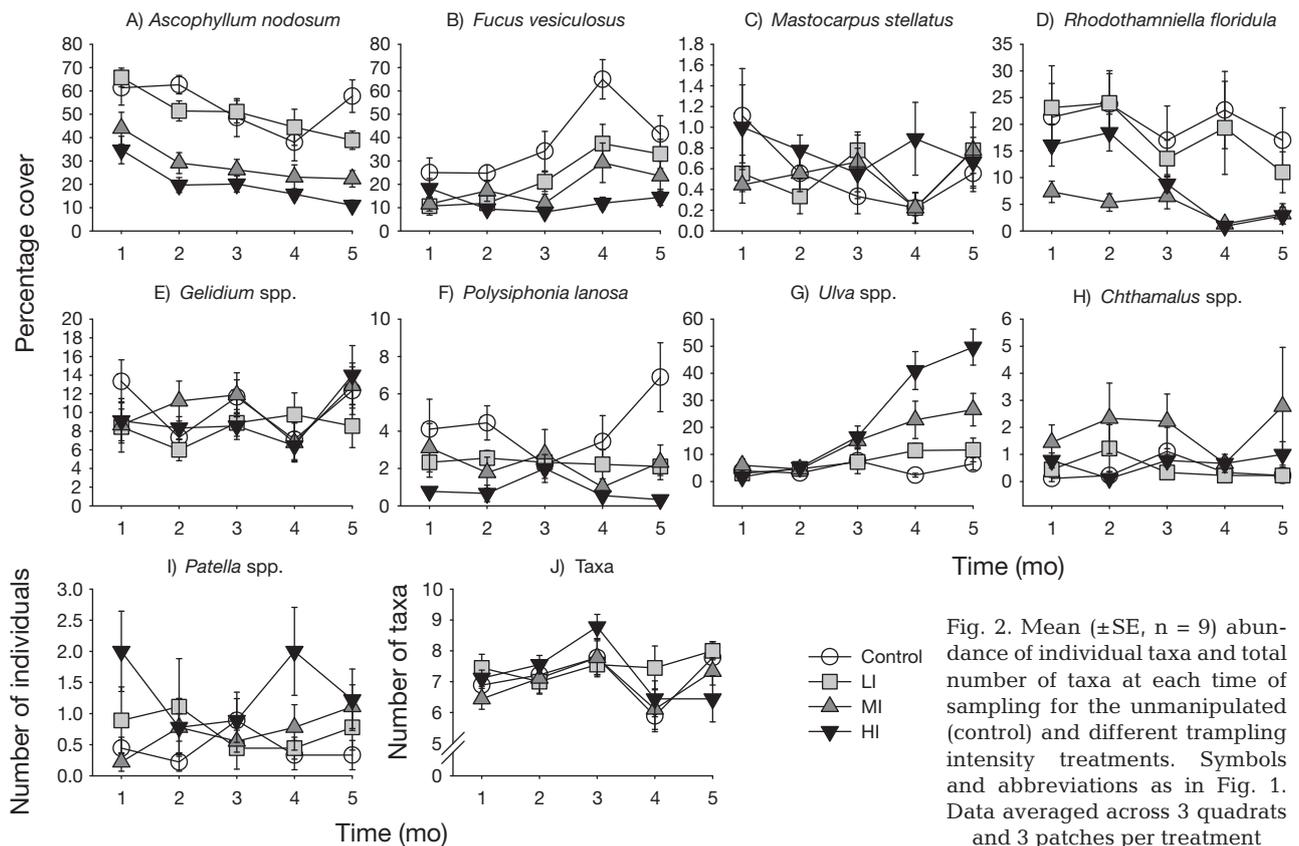


Fig. 2. Mean (\pm SE, n = 9) abundance of individual taxa and total number of taxa at each time of sampling for the unmanipulated (control) and different trampling intensity treatments. Symbols and abbreviations as in Fig. 1. Data averaged across 3 quadrats and 3 patches per treatment

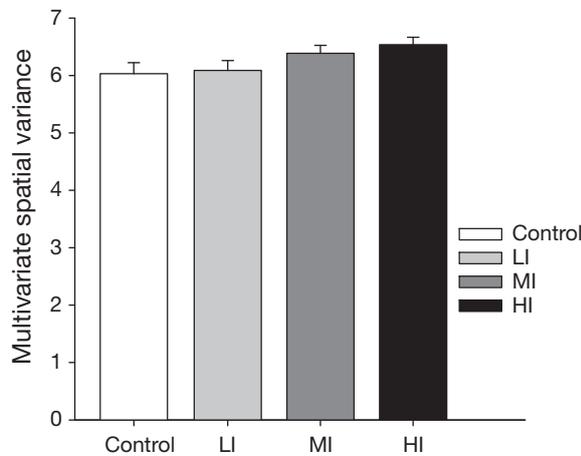


Fig. 3. *Ascophyllum nodosum*. Spatial variance (mean ± SE, n = 15, on a logarithmic scale) of the structure of assemblages in the unmanipulated (control) and different trampling intensity treatments. Abbreviations are as in Fig. 1. Data averaged across 3 patches and 5 sampling dates

(Table 2, Fig. 4D). Conversely, high disturbance intensity was associated with larger spatial heterogeneity of grazing limpets of the genus *Patella*, compared to the other manipulated treatments and the control (Table 2, Fig. 4I). Similarly, the small-scale distribution of *Ulva* spp. was more heterogeneous under very intense trampling than in unmanipulated patches, with the other treatments being inconsistently ranked (Table 2, Fig. 4G). *Ulva* spp. was the only taxon showing significant differences among sampling times independently of treatments (Table 2). No significant effects were documented for all other macroalgae (Table 2, Fig. 4B,C,E) and animals (Table 2, Fig. 4H) examined.

DISCUSSION

According to the well documented positive relationship between the mean and the variance in the abundance of natural populations (Taylor 1961, McArdle & Gaston 1992, Gaston & McArdle 1993), we hypothesized that experimental treatments that are able to decrease individual abundances of taxa to very low values would also cause drastic reductions in their temporal and spatial measures of variability. Conversely, larger heterogeneity in space and time would be possible for taxa responding positively to the disturbance applied, in agreement with the expected differential effects of disturbance depending on taxon-specific life traits of organisms (e.g. Bertocci et al. 2005). Findings basically consistent

Table 2. ANOVA examining the effects of time and intensity of trampling on spatial variance of the total number of taxa and the abundance of individual taxa. *p < 0.05, **p < 0.01, ***p < 0.001; ns: not significant (p > 0.05). Denominators for F tests are as in Table 1

| Source of variation | df | Number of taxa | | Ascophyllum nodosum | | Fucus vesiculosus | | Mastocarpus stellatus | | Rhodothamniella floridula | |
|---------------------|----|----------------|---------------|---------------------|---------------|-------------------|---------------|-----------------------|-------------|---------------------------|---------------|
| | | MS | F | MS | F | MS | F | MS | F | MS | F |
| Time, T | 4 | 0.402 | 1.53 | 76203.65 | 1.71 | 3.30 | 2.04 | 0.48 | 1.09 | 4.72 | 2.10 |
| Intensity, I | 3 | 0.031 | 0.11 | 278550.47 | 4.67* | 6.41 | 3.23 | 0.51 | 1.48 | 13.94 | 8.02** |
| T × I | 12 | 0.270 | 1.03 | 59668.18 | 1.34 | 1.98 | 1.22 | 0.34 | 0.78 | 1.74 | 0.77 |
| Residual | 40 | 0.262 | | 44566.98 | | 1.62 | | 0.44 | | 2.25 | |
| Cochran's C test | | | C = 0.172, ns | | C = 0.267, ns | | C = 0.226, ns | | C = 0.561** | | C = 0.258, ns |
| Transformation | | | Ln(x+1) | | None | | Ln(x+1) | | None | | Ln(x+1) |
| Source of variation | df | MS | F | MS | F | MS | F | MS | F | MS | F |
| Time, T | 4 | 1998.02 | 1.49 | 0.40 | 0.46 | 21.23 | 9.68*** | 254.45 | 0.86 | 0.21 | 0.54 |
| Intensity, I | 3 | 954.59 | 1.50 | 5.70 | 6.93** | 12.34 | 3.87* | 472.07 | 1.83 | 2.63 | 10.45** |
| T × I | 12 | 635.65 | 0.47 | 0.82 | 0.96 | 3.19 | 1.45 | 258.29 | 0.87 | 0.25 | 0.65 |
| Residual | 40 | 1341.26 | | 0.86 | | 2.19 | | 296.52 | 2.25 | 0.39 | |
| Cochran's C test | | | C = 0.258, ns | | C = 0.157, ns | | C = 0.259, ns | | C = 0.883** | | C = 0.270, ns |
| Transformation | | | None | | Ln(x+1) | | Ln(x+1) | | None | | Ln(x+1) |

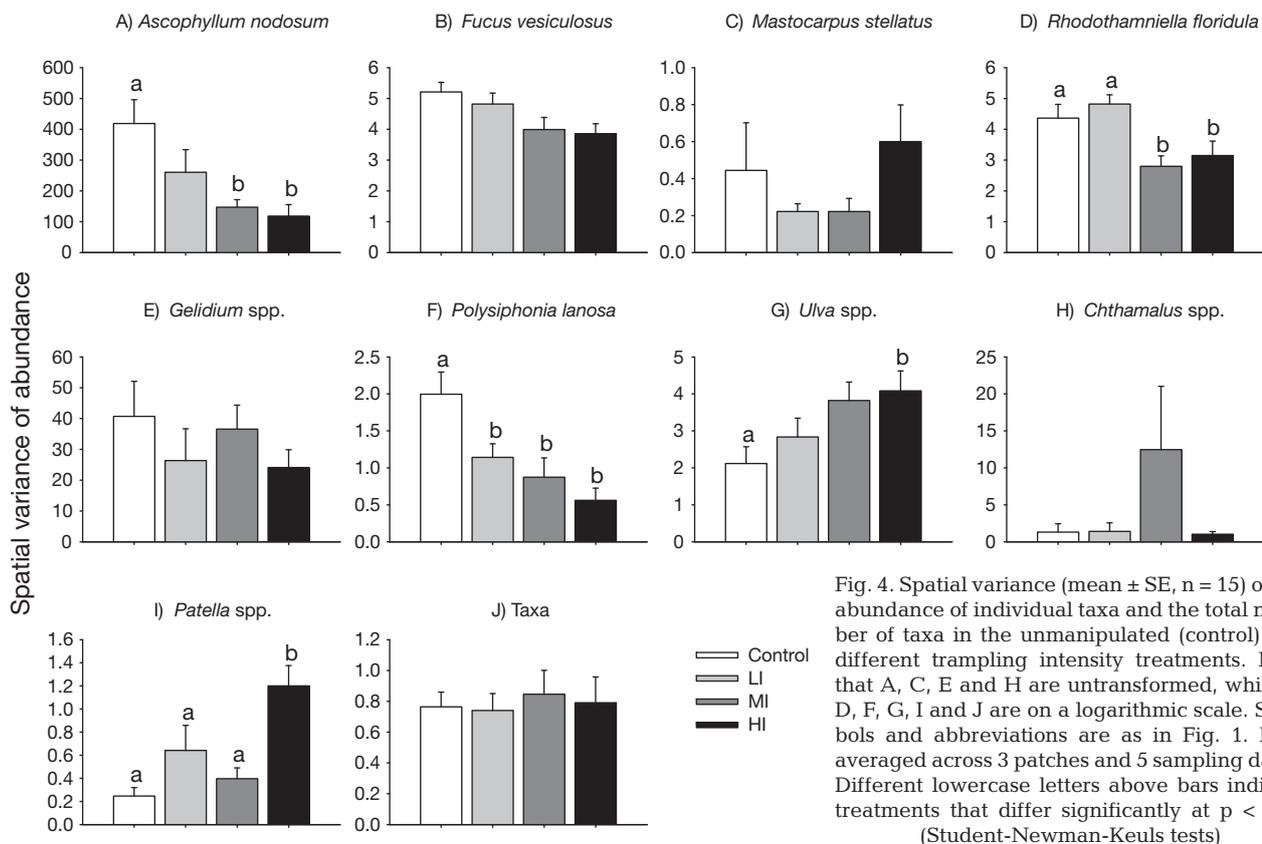


Fig. 4. Spatial variance (mean ± SE, n = 15) of the abundance of individual taxa and the total number of taxa in the unmanipulated (control) and different trampling intensity treatments. Note that A, C, E and H are untransformed, while B, D, F, G, I and J are on a logarithmic scale. Symbols and abbreviations are as in Fig. 1. Data averaged across 3 patches and 5 sampling dates. Different lowercase letters above bars indicate treatments that differ significantly at p < 0.05 (Student-Newman-Keuls tests)

with such predictions were obtained for temporal patterns in the abundance of *Fucus vesiculosus* and the ephemeral green algae of the genus *Ulva* and for spatial patterns in the abundance of *Ascophyllum nodosum*, the turf-forming algae *Polysiphonia lanosa* and *Rhodothamniella floridula*, limpets and *Ulva* spp. The other response variables examined were generally not affected by trampling.

The small-scale spatial heterogeneity of *Ascophyllum nodosum* was negatively affected by the medium and high intensity of trampling, which also drastically reduced the abundance of this species throughout the experiment compared to the less or undisturbed treatments. Such a response was likely due to the mechanical impact of trampling on the canopy, which removed plants and generated haloes of bare space that increase in size with increasing intensity of disturbance. This led to an increasing spatial homogenization of the distribution of this alga, which levelled off around low abundance values. Although specifically examining long-term responses to trampling is beyond the goals of the present study, we could also hypothesize that the new spatial patterns might further compromise the recovery of the canopy due to species and population specific traits of

A. nodosum. It has been documented that due to its low dispersal abilities, the growth and expansion of this species mostly depend on the development of recruits established under the canopy created by adults of the same species (Åberg & Pavia 1997, Cervin et al. 2005); this canopy provides protection against excessive temperatures and hydrodynamics (Vadas et al. 1990) and prevents the establishment of potential competitors for space (Dudgeon & Petraitis 2001). By creating patches of bare space, disturbance may, therefore, drastically prevent recolonization by *A. nodosum* as the distance from parental algae increases—an effect that would be proportional to the intensity of disturbance. A similar mechanism was considered responsible for the occurrence of alternative communities on the rocky shores of Maine, where intertidal areas subject to low disturbance are dominated by *Ascophyllum*, which are able to recolonize the small patches produced by disturbance despite its very limited dispersal; areas with a history of larger disturbances are colonized by mussels and barnacle species with relatively wider dispersal abilities (Petraitis & Dudgeon 1999). Moreover, the potential negative effects of the spatial patterns of distribution of *A. nodosum* determined by

disturbance might be exacerbated by the isolation of the studied marginal population from nearby sources of propagules (Guo et al. 2005). Conversely, where *A. nodosum* was more abundant, such as in control patches, a larger spatial heterogeneity could have been generated and maintained by abiotic and biological processes, including wave action (Vadas et al. 1990) and grazing (Pavia & Toth 2000, Davies et al. 2007). In principle, we could have obtained analogous results for the temporal variability of *A. nodosum*, but this was not the case, as this response variable was comparable among all trampling intensities and not different from the unmanipulated condition. In fact, the abundance of this species during the experiment was generally stable under all experimental conditions, either where percentage cover values were relatively low due to severe (MI and HI) disturbance, or large due to mild (LI) or no (control) disturbance.

Several studies have documented large changes in associated assemblages after natural (e.g. Davies et al. 2007), anthropogenic (e.g. Keser et al. 1981, Ang et al. 1996) and experimental (e.g. Jenkins et al. 1999, Viejo et al. 1999, Dudgeon & Petraitis 2001, Bertness et al. 2002) disturbances affecting *Ascophyllum nodosum*. Species occurring in close association with *A. nodosum* are particularly expected to show patterns of variability analogous to those of the canopy-forming species (Cervin et al. 2005). In the present study, this clearly occurred for the turf-forming red algae *Polysiphonia lanosa* and *Rhodothamniella floridula*, the former being an obligate epiphyte of *A. nodosum* (and, more rarely, of other fucoids), and the latter being a typical understory species of large brown seaweeds (Hayward et al. 1996). Nevertheless, corresponding variations were not documented for spatial and temporal patterns in the structure of the whole assemblage, the total number of taxa and the abundance of most of the other *A. nodosum* associated organisms, as such variables were generally not affected by trampling. For *Gelidium* spp., results agree with the previously documented resistance of algal turfs to trampling and are likely due to their morphology (Brosnan & Crumrine 1994, Schiel & Taylor 1999, Milazzo et al. 2004, Goodsell & Underwood 2008). More surprising was the lack of significant responses of *Chthamalus* spp. and the red macroalga *Mastocarpus stellatus*, as Brosnan & Crumrine (1994) reported relevant negative effects of trampling on both barnacles and algae of the same genus. It is worth noting, however, that the intensity of experimental trampling applied by those authors was approximately double the most

severe disturbance applied here (Brosnan & Crumrine 1994, Araújo et al. 2009) and, therefore, might have been more effective in damaging these taxa.

High trampling intensity was associated with relatively higher mean abundance and spatial and/or temporal heterogeneity of limpets and *Ulva* spp. On the contrary, large fluctuations of limpets in space did not occur in unmanipulated patches and in treatments (LI and MI) where they were relatively less abundant, and cover values of algal turfs, such as *Rhodothamniella floridula* (the most abundant filamentous species here), were larger. It is known that grazing invertebrates tend to be excluded from substrates monopolized by algal turfs (Underwood & Jernakoff 1981), while they can be favoured by relatively large gaps of free space made available by intense disturbance (e.g. Bertocci et al. 2005), such as in the HI treatment here. Patterns of distribution of limpets could have affected those of the grazed *Ulva* spp. in the same direction. There is evidence that changes in spatial or temporal variance of the abundance of consumers may drastically affect patterns of resources (Berlow 1999, Benedetti-Cecchi 2000, Benedetti-Cecchi et al. 2005). In addition, the genus *Ulva* includes opportunistic species that typically attain large cover values on rocky shores only where the abundance of potential competitors for space is reduced (e.g. Denny & Gaines 2007). These ecological mechanisms could have contributed to maintaining the low cover of these algae in undisturbed or less disturbed treatments, where canopy-forming species such as *Ascophyllum nodosum* and *Fucus vesiculosus* were conversely more abundant.

The present findings indicate that intense anthropogenic disturbance may cause homogenization of spatial patterns of distribution of the population of *Ascophyllum nodosum* in North Portugal, with cover being stabilized around low values and its possible replacement by opportunistic algae. Although this population shows life-history traits that likely resulted in adaptation, on evolutionary scales, to sub-optimal conditions (Araújo et al. 2011), the increasing intensity and rates of human use of the studied shore may represent a relevant extinction threat. Under such circumstances, for instance, a further reduced and isolated population might not be able to respond efficiently to more extreme environmental conditions, such as those due to predicted climate change. This highlights the need for management and protection measures that would allow the conservation of the distinctive traits of this peripheral *A. nodosum* population and the preservation of an important component of the biodiversity of European rocky shores.

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