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Seasonal dynamics of soil nutrients and microbial activity due to colonization by bracken ferns (*Pteridium aquilinum* (L.) Kuhn) in a pine forest

Manuel Aira [*], Andrea Tato, Jorge Domínguez

Grupo de Ecoloxía Animal (GEA), Universidad de Vigo, E-36310, Spain

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ABSTRACT

Bracken (*Pteridium aquilinum*) is an aggressive colonizer of disturbed and other successional habitats in temperate forests. However, little is known about how bracken colonization modifies soil microbial activity and nutrient cycling. We questioned whether bracken presence alters soil nutrient pools and soil microbial respiration throughout a growing season and whether this effect depends on the size of the bracken patch. To answer these questions, we sampled the soil in bracken patches of different sizes (large, medium and small) and in the surrounding pine forest (paired sampling design) in summer, autumn, winter and spring. We analyzed the samples to determine nutrient contents (C, N and P) and soil microbial respiration. Patch size did not influence soil microbial activity or nutrient pools. Bracken acted as nutrient sink for N pools through the growing season and as source or sink for C and P pools depending on season. Moreover, the effect on nutrient pools did not depend on bracken characteristics (area, density or height). Bracken presence enhanced soil microbial respiration proportionally to patch area. The control that bracken exerts over nutrient pools may determine the successful (or otherwise) establishment of other plant species. This contributes to making bracken a successful colonizer as no particular population threshold (area, density) has to be reached before nutrients becomes limiting to other plant species.

1. Introduction

Bracken (*Pteridium aquilinum* (L.) Kuhn) is a common aggressive ruderal in European forests, but little is known on how this species influences soil microbial activity and nutrient pools during its growth cycle. Bracken is one of the most widely dispersed and common plant species worldwide [1,2]. Several of its characteristics contribute to bracken being a successful colonizer. First, the rhizome system stores nutrients and carbohydrates, enabling fast rapid recovery of the plant after disturbance such as fire or harvesting. Second, the high productivity of bracken yields a massive frond canopy, resulting in litter accumulation, water interception and limiting access to light by other plant species. Third, the plant releases several toxic chemicals [3–6], and fourth the bracken reallocates nutrients to the rhizome that will be used to trigger growth in spring [7]. These traits make it difficult for other plant species to become established once bracken colonizes the soil [7]. Bracken has been widely studied as a modifier of plant succession because it can even suppress colonization by trees [7]. Further, research has also focused on bracken because it produces a carcinogenic agent (ptaquiloside) that can affect livestock [8]. In addition, variation in soil nutrient pools has been attributed to uptake and storage as bracken is a very efficient nutrient recycler, sequestering nutrients even after senescence [3,6,9]. However, although there are important contributions studying how the presence of bracken modifies soil microbial respiration and nutrient pools in soils where the plants are established [10–12]; little is known about how the influence of bracken varies between seasons and with the size of bracken patches.

The main aim of the present study was to determine whether bracken affects the nutrient pools and soil microbial respiration in soils where it is present. However, due to the particular growth habits of bracken, it is difficult to compare the effects on soil biochemical parameters in colonized and uncolonized (control) areas, because the bracken forms dense, uniform patches [7]. However, bracken stands may occur in patches due to habitat variability, competition, or even to the effects of bracken on itself [7]. Size of the patches has been related with its age and with the number of clones they comprise [13,14]. In this way, and according to

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* Corresponding author.
E-mail address: aira@uvigo.es (M. Aira).

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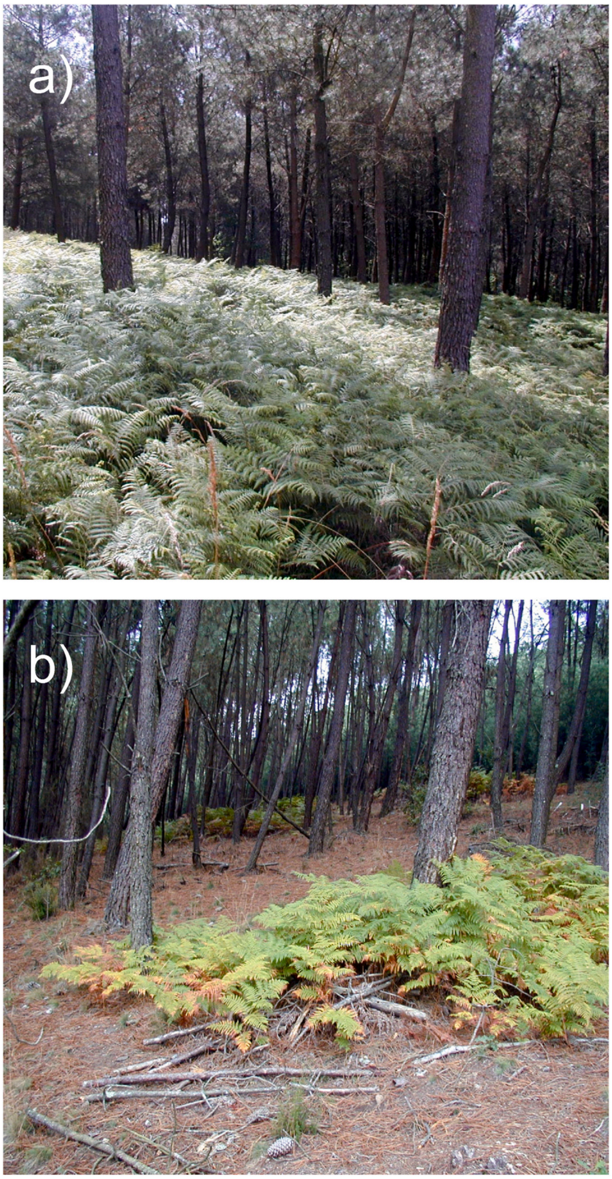

Fig. 1. The study system. (a) a typical pine forest (*Pinus pinaster*) with homogeneous bracken cover (*Pteridium aquilinum*) and (b) the study site, a pine forest with bracken distributed in patches of different size.

the home-field advantage hypothesis [15] microorganisms should be more adapted to decompose bracken litter more efficiently in larger patches. However, this should largely depend on how fast patches grow. Thus, it could be expected that the influence of bracken being larger in the inner than at the edge of the patches would increase with patch size.

These defined patches of different sizes can be considered habitat-islands (Fig. 1). Habitat-islands play an important role in the study of ecology and evolution, and their particular characteristics (small isolated areas and defined boundaries with surrounding ecosystems) make them suitable sites for scientific research [16]. Habitat-island systems have been studied as oceanic islands *per se* [17,18] and even as "isolated patches" of communities different from the surrounding communities [19].

We questioned whether the presence of bracken effectively modifies basal soil microbial respiration and nutrient dynamics and whether the particular traits governing growth cycle of brackens, i.e. reallocation of nutrients from the frond to the rhizome in autumn and winter during senescence [20,21], alter the nutrient pools and soil microbial respiration of soil colonized by the bracken. We should expect higher levels of nutrients in autumn, winter and even spring, as a result of decomposition of dead fronds and also because nutrients are provided by the rhizome during the initial stages of growth of fronds [21]. Moreover, if bracken behaves as an invasive species, we would expect increased nutrient contents, especially of nitrogen, underneath the plants, relative to bracken free areas, as it has been shown that bracken, as other invasive plant species, enhance nitrogen pools [10–12,22]. However, for brackens this effect is strongly modulated according to pH [12]. Secondly, we also questioned whether the effects of bracken on soil nutrient pools and basal soil microbial respiration depend on the size of the bracken patch. It is known that habitat-island size (hereafter bracken patch) is associated with ecosystem properties and function, as litter mass loss, nutrient content and microbial biomass and activity [17,19]. We, therefore, hypothesized that the effects of bracken on soil nutrient pools and basal soil microbial respiration will increase with patch size and even with bracken density and height.

2. Material and methods

2.1. The study area and sampling procedure

The study site, (12.33 Ha), is located in Ribadavia, NW Spain (42°18′44″ N, 8°05′45″ W, at 165 m above sea level). The climate is temperate Mediterranean with a mean annual precipitation of 800 mm (range 759–818 mm) and mean annual temperature of 14.5 °C (range 4.4–36.3 °C). The dominant tree in the site is pine (*Pinus pinaster* Ait.), and the sparse understorey is composed of gorse (*Ulex europaeus* L.), broom (*Chamaespartium tridentatum* L.) and bell heather (*Erica cinerea* L.), with young individual specimens of oak (*Quercus robur* L.) and strawberry tree (*Arbutus unedo* L.). Pine tree density was 620 ± 70 trees m^{-2} and the trunk diameter (at breast height) was 70 ± 3 cm. The experimental site is located on a sandy loam soil, with a mean organic matter content of 25% ± 1% and a pH of 5.8 ± 0.1 in the first 5 cm.

In summer 2007, we located and flagged 20 bracken patches. We recorded the location of each patch with a GPS (N and W in decimal degrees). We measured patch area (length x breadth) and the height and density of bracken fronds (0.5 × 0.5 m square). The mean patch area was 33.1 ± 5.7 m^2 (minimum, 2.8 m^2 and maximum 88.2 m^2), and patches were classified (on the basis of the area occupied) as small (area<15 m^2, mean area = 6.96 ± 1.22 m^2, n = 6), medium (15<area<35 m^2, mean area = 23.33 ± 2.31 m^2, n = 7) or large (area>35 m^2, mean area = 65.66 ± 5.49 m^2, n = 7) ($F_{2,17} = 66.12$, $P < 0.0001$). We obtained paired soil samples on 6 August (summer, bracken fronds grown), 14 November (autumn, with bracken fronds starting to fade away in second week of October), 5 February (winter, bracken fronds completely faded away) and 5 May (spring, bracken frond actively growing since the fourth week of March) in bracken patches and surrounding soil (3 m apart). With this sampling, we covered all stages in bracken seasonal growth cycle. We removed the litter layer and collected five samples randomly but avoiding the edge of the patch (0–10 cm deep) in each bracken patch and in the corresponding surrounding soil (at a distance of 3 m) to make composite samples (total 100 g per sample).

2.2. Analytical procedures

Samples were processed the same day that were taken. Firstly, samples were sieved (2 mm) before the analysis. Subsamples were dried at 105 °C for 24 h, to determine the moisture content, and at 550 °C for 4 h, to determine the organic matter content. Other fresh soil subsamples were used for 0.5 M K_2SO_4 extracts (1:5 wt/volume). Ammonium-N (NH_4^+-N), nitrate-N (NO_3^--N) and total extractable N were determined in 0.5 M K_2SO_4 extracts by a modified indophenol blue technique and alkaline persulfate oxidation respectively [23,24]. Dissolved organic C (DOC) in the samples was determined colorimetrically after moist digestion ($K_2Cr_2O_7$ and H_2SO_4) of aliquots of the samples extracted with 0.5 M K_2SO_4. Phosphate was extracted from soil samples (2 g dw) with

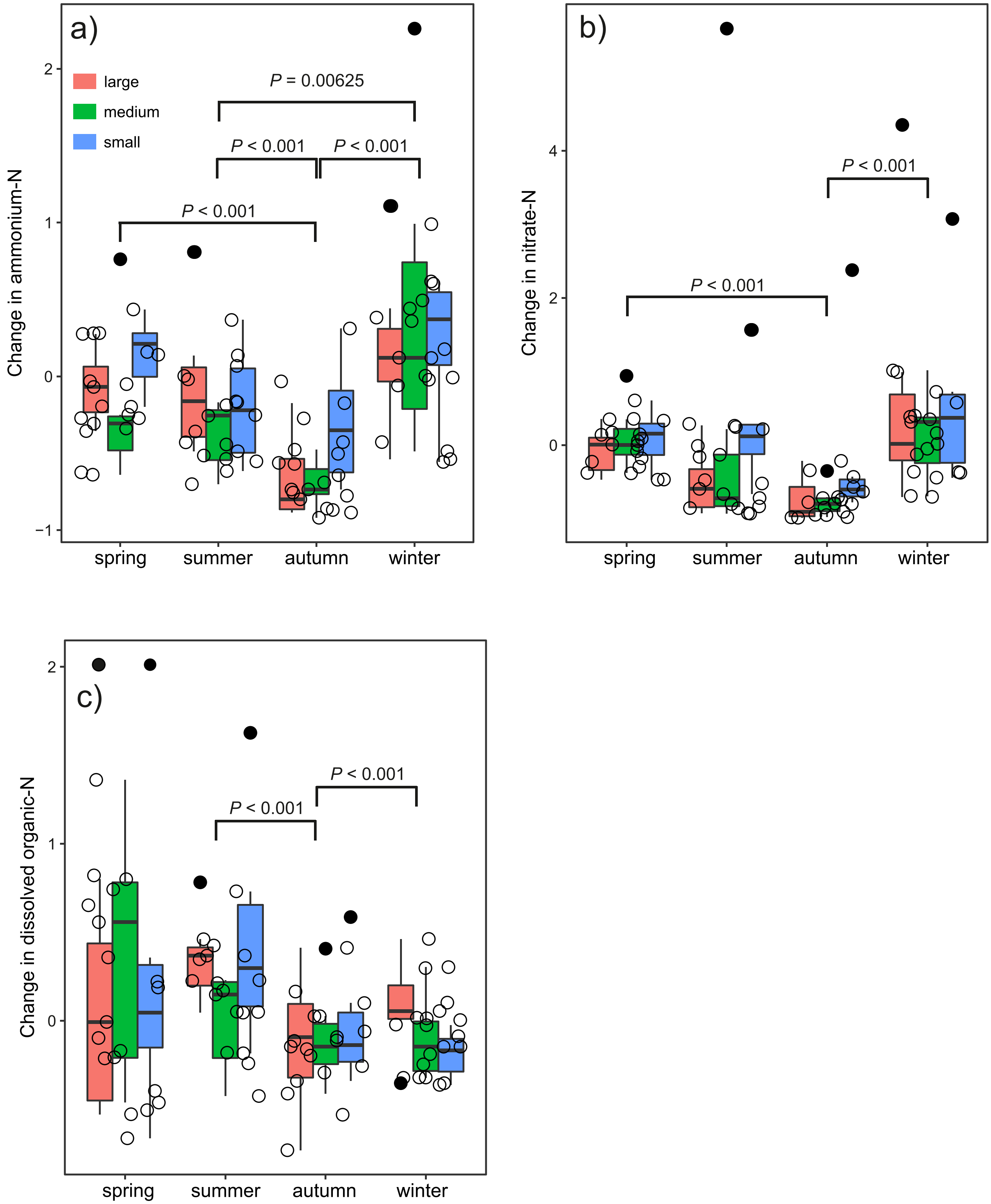

Fig. 2. Effects of bracken patch size (small, medium and large represented by blue, green and red bars respectively) and season on N pools. Changes in different parameters are shown: a) ammonium-N, b) nitrate-N and c) dissolved organic-N relative to control (soil below pines) calculated as $(V_b\text{-}V_p)/V_p$, where V_b and V_p are the values of the variables in samples of bracken and pine soils. Different letters indicate significant differences between the different seasons (Tukey HSD test). In the boxplot lower and upper hinges correspond to the 25th and 75th percentiles, and the upper and lower whisker extends from the hinge to the largest and smallest value no further than 1.5 * IQR (IQR is the inter-quartile ranges) respectively. Black and white dots represents outliers and sampled data respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

acetic acid (2.5%) and filtered. The absorbance was read at 700 nm after the addition of ammonium molybdate (0.1 M) and tin chloride [25]. The absorbance of all samples was read in a Bio-Rad Microplate Reader 550. Soil microbial respiration was assessed by measuring the rates of evolution of CO_2 from samples after 6 h incubation at field moisture and 20 °C. The evolved CO_2 was trapped in 0.02 M NaOH and measured by titration with HCl to a phenolphthalein endpoint, after adding excess $BaCl_2$ [26]. We used an incubation time of 6 h to capture the status of the soil just sampled. Cumulative respired C over a very long term incubation would be more suitable to assess the C availability to heterotrophs in the soil.

2.3. Statistical analysis

We used the Mantel test based on dissimilarity matrix of geographic position and properties of patches (area, height and density of bracken) to test for the existence of any pattern of spatial aggregation of patches on the study site due to their attributes. The test computes a correlation between two distance matrices, one with spatial distances, and another with differences between the selected properties of patches. The null hypothesis is that the observed relationship between the two distance matrices could have been arisen by any random arrangement in space of the observations through the area [27]. Dissimilarity matrix were obtained with vegdist function (Euclidean distance) and tested with the Mantel test (10,000 permutations) implemented with the mantel function of the vegan package [28].

We determined the strength and direction of the presence and life cycle of bracken as the change in the soil parameter in presence of bracken relative to control (no bracken) as $(V_b\text{-}V_c)/V_c$, where V_b and V_c are the values of the soil parameters of samples from bracken patches and controls respectively [29]. Expressing data as a fraction of controls simplifies interpretation making response values negative or positive [29]. Thus, negative values indicate that brackens reduce the nutrient content and activity of microbial community, whereas positive values indicate enhancement of nutrient pools and overall microbial activity. The actual nutrient concentrations are shown in Supplementary Table 1. Prior to statistical analysis, the data on bracken density and height, nutrient pools and microbial activity were transformed using the boxcox function in the MASS package [30], in order to meet the conditions of normality and homoscedasticity. We analyzed the data by fitting linear mixed models with nlme package [31], with patch size and season as fixed factors and patch identity and season as random factors, to control for pseudoreplication due to repeated measures on patches between sampling dates. We removed the size × season interaction whenever it was not significant [32]. We conducted post hoc comparisons (Tukey HSD) with the glht function of the multcomp package [33]. We used regression analysis to assess the effects of patch characteristics (area, density and height of brackens) on the chemical and microbiological variables separately in the two months when the plants were living, because density and height of brackens differed between these times but not between patch sizes (summer and spring). All statistical analyses were performed using R [34].

3. Results

Patch size did not differ between summer (33.23 ± 6.01 m^2) and spring (33.51 ± 6.05 m^2, $F_{1,17} = 2.85$, P = 0.11), indicating that colonization of bracken in this area occurs very slowly. Bracken density did not depend on patch size ($F_{2,17} = 1.54$, $P = 0.24$), although it was lower in spring (6.04 ± 0.36 fronds m^{-2}) than in summer (10.01 ± 0.68 fronds m^{-2}, F1$_{,17}$ = 28.51, P=0.0001), indicating that the patches had not yet reached their previous density. The same occurred with bracken height, which was lower in spring (100 ± 7 cm) than in summer (102 ± 8 cm, $F_{1,17} = 8.16$ $P = 0.011$) and did not depend on patch size ($F_{2,17} = 1.40$, $P = 0.27$). Patch location was not correlated with patch area (Mantel test, r statistic = −0.008, $P = 0.47$) or bracken height (Mantel test, r statistic = 0.007, P = 0.42), although bracken density tended to increase with distance among bracken patches (Mantel test, r statistic = 0.265, P = 0.008).

Table 1
Table summarizing the statistical output of linear mixed models analysing the effect of bracken patch size and season on the response ratio (calculated as (Vb-Vp)/Vp, where Vb and Vp are the values of the variables in samples of bracken and pine soils) of the different variables analyzed. We give the numerator and denominator degrees of freedom.

		d.f.	F	P
N–NH_4^+ (μg g^{-1} dw soil)	patch size	2,17	2.70	0.0958
	season	3,57	25.49	**<0.0001**
N–NO_3^- (μg g^{-1} dw soil)	patch size	2,17	1.20	0.3254
	season	3,57	12.78	**<0.0001**
Dissolved organic nitrogen (μg g^{-1} dw soil)	patch size	2,17	1.86	0.1854
	season	3,57	7.48	**0.0003**
Dissolved organic carbon (μg g^{-1} dw soil)	patch size	2,17	3.73	**0.0455**
	season	3,57	5.49	**0.0022**
P-PO_4 (μg g^{-1} dw soil)	patch size	2,17	5.19	**0.0174**
	season	3,57	7.91	**0.0002**
Soil microbial respiration (μg CO_2 g^{-1} dw soil h^{-1})	patch size	2,17	9.93	**0.0014**
	season	3,57	0.31	0.8214

The presence and seasonal dynamics related to the bracken life cycle strongly affected the soil nutrient content and basal soil microbial respiration. Thus, bracken appeared to act as a sink of available N (both mineral and organic), as most of response ratio were negative for the three N pools (Fig. 2, Supplementary Table 1 for actual nutrient concentrations). Moreover, N–NH_4^+ dynamics showed a marked seasonality (Table 1), with lower response ratios in summer and autumn than in winter (Fig. 2a, Supplementary Table 1). This trend was similar to those of nitrate content, which also showed a marked seasonality (Table 1, Fig. 2b, Supplementary Table 1), mainly due to the low response ratio observed in autumn. However, we found positive response ratios for DON contents in summer and spring, when bracken was actively growing (Table 1, Fig. 2c, Supplementary Table 1). None of the available N forms depended on bracken patch size. DOC response ratio was significantly higher in small patches than in medium-sized patches (post-hoc comparison $P = 0.0247$, Table 1). Furthermore, DOC response ratios were significantly higher in spring than in summer and autumn (Table 1). Phosphate response ratio was significantly higher in small and large patches than in medium-sized patches (P = 0.0061 and P = 0.0497 respectively for post-hoc comparisons, Table 1); phosphate response ratio was higher in winter than in autumn (Table 1, Fig. 3b, Supplementary Table 1). Soil microbial respiration response ratio was significantly higher in large than in small and medium-sized patches (P = 0.00196 and P < 0.0001 respectively for post-hoc comparisons, Table 1), and it generally remained positive throughout all the stages of the seasonal growth cycle of bracken (Table 1,Fig. 4, Supplementary Table 1).

We did not find any effect of patch size on any of the variables analyzed in August and May, when the fronds were above-ground (regression analysis, data not shown). However, dissolved organic N (DON) was significantly and negatively related to both density and height of bracken fronds in summer in mature bracken (whole model R^2 = 0.48, $F_{3,16}$ = 3.63) but not in spring in actively growing bracken (Fig. 5a). Height of bracken was also related to dissolved organic C (DOC), although only in spring (whole model R^2 = 0.28, $F_{3,16}$ = 2.06, P = 0.14; Fig. 5b).

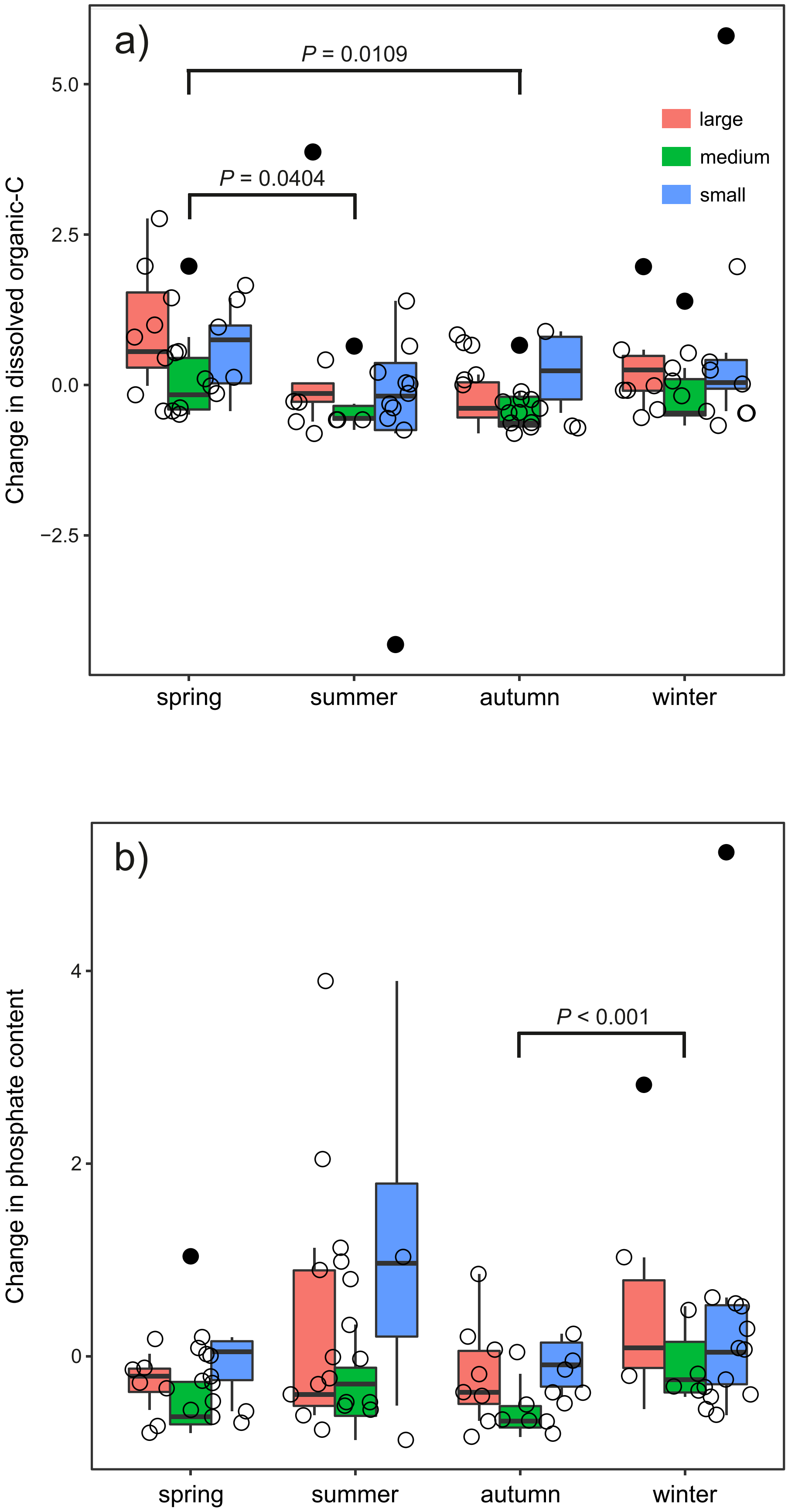

Fig. 3. Effects of bracken patch size (small, medium and large, represented by blue, green and red bars respectively) and season on C and P pools. Changes in different parameters are shown: a) dissolved organic-C, and b) phosphate content relative to control (soil below pines) calculated as $(V_b - V_p)/V_p$, where V_b and V_p are the values of the variables in samples of bracken and pine soils. In the boxplot lower and upper hinges correspond to the 25th and 75th percentiles, and the upper and lower whisker extends from the hinge to the largest and smallest value no further than 1.5 * IQR (IQR is the inter-quartile ranges) respectively. Black and white dots represents outliers and sampled data respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

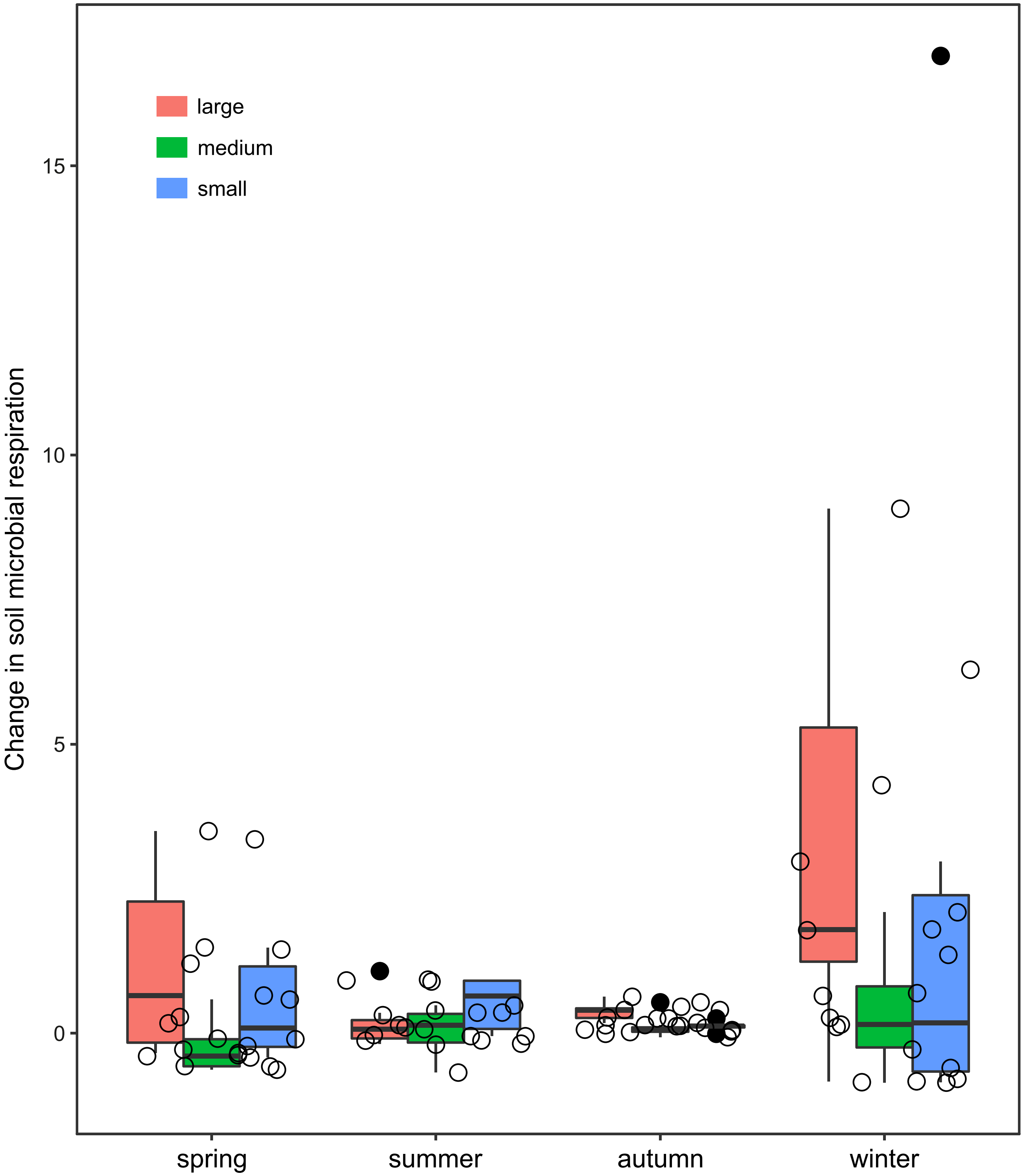

Fig. 4. Effects of bracken patch size (small, medium and large represented by blue, green and red bars respectively) and season on soil microbial respiration. The graph shows changes in microbial activity, measured as soil respiration relative to the control (soil below pines) and calculated as $(V_b-V_p)/V_p$, where V_b and V_p are the values of the variables in samples of bracken and pine soils. In the boxplot lower and upper hinges correspond to the 25th and 75th percentiles, and the upper and lower whisker extends from the hinge to the largest and smallest value no further than 1.5 * IQR (IQR is the inter-quartile ranges) respectively. Black and white dots represents outliers and sampled data respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

The study findings showed that the bracken seasonally affected soil nutrient pools but not soil microbial respiration. Height and density of bracken decreased and increased the DON and DOC contents in summer and spring respectively. We also found that patch size only affected the DOC and phosphate contents as well as soil microbial respiration, with the lowest values always associated with the medium-sized patches. Contrary to our hypothesis (i.e. high availability of nutrients in autumn, winter and spring due to bracken senescence and subsequent

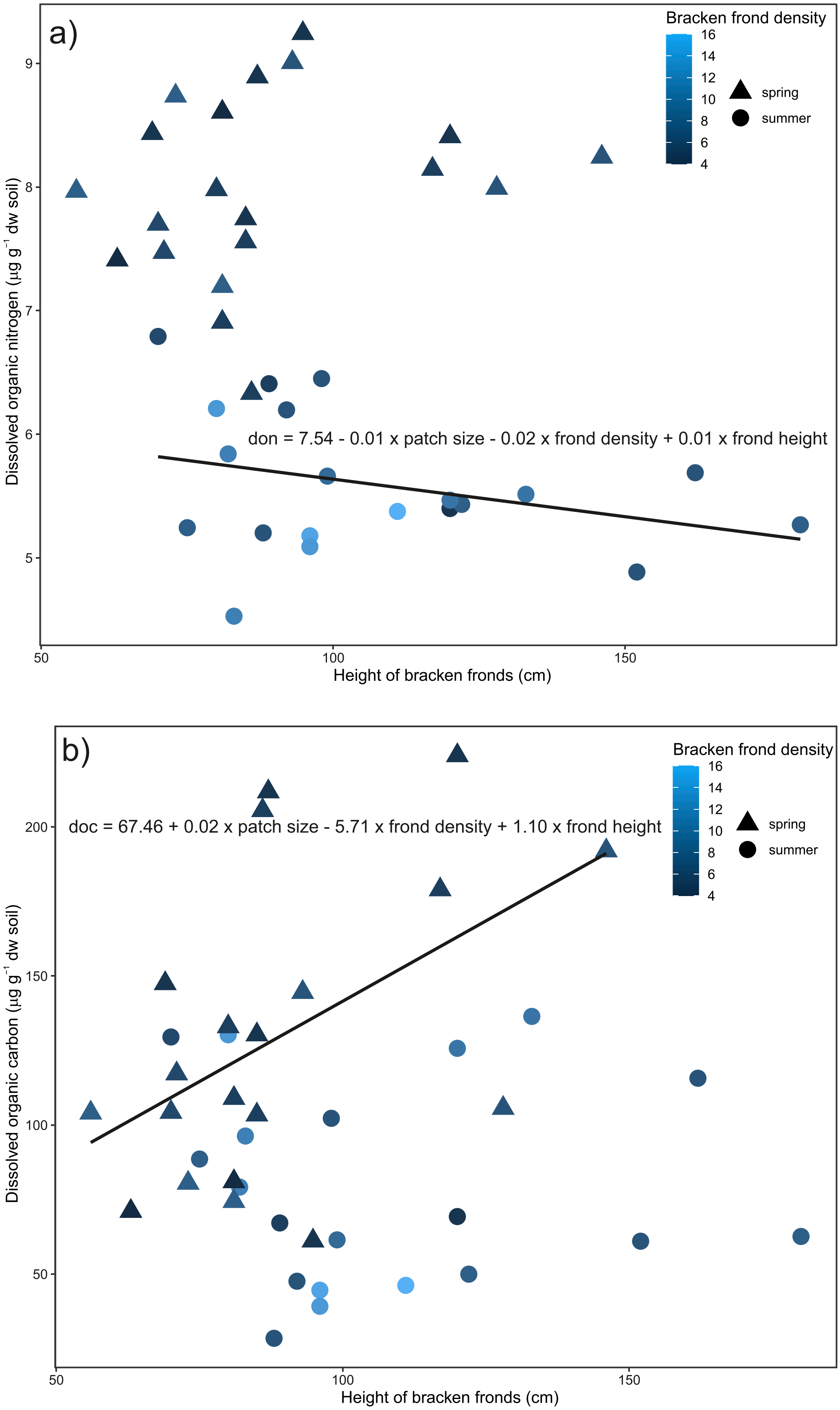

Fig. 5. Effects of bracken frond density and height and season on a) dissolved organic nitrogen and b) dissolved organic carbon. Triangles and circles represent data from spring and summer seasons respectively.

decomposition of fronds), we found that nutrient levels (available forms of C, N and P) were lower in autumn, but increased in winter (except for DON, Supplementary Table 1). In spring, phosphates and N–NH_4^+ decreased, suggesting that the plants were actively absorbing these compounds, unlike other N forms and DOC. This has important implications for N cycling, which begins with the release of polymeric organic N to DON, which is either then mineralized by microorganisms or directly absorbed by plants [35,36]. It has been suggested that microorganisms in N limited ecosystems immobilize N in autumn and winter, and release it in spring [37]. Our data support this statement, as most of the available N (DON and N–NO_3^-) contents were higher in spring, despite there being no seasonal effect on microbial activity, which was always higher underneath brackens than underneath pines. The N pool data are partly consistent with those reported by Smart et al. [38], who observed lower levels of N (mineral and organic) below brackens than below a grass crop, mainly due to differences in the study system (grassland vs forest soil). These authors reported that N was mainly present as N–NH_4^+ and DON and to a lesser extent as N–NO_3^-; however, we found that N was mainly present as DON (70 ± 5 μg g^{-1} dw, overall mean joining patch size and season, Supplementary Table 1), with no differences between the two mineral forms (7.3 ± 0.3 and 9.6 ± 0.8 μg g^{-1} dw for N–NH_4^+ and N–NO_3^- respectively, Supplementary Table 1). In addition, soils colonized by bracken ferns showed increased levels of total N and C pools [11,12,39]. This trend was reversed when bracken was removed from soils [40].

Ecosystem C loss occurs due to microbial respiration (CO_2) or to leaching of dissolved organic C [41]. Decomposition of plant material and production of root exudates are the main sources of DOC [42]. In the present study, the significant correlation between DOC and soil microbial respiration ($r = 0.58$, $P < 0.0001$) indicate that the substrate availability, and therefore the potential for decomposition, was higher in winter and spring. Our data are not consistent with the hypothesis predicting low DOC production with increasing N–NO_3^- availability [[43–45], but see Refs. [46,47]). Indeed, we found that DOC and N–NO_3^- were closely correlated ($r = 0.41$, $P < 0.001$ and $r = 0.52$, $P < 0.0001$ for soil below bracken and pines respectively). The dynamics of phosphate content partly matched our expectations, and the contents were higher in summer and winter. Moreover, the bracken acted as a phosphate sink (4.31 ± 0.28 and 5.88 ± 0.42 μg g^{-1} dw for bracken and pine soil, overall mean joining patch size and season, Supplementary Table 1). This may be due to the ability of bracken rhizomes to mobilize, as well as to immobilize, large amounts of phosphates [48] which is of critical importance in P limited soils [49]. We used changes in pools of nutrients as a proxy for nutrient immobilization or release from brackens. However, both mineral and organic constituents of these pools arise from the balance between multiple production versus immobilization/consumption processes.

The regulation that bracken exerts over nutrient pools may be another way of controlling the establishment of other plant species. In contrast to the general trend of increasing soil stocks, pools, and fluxes of nitrogen [22], soils under the influence of bracken fern contained significantly lower levels of nutrients than uncolonized soil. This suggests that the mechanisms used by the bracken fern to control other species may rely on limiting the available nutrients, in part due to its ability to sequester and store them in its rhizome. In fact, productivity in bracken stands is independent of soil total N and P [50]. Importantly, this does not depend on patch size, thus challenging island theory (at least for this system), i.e. that island size governs the island ecosystem properties [17,19]. This occurred independently of the other two patch characteristics (density and height of brackens), which were not related to patch size. This mechanism therefore seems to be independent of the amount and extension of area colonized by the bracken ferns, making them successful colonizers as they do not have to reach any threshold (area, density) before nutrient limitation occurs.

We found that soil microbial respiration remained higher in bracken than pine soil (12.67 ± 0.99 and 10.92 ± 0.83 μg CO_2 g^{-1} dw h^{-1} for bracken and pine soil, overall mean joining patch size and season) despite the lower mineral N and phosphate contents of soils below bracken. This is opposed to lower levels of soil microbial respiration in soils due to bracken colonization found by Potthast et al. [51]. Bracken litter is very resistant to decomposition [52,53] and contains ptaquiloside, a compound that enhances soil microbial respiration and growth [54,55] so that the increased potential for decomposition found in winter corresponds with the new input of dead fronds due to senescence. Global warming is increasing the rate of soil respiration [56] and is expected to boost the expansion of bracken because the main limitations to bracken growth are frost and waterlogging [7].

5. Conclusions

Bracken ferns act as nutrient sinks, only releasing nutrients in winter; this effect was independent of patch size, density or height of brackens. More importantly, since patch size it is related with its age [10,11] this data suggests that bracken does not need to reach any population threshold (area, density) before limiting other plant species. Bracken colonization significantly enhanced soil microbial respiration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2021.103295.

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