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The impact of human frequentation on coastal vegetation in a Biosphere Reserve

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ABSTRACT

We aimed to assess the impacts of recreational trampling on rare species, plant communities and landscape structure in the Iroise Biosphere Reserve (western France). Focusing on coastal grasslands, we first identified indicators discriminating human-induced short grasslands (i.e. maintained short by intensive trampling) from natural short grasslands (i.e. maintained by environmental constraints): the presence of lichens and succulent or woody species, which are known to be highly sensitive to trampling, as well as a shallow soil were good indicators of natural short grasslands. Recreational activities affected the majority of plots containing rare species, but one third of rare species (according to their habitat preference) appeared currently not threatened by recreational activities. The other rare species were found in grasslands with low trampling intensity and were not found in grasslands with greater trampling intensity. One lichen species (*Teloshistes flavicans*) was not affected by trampling intensity, while two plants species (*Scilla verna* and *Ophioglossum lusitanicum*) showed higher abundances when trampling was low to medium. When it occurs in natural short grasslands, tourist trampling reduced drastically plant species richness. However, when considering maritime high grasslands, we observed that species richness was higher under low trampling vs. no trampling, but decreased at higher trampling intensity. At a landscape scale, the mean annual rate of path creation was about 1,6% and trampling has already completely destroyed 3.5 ha of natural coastal vegetation, created 31 ha of short grasslands which represent 50.8% of the whole short grassland habitat of the island, and affected respectively 41% and 15% of natural short grasslands and maritime-high grasslands. One of the main suggestions for managers to minimise trampling impacts should be to protect totally areas of rocky soil covered by short grassland that are still non-trampled and not impacted. Fortunately, this appears compatible with a relatively free access of visitors to coastal areas, as tourists can be redirected towards high maritime grasslands, a habitat which is less impacted by tourism in terms of affected surface, soil cover, loss of species, or presence of rare species host.

Keywords: trampling, littoral, species richness, rare species, Biosphere Reserve,

1. Introduction

Protection status, arising from the presence of rare and endangered species, high biological diversity and/or preserved ecosystems sometimes leads to an increase in eco-

tourism: increased use of natural and wild areas for eco-tourism and recreation has already been identified as a worldwide trend (Buckley, 2000). Tourism in protected areas can provide resources for sustainable development to regions with often little other economical activities (Buckley, 2002; Ceballos-Lascurain, 1991; Epler-Wood, 1996; Guerrero and Munoz 2002; U.S. Congress, 1992). However, many of these protected areas have been designed for species and habitat protection, with limited or no consideration for tourism access or accommodation (Ashton, 1991; Boo, 1990). Some authors recently suggested that eco-tourism may generate important perturbation of wildlife and alteration of habitats (Buckley, 2000; Buckley, 2002; Kelly et al., 2002; Taylor and Knight, 2002). As recreation is a legitimate use of wilderness areas, the challenge for managers is to evaluate the acceptable level of negative impacts on resources based on wilderness management goals and mandates. Furthermore, studies underlined that tourist perception of the impact (soil erosion, path…) can degrade the quality of visitor experiences (Roggenbuck et al., 1993; Vaske et al., 1982). These perceptions are based on how visitors believe impacts affect the overall attributes of the setting like scenic appeal or solitude (Whittaker and Shelby, 1988). However, international and national reports have underlined the small amount of data about tourism impact on biodiversity (Bhandari 1999; Harriot, 2002; IUCN, DFID and European Commission, 2002; Minister of the Environment and Governments Services Canada, 1998; Office of Technology Assesment, 1992; U.K. CEED, 2000; U.S. Congress, 1992).

One of the first degradation resulting from the presence of tourists is vegetation trampling, which often affects ecosystems of high conservation value (Andres-Abellan et al.,. 2005; Liddle, 1975; Liddle, 1997; Yorks et al., 1997). Many ecological studies of tourist impact on vegetation have been conducted on sand dunes (Blom, 1976; Lemauviel, 2000; Lemauviel and Rozé, 2003; Liddle and Greig-Smith, 1975; Van der Maarel, 1971), forest (Roovers et al., 2004; Sun and Walsh, 1998), riparian areas (Marion and Cole, 1996) alpine environments (Whinam and Chilcott, 2003), but there have been few studies on coastal vegetation on rocky soil (Gallet and Rozé, 2001). Such vegetation is likely to be highly sensitive to trampling, due to poor productivity. Plants are generally resilient to perturbation, but their ability to recover after intensive trampling disturbance vary substantially across habitats, with slower recovery in less productive environments such as alpine grasslands (Hartley, 1999; Stohlgren and Parson 1986, Whinam and Chilcott, 2003). It has been shown in alpine grasslands that recovery can run on many year (Godefroid et al., 2003), so that the effects of the disturbance can sometimes be detected 20 years after it occurred (Charman and Pollard, 1994). Coastal cliff vegetation is very similar to alpine grasslands (close species such *Armeria sp, Festuca sp., Scilla sp, Jasiona sp, Sedum sp…*), is characterized by a growth on thin soil and poor productivity, so that trampling could potentially generate major, long-lasting damage to this vegetation as well.

Coastal habitats (maritime-high grassland and dry heathland) are classified as Habitat of Community Value by the European 'Habitats' Directive on the conservation of natural habitats (Directive 94/43/CEE; Romao, 1997) and may shelter species of great conservation concern (Rodwell et al., 1991; Rodwell et al., 2000; Thompson et al., 1995). Nevertheless, nearly total destruction of such vegetation had already occurred on large coastal areas, due to tourism activities at several sites along the French Atlantic coast (for example, "Pointe du Raz" in Brittany). Landscape rehabilitation of such areas has led to large public spendings (10 millions euros) and ecological restoration runs on many years (official source from Bretagne Regional Council and Syndicat mixte pour l'aménagement de la pointe du Raz et du Cap Sizun).

Here, we explore the impact of tourism on the coastal vegetation of Ouessant, a small French island hosting rare plant and animal species, as well as noticeable habitats,

but receiving increasing numbers of tourists, which represent the main source of income for the inhabitants. By first checking that short coastal grasslands were natural plant communities maintained by environmental constraints, not by human trampling, we studied the impact of trampling at different scales and from different perspectives:

From a Park manager point of view, we assessed the potential and actual impacts of trampling by visitors on rare species. This was performed first at a landscape scale by mapping tourist flow and rare species. Several studies have shown that recreation impacts a relatively small proportion of wilderness areas (see review in Leung and Marion, 2000) and that effects are usually distributed unevenly due in part to visitor use patterns (Lucas, 1990). However, even localized impact can harm rare or endangered species. Thus, in addition to studying trampling at a landscape scale, we also identified the habitats of rare species, some of which (e.g. maritime-high grassland and short grassland) are more submitted to tourist frequentation than others, depending notably on accessibility via vegetation height and absence of thorny species like blackberry bush (*Rubus sp.*) or gorse (*Ulex sp*.). Finally, at a species scale, we assessed how rare species responded to human perturbation.

From a conservation biologist point of view, we considered the potential and actual impacts of trampling on plant communities by assessing the proportion of trampled habitat and by analysing species richness and species assemblage in trampled vs. preserved areas.

Finally, we attempted to assess the current dynamic induced by recreation activities, via indicators of damage widely used in previous studies, such as variation of path length (Cole, 1995; Roovers et al., 2004; Whinam and Chilcott, 2003).

Because there is a strong social and economical pressure for developing tourism in protected, and notably coastal, areas (Laurans, 2002), zero perturbation is generally not an acceptable goal. Conservation biologists should better assess the rates of habitat alteration and diversity loss, and evaluate a sustainable level of perturbation, or propose compensatory landscape management that will ensure a suitable and a sustainable habitat conservation state. Tourist pressure on natural costal resources is becoming really obvious in Ouessant, a small island at the western tip of Brittany, France. This island is highly protected because it hosts rare plant and animal species and noticeable habitats, but it receives nowadays an increasing number of tourists, with currently about 140,000 visitors per year. Tourism is nowadays the main source of income for local inhabitants since the abandonment of traditional agriculture and the decline of resident human population. Given that tourism development is vital for the island economy and given the importance of Ouessant for the conservation of many threatened plants and habitats (Bioret, 1993; Bioret and Magnanon, 1993), we carried out a study for assessing the impact of tourism frequentation on coastal vegetation, the latter being considered at various spatial scales, from local species assemblage to the landscape. Most of the developed analyses could be hindered by the fact that the trampling pressure in coastal habitats may itself creates short grasslands. One of the first goal of this study is thus to discriminate grasslands kept short by human trampling from those kept short by environmental constraint such as wind, sea spray and soil depth and composition.

2. Materials and methods

2.1 Study area

Ouessant is a small island (1,541 ha) located 20 km off the western end of Brittany, France (48°28’N, 5°5’ W). Ouessant has long been recognised as an exceptional ecosystem, representative of the biodiversity of the Atlantic domain, and was therefore listed in national and European inventories such as Important Bird Areas or Special Protection Areas. The island is thus highly protected, as it has been declared as a Regional

Nature Park since 1969 and as a Man and Biosphere Reserve since 1988; in addition, the 40 km of the island coastline have received the status of ”Classified Site” in 1979, which led to total protection against any human construction (fig. 1)
From the sea border to inland, a limited number of vegetation series occur on the island. On the coastal line, vegetation of Atlantic sea cliff consists of three classes: (1) maritime rock crevice vegetation; (2) maritime-high grassland; (3) short grassland on rocky soil. The second main vegetation series of the coast stripe is European dry heathland, consisting of two main classes (tab.1). More inland, pastures with low grazing pressure and crop abandonment had led to the development of fallow-lands. Currently fallow lands, dominated by braken (*Pteridium aquilinum*) and brambles (*Rubus fructicosus*) occupy more than half of the island area (Gourmelon et al., 2001). Species and habitats of high conservation values are present in Ouessant; for some of them (e.g. *Isoetes histrix*, *Ophioglossum lusitanicum*), the island is one of very few stations in Western France (Annezo et al., 1998; Bioret, 1989).
Man exploited the entire island until the early 20th century. During the 20th century, inhabitant number declined drastically from 2661 in 1911 to about 1000 in 1999 (Péron, 1997). Consequently, cropping, which was exclusively directed towards self-production of food resources, almost disappeared from local farming practices. Only residual sheep breeding maintained a remnant traditional agriculture (Gourmelon et al., 2001). During the last fifty years, tourism activities have greatly increased on the island: annual number of ferry passengers increased from 10,000 in 1950 to about 140,000 in 2004. The annual growth rate of the ferry traffic was about +2,500 passengers per year during the last twenty years (fig. 1). Tourism is currently the main source of economical incomes of the island. Most visitors undertake a one-day excursion to the island, and are mainly interested by discovering coastline landscapes by walking or cycling along paths all around the island.

2.2. Data collection and analysis

Generally, the impacts of trampling on vegetation are studied via a comparison of protected vs. experimentally trampled plots (Cole, 1995; Gallet and Rozé, 2002; Whinam and Chilcott, 2003). This was not achievable on Ouessant, where most land is privately owned which renders plots enclosure very problematic. Hence, we chose to consider the whole costal area of Ouessant Island as a life-size experience and to take advantage of the existing variation in trampling intensity.

2.2.1 Spatial pattern in tourist visits

During the 1993 and 1994 summers and year round between 1995 and 2001, numbers of tourists walking along the main tourist flow (tips of the island, main beaches, main littoral paths...) were routinely counted by the same observer in 12 coastal areas, where botanical patrimonial index was also estimated (see below). The average coastline length of these areas is 2.6 Km ± 0.13 (Fig. 1). Counts were performed at least once a month (sometimes many more times depending on the daily activity of the observer), on average 7 times a day, between 8 am and 8 pm. Overall, there were a total of 7,915 counts, split among 1113 days, which represents an average of 8 records per area and per month. To transform tourist number into a flux of tourists crossing the area, a specific survey of the time tourists spend at a given location was carried out in two specific sites (Ouessant tips: Porz Doun in 1998 and Kadoran in 1999) for a total of 56 hours of survey. Most tourists walked along the coastline and their presence in such area was ca. 21 ± 4 minutes. Estimates of the annual number of tourists per area were obtained after accounting for monthly and daily variations.

Average of tourist within in a typical day of a month (m) in a tourist area x (ADMnTx) :

$$ADMnTx = \sum_i (n_i/N_i).Jm.(60/s_x)$$

Were : i is the hour of the day concern,
n is the count of tourist at the hour i,
N is the number of count at the hour i,
Jm is the number of days in the month,
s_x is the average of time (in minutes) that tourist stay in a tourist area (Tx)

Then estimates of the annual number of tourists in an area are asses through the addition of the 12 tourist month estimation.

2.2.2. Botanical sample used to discriminate short grassland origin

Some impacts of tourist trampling on vegetation, such as path creation, appear quite easy to identify and quantify. But when tourist impact occurs for a long time, the increase number of paths, which eventually connect to one another, can create large areas of short grassland and even soil erosion. To distinguish short grassland arising from natural, environmental constraints from those created by human trampling, we performed 157 botanical samples. 137 samples were performed on short grassland (European habitat classification 1230-6, Sedum anglicum-Dactlis glomerata or Scilla verna-Jasione crispa maritima or Plantago coronopus-Armeria maritime) This samplings were split among the 12 tourist areas following, as much as possible, the surface of grassland present in each area (stratified sampling, yielding between from 4 and 34 sampling sites per area, linear regression between grassland areas and number of sampling sites: R^2=0,72). An intensity of human trampling was estimated for each sampling, to assess correlation between species, soil characteristics and tourist trampling impact.

Whenever possible, sampling was performed on plots of standardized size (10 m^2); however, because of field constraint (size of patch vegetation), some samples were done on slightly smaller areas (minimum 6m², average 9.59 ± 0.59). We listed all species present in each plot and attributed a cover index for each species (1: cover < 5% ; 2: 5% < cover < 25% ; 3: 25% < cover < 50% ; 4: 50% < cover < 75% ; 5: cover > 75%; Braun-Blanquet, 1965). All these samples were performed in areas where there was no doubt on the intensity of human trampling. The rate of human visits on the plot was estimated with four classes: none, low, medium and high. Plots free from human trampling were located in non-accessible areas (n = 48 samples, 54 species have been founded and *Plantago Coronopus, Cladonia furcata, Thrincia hirta, Agrostis stolonifera maritima and Jasiona montana* occurred the most). Plots with low trampling were located in areas known to be faintly visited (n<15 000 visitor per year) or on secondary paths (n = 19 samples, 47 species have been founded and *Plantago Coronopus, Agrostis stolonifera maritima, Festuca rubra pruinosa, Jasiona montana* and *Thrincia hirta,* occurred the most). Plots located on secondary paths of the main tourist areas (n>15 000 visitor per year) were attributed a medium intensity of trampling (n = 38 samples, 49 species have been founded and *Plantago Coronopus, Agrostis stolonifera maritima, Thrincia hirta, Festuca rubra pruinosa and Scilla verna* occurred the most), whereas those located on the main pathways of the main tourist areas were scored as high human trampling (n = 32 samples, 34 species have been founded and *Agrostis stolonifera maritima, Plantago Coronopus, Festuca rubra pruinosa, Thrincia hirta, and Lotus corniculata* occurred the most). Twenty additional samples were performed near the frontier between maritime-high grassland (5 to 15 cm high) and natural short grassland (under 5 cm high), to provide potential indicators of the factors limiting the establishment of short grassland. Maritime grassland matches to the European classification 1230-3, *Festuca rubra-Armeria maritima* or *Festuca rubra-Holcus*

lanatus or *Festuca rubra-Daucus carota gummifer*. 27 species have been founded and *Festuca rubra pruinosa, Daucus carota* gummifer, *Armeria maritime, Lotus corniculata and Agrostis stolonifera maritima* occurred the most). In addition to human trampling intensity, distance from the sea, slope, orientation and soil depth were recorded for each plot. Soil depth was calculated as the mean of 30 measurements performed every 5cm along the two diagonals of each plot. Principal Components Analysis and Discriminant Analysis were used to identify potential indicators of human trampling.

2.2.3. Localization of hot spots of rare species in Ouessant

As the preservation of rare species is one of the main goals of the various protection statuses, we built a patrimonial flora index to localize hot spots of rare species. We considered only plants protected at the European (Annexe II of European Community Habitat Directive 21 may 1992), National (law of the10 July 1976 and 20 January 1995) or Regional (law of the 23 July 1987) scale, listed on the national Red List (Olivier et al., 1995) or listed in the appendix I of the regional Red List (published by the National Botanical Conservatoire of Brest, Annezo et al., 1998). The retained species were: *Centaurium marinum, Cytisus scoparius ssp. maritimus, Heterodermia leucomelos, Isoetes histrix, Ophioglossum lusitanicum, Rumex rupestris, Scilla verna, Solanum dulcamara ssp. marinum, Solidago virgaurea ssp. rupicola, Teloschistes flavicans, and Trichomanes speciosum.* Two species of lichens considered as very rare ([Nom des espèces] Pr Masse / Rennes University comm. pers.) were retained to build up the index. Two species (*Daucus carota ssp. gadecaei* and *Silene dioïca ssp. zetlandica*) were removed due to obvious problems during field identification. All detected stations of each species were mapped on aerial ortho-photographs (IGN 2002), implemented in a Geographical Information System (G.I.S. Arc-Info, Environmental Research System Institute Inc). The data were then pooled using a geo-referenced grid of 250m squares (n = 292 squares) to calculate the patrimonial index, using the formula:

Index value of a square = $\sum_i (n_i/N_i)$

Where n_i is the number of spots of rare species a in the considered square.
N_i is the total number of spots of rare species on Ouessant island.

As the delimitation of local stations was not easy for species covering large unfragmented areas, like *Scilla verna* or *Cytisus scoparius maritimus*, we considered only presence/absence of these two species in each square.

2.2.4. Distribution of rare species along coastal habitat and their response to trampling intensity.

Using the result from the analysis of trampling effect on vegetation, a coastal vegetation map was drawn using field plotting and aerial ortho-photographs interpretation, and implemented in the G.I.S. Habitats were categorized according to vegetation height and floral composition, while for short grasslands two other features were considered: trampling intensity (trampled or non-trampled) and their potentiality (corresponding to the vegetation expected on a plot without human trampling, derived from results of Discriminant Analyses on natural vs. trampled short grassland). As paths could not be accurately digitalised directly from aerial photographs, they were first defined as lines. In a second step, path width was measured in the field and their vegetation cover was recorded. A polygon cover of paths was then created as a buffer along the path length cover, using data on path width as the buffer coefficient. The final coastal vegetation cover was obtained by updating the vegetation cover with the polygon path cover. We

super-imposed this vegetation coverage with the rare species coverage to describe the distribution of rare species within coastal habitat. We further used Logistic models to explore variations of rare species occurrence (Presence/absence in samples) along the trampling gradient established previously (see Discriminant analysis).

2.2.5. Plants community diversity.
We studied variations in species richness as a function of levels of human trampling. Assumptions of equal detectability of all species are generally not met, which can invalidate comparisons of plots (Boulinier et al.,1998; Nichols et al., 1998). We therefore used statistical methods, derived from the capture-recapture approaches used in population or community dynamics, and incorporating differences in species detectability, to provide an estimator of species richness and of changes in community composition. The basic estimator of species richness is the jack-knife estimator proposed by Burnham and Overton (1979) and implemented in COMDYN (Hines et al., 1999). We studied variations in species richness in two vegetation types (maritime-high grassland and natural short grassland) across the four trampling levels (none, low, medium and high). Within each vegetation type, sample sizes varied across trampling levels. To correct for sample size bias, we set all sample sizes to the minimum sample size observed within each group (n = 14 for short grassland and n = 5 for maritime-high grassland) via sampling methods: we sampled randomly 14 (respectively 5) plots in each of the three trampling levels containing supernumerary plots. This sampling was performed 20 times, and the resulting samples were analyzed with COMDYN, to obtain estimators of (1) species richness, (2) extinction rate Φ in pair wise comparisons (i.e. proportion of group 1 species found in group 2) and rate of species turnover γ (i.e. proportion of group 2 species present in group 1).

2.2.6. Relationship between trampled areas and tourist visits
We used Linear models to explore correlation between trampled areas assess by GIS (m²) and tourist visits (number of tourists per year).

2.2.7. Rate of creation of artificial short grassland
As creation of new areas of short grassland is mostly linked to path creation, we used the rate of additional path length from 1998, to 2000 and 2004 as indicators of short grassland creation dynamic. Aerial photographs and field measurements were used for this estimation.

3. Results

3.1. Spatial distribution of tourists

The distribution of tourists (Fig.2) showed great spatial variations, ranging from 100,000 visits per year at the North-Western tip to only 3000 in the South-Eastern Island. In the followings analyses, we used this annual average estimation of tourist number obtained in each coastal area.

3.2. Distinguishing natural from human-created short grassland

We observed a significant correlation between soil depth, vegetation type and trampling intensity (Fig.3 ; $F_{4,152} = 22.9$, $P < 0.0001$). Soil depth appears to constrain the establishment of natural, non-trampled short grassland (Fig.3), which was encountered only on soil shallower than 10cm. This type of vegetation had an average soil depth of 4.8 ± 0.2 cm. This pattern was not attributable to a spurious correlation with distance to seashore (soil generally gets shallower as distance to seashore decreases, and vegetation

type is also constrained by proximity to the sea), as no correlation between soil depth and distance to seashore was observed in our data (not shown). Maritime-high grassland appeared not to be able to settle in areas with a soil shallower than 10 cm. We can therefore assume that trampled vegetations with a soil depth under 10 cm were previously natural short grassland and those with a soil depth over 10 cm are kept short by human trampling only. Soil depth thus appeared as a first powerful indicator to classify natural vs. human-maintained vegetation, and was used to build a map of the whole coastline (see below).
To identify additional indicators of human trampling, a PCA was performed on the floristic composition of the 137 samples of short grassland using their cover indices. This analysis revealed an obvious gradient in species composition across trampling levels (Tab. 2, Fig. 4), located roughly along the second principal component axis. Natural (non-trampled) short grassland appeared to be characterized by the presence of *Cladonia furcata, Cladonia firma, Sedum anglicum,* and *Jasiona crispa maritima*.

We performed parametric a Discriminant Analyses and then assess error rate of estimation in classification (Mathsoft 1999). We test how species composition of botanical sample (n = 137; species cover as variable, only the first 45 most frequent species were taken into account) from distinct trampling intensity (none, low, and a third group gathering medium and high trampling levels) could distinct trampling intensity. This technique provides an upper limit of error count estimates, and cross-validation is necessary. The cross-validation technique uses functions computed from all data except the group being classified. Conceptually, each observation is systematically dropped, the discriminant function is reestimated, and the excluded observation is classified. All error rate estimates presented in this study are based on posterior probabilities (see Mathsoft 1999 and McLachlan 1992 for more details). Multivariate Analysis of Variance was highly significant (Wilk's Lambda = 0.051, $F_{90,180} = 6.873$, $P < 0.0001$). Overall, this classification generated only 4% of posterior error in jack-knife classification, most of these errors coming from the low intensity group (Tab.3). Furthermore, none of the samples of medium to high trampling group were classified in the "non-trampled" group, and only one sample in the converse way.
According to Sidak's test (Tab 4), lichens such as *Cladonia firma and C. furcata* contributed highly to discriminate the natural short grassland group from trampled short grassland. In addition, *Aira caryophylea, Armeria maritime, Jasiona crispa maritima, Sedum anglicum, Plantago coronopus, Bellis perennis* discriminated the natural short grassland group from short grassland with medium and high trampling intensity, with the first five species being mostly specific of non-trampled sites, whereas *Plantago coronopus* and *Bellis perennis* are specific of highly trampled sites.

3.3. Location of rare species hotspots

As excepted, rare taxa on Ouessant are species or subspecies linked to marine environmental constraints and are hence naturally found essentially along the coastline (Fig.5). Littoral 250m x 250m cells (i.e., cells including a fragment of coastline, $n = 117$) have an average of patrimonial index (0.095 ± 0.013) twenty times higher than inside cell (0.005 ± 0.002). The North coast, more exposed to dominant winds, appeared to host the largest part of rare species.

3.4. Distribution of rare species along coastal habitats and their response to trampling intensity.

Some habitats were obviously devoid of human trampling (Table 1), such as submerged or partially submerged sea caves, maritime rock crevice or other little human trampled habitats such as European dry heaths; they host species that are not found elsewhere (*Rumex rupestris, Trichomanes speciosum, Cytisus scoparius maritimus, Solanum dulcamara and Solidago virgaurea*) and that were then not considered in the following, as we chose to focus on human-accessible habitats only. In such habitats, one species was noticed only in non-trampled habitat (*Teloshistes flavicans*). Conversely, some species such as *Isoetes histrix, Ophioglossum lusitanicum, Centaurium maritimum, Scilla verna,* and *Heterodermia leucomelos* occurred both in natural and trampled short grassland. We thus focused our subsequent analyses on these species, studying their occurrence throughout samples to discriminate short grassland origin. Except *S. verna* and *O. lusitanicum*, rare species have their maximum occurrence frequency in non-trampled short grassland (Table 1). But no significant difference could be detected between non-trampled and low trampled group for *I. Histrix* (χ^2, ddl 1 = 2.31, P=0.13), *C. maritimum* (χ^2, ddl 1 = 0.05, P=0.82) and *H. leucomelos* (χ^2, ddl 1 = 0.05, P=0.82). *S. verna* and *O. lusitanicum* appeared to have their optimum in short grassland with medium trampling intensity; the difference with the non-trampled group were significant for *O. lusitanicum* (χ^2, ddl 1 = 4.21, P=0.04) and non-significant for *S. verna* (χ^2, ddl 1 = 0.53, P=0.47).
In addition, as human trampling created new areas of short grassland, we focused on two widespread species, *I. histrix and O. lusitanicum*, and identified plots located in this newly-created areas. Twenty-five % of the 159 *I. Histrix* plots and 38% of the 195 *O. lusitanicum* plots were found in the human-maintained short grasslands (the other plots were all found in natural short grasslands). These species were never found in tall grasslands).

3.5. Plants community diversity.

Species richness (estimated via capture-recapture methods) significantly decreased with increasing intensities of trampling in maritime high grasslands ($F_{1,78} = 134.87$; $P < 0.0001$; Fig. 6). The same pattern was found in maritime-high grassland ($F_{1,78} = 3.83$; $P = 0.05$; Fig. 6), although the decrease was less significant due to an initially relatively poor species richness in non-trampled maritime-high grasslands. In addition to species richness, we also consider estimators of species changes across the gradient of trampling, to test whether the observed decreased species richness with increased trampling intensity could be linked with losses and/or replacement of species.

3.6. Changes occurring in natural short grassland affected by trampling

In trampled plots, the proportion of species observed in non-trampled natural short grassland decreased significantly with trampling intensity, by about 20% (Figure 6 and Table 5; Φ; $F_{1,58} = 22.51$; $P < 0.0001$). Similarly, the number of species observed at a given trampling intensity was always smaller than that of immediately lighter trampling intensity (Table 5; γ; $F_{1,58} = 5.56$; $P = 0.022$). The proportion of new species appearing when trampling intensity increases remained relatively minor with respect to loss of species.

3.7. Changes occurring in maritime-high grassland affected by trampling

In trampled plots of maritime high grasslands, the proportion of species observed in non-trampled plots also decreased significantly with trampling intensity (Table 6; Φ; $F_{1,58} = 10.98$; $P < 0.002$) and the number of species observed at a given trampling intensity was smaller than that of immediately lighter trampling intensity (Table 6; γ; $F_{1,58} = 50.02$; $P <$

0.0001). However, the estimated species richness increased from 23 to 46 species between non-trampled plots and plots of low trampling intensity (Fig. 6), which results in a low γ (0.50, Table 6). As Φ, the proportion of species observed in non-trampled plots and still found at low trampling intensity, was relatively high (0.84 Table 6), we can infer that most changes between the two states are essentially due to a contribution of new species. Further increases in trampling intensity resulted in patterns similar to those observed in short grasslands, i.e. decreasing number of species and loss of species (Table 6).

3.8. Impact of human trampling at the landscape scale

Using the indicators of natural vs. human-induced grassland identified above (i.e. soil depth < 10 cm and presence of species non-tolerant to trampling, such as lichens, inferred from the Discriminant Analysis), a map of coastal grasslands was built in the GIS as described below. Four grassland types were distinguished: natural, non-trampled short grassland, maritime-high grassland, short grassland induced by human trampling (i.e. predicted to be maritime-high grassland without tourist impact) and short grassland affected by human trampling (i.e. predicted to remain short grassland without tourist impact).

As expected, path surface in a given area was strongly correlated with the number of tourists crossing the area (regression of path surface on number of tourists: $y = 0.358x + 8004$, $F_{1,10} = 46.79$; $P < 0.0001$). Total surface of trampled short grassland was also strongly correlated with the number of tourists crossing the area (regression of surface of trampled short grassland on number of tourists: $y = 1.437x + 9292$, $F_{1,10} = 45.20$; $P < 0.0001$).

Indicators of trampling, such as soil depth or plant species and assemblages, and obvious field observations, such as tourist paths, were then used to infer the short grassland cover (of the whole coastline Fig.7). Human trampling on the coast appears to have destroyed 3.5 ha of natural coast vegetation by creating numerous paths without vegetation cover. This trampling also created 31 ha of short grassland, which represents 50.8% of the whole short grassland of Ouessant, and appears to affect 41.4% of the original natural short grassland.

3.9. Creation dynamics of short grassland link with human trampling.

From 1998 to 2004, 7.5 km of additional paths were created by human trampling, so that Ouessant coastline is traversed today by a total of 85 km of littoral paths. The mean annual rate of path creation was 1.1% from 1998 to 2000 and 1.8 from 2000 to 2004. Creation of new paths appeared more intensive in areas with large tourist flow ($F_{1,10} = 4.89$; P = 0.051) . Given the previously observed relationship between path surface and tourist flow (Regression of path surface on number of tourists: $y = 0.358x + 8004$, $R^2 = 0.82$), and the constant increase in the number of boat passengers (+2500 per year), we expected a 13.3 km increase in path length between 1998 and 2004. This prediction is somewhat higher than the estimation obtained by field surveys (7.5 km), but remains in the same order of magnitude.

4. Discussion

4.1. Trampling indicators

Our study underline that indicator species to discriminate natural short grassland from grassland maintained short by human trampling are mainly species that do not resist trampling, such as thallophyte (lichens*: C. firma, C. furcata, T. flavicans, H. leucomelos*), succulent (*Sedum anglicum*) or perennial woody-stems species (*Armeria maritima*). As shown by Yorks *et al* (1997), this sensitivity is probably linked with their breakable nature,

which increases in summer when plants, especially shrub lichens, dry. The species mentioned above thus appear as good indicators of non-trampled areas. A couple of species were associated with human-maintained short grassland: (1) *P. coronopus* and *B. perennis*, which is probably due to the presence of a rosette stage in their life cycle, yielding greater resistance to trampling (Liddle and Greig-Smith, 1975; Cole, 1987; Enoul, 1999) and (2) graminoids (grass, here *Festuca sp.*), which are already known as trampling-resistant species (Cole, 1995; Yorks et al., 1997).

4.2. Rare species

Focusing on patrimonial species, we showed that at least on third of rare species occurring in potentially-trampled habitats were never found in trampled sites. One species, *T. flavicans*, was never seen in trampled vegetation, even under a low intensity of trampling, which suggests zero tolerance to trampling. However, most rare species on Ouessant seem to be able to tolerate a low intensity of trampling (xxx visitors per year), and disappear only at greater trampling intensities. Two species, *S. verna* and *O. lusitanicum*, even appear to be favoured by low and medium trampling. This may be caused the fact that trampled soil are generally less permeable, so that raining water can stagnate in winter, creating suitable conditions for these species. For *I. histrix* and *O. lusitanicum*, trampling has even created a rather large number of new stations, respectively 40 (+25%) and 74 (+38%). Recent extinctions of spots of *O. lusitanicum* in Ouessant could be detected through differences between a map drawn during the period 1984-1986 (Bioret, 1989) and this study. The few detected extinctions (at least 5) are mainly located inland and are probably associated with fallow-land process rather than tourism impacts; a single extinction might have been due to human trampling.

4.3. Community scale

When it occurs in natural short grassland, coastal tourist trampling appears to reduce drastically species diversity and results mainly in loss of species not tolerant to trampling. Such results are globally consistent with earlier studies (Lemauviel and Rozé, 2003; Roovers et al., 2004; Whinam and Chilcott, 2003); however, in contrast to other studies, species were lost gradually with increasing trampling intensity, i.e. we did not observed a more severe loss of species in the first stage (no trampling to low-intensity trampling) than in the later stages.

When trampling occurs on maritime-high grassland, low intensity of trampling results in larger species richness than in non-trampled plots. At higher trampling intensities, species richness decreases with increased trampling, as in natural short grasslands. Such transient increase in number of species at low intensity of trampling has been also observed by Van der Maarel (1971) on sand dune. This result can be explained by the fact that dominant species of maritime-high grasslands, which are mainly perennial (*Agrostis stolonifera maritima, Armeria maritima, Dactylis glomerata oceanica, Festuca rubra pruinosa*) are not resistant to trampling, so that small clearings produced by trampling enable establishment of numerous annual species such as *Aira sp., Catapodium loliaceum,* or *Radiola linoides*.

4.4. Landscape scale

Considering the landscape scale is crucial for managers who want an accurate picture of how natural patrimony is affected by tourism pressure. In contrast to many studies (see review by Leung and Marion, 2000), recreational impacts on Ouessant are not limited to a relatively small and negligible proportion of the habitat of rare species: the major parts of noticeable habitats are affected. According to vegetation coverage, trampling currently

affects 12 ha of natural short grassland (i.e. 41% of this vegetation type) and 31 ha of maritime-high grassland (15%) and tourist visits have already led to the destruction of 3.5 ha.
In addition, yearly rate of increase in tourist number (+2500), dynamics of path creation (+1.6% per year) and decrease in vegetation cover (-6.6% per year on shallow soil (< 10 cm) and - 0.6% on thicker soil (> 10 cm), unpublished survey of 12 permanent quadrats between 1998 and 2003) are a source of major concern for the conservation of the natural patrimony of the Biosphere Reserve.

4.5. Management implications

The results of this study have direct implications for managers attempting to minimise trampling impacts in wilderness recreation areas with nature preservation goals (Cole and McCool, 2000; Gómez-Limón and Lucio, 1995; Lande et al., 2000; Yorks et al., 1997). Our results are relevant to issues such as how natural patrimony is affected by this process on this Biosphere Reserve; which plants communities are more affect by trampling impacts and whether concentration or dispersal of tourists is more appropriate in a given environments.
Managers should influence spatial distribution of visitors at a large scale to (1) fully protect non-trampled areas of natural short grassland, where rare and non-tolerant to trampling species like *T. flavicans* are present, and (2) protect areas favourable to the establishment of natural short grasslands that have been turned into bare soil by trampling, to limit the current decrease in vegetation cover.
Fortunately, a compromise between tourist access to the coast and species protection seems possible. Maritime-high grasslands, dominated by perennial grass species like *Festuca rubra pruinosa* and *Agrostis stolonifera maritima*, appears currently less impacted by tourism in term of affected surfaces, soil cover or species loss. Tourist flow should thus be redirected towards such habitat. With a moderate and controlled flow of visitors flow in this habitat, new areas of short grassland would be created, which could enable the establishment of rare species.
In addition to landscape management, a threshold of sustainable number of visits on the coast should be defined to preserve species and habitat of great value, as the continuous increase in visitor number currently observed will eventually creatie serious and irreversible damage to the coastal ecosystem, even if tourist paths are strongly constrained.

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Table 1. Protection status of rare species and number of spots where they were observed on Ouessant; habitats of Annexe I directive habitat hosting these species. For short grassland habitat, occurrence (%) of species under various intensities of trampling is given

	Number of plots	Species status	Annexe I European Habitat								
			Caves (8300)	Vegetated sea cliff of the Atlantic coasts (1230)						European dry heaths (4030)	
			8300-1 Submerged or partially submerged sea caves	1230-1 *Crithmum maritimum-Spergularia rupicola* : maritime rock crevice	1230-3 *Festuca rubra-Armeria maritima* or, *Festuca rubra-Holcus lanatus* or, *Festuca rubra-Daucus carota* ssp. *Gummifer*: maritime grassland	1230-6 *Sedum anglicum-Dactlis glomerata* or, *Scilla verna-Jasione crispa* maritima or *Plantago coronopus-Armeria maritima* : short grassland				4030-2 *Calluna vulgaris-Scilla verna* : heath	4030-3 *Calluna vulgaris-Ulex gallii* : heath
						Trampling intensity					
						none	low	medium	high		
Rumex rupestris	10	1,2,3,4		X							
Trichomones speciosum	8	1,2,4	X								
Isoetes histrix	159	2,4				0.19	0.05	0.05	0		
Daucus carota gadecaei	1+	3,4			X						
Solidago virgaurea rupicola	23	3,4								X	
Silene dioica zetlandica	3+	4			X						
Ophioglossum lusitanicum	195	4				0.02	0.05	0.13	0.06		
Centaurium maritimum	49	4				0.13	0.11	0	0		
Cytisus maritimus	28*	4								X	(X)
Scilla verna	75*	4				0.50	0.53	0.58	0.28	X	
Solanum dulcamara marinum	8	4		X							
Heterodermia leucomelos	53	5				0.13	0.11	0	0		
Teloshistes flavicans	40					0.06	0	0	0		

+ : minimum number, due to problem with field determination ; * Species with spread distribution : plots correspond to 250x250m squares and not to populations ;

Species status: Species of the European directive habitat (1), species with national protected status (2); species listed in the National Red List (3); species listed in the Regional Red List (4), Lichens consider as rare at National Scale, Pr Masse comm.. pers., (5).

X presence of this specie in this habitat.

Table 2: First five axes of the principal component analysis performed for floristic composition

	PC1	PC2	PC3
% Variance	18,1	13,7	11,5
Cumulative %	18,1	31,7	43,2

Table 3: Result of a Discriminant Analysis performed on 137 short grassland samples using six variables.

	In classification matrix			In jack-knife classification matrix		
Trampling intensity	None	Low	Medium to high	None	Low	Medium to high
None	47	0	1	41	6	1
Low	1	15	3	5	8	6
medium to high	0	0	70	0	4	66

Table 4: Species contributing significantly to group discrimination under 95% simultaneous confidence intervals, using the Sidak's test of SPLUS package.

Species	estimate	standard error	lower bound	upper bound
Species showing significant differences between the "no trampling" group and the "low trampling" group				
Cladonia firma	0.69	0.12	0.27	1.10
Cladonia furcata	1.31	0.21	0.61	2.02
Species showing significant differences between the "no trampling" group and the "medium to high trampling" group				
Aira caryophyllea	0.41	0.07	0.18	0.66
Cladonia firma	0.77	0.09	0.48	1.06
Cladonia furcata	2.09	0.14	1.61	2.57
Jasiona crispa maritima	0.58	0.09	0.29	0.87
Sedum anglicum	0.69	0.10	0.35	1.03
Bellis perennis	-0.21	0.06	-0.42	-0.01
Plantago coronopus	-0.51	0.15	-1.00	-0.01
Species showing significant differences between the "low trampling" group and the "medium to high trampling" group				
Armeria maritima	0.59	0.14	0.13	1.05
Cladonia furcata	0.78	0.20	0.11	1.44
Jasiona crispa maritima	0.65	0.12	0.25	1.04

Table 5: Changes in species composition of natural short grassland along a gradient of trampling intensity. Φ is the proportion of group 1 species still present in group 2 and γ is the proportion of group 2 species present in group 1, with group 1 (lines) being less trampled than group 2 (columns).

	Φ			γ		
Trampling level	Low	Medium	High	Low	Medium	High
None	0.88±0.07	0.73±0.04	0.68±0.16	0.89±0.06	0.83±0.08	0.89±0.08
Low		0.81±0.05	0.71±0.16		0.91±0.07	0.99±0.03
Medium			0.75±0.12			0.97±0.03

Table 6: Changes in species composition of maritime grasslands along a gradient of trampling intensity. Φ is the proportion of group 1 species still present in group 2, γ is the proportion of group 2 species present in group 1, with group 1 (lines) being less trampled than group 2 (columns).

	Φ			γ		
Trampled level	Low	Medium	High	Low	Medium	High
None	0.837±0.07	0.748±0.16	0.56±0.10	0.51±0.09	0.53±0.12	0.63±0.16
Low		0.87±0.14	0.65±0.17		0.99±0.03	0.95±0.04
Medium			0.71±0.15			0.92±0.09

Figure 1: Location of protected areas on Ouessant, survey areas and variations of the number of tourists through time.

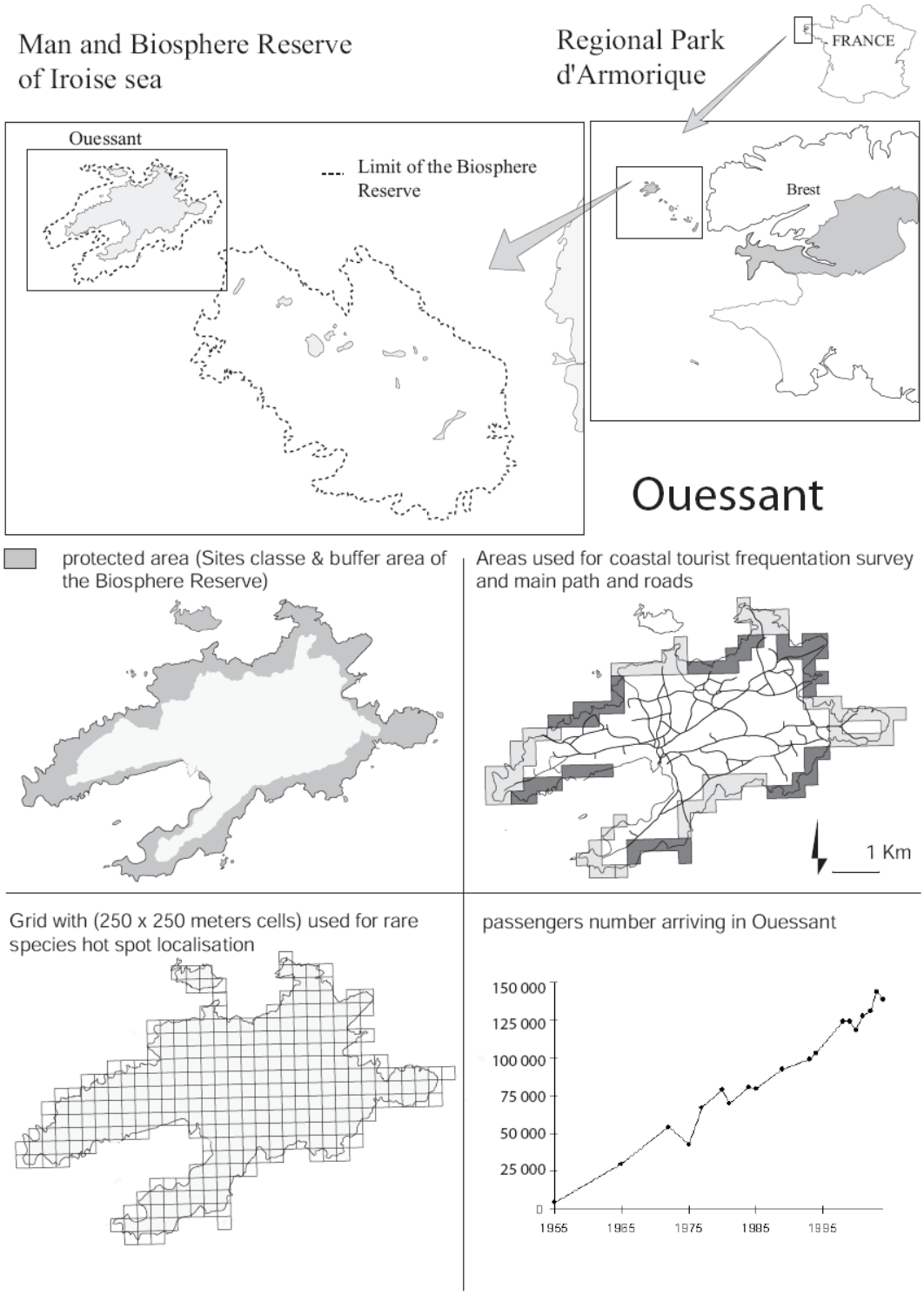

Figure 2: Spatial distribution of tourists on Ouessant Island. The estimated annual number of visitors is given for each survey area.

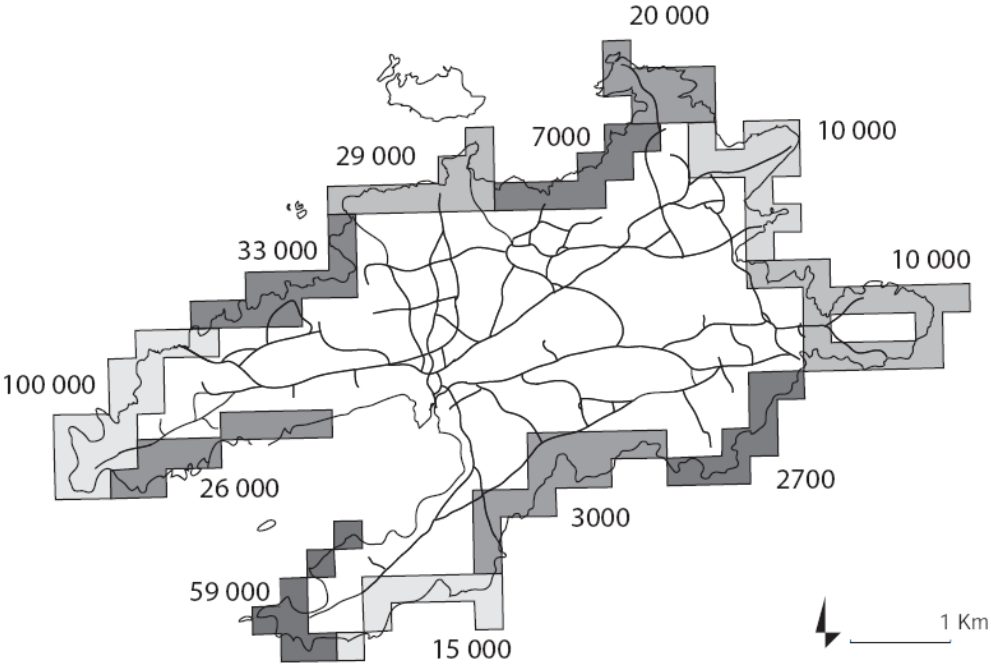

Figure 3: Soil depth in plots of maritime high grasslands and short grasslands under various trampling intensity (Maritime grassland n = 20 ; Short grassland with no trampling n = 48, with low trampling n = 19, with medium trampling n = 38 and with important trampling n = 32).

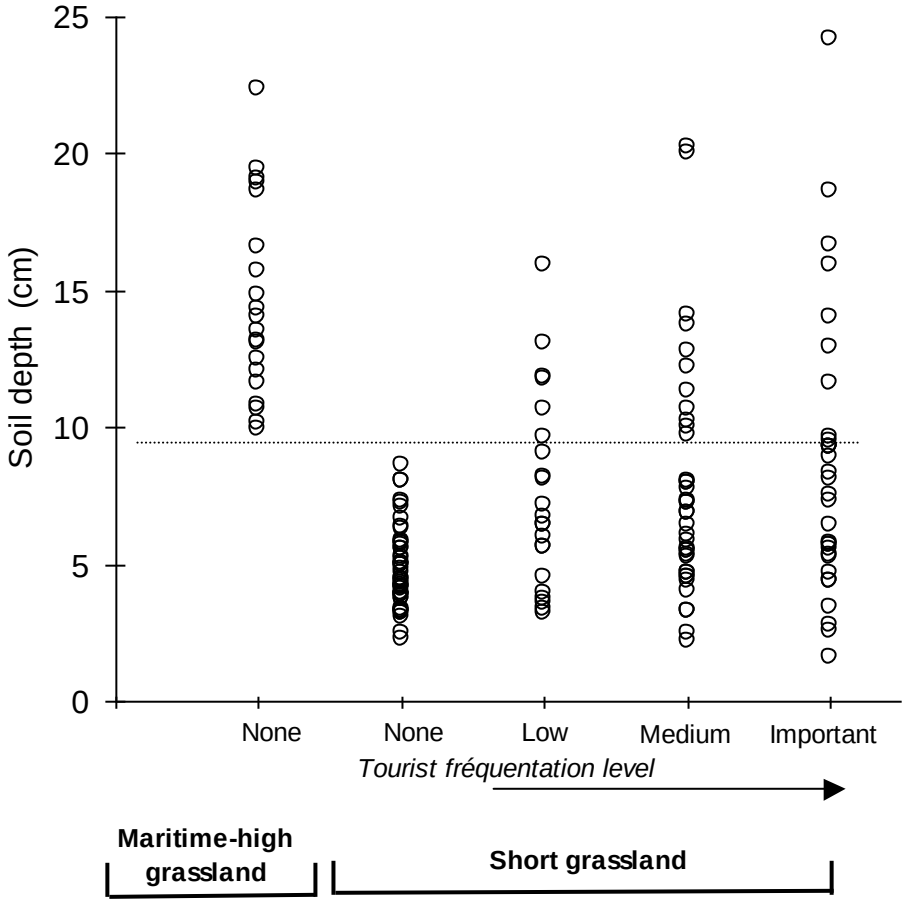

Figure 4: Plot of the first two principal components from the PCA analysis of floristic composition in 137 sites of short grassland. Sites (A) ; Plants species (B).

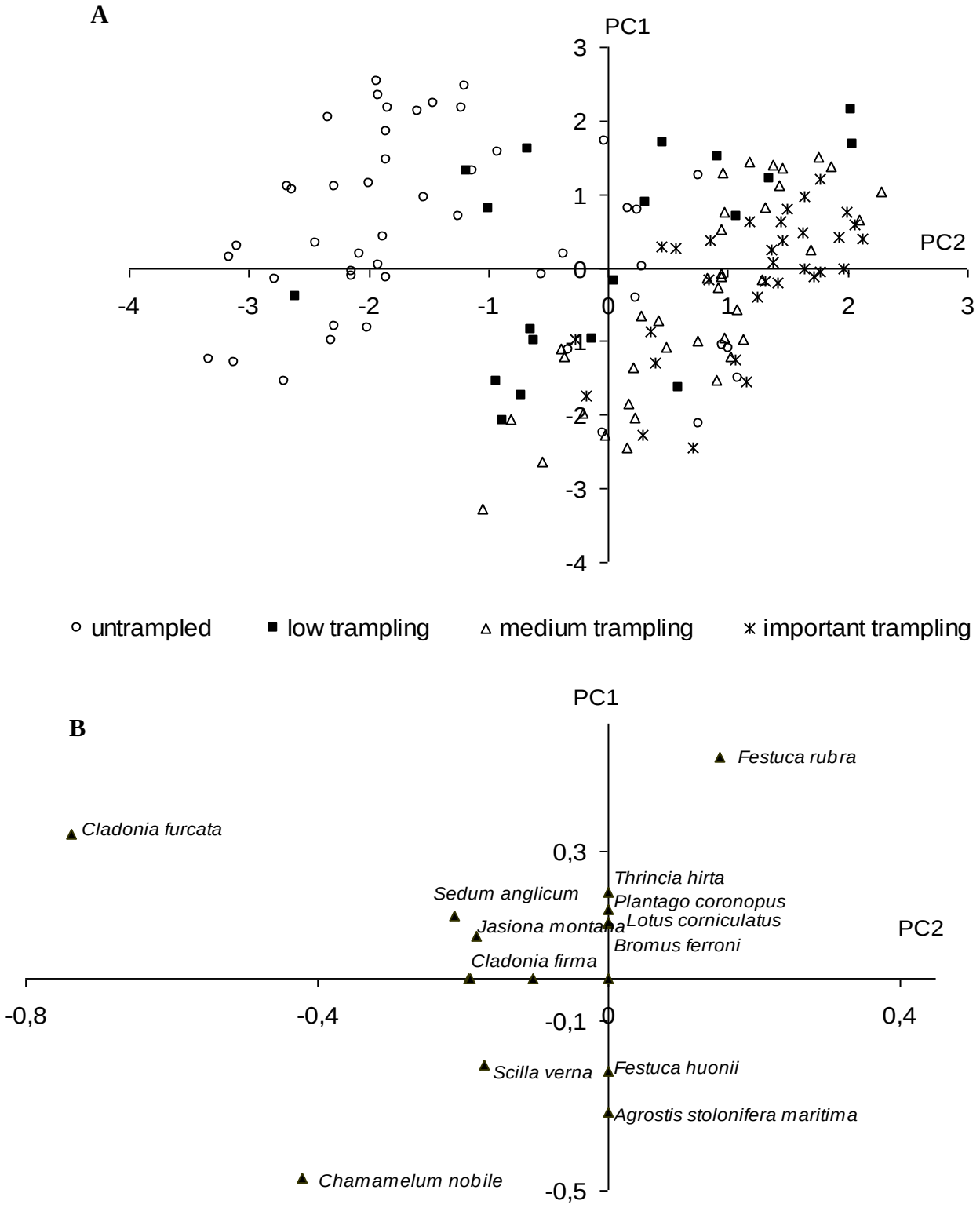

Figure 5: Protected coastline areas and hotspots of rare plant species on Ouessant

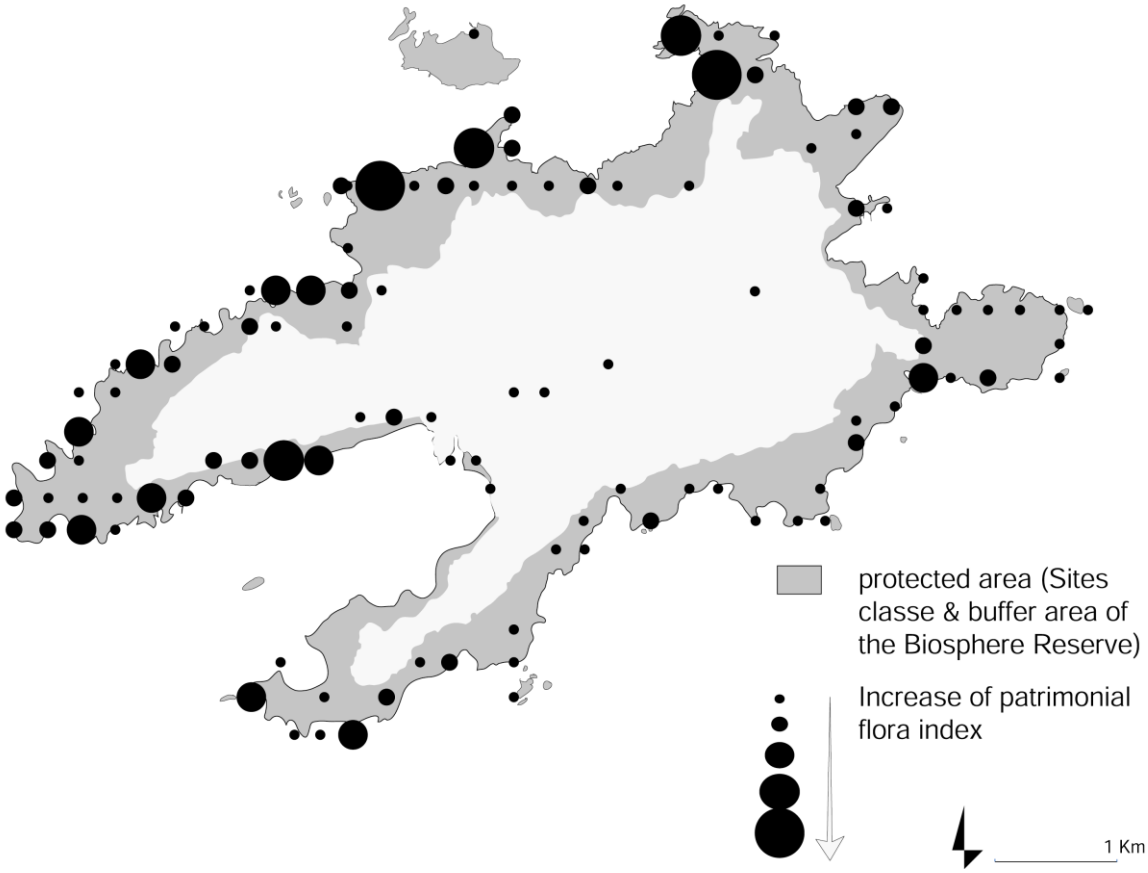

Figure 6: Variation in species richness estimation, access using jack-knife estimator, across a gradient of trampling intensity in two grassland habitats of Ouessant.

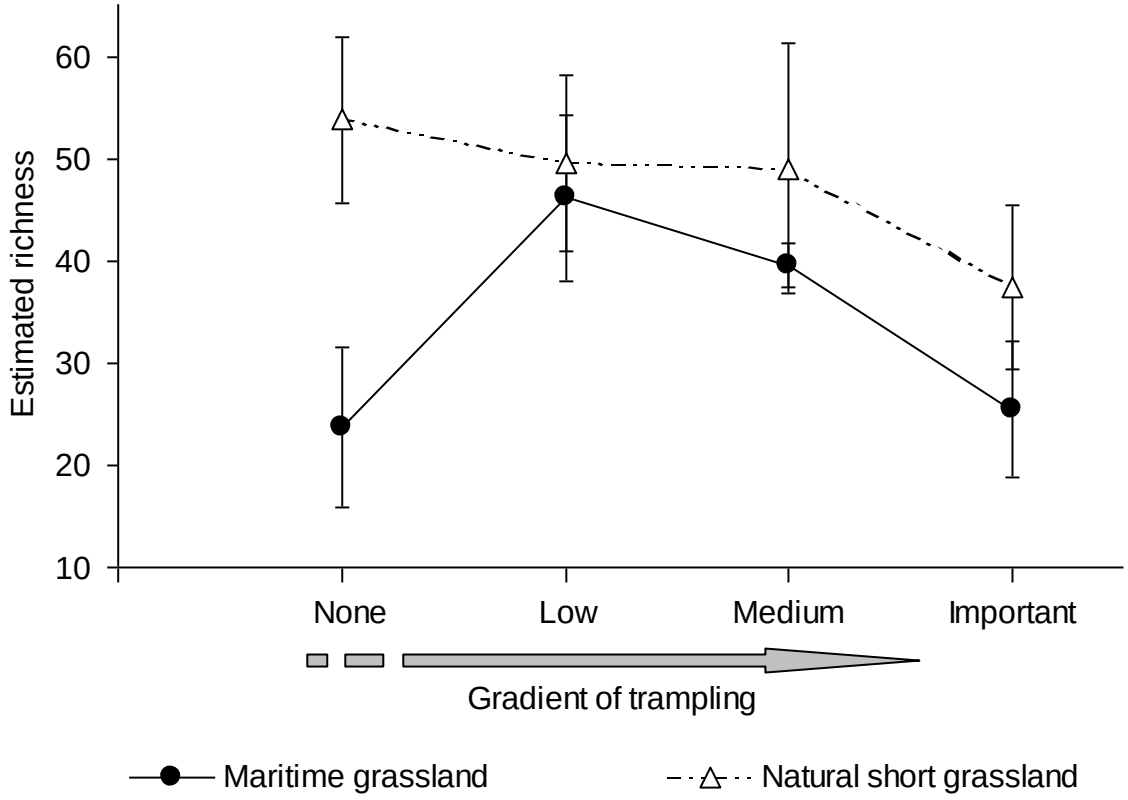
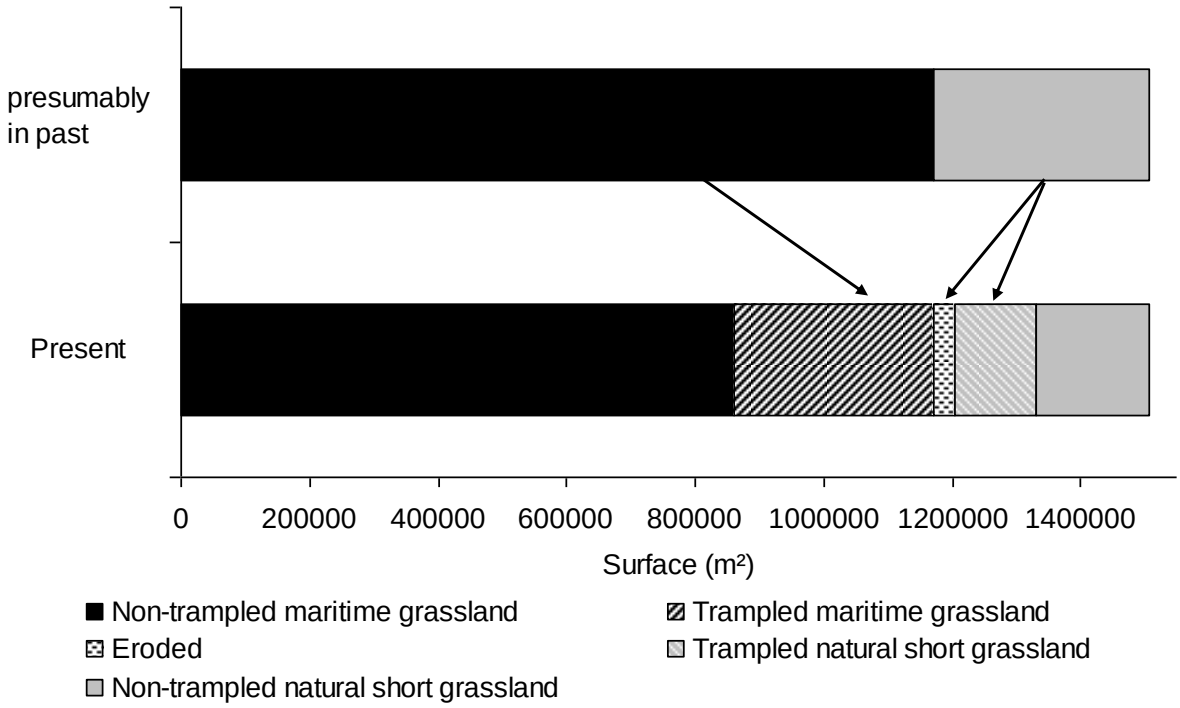
Figure 7: Distribution of surfaces of the different grassland types on Ouessant.