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Ecology, demography and conservation of *Coscinodon horridus* (J. Muñoz & H. Hespanhol) Hugonnot, R. D. Porley & Ignatov in France

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This study provides the first comprehensive evaluation of the population of *Coscinodon horridus* (J. Muñoz & H. Hespanhol) Hugonnot, R. D. Porley & Ignatov in France, a recently discovered species in Meygal (Haute-Loire). A total of 876 individuals (one cushion = one individual) were recorded amongst lava scree on three scree (volcanic summits), of which 99.6% occur on a single summit. The detailed population counts provide an accurate base-line for future monitoring. Male plants are very rare and the sex-ratio is strongly biased towards females. Sporophytes are also very rare. *Coscinodon horridus* is a mountain species, strongly linked to harsh environments, mostly on steep exposed slopes of south-east aspect yet is predominantly associated with sheltered niches that are protected from direct precipitation and insolation. Sheltered individuals tend to be vegetatively more robust than those growing in more exposed situations. The unique hairpoint anatomy of *C. horridus*, complex water relations and competitive interactions may explain the narrow niche that this species occupies. Due to the very small area of occupation in France and the low number of individuals, *Coscinodon horridus* is considered to be threatened in France and is classified as Endangered.

Keywords: conservation, *Coscinodon horridus*, harsh environments, niche competition, population counts, scree, water relations

Coscinodon horridus (J. Muñoz & H. Hespanhol) Hugonnot, R. D. Porley & Ignatov, formerly *Grimmia horrida* J. Muñoz & H. Hespanhol, is a globally very rare bryophyte in the Grimmiaceae, a European endemic known from a few localities in the Iberian Peninsula (four in northern Portugal and one in north-west Spain) and in Meygal Massif, France (Haute-Loire). It was recently added to the French bryoflora (Hugonnot et al. 2018). From the limited data available for the Iberian Peninsula (Sérgio et al. 2019), the French population may represent the most important site for the plant in the world.

The French population is located in a Natura 2000 site which is characterized by massive scree slopes which are essentially devoid of tracheophytic vegetation. Upland heath and scree are widely being colonized by shrubs and trees as a result of abandonment of grazing. Up until 30 years ago, sheep grazing was practised on Pic du Lizieux. With the removal of stock, woody species including *Sorbus aria*, *Corylus avellana* and *Pinus sylvestris*, begin to invade. Shrubs

also benefit from cavities in scree where small quantities of organic material accumulate, and eventually individual shrubs form small stands. Hence, the main conservation issue is related to maintaining the biological quality of this peculiar fragile habitat which supports a variety of specialized species, among which are several notable bryophytes.

Nonetheless, the precise geographical extent, population size and ecological requirements of *Coscinodon horridus* in Meygal Massif are virtually unknown. In particular the reproductive strategy of the species is crucial since in dioicous Grimmiaceae dispersal is largely dependent upon spore production. Such precise data are fundamental to inform conservation policy.

Material and methods

Study site

The study site is located in the ecological region of Meygal, in Haute-Loire department (between 45°01' and 45°05'N; 4°02' and 4°12'W), France. The climate is continental-montane with Mediterranean influence (Jouve 2001, Darnis 2010). The mean annual temperature is 6.5°C (January:

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Table 1. Main characteristics of the six studied sucs.

Sucs	Altitude	Scree surface (ha)	Scree type	Medium size of blocks (L × l) [evaluated in the field]
Tortue	1130–1327 m	18	Phonolithe (with agpaïtic tendencies) dome	1 × 1 m
Mounier	1210–1407 m	13.6	Nepheline trachyte and miaskitic phonolite dome	1 × 1 m
Pic du Lizieux	1260–1388 m	7.6	Trachyte and phonolite dome	0.5 × 0.5 m to 1 × 1 m
Testavoivre	1350–1436 m	5	Trachyte and phonolite dome	0.4 × 0.4 m to 1 × 1 m
Montivernoux	1276–1371 m	unknown	Trachybasalts and basaltic trachyandesites	0.5 × 0.3 m
Mont Pidgier	850–1074 m	unknown	Phonolites with agpaïtic tendencies	0.3 × 0.3 m

–1 to 0°C; April: 4–5°C; July: 15–16°C; October: 7°C). The average number of freezing degree-days is 110, with a mean of 30 days with snow. Average rainfall is 1050–1100 mm year⁻¹. Locally known as sucs, the volcanic summits are regularly exposed to strong winds from southeast and west.

The main interest of the Natura 2000 site 'FR8301086 – Sucs du Velay-Meygal' is the occurrence of five massive volcanic sucs, made of trachyte and phonolithe: Tortue, Mounier, Montivernoux, Pic du Lizieux and Testavoivre, which were all surveyed. Mont Pidgier was added to the study site because it shares similar geologic characteristics (Feybesse et al. 1998) (Table 1). The highest elevation is 1436 m, in Testavoivre site. Typically, from the top to the bottom of the slope, diverse rock assemblages are encountered where gravity (on steep slopes, > 30 deg.) and gelifluction are the main governing processes.

Apart from small patches of trees and shrubs (*Pinus sylvestris*, *Sorbus aucuparia*), the Tortue site offers a large open area almost devoid of vascular vegetation. The few vascular species are sparse and have little overlap (*Campanula rotundifolia*, *Cryptogamma crispera*, *Avenella flexuosa*, *Dryopteris filix-mas*, *Silene rupestris*, *Valeriana tripteris*). Some heathland plants (*Vaccinium myrtillus*, *Calluna vulgaris*, *Rubus idaeus*) are mostly found on the edge of rocky areas. The vegetation of the other sucs is very similar.

***Coscinodon horridus* population localization and description**

Field work was conducted during March–April–May 2018. To locate *Coscinodon horridus* populations, each of the six sucs were systematically surveyed. The method used was to ascend the slope of the suc by following compass directions, and shifting 5 m laterally once the top of the slope was reached, and then return down. During the repetitive ascents and descents, *C. horridus* cushions were visually spotted due to their blackish-olive green color and confirmed by the long spinulose hair-points with a ×20 hand lens. This approach allows a comprehensive survey of the populations on each suc. Once an individual (one individual = one discrete cushion constituting numerous shoots) or a colony (a group of cushions colonizing the same block and thus sharing the same environmental conditions) was identified, its position was logged using GPS. For each colony the number of individuals was recorded, and the length, width and height (or thickness, from substrate surface to terminal leaf hyaline apex) of the smallest cushion and tallest cushion in the colony was measured to provide a range. Inaccessibility

due to certain rock formations meant that these parameters were sometimes visually estimated. The length, width and thickness of all the individuals of the colony were estimated and averaged. The general appearance (dry, vigorous growth, spherical, oblong) of cushions and occurrence of sporophytes was also noted. Finally, 100 shoots from 100 distinct individuals from 100 distinct colonies were collected and a thorough search for gametangia (archegonia and antheridia) made in the lab.

Ecological parameters

For each *Coscinodon horridus* colony location, ecological parameters were measured at two scales: at the habitat scale (i.e. approximately 100 m² of scree surrounding the location, representative of the global environment of the colony), and at the microhabitat scale (i.e. the actual block colonized by the colony). At the habitat scale, slope and exposure were measured. At the microhabitat scale, block size (length, width and height) and the slope were measured and the exposure of the block surface estimated. Elevations were determined later by projecting each location on Google Earth. Additionally, we classified the colonies into three categories of microhabitat depending on the degree of protection from wind and sun afforded by the surrounding blocks. The three categories were: sheltered (when the area occupied by the colony was in a cavity or sheltered by an overhang); moderately sheltered (when sun and wind exposure was moderate, for example when the colony was in a crack or fissure), and exposed (when the occupied area was fully exposed to sun and wind). In total 100 colonies were sampled.

Bryophyte assemblages

The area covered by *Coscinodon horridus* within each colony was recorded. Companion species (i.e. species that grow on the same block together with *C. horridus* colony) were recorded and their surface cover was visually estimated.

Mapping and data analysis

Maps of *Coscinodon horridus* distribution were generated using Qgis software (ver. 2.18.18). Individuals' length, width, thickness (maximal and average per colony), number of individuals per colony and surface area covered between categories of microhabitats were compared using the non-parametric Kruskal–Wallis test, followed by Dunn's test when the result was significant. The degree of association

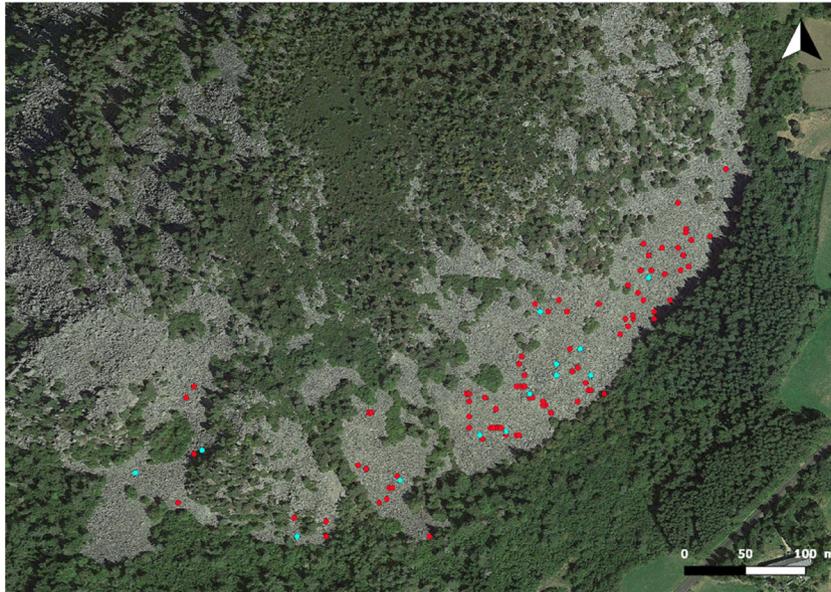


Figure 1. Distribution of *Coscinodon horridus* on Tortue site (1 dot=1 colony). Light blue dots represent colonies with sporophytes, and red dots represent colonies without sporophytes.

between the surface area occupied by *C. horridus* and the surface area occupied by companion species on the block were tested using Spearman's correlation. All statistical analysis were conducted on R (ver. 3.5.1, <www.r-project.org>).

Results

Demography

Coscinodon horridus was found on three sites: Tortue, Mounier and Testavoivre. It was not found on Montivernoux, Pic du Lizieux and Mont Pidgier. 99.6% of *C. horridus* individuals (873 cushions) are mainly grouped, more or less, within the central core of the population. The number of sporophytes per colony rarely exceeded five. Out of 100 individuals selected, 99

slope (Fig. 1). On this site, the area containing all the colonies is estimated at 24 110 m²: this corresponds to an average density of 3.6 individuals/100 m². Only two individuals (cushions) were observed on the southern slope of the Mounier, and one on the Testavoivre (Fig. 2, 3). In total, 876 individuals/cushions were recorded.

Reproduction

Thirteen colonies of *Coscinodon horridus* contained sporophytes and they were all located on Tortue (Fig. 1). No sporophytes were observed on Mounier or Testavoivre. Sporophytes were observed on Mounier or Testavoivre. Sporophytes were observed on Mounier or Testavoivre. Sporophytes were observed on Mounier or Testavoivre.

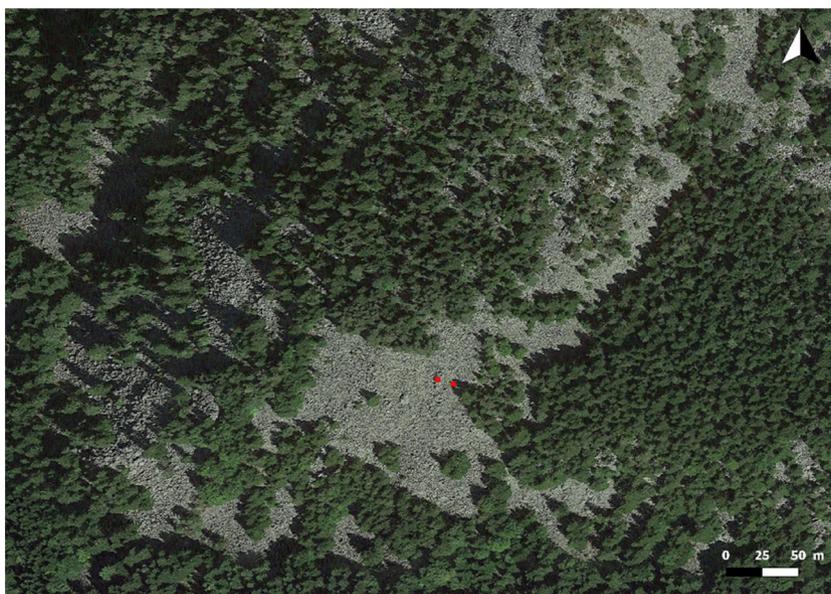


Figure 2. Distribution of *Coscinodon horridus* on Mounier site (1 red dot=1 colony).



Figure 3. Distribution of *Coscinodon horridus* on Testavoivre site (1 red dot = 1 colony).

presented female gametangia and only one presented a male gametangium. The male individual was of a similar same size as the females, with antheridial buds at the apex of long, relatively attenuated shoots. The reddish perigonal leaves were concave and differentiated at the base. No sterile shoots were observed.

Ecology

Individuals were found at elevations between 1174 m and 1283 m on Tortue, 1345 and 1346 m on Mounier and 1400 m on Testavoivre. *Coscinodon horridus* occurs predominately on steep scree slopes (from 45° to 50°); only one extreme of 5° was recorded. Aspect was mainly south-east (88%). No individuals were observed on north or west facing slopes.

The blocks colonized by *Coscinodon horridus* had an average dimension of 1.3/1/0.7 m (l/w/h) and their configurations varied very little. The slope of colonized block surfaces is variable, but is mostly below 90° (except for two extremes recorded at 95° and 110°, under overhangs). Number of individuals in each colony was significantly different between sheltered and exposed niches (Fig. 4). Sheltered blocks support the most extensive colonies, consisting of 15 cushions/individuals on average, up to a maximum of 60 cushions/individuals. No difference was found between moderately sheltered and exposed niches.

In 39% of cases exposure of exposed blocks colonized by *Coscinodon horridus* was the same as the slope of the suc (SE), the other 61% being S (19%), NW (15%), W (11%), SW (8%), NE and E (4% each). On the contrary, exposure of 44% of sheltered blocks was in the opposite direction (NW). The other 56% are SE (16%), W (14%), N (11%), NE, E and SW (5% each). No exposure seemed to prevail over another in the case of moderately sheltered blocks. Finally, no blocks were covered with humus.

Cushion height (mean and max) was significantly different between the three microhabitats, with the largest

cushions found on sheltered blocks (Fig. 5) interspersed with shorter cushions. The larger cushions often had a semi-spherical shape, with an olive green to dark green colour and long hyaline spinulose hair-points (Fig. 6A). Cushions growing on moderately sheltered and exposed blocks had shorter stem length, and it is well known that cushions in exposed wind-swept places are more compact (Proctor 1979). Cushions in exposed niches often had a dry appearance with cracks, a blackish colour and short heterogeneously distributed hair-points, with some sectors exhibiting long hairs and others shorter ones (Fig. 6B–C).

Bryological assemblages and abundance

The surface area covered by other bryophytes was significantly higher on sheltered blocks by an average of 28% than

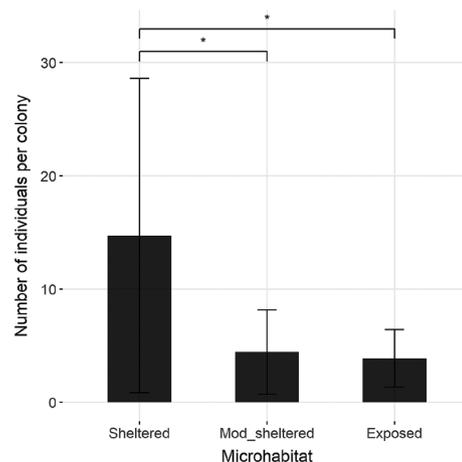


Figure 4. Number of *Coscinodon horridus* individuals per microhabitat (mean \pm SD). Significant differences between the three categories of microhabitats are indicated with an * (Dunn test, p-value < 0.05). Mod_sheltered: moderately sheltered.

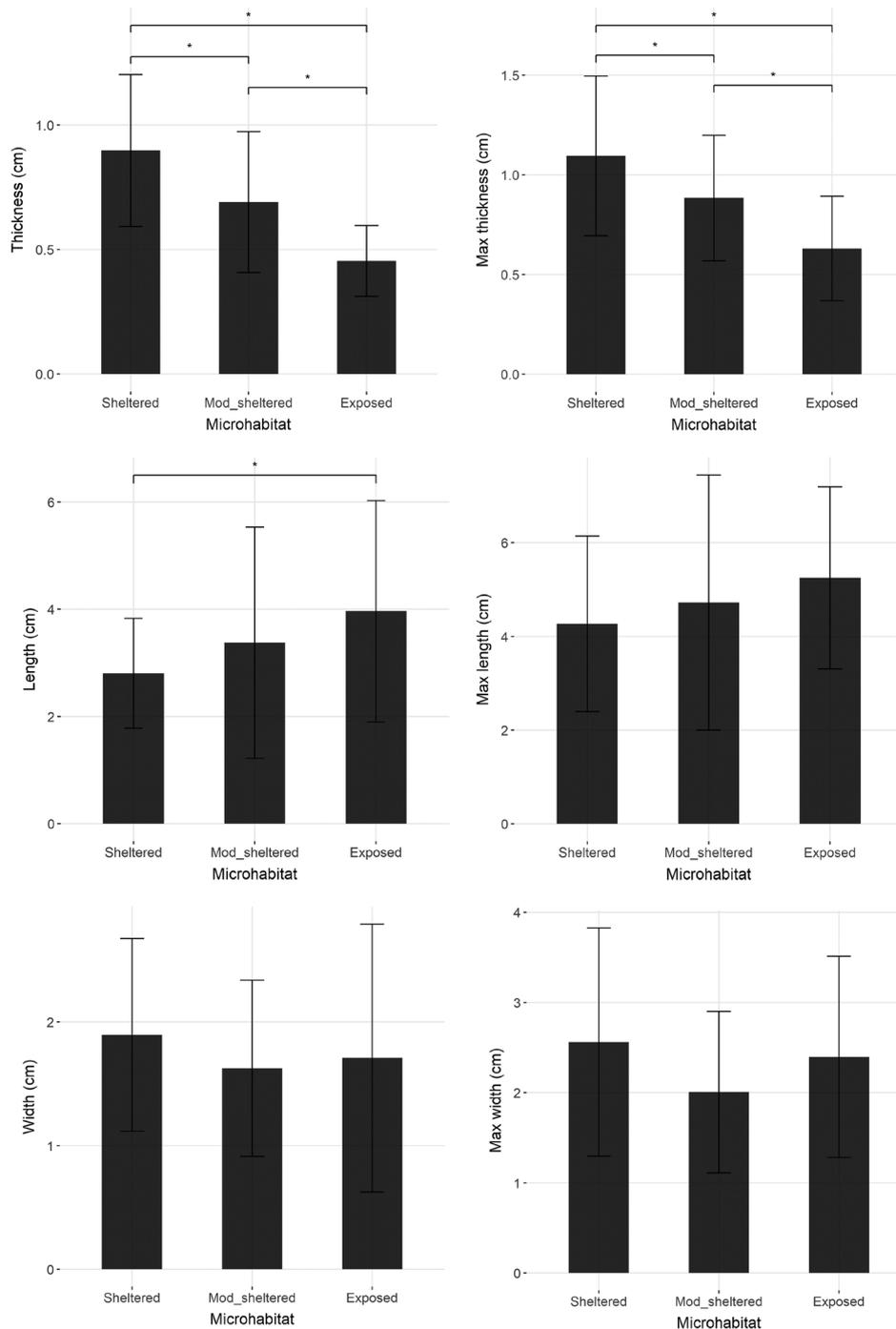


Figure 5. Mean and max thickness, length and width of *Coscinodon horridus* individuals between the three categories of microhabitats (mean \pm SD). Significant differences between the three categories of microhabitats are indicated with an * (Dunn test, p-value < 0.05). Mod_sheltered: moderately sheltered.

on moderately sheltered (8%) and exposed blocks (4%) (Fig. 7). *Coscinodon horridus* also occupied a larger surface area on sheltered blocks (Fig. 7, Table 2).

The main companion species of *Coscinodon horridus* are bryophytes: *Grimmia montana*, *G. donniana*, *G. incurva*, *Andreaea heinemanii* and *A. rupestris*. At a much lower frequency (3%), two other species were noted: *Grimmia muehlenbeckii* and *Racomitrium lanuginosum* (Table 2). On sheltered blocks, *Coscinodon horridus* individuals

were mainly found associated with *Grimmia incurva* and *Andreaea heinemanii* (Table 2). On moderately sheltered to exposed blocks, occurrence of *Grimmia montana* and *G. donniana* increases. *Grimmia incurva* was notably absent on the exposed blocks. Positive correlations were found between the surface occupied by *Coscinodon horridus* and the surface occupied by *Andreaea heinemanii*, *Andreaea rupestris* and *Grimmia incurva*. A negative correlation was found with *Grimmia montana* occupied surfaces.

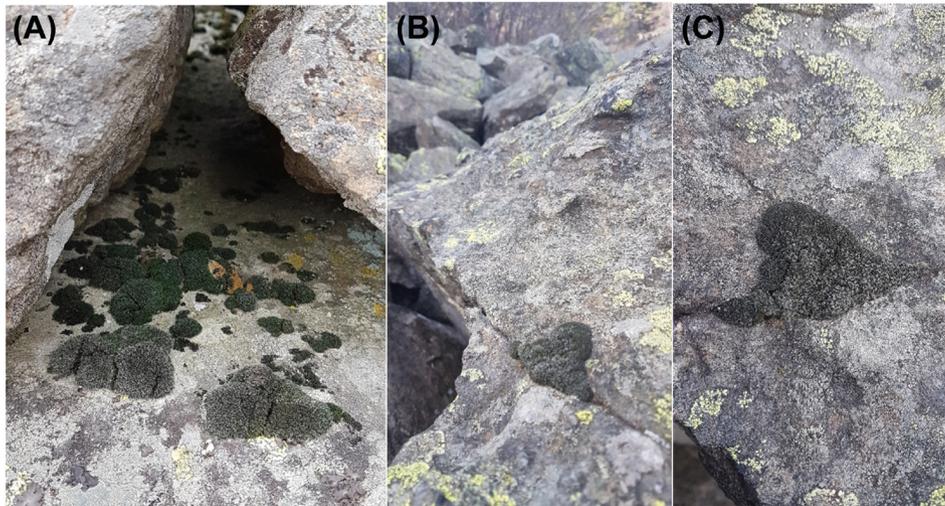


Figure 6. *Coscinodon horridus* colony on a sheltered block (A), and one individual on an exposed block (B) presenting typical short heterogeneously distributed hair-points and cracks (C).

Discussion

The extremely restricted geographical occurrence of *Coscinodon horridus* is remarkable (more than 99% of the population occupies approximately 2 ha), particularly since the Haute-Loire populations are the only colonies at the national level, and the only other known populations are located in the Iberian Peninsula. *Coscinodon*, a genus of 12 or so species, is known to show restricted global ranges and some are endemics or near endemics (Ochyra 2004, Ignatova et al. 2008). The recent taxonomic description combined with a lack of systematic survey may explain why *C. horridus* has remained undetected in France. Nevertheless, targeted local searches on neighbouring sites were unsuccessful except for the tiny populations observed on Mounier and Testavoire (3 individuals compared with 873 individuals of Tortue site), hence we are confident that the species is not under-recorded. *Coscinodon horridus* may be a recent colonizer, in the process of expansion from a core population (Tortue site) which may offer an explanation for the species unusual distribution pattern. This would, theoretically, be possible

to test in the future, by permanent monitoring of sink-sites (Mounier and Testavoire).

The rare occurrence of sporophytes at the Tortue site provides indirect evidence that male individuals are present. However, repeated and systematic search revealed only a single antheridial individual. Muñoz et al. (2009) and Porley (2012) also observed only female individuals in populations from the Iberian Peninsula. A high female-biased sex-ratio in dioicous bryophytes is well documented (Bisang and Hedenäs 2005) and is likely to be a factor explaining the absence or rarity of sporophytes. Vegetative reproduction is likely to be important in the spread of *C. horridus*, either by means of leaf fragments or other gametophyte parts (flagelliform shoots). Vegetative reproduction is assumed to be effective mostly over relatively short distances compared to long-distance transport by spores (Frey and Kürschner 2011) and would offer an explanation to account for the inability of the species to extend to other sites. Strong winds undoubtedly could carry gametophyte fragments for considerable distances (Miller and Ambrose 1976) but for some unknown reason establishment and colonisation events seem to be exceptional.

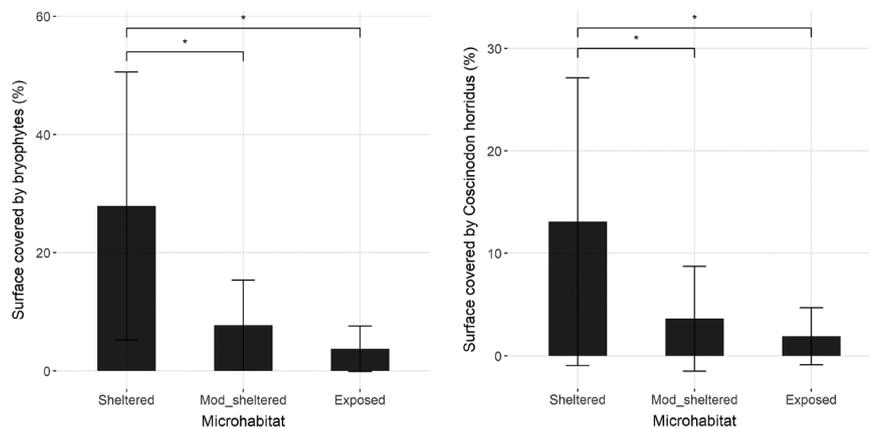


Figure 7. Block surface covered by bryophytes, and block surface covered by *Coscinodon horridus*, between the three categories of microhabitats. Significant differences between the three categories of microhabitats are indicated with an * (Dunn test, p-value < 0.05). Mod_sheltered: moderately sheltered.

Table 2. Observation frequency of *Coscinodon horridus* and its companion species, and their respective surface cover on the block. Rho: correlation between surface covered by *Coscinodon horridus* and surface covered by its companion species (Spearman's correlation coefficient). *: p-value < 0.05. **: p-value < 0.01. ***: p-value < 0.001. NS: no significance. Mod_sheltered: moderately sheltered.

Species	Observation frequency (left) and surface covered (right) between the three categories of micro-habitats (%)						Rho
	Sheltered		Mod_sheltered		Exposed		
<i>C_horridus</i>	43	13.08	31	3.61	26	1.90	/
<i>A_heinemanii</i>	28	3.22	16	1.25	2	0.04	0.35***
<i>A_rupestris</i>	16	4.07	3	0.08	0	0	0.46***
<i>G_montana</i>	5	0.55	13	1.45	15	1.25	-0.38***
<i>G_donniana</i>	6	0.43	13	0.50	16	0.48	NS
<i>G_incurva</i>	22	6.49	6	0.80	0	0	0.52***
<i>G_muehlenbeckii</i>	1	0.06	0	0	2	0.04	NS
<i>R_lanuginosum</i>	2	0.02	0	0	1	0.02	NS

Alternatively, the absence of *C. horridus* from apparently suitable sites could be related to specific ecological requirements. The majority of the populations of *C. horridus* are on SE facing slopes, and strong winds blow from SE and SW direction, influenced by the nearby Cévennes mountain range. Although not excessively cold, the prevailing winds are nevertheless cool. It is conceivable that warmer air at lower elevations is deflected up the slope by orographic lifting, and as the air gains altitude it undergoes rapid adiabatic cooling which can raise the relative humidity of the air to 100%, leading to cloud formation on windward slopes and ridges (Jiang 2003, Smith and Barstad 2004). Additionally, condensation may be involved, where the saturated air condenses (dew point) on cold surfaces, for example, on the hairpoints of *Coscinodon*, where the liquid water is then transferred to living tissues in the interior of the cushion. Many mosses of harsh environments, particularly in the families Grimmiaceae and Pottiaceae, possess hairpoints which have been shown to play a key role in water relations (Tao and Zhang 2012). The strongly spinulose hairpoints of *C. horridus* provide a much greater surface area for condensation to take place compared with species of *Grimmia* which normally have smooth to only weakly toothed hairpoints. It is reasonable to conjecture that the strongly ciliate hairpoints, with their large surface area, providing an increase in the diffusion path length for water vapour, endows *C. horridus* cushions with a very high efficacy of pulling moisture from the air and in reducing water loss. Furthermore, it is probable that the efficiency of spinulose hairpoints is further enhanced when massed together in a cushion. It is argued that spinulose hairpoints gives *C. horridus* a critical adaptive advantage over its companion species enabling it to grow in sheltered niches such as under overhangs, where direct precipitation is reduced. On more exposed surfaces receiving direct precipitation, *Grimmia montana* and other species tend to predominate. Physiological studies and precise meteorological data would be required to substantiate such a hypothesis.

A cursory examination of the tracheophytic vegetation did not reveal significant differences between sites (Darnis 2010). *Coscinodon horridus* only grows on strongly insolated sites, in France and in Portugal (Porley 2012). However, at the micro-habitat scale, subtle processes may be contributing to the presence or exclusion of *C. horridus*. The results from the present study support this hypothesis. On Tortue most individuals of *C. horridus* are located in sheltered niches and,

notably, sheltered individuals cover a greater surface and are taller compared to exposed cushions. In Portuguese populations Porley (2012) made similar observations, with *C. horridus* preferring sheltered niches and under overhangs. Furthermore, in France, overall cover of bryophytes is also significantly higher in sheltered niches (in average remaining nevertheless very low, 28%), an observation previously underlined by Alpert (1986). The sheltered micro-environment may allow settlement of individuals (diaspores) and favour their growth by offering more effective water uptake and reduced evaporation. Hespanhol et al. (2011) suggested similar water relationships for scree-bryophytes.

It was noticed repeatedly that blocks of small size appear to be unsuitable for the creation of sheltered niches (e.g. on Mounier and Testavoyre) although the study did not directly address this factor. Further work is needed to determine if trickling water converging within cavities (Fig. 8) of large blocks play a role in the establishment of *C. horridus*. At the micro-habitat scale, almost 50% of *C. horridus* individuals colonizing the sheltered niches were found on north-west aspects of blocks, whereas the overall aspect of the scree slope is the opposite (south-east). The north-west aspect of blocks provides some shelter from direct sun and desiccating winds.

On sheltered blocks, *C. horridus* was mainly found associated with *Grimmia incurva* (forma *longifolia*) and *Andreaea heinemanii*, two species that are known to be associated with sheltered niches (Dierssen 2001, Blockeel et al. 2014). Although *C. horridus* is occasionally able to colonize exposed blocks, *G. incurva* is largely absent. Conversely, as previously noted by Porley (2012), *G. montana* is able to extend onto more exposed surfaces than *C. horridus*. *Grimmia montana* may be less efficient in scavenging moisture from the air in sheltered niches not receiving direct precipitation, and smooth reflective hairpoints are more efficient in reflecting high UV levels and possibly keeping down the temperature of the cushion. These observations support the view that scree bryophytes, although commonly associated at the habitat scale, are segregated at the fine ecological niche scale.

The question arises as to why *C. horridus* is apparently unable to colonize less exposed slopes of north aspect or other less insolated sites where water relation issues would be less restrictive. The bryophytic assemblages of northern slopes are typically radically distinct from sites favoured by *C. horridus*, both in terms of floristic composition and structure: they are colonized by cold-adapted Gymnomitriaceae such as *Marsupella sprucei*, *Gymnomitrium concinnatum*,



Figure 8. Block configuration inducing shadows and a runoff of water towards the surface of the block colonized by *Coscinodon horridus*. Red arrows: the possible path that the water can take.

and other species like *Barbilophozia sudetica* or *Kiaeria blyttii*, that form extensive thin carpets over the rock. A strictly lithophilic early colonizer of large blocks is probably unable to compete with dynamic liverworts in colder environments.

Conservation

Testavoire and Pic du Lizieux are the most well known succs within the Natura 2000 site and are frequented by a relatively high number of tourists, mostly hikers. Nonetheless, the degree of human disturbance still remains low, but repeated trampling may have adverse effects on *Coscinodon horridus* population. Tortue site, which hosts the largest population, has no walking trails and therefore is not currently under threat from tourist pressure.

Coscinodon horridus is typically linked to open habitats, without any shrubs and may be threatened in the future by closing of the vegetation. Although no visible signs of tree expansion were detectable by comparison of 1977 and 1999 aerial photographs, we recommend that medium-term monitoring should be undertaken. For the time being, we consider that no management action is needed and that a better evaluation of the dynamic of tree colonization is necessary.

Coscinodon horridus was previously known only from the Iberian Peninsula, and was classified as VU (Sérgio et al. 2019). With the subsequent discovery of the species in France, it was later assigned to the category DD in Europe (Hodgetts et al. 2019) mainly because of its recent discovery and lack of systematic bryoflora recording in France. Recent targeted searches for new populations of *C. horridus* in screes of Haute-Loire, Puy-de-Dôme and Cantal were unsuccessful so that we consider that the species is a genuinely localized species.

The current population trend is unknown but the species does not appear to be under direct threat. Nevertheless, in France the population has fewer than 1000 individual-equivalents and has a very low number of localities that are very spatially restricted. Both abundance and range size are linked strongly with extinction risk (IUCN 2012). Accord-

ingly, pending more information on its demographic status, it should be considered EN.

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