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Ecology, demography and biology of four populations of *Mannia fragrans* (Balb.) Frye & L.Clark in the upper Allier Valley (Haute-Loire, France) – Conservation implications

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Abstract

The populations of *Mannia fragrans* (Balb.) Frye & L. Clark in Haute-Loire, particularly at Blassac and Saint-Privat-d'Allier, are among the most demographically robust in Western Europe, with large population sizes and surface cover. This contrasts with marginal populations elsewhere, such as in Spain or Belgium. Unlike most European populations found on calcareous substrates, these occur on siliceous volcanic rocks. *M. fragrans* occupies transitional habitats between rocky outcrops and dry grasslands, where competition is limited and soil depth is sufficient. Dense bryophyte mats (e.g., *Tortella squarrosa* (Brid.) Limpr, *Rhytidium rugosum* (Hedw.) Kindb) and vascular competitors (e.g., *Centaurea stoebe* L.) restrict its development, particularly at Chilhac. The species thrives under harsh ecological conditions - steep slopes, shallow soils, and high rock cover - which limit plant competition. Its reproductive strategy is adapted to environmental variability, with spores released in spring and germination occurring in late summer, typically in microsites created by disturbances. Sporophyte abortion and rare germination events suggest constraints on sexual reproduction, though vegetative propagation is probably effective. Spatial distribution is patchy, conistent with by microtopographic factors and diaspores' downslope movement via gravity and water runoff. These mechanisms promote local recolonization and delay succession. Conservation-wise, the Blassac population remains stable despite land abandonment, thanks to natural abiotic filters. Conversely, Chilhac shows signs of succession and competition, indicating a potential need for restored grazing. The spread of invasive *Opuntia* species, though limited for now, represents a latent threat. Continued monitoring and context-specific management may be required to preserve these rare liverwort habitats.

Keywords
Mannia fragrans
Xeric habitats
Vegetative reproduction
Bryophyte conservation
Habitat disturbance

Résumé

Les populations de *Mannia fragrans* (Balb.) Frye & L. Clark en Haute-Loire, notamment à Blassac et à Saint-Privat-d'Allier, comptent parmi les plus importantes de l'Europe de l'Ouest sur le plan démographique, avec des effectifs élevés et de grandes surfaces occupées. Cela contraste avec des populations marginales observées ailleurs, comme en Espagne ou en Belgique. Contrairement à la plupart des populations européennes situées sur substrats calcaires, celles-ci se trouvent sur des roches volcaniques siliceuses. *M. fragrans* occupe des habitats de transition entre affleurements rocheux et pelouses sèches, où la compétition reste limitée et l'épaisseur du sol suffisante. Des tapis bryophytiques denses (par ex. *Tortella squarrosa* (Brid.) Limpr., *Rhytidium rugosum* (Hedw.) Kindb.) ainsi que des compétiteurs vasculaires (par ex. *Centaurea stoebe* L.) restreignent toutefois son développement, notamment à Chilhac. L'espèce prospère sous des conditions écologiques sévères - fortes pentes, sols peu profonds, couverture rocheuse élevée - qui limitent la concurrence. Sa stratégie reproductive est adaptée à la variabilité environnementale : les spores sont libérées au printemps et la germination se produit en fin d'été, généralement dans des microsites créés par des perturbations. L'avortement des sporophytes et la rareté des germinations indiquent des contraintes sur la reproduction sexuée, tandis que la propagation végétative semble efficace. La distribution spatiale est discontinue, probablement déterminée par des facteurs microtopographiques et par le déplacement des diaspores vers l'aval sous l'effet de la gravité et du ruissellement. Ces processus favorisent la recolonisation locale et retardent la succession. Sur le plan de la conservation, la population de Blassac demeure stable malgré l'abandon des pratiques agricoles, grâce aux filtres abiotiques naturels. À l'inverse, Chilhac montre des signes de succession et de compétition, suggérant un éventuel besoin de rétablir un pâturage. La progression d'*Opuntia*, encore limitée, constitue une menace latente. Un suivi continu et une gestion ciblée pourraient être nécessaires pour préserver ces habitats rares d'hépatiques.

Mots-clés
Mannia fragrans
Habitats xériques
Reproduction végétative
Conservation des bryophytes
Perturbation des habitats

Introduction

Mannia fragrans (Balb.) Frye & L. Clark is a well-known robust thalloid liverwort typically restricted to warm, open habitats on calcareous or basic substrates (Müller 1954; Schuster 1992; Damsholt 2002). Its global distribution is Holarctic, with occurrences across temperate regions of Europe, Asia, North America, and Greenland (Hodgetts *et al.* 2020; Schuster 1992; Choi *et al.* 2020). In Europe, the species is mainly concentrated in central and eastern regions, with outposts in Scandinavia and the Alps. Western records are scarce and scattered, often involving small, threatened populations (Clesse & Sotiaux 2015; Jover 2021) (Fig. 1).

Figure 1 - *Mannia fragrans* (Balb.) Frye & L. Clark.

Hock *et al.* (2009) investigated the impact of the polyoicous reproductive system on the genetic structure of *Mannia fragrans* populations. Despite frequent sexual reproduction, genetic diversity was low, likely due to predominant clonal propagation and mating among genetically identical individuals. Rare bisexual and asexual plants showed traits favouring colonization, suggesting selection for reproductive assurance. Occasional recombination and mutation occurred but are limited by large spore size and small, isolated populations. Overall, asexual reproduction appears to play a dominant role in shaping population genetics.

In France, *M. fragrans* is considered as a rare and threatened species, known from a handful of localities in Alsace, the Alps, and the southern Massif central (Frahm & Bick 2013; OpenObs platform [OpenObs is the national portal providing access to public biodiversity observation data in France]). The populations discovered in the Haute-Loire, in the upper Allier valley, are remarkable in several respects. They lie at the westernmost limit of the species' European range, occupy steep basaltic slopes, and comprise several thousand fertile thalli that have been consistently observed for over two decades. This makes them model sites for investigating the species' ecology, reproduction, and long-term viability.

Despite its persistence in the Haute-Loire populations, little is known about the demographic dynamics or microhabitat specificity that sustain such populations. Their isolation, high fertility, and occupation of a structurally extreme environment raise important questions regarding habitat suitability, recruitment processes, and conservation needs. The present study aims to (1) describe the microhabitat and ecological constraints of the upper Allier valley populations, (2) quantify the demography and reproductive effort, and (3) discuss its conservation relevance in light of the species' overall distribution, biology and habitat specificity.

Material and methods

Study sites

The study was carried out in the Haute-Loire department (south-central France) across four basalt-based sites located along the upper Allier River: Blassac, Chilhac, Le Blot, and Saint-Privat-d'Allier. All populations occur on basaltic outcrops forming a common geological substrate. The local climate, however, differs markedly from the standard regional classification. Although broadly situated within the French Massif central, the upper Allier valley is characterised by a sheltered microclimate shaped by strong foehn effects and marked thermal contrasts. This results in a distinctly semi-continental regime, with relatively dry summers, a clear winter precipitation minimum, and warm, sometimes Mediterranean-like episodes during the growing season (Fig. 2). In parallel, elevation gradients introduce a montane influence, especially on exposed upper slopes where annual mean temperatures decrease rapidly with altitude. Together, these factors create a hybrid climatic setting that departs from oceanic expectations and instead shows affinities with the subcontinental to continental climates typical of central and eastern Europe (Antonetti 2006). Such conditions likely play an important ecological role in shaping the microhabitats and bryophyte communities found on these basaltic cliffs and slopes.

The four sites also share a historical context of agropastoral use, with several sectors still subjected to grazing or local agricultural pressure (notably near Chilhac). In contrast, the Falaises du Blot benefit from a protected status (ZNIEFF Type I, Natura 2000).

The sites of Blassac, Chilhac, and Saint-Privat-d'Allier were identified via the OpenObs platform, based on previous observations by V. Hugonnot. The site of the Falaises du Blot was discovered during a field survey targeting *Gagea bohemica* on January 1st, 2025. Within the different populations (Blassac, Chilhac, and Saint-Privat-d'Allier), a classical sigmatist phytosociological survey was carried out to better characterize the vegetation of *Mannia fragrans* sites as well as ecological setting.

Demographic assessment method

Conducting this study required 245 hours of fieldwork. We systematically collected and identified all the bryophytes encountered in the habitat of *Mannia fragrans*. We then ranked the species from most to least abundant based on our observations.

The aim of the general protocol for demographic data collection was to complement the IUCN individual count with a demographic analysis of *Mannia fragrans* (Fig. 3):

- Quantifying areas occupied by *M. fragrans*: to this end, we surveyed pre-identified areas using a mapping system,

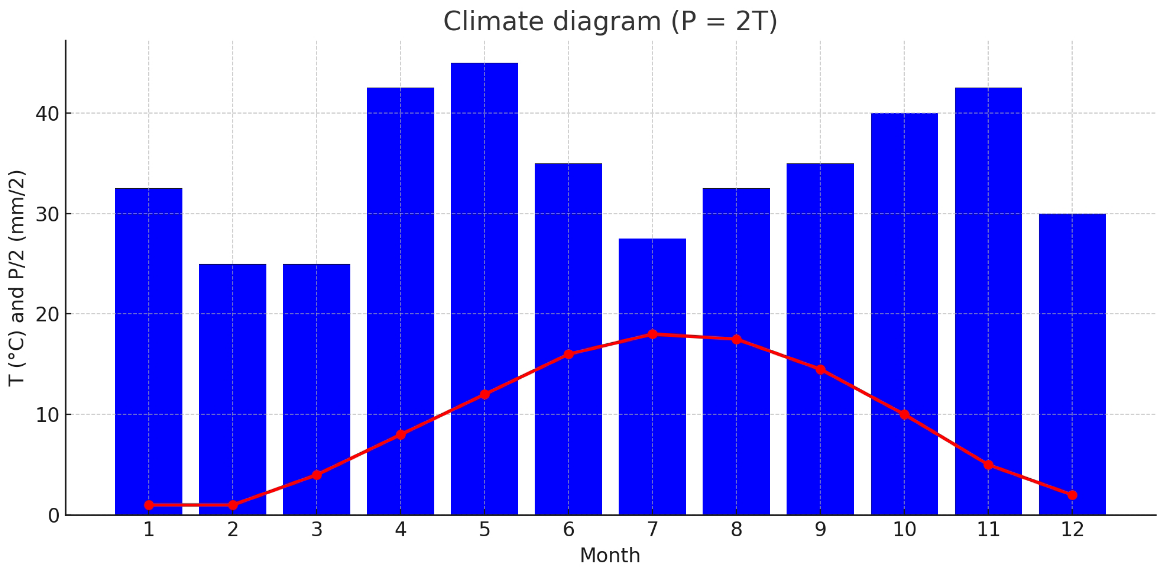

Figure 2 - Ombrothermic diagram of Lavoûte-Chilhac municipality (data from 1991 to 2021).

attempting to delineate the probable extent of occupancy. Starting at the lower part of the zone, we placed a measuring tape (decameter) perpendicular to the slope. The quadrat was then moved along each square meter intersected by the transects wherever *M. fragrans* was observed;

- Quantifying *M. fragrans* cover within occupied quadrats: cover estimation was carried out using our fists as a standard unit, each representing approximately 100 cm², i.e., 1% of a square meter. This method allowed us to calculate the total surface area covered by *M. fragrans*. It also enabled us to determine the number of IUCN individuals, defined as any occurrence of the species within a standardized 1 m² area. These data are exhaustive for the surveyed areas; every thallus of *M. fragrans* was counted, and the survey area was extended whenever new occurrences were found beyond the initially defined limits. Figure 4 illustrates the white markers which were placed to indicate individual IUCN units;

- Quantifying rock surface per square meter of *M. fragrans* presence: concurrently with the abundance survey, while the quadrat was in place, we estimated the percentage of rock cover using the same fist-based method (each fist representing ~100 cm² or 1% of the quadrat). When rock was dominant, we estimated the proportion of soil and subtracted it from 100% to calculate rock cover.

- Comparison of mean densities per altitude range: to improve the reliability of these estimates, outlying or marginal individuals were removed, restricting the analysis to the core population. Accordingly, the dataset includes 741 individuals from Blassac, 171 from Chilhac, and 405 from Saint-Privat. The Falaises du Blot population was omitted due to insufficient sampling and because its altitude does not differ meaningfully from the other sites.

Method for describing ecological and mesological parameters

General protocol for ecological data collection: using a GPS device containing the occurrence area of *Mannia fragrans*, which had been delineated in QGIS following the demographic survey, we classified each sampling point (1 m²) as either a presence point (if located within the mapped occurrence zone) or an absence point (if located outside this zone). A total of 100 sampling points were recorded, including 50 located within the distribution area of *Mannia fragrans* and 50 outside of it on Blassac's, Chilhac's and Saint-Privat d'Allier's population. Each point systematically included the following parameters (Fig. 3):

- Slope and exposure: to obtain accurate and consistent topographic data, we used LIDAR point clouds available from the French National Geographic Institute (IGN) platform. These data were processed into a Digital Terrain Model (DTM), from which slope and aspect were extracted for both demographic and ecological sampling points using spatial analysis tools. This approach ensured a high-resolution and harmonized dataset describing the topographic conditions across all study sites;

- Substrate depth: at each sampling point along the transects, a ruler was vertically inserted into the soil until resistance was encountered. The depth (in cm) was recorded at the point of contact with the mineral substrate, excluding the superficial organic layer;

- Evaluation of the surface covered by bryophytes indicating vegetation closure: only a restricted set of taxa were considered as indicators of hem formation: *Tortella squarrosa* (Brid.) Limpr., *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr, and all pleurocarpous mosses (e.g., *Hypnum cupressiforme* Hedw, *Rhytidium rugosum* (Hedw.) Kindb, etc.). For each sampling point, the surface area covered by these taxa was estimated using the same fist-based method employed for assessing the cover of *Mannia fragrans*, with each fist corresponding to approximately 100 cm²;

- Measurement of vegetation strata: the technique is the same as that used for estimating the surface area of bryophytes indicative of vegetation closure and is applied here to the moss and herbaceous strata.

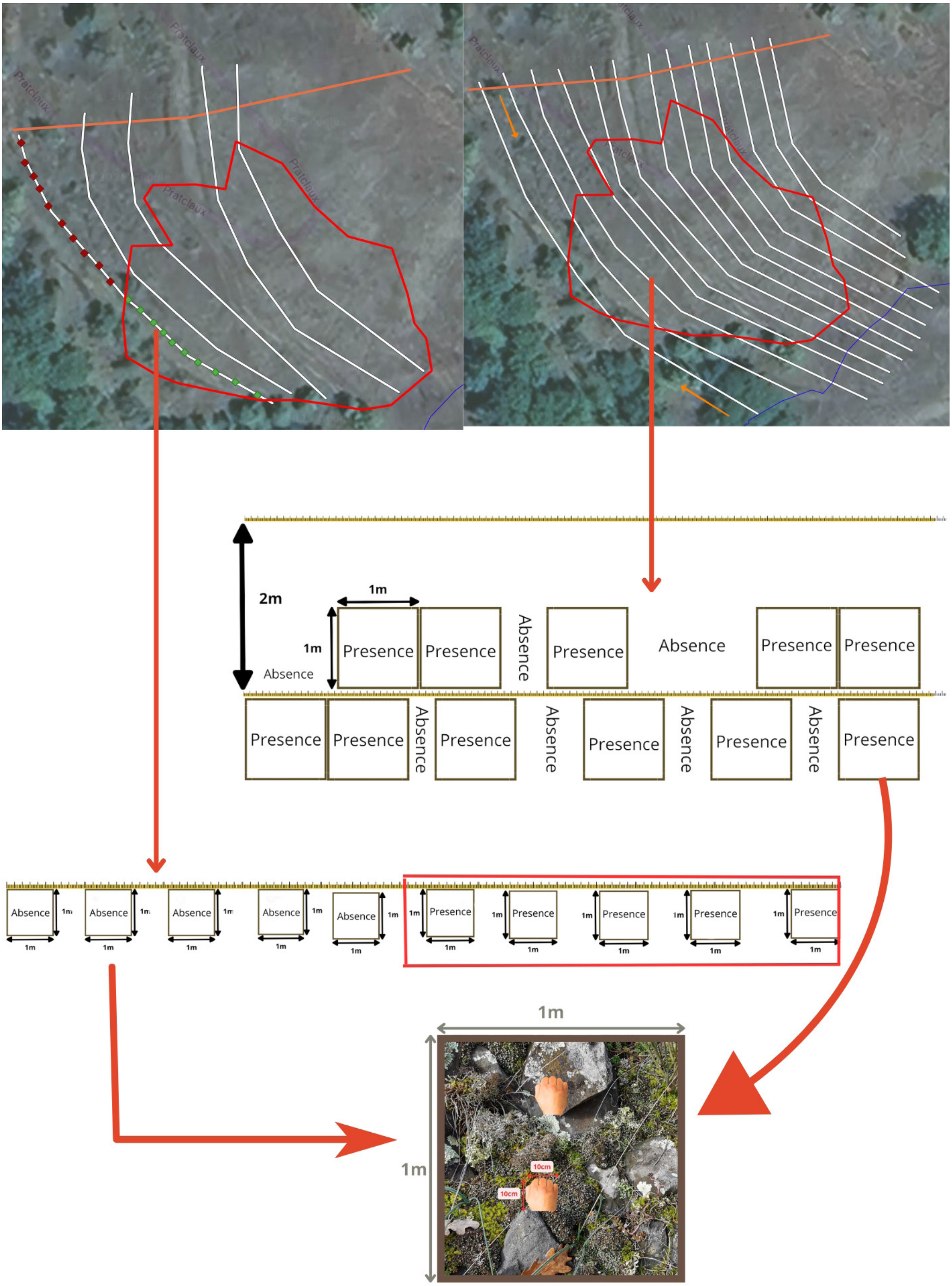

Figure 3 - Method used to collect data on the demography (right) and ecology (left) (ecological sampling locations were positioned at equal distances along the transect to ensure uniform spatial coverage) of *Mannia fragrans*, using the Saint-Privat-d'Allier population as an example.

Counting fertile individuals - Laboratory protocol

Fourteen samples were collected from the central parts of colonies at the Blassac site, which harbours the largest known population. The sampled surfaces ranged from 9 to 25 cm². Each sample was examined under a stereomicroscope. The precise surface area was measured using a ruler, and all apices bearing carpophores were counted. Carpophores were identified by the presence of numerous distinctive hyaline scales. To avoid double counting, each fertile apex was marked with red ink during the observation process. The carpophore density was then calculated as the number of carpophores per cm². Results are expressed as a range, representing the minimum and maximum densities observed across the different samples. We extrapolated the data from Blassac to apply them to the other populations.

Results

We found the same assemblage of bryophytes at all populations, ranked in decreasing order of abundance: *Tortella squarrosa*, *Hedwigia emodica* (Mitt.) H.A. Crum, *Racomitrium canescens* (Hedw.) Brid, *Grimmia laevigata* (Brid.) Brid, *Imbribryum alpinum* (Huds. *ex* With.) J.R. Spence, *Targionia hypophylla* L., *Reboulia hemisphaerica* (L.) Raddi, *Riccia sorocarpa* Bisch., *Weissia controversa* Hedw., *Syntrichia ruralis*, *Rhytidium rugosum*, *Hypnum cupressiforme*, *Riccia ciliifera* Hoffm. The recurrent vascular species (*Sedum album* L., *Prospero autumnale* (L.) Speta, *Festuca arvernensis* Auquier, Kerguélen & Markgr.-Dann, *Logfia minima* (Sm.) Dumort, *Sedum reflexum* L.) in the 3 phytosociological relevés (Table 1) reflect xeric conditions and a rather acidic soil.

The four surveyed sites-Blassac, Saint-Privat-d'Allier, Chilhac, and the Falaises du Blot-exhibit marked variation in surface area, topography, and edaphic conditions (Table 2). *M. fragrans* populations are associated with a wide range of microhabitats, from extreme xeric rocky slopes to more mesic, moderately inclined terrains, south-facing exposure though highest abundance is found in sites combining steep slopes, shallow soils, and high rock cover (Table 2, Fig. 4 & 5).

Blassac presents the largest study area (3,780 m²) and is characterized by a steep mean slope (37.4°) and moderate east-southeast exposure (129°). The site also exhibits high rock cover (mean of 57.8% per m²) and a shallow soil depth (2.15 cm), typical of xeric rocky habitats. Chilhac features a gentler slope (24.9°) and south-facing exposure (197°), with considerably lower rock cover (22.9%) and slightly deeper soils (2.37 cm), potentially indicating a transitional zone between rocky outcrops and more developed grasslands.

The phenology of *Mannia fragrans* shows a predominantly cold-season life cycle (Fig. 6). Germination begins in August, followed by vegetative development - including hyaline scales and mature antheridial cushions - from September to April. Carpophores develop from December, reaching maturity between February and March, with spore release occurring mainly in March.

Table 1 - Phytosociological surveys of the three sites (*= recorded outside the relevé).

Sites	Chilhac	Blassac	St-Privat d'allier
Coordonnates	45,156913 3,428188	45,163903 3,411318	44,9777843 3,6435278
Date	04/08/2025	04/09/2025	04/10/2025
Altitude(m)	508	530	690
Slope(%)	24,9	37	37
Exposition	S-SW	S-SE	S-SW
Area(m²)	50	50	50
Total vegetation cover (%)	77	43	43
Number of taxa	29	26	18
Xeric rocky outcrop			
Anarrhinum bellidifollium L.		r	1
Asplenium ceterach L.	r	r	
Asplenium septentrionale (L.) Hoffm.		2a	
Diantus graniticus Jord.			1
Helianthemum apenninum (L.) Mill.	2		
Saxifraga fragosoi Font Quer		+	3
Saxifraga granulata L.	*		
Sedum album L.	2	2b	2a
Sedum reflexum L.	1	+	+
Xeric grasslands			
Andryala integrifolia L.	2		
Centaurea stoebe L.	1	1	
Crepis sancta (L.) Bornm.	r		
Crucianella angustifolia L.	*		
Dichanthium ischaemum (L.) Roberty	3		
Fetusca arvernensis Auquier, Kerguélen & Markgr.-Dannenb.		2	2b
Genista sagittalis L.		i	
Hypocaeris radicata L.		r	
Logfia minima (Sm.) Dumort.	1	+	r
Muscari comosum (L.) Mill.		2b	
Poa bulbosa L.			+
Potentilla neumanniana Rchb.	2	*	+
Poterium sanguisorba L.	3	+	
Prospero autumnale (L.) Speta	2	2	+
Stachys recta L.	1		
Veronica triphyllos L.			r
Others			
Anisantha sterilis (L.) Nevski	+		
Cardamine hirsuta L.	r		
Centaurium sp.			1
Diantus sp.		r	
Geranium sp.			+
Jacobaea vulgaris Gaertn.	r	i	r
Jacobea sylvatica (Willd.) G.Gaertn., B.Mey. & Scherb.		r	
Lamium purpureum L.	r		
Medicago sp.	2		+
Myosotis arvensis (L.) Hill	+	r	
Myosotis stricta Link ex Roem. & Schult.			r
Rumex acetosella L.			1
Spergularia sp.		i	
Thymus sp.	r	+	1
Trifolium sp.	+		
Veronica persica Poir.	+		
Vicia sp.	r		
Lotus corniculatus L.		*	
Bryophytes			
Tortella squarrosa (Brid.) Limpr.	3	3	+
Mannia fragrans (Balb.) Frye & L. Clark	+	1	r
Imbribryum alpinum (Huds. *ex* With.) J.R.Spence	+	r	
Grimmia laevigata (Huds. *ex* With.) J.R.Spence		r	

Table 2 - Habitat characteristic of the different populations.

Site	Surface of study area (m²)	Mean altitude	Mean exposure (°)	Mean slope (°)	Altitudinal range (m)	Mean rock cover (% per m²)	Mean soil depth (cm)
Blassac	3780	530	129,14	37,36	36,35	57,8	2,154
Saint-Privat-d'Allier	2180	702	214	37	23,53	57	3,23
Chilhac	2792	516	197,15	24,89	12,76	22,88	2,37
Falaises du Blot	122	543	222,75	23,02	3,24	16,25	3

Figure 4 - Field protocol procedure for *Mannia fragrans* on the Blassac population (white dots correspond to IUCN-recorded individuals).

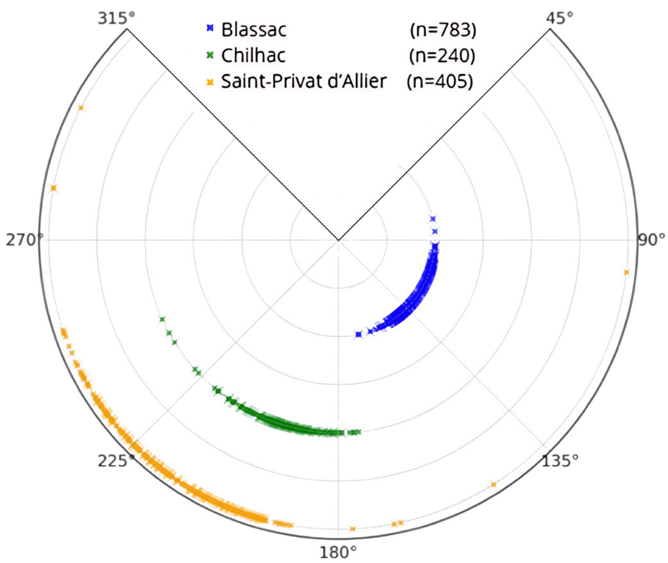

Figure 5 - Exposure of IUCN-assessed *Mannia fragrans* individuals across the 3 study sites.

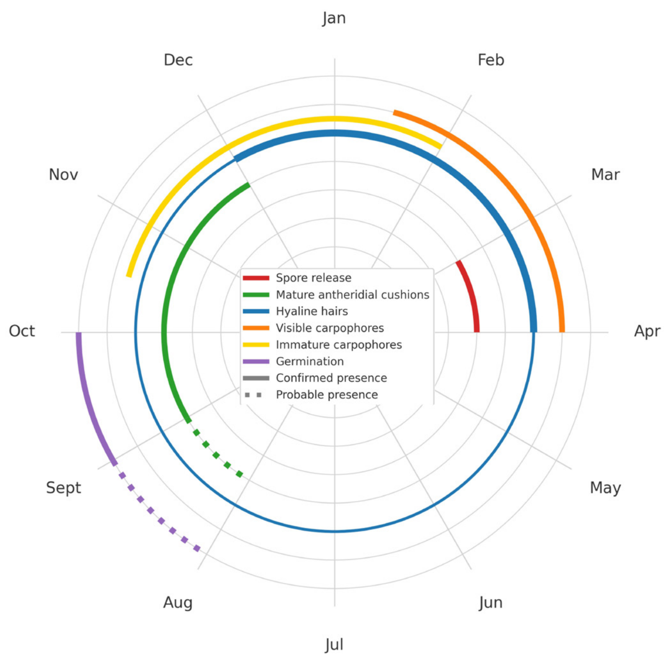

Figure 6 - Phenological calendar of *Mannia fragrans*.

Mannia fragrans exhibits considerable variability in demographic, reproductive, and vegetation cover across the four studied populations (Table 3 and Fig. 7). Blassac shows the highest number of IUCN individuals (784 m² of occupied area) and the most extensive occurrence area (1,101 m²). It also shows the greatest total cover of the species (35.15 m²), the highest mean cover per m² (4.36%), and the maximum local density (21% cover per m²). Reproductively, Blassac supports an estimated 2.7 to 5.1 million potentially fertile individuals, capable of producing between 2.38×10^{10} and 4.46×10^{10} spores-values far exceeding those of other sites.

The results indicate a general trend of decreasing density with increasing altitude across the studied sites. The mean density of *Mannia fragrans* is highest at lower margin of the slope (Fig. 8).

Table 3 - Demographical, ecological and biological results.

Site	Blassac	Chilhac	St Privat d'Allier	Blot
IUCN individuals (m²)	784	240	405	20
Area of occupancy (m²)	1101	379	867	39
Total cover of *M. fragrans* (m²)	35,153	5	9,572	0,589
Mean cover of *M. fragrans* per m² (%)	4,356	2,087	2,36	2,94
Maximum cover of *M. fragrans* per m² (%)	21	9,5	15	9,5
Estimated number of potentially fertile individuals (n)	2,72E+6 - 5,10E+6	4.00E+5 - 7.50E+5	7.66E+5 - 1.44E+6	4,71E+4 - 8,80E+4
Estimated number of potential spores (n)	2,38E+10 - 4,46E+10	3,50E+9 - 6,56E+9	6,70E+9 - 1,26E+10	4,12E+8 - 7,73E+8
Cover of ecotonal bryophytes per 100 m² (P/A)	19,46	47,62	14,37	-
Herbaceous layer cover per 100 m² (P/A)	29,54	28,97	15,02	-
Bryophyte layer cover per 100 m² (P/A)	42,33	78,86	49,71	-

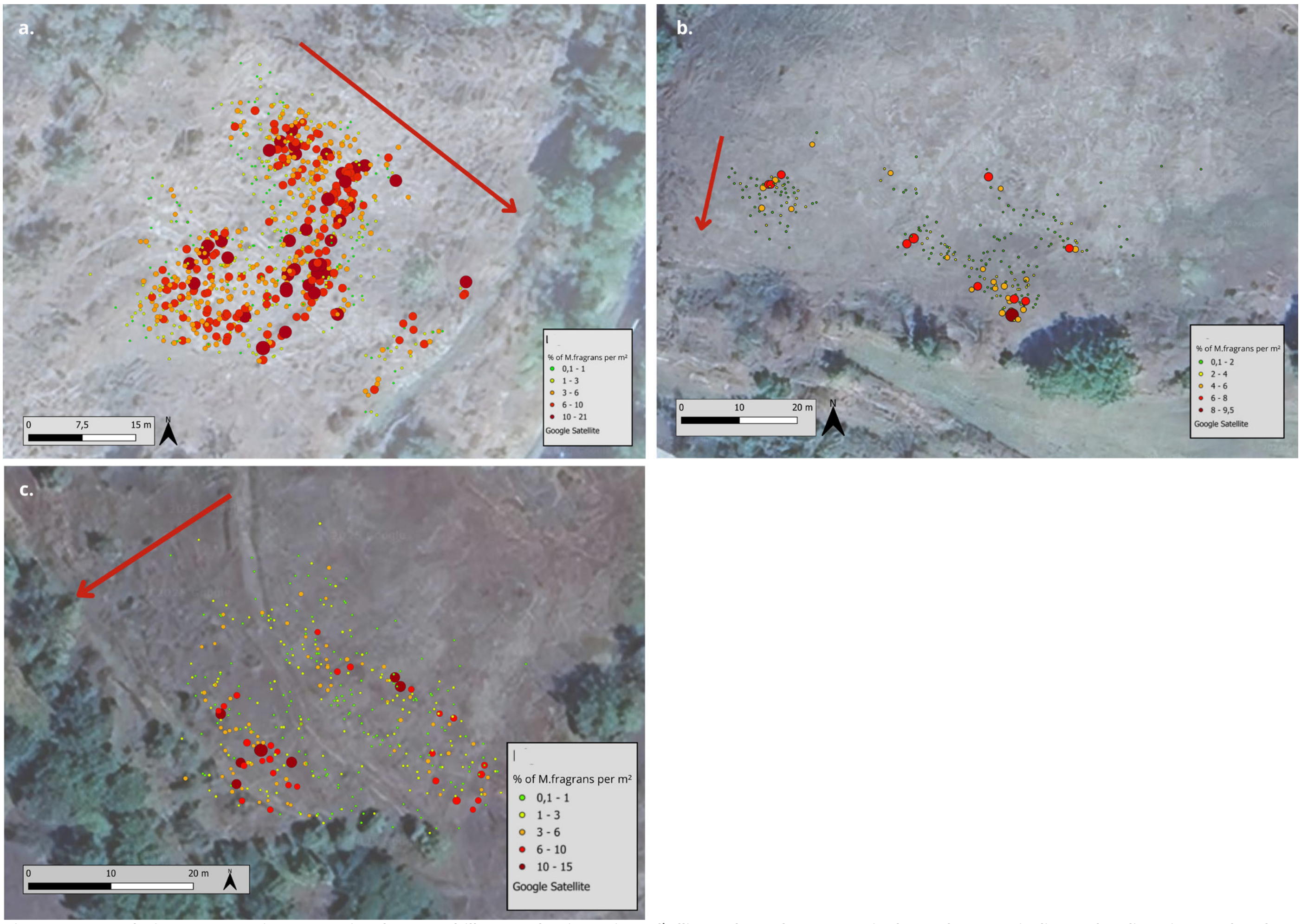

Figure 7 - Populations of *Mannia fragrans* in Blassac, Chilhac, and Saint-Privat-d'Allier, a, b, and c, respectively. Red arrows indicate the direction of the slope (from high to low elevation).

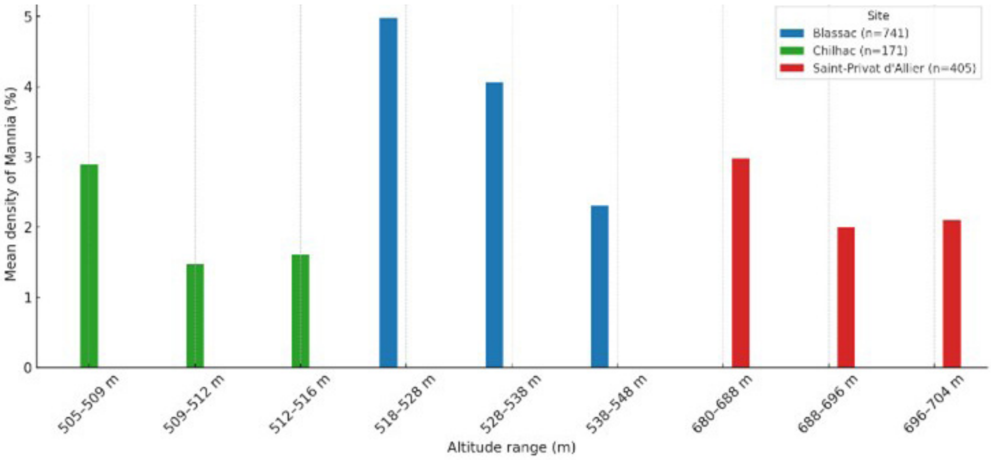

Figure 8 - Comparison of mean densities of *Mannia fragrans* by altitude (n equals the sample size, see methods).

Discussion

Demographic patterns and regional comparisons

Among the studied sites, the *Mannia fragrans* population at Blassac clearly stands out due to its demographic robustness-marked by the highest number of individuals, occupied surface area, and cover. These results contrast with the more moderate values observed at Saint-Privat-d'Allier and Chilhac, and the marginal status of the Falaises du Blot population. Demographic data for *M. fragrans* remain scarce in Europe. In Switzerland, the species is described as locally abundant yet geographically isolated (Meylan 1924). In southern Germany, approximately 60 populations have been reported, all of small to very small size (Meinunger & Schröder 2007). Within the unique Belgium population, 48 micro-populations have been found (Clesses & Sotiaux 2015), while the single population reported in Spain consists of only 10 IUCN individuals and 903 cm^2 of total cover (Jover 2021). In this context, the Haute-Loire populations-particularly at Blassac and Saint-Privat-d'Allier-rank among the most extensive and demographically significant known in Europe, highlighting their potential importance for long-term conservation.

Ecological niche and competitive context

Most known populations in Western Europe occur on substrates derived from calcareous rocks (Belgium, Switzerland, southern Alps); here, the distinctive feature lies in their occurrence on siliceous volcanic rocks. The ecological position of M. fragrans is transitional between saxicolous plant communities and dry grasslands. Neither extreme fully favors its persistence: saxicolous habitats are probably too shallow and harsh, while grasslands generally present excessive competition due to denser vegetation cover. The transition zone offers a narrow but favorable window, combining sufficient soil depth for anchorage with limited competitive pressure. From a phytosociological perspective, the vegetation observed lies at the interface between the *Asplenietea trichomanis* class (chasmophytic species) and the *Koelerio-Corynephoretea canescentis* class (*Sedo albi-Veronicion dillenii* alliance), characteristic of xeric grassland habitats with terricolous species (Thébaud *et al.* 2014). At Chilhac, increased cover of competitive bryophyte species such as *Tortella squarrosa*, *Rhytidium rugosum*, and *Syntrichia ruralis* likely restricts *M. fragrans* development. These species are tolerant and plastic, form dense social stands, and are generally robust or large in size (Hurtado *et al.* 2022). These species contribute to organic matter accumulation and soil formation, favoring successional closure. In addition, in North America, *Centaurea stoebe* L. is considered an invasive species and exhibits a remarkable dynamic behavior in a distinct biogeographical context. Its invasive success has been attributed to both aerial and subterranean expansion strategies (Wilson & Randall 2005; Callaway *et al.* 2011). Although this species is native in France the presence of this highly competitive hemicryptophyte at the study site further supports the hypothesis of competitive exclusion (Fig. 9). Our data suggest that *M. fragrans* thrives under highly selective conditions: steep slopes, shallow soils, high rock cover, and marked dryness. These parameters likely reduce vascular plant colonization and support this poikilohydric liverwort's survival and expansion. Its physiological tolerance to desiccation (Glime 2017; Nebel & Philippi 2005) allows persistence under intermittent water availability.


Figure 9 - Vegetation cover at Chilhac's site.

Reproductive ecology and germination constraints

The reproductive strategy of *M. fragrans* is tightly linked to environmental variability. As evidenced by our phenological observations, spore release occurs predominantly in March, while germination becomes visible from late August or September. This temporal gap likely reflects a dormancy period driven by unfavorable summer conditions.

Field observations show that germination events are rare and mostly restricted to bare soil patches, often created by thallus detachment or local rock movement. These disturbances expose microsites conducive to germination, yet such events remain sporadic given the near-complete vegetation cover observed at all sites. This rarity highlights the importance of canopy openings and bare substrate availability for regeneration.

We also observed numerous cases of sporophyte abortion, which may result from moisture stress or energetic trade-offs. The combination of high spore production, low dispersal efficiency, and patch detachment reinforces the hypothesis that *M. fragrans* primarily relies on short-distance vegetative propagation, while maintaining a limited but significant sexual reproductive potential. This is in line with the results of Hock *et al.* (2009).

Spatial structure and colonization dynamics

Population distribution within each site is heterogeneous, with *M. fragrans* generally restricted to specific zones of rocky outcrops. Two main, non-exclusive hypotheses can explain this asymmetry: 1. Ecological filtering: microtopographic features, such as slope base accumulation zones, cast shadows, and moisture retention pockets, may locally enhance establishment and growth. Gravitational soil and water movement may create more stable hydrological conditions conducive to persistence (Greco *et al.* 2023); 2. Diaspore dynamics: spores and thallus fragments may accumulate downslope through gravity and water runoff. Detached thallus patches can re-anchor further downslope, a mechanism we observed in the field. This process probably contributes to local recolonization and the maintenance of open microhabitats, delaying ecological succession.

Our observations contrast with those from Spain (Jover 2021), where fallen patches are reported to be lost due to limited habitat availability. In contrast, our sites remain large and heterogeneous enough to enable successful re-establishment.

Conservation implications

Mannia fragrans typically occurs in scalded grasslands or rocky outcrops over basaltic or calcareous substrates, habitats often considered secondary formations resulting from historical anthropogenic disturbance. These open environments have long been maintained through extensive pastoral practices, particularly sheep grazing, which prevent ecological succession and maintain low competition habitats (Dutoit 1996; Poschlod *et al.* 2005).

Our study highlights a strong correlation between ecological harshness and population robustness. The Blassac site, among the most restrictive for vascular plants-owing to steep slopes, high rock density, and shallow soils-hosts the densest and most extensive *M. fragrans* population. Despite the abandonment of traditional land use several decades ago (cf. aerial photograph series, Géoportail), no significant vegetation closure has been observed to date, likely due to the extreme edaphic constraints. These findings suggest that in such environments, the absence of active management does not currently threaten *M. fragrans* and that natural abiotic filters suffice to maintain suitable conditions.

In contrast, the situation at Chilhac is more concerning. This site, although less topographically constrained, exhibits clear signs of ecological succession. Bryophyte cover-particularly *Tortella squarrosa*-exceeds 78%, more than twice the levels recorded at other sites. This expansion dramatically reduces the availability of colonizable microsites for *M. fragrans*. Our field observations suggest a potential link between the progressive dominance of *T. squarrosa* and the encroachment of vascular plants. While this correlation remains to be formally tested, it raises the possibility that *T. squarrosa* could serve as an early bioindicator of successional dynamics leading to habitat closure. If this hypothesis proves correct, pastoral management may become a necessary conservation tool. Reintroducing low-intensity grazing could help delay or reverse successional processes, maintaining open microsites favorable to *M. fragrans* and other pioneer bryophytes.

Additional threats to habitat integrity stem from the presence of alien species. At Chilhac, we confirmed the presence of *Opuntia humifusa* × *macrorhiza*, a hybrid cactus previously suspected at this location (Bulot 2007). *Opuntia* species were introduced to France during the Middle Ages and have since spread extensively in the upper Allier valley. In the Blassac's municipality, for example, *Opuntia* established during the 1970s (Fig. 10) and now dominates large areas, displacing native vegetation. Although not currently a threat at our main study site, the potential for further expansion warrants close monitoring.

Figure 10 - Example of *Opuntia*'s invasion on a slope near Blassac's municipality.

References

Antonetti P., Brugel E. & Kessler F., 2006. *Atlas de la flore d'Auvergne*. Éd. Conservatoire botanique national du Massif central, 981 p.

Bulot L.-G., 2007. Les espèces d'*Opuntia* (*Cactaceae*) naturalisées dans la haute-vallée de l'Allier (Haute-Loire). *Digitalis*, **6** : 50-53.

Callaway R.M., Thelen G.C., Rodriguez A. & Holben W.E., 2011. Soil biota and exotic plant invasion. *Nature*, **427**: 731-733. https://doi.org/10.1038/nature02322

Choi S.-S., Bakalin V.A., Park S.J., Sim S.H. & Hyun C.-W., 2020. Unrecorded liverwort species from Korean flora III: New data on the distribution of *Mannia fragrans* (Balb.) Frye & L. Clark. *Korean Journal of Plant Taxonomy*, **50**(2): 227-231. https://doi.org/10.11110/kjpt.2020.50.2.227

Clesse B. & Sotiaux A., 2015. *Mannia fragrans* (*Hepaticae*), espèce nouvelle pour la bryoflore belge à Viroinval (province de Namur). Une remarquable extension de son aire de répartition. *Dumortiera* **107** : 31-34.

Damsholt K., 2002. *Illustrated Flora of Nordic Liverworts and Hornworts*. Oikos Editorial Office, Lund University, Nordic Bryological Society, Lund, 837 p.

Dutoit T., 1996. *Chapitre second. Mécanisme d'une succession végétale secondaire en pelouse calcicole : une approche historique*. Presses universitaires de Rouen et du Havre, 91-108 p. https://doi.org/10.4000/BOOKS.PURH.8094

Frahm J.-P. & Bick F., 2013. *La bryoflore des Vosges et des zones limitrophes*. 3e éd. *Archiv für Bryologie*, **169** : 135.

French National Geographic Institute (IGN). https://geoservices.ign.fr/lidarhd

Géoportail. https://www.geoportail.gouv.fr/

Glime J.M., 2017. *Bryophyte Ecology. Volume 1: Physiological Ecology*. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. https://digitalcommons.mtu.edu/oabooks/4

Greco R., Marino P. & Bogaard T.A., 2023. Recent advancements of landslide hydrology. *WIREs Water*, **10**(6): e1675. https://doi.org/10.1002/wat2.1675

Hock Z., Szövényi P., Schneller J.J., Urmi E. & Toth Z., 2008. Population genetic consequences of the reproductive system in the liverwort *Mannia fragrans*. *Plant Ecology*, **202**: 123-134. https://doi.org/10.1007/s11258-008-9541-8

Hodgetts N.G., Söderström L., Blockeel T.L., Caspari S., Ignatov M.S., Konstantinova N.A., Lockhartg N., Papp B., Schröck C., Sim-Sim M., Bell D., Bell N.E., Blom H.H., Bruggeman-Nannenga M.A., Brugués M., Enroth J., Flatberg K.I., Garilleti R., Hedenäs L., Holyoak D.T., Hugonnot V., Kariyawasam I., Köckinger H., Kučera J., Lara F. & R. D. Porley, 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology*, **42**(1): 1-116. https://doi.org/10.1080/03736687.2019.1694329

Hurtado F., Estébanez B., Aragón P., Hortal J., Molina-Bustamante M. & Medina N.G., 2022. Moss establishment success is determined by the interaction between propagule size and species identity. *Scientific Reports*, **12**: 20777. https://doi.org/10.1038/s41598-022-24354-8

Jover M., 2021. *Seguiment de l'hepàtica Mannia fragrans a la Reserva Natural del Volcà de la Garrinada 2021*. Generalitat de Catalunya, Parc Natural de la Zona Volcànica de la Garrotxa, 22 p.

Meinunger L. & Schröder W., 2007. *Verbreitungsatlas der Moose Deutschlands*. Band 1. Re-gensburgische Botanische Gesellschaft, 2045 p.

Meylan C., 1924. *Les Hépatiques de la Suisse*. Band IV, Heft 1,. Beiträge zur Kryptogamenflora der Schweiz, 318 p.

Müller K., 1954. *Die Lebermoose Europas*. Akademische Verlagsgesellschaft Geest & Portig, Leipzig, 756 p.

Nebel M. & Philippi G., 2005. *Die Moose Baden-Württembergs. Band 3 : Spezieller Teil (Bryophyta, Sphagnopsida, Marchantiophyta, Anthocerotophyta)*. Verlag Eugen Ulmer, Stuttgart, 512 p.

OpenObs, Inventaire National du Patrimoine Naturel (INPN), Muséum National d'Histoire Naturelle (MNHN). https://cat.opidor.fr/index.php/OpenObs

Poschlod P., Bakker J.P. & Kahmen S., 2005. Changing land use and its impact on biodiversity. *Basic and Applied Ecology*, **6**: 93-98. https://doi.org/10.1016/j.baae.2004.12.001

Schuster R.M., 1992. *The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Volume VI*. Field Museum of Natural History, Chicago, 937 p.

Thébaud G., Roux C., Bernard C.-E. & Delcoigne A., 2014. *Guide d'identification des végétations du nord du Massif central : Associations végétales et habitats naturels*. Presses universitaires Blaise Pascal, Clermont-Ferrand, 274 p.

Wilson L.M. & Randall C.B., 2005. Biology and Biological Control of Knapweed. *USDA Forest Service / UNL Faculty Publications*, 113. https://digitalcommons.unl.edu/usdafsfacpub/113