

How ‘alpine’ are nivicolous myxomycetes? A worldwide assessment of altitudinal distribution

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Abstract: Nivicolous myxomycetes constitute an ecologically well defined group of organisms occurring at the edge of melting winter snow cover. They often are considered and described as alpine species, occurring exclusively or most frequently in the alpine belt. We reviewed and synthesized available published data on the altitudinal occurrences of nivicolous myxomycetes in 22 massifs worldwide and attributed the records to main altitudinal belts (montane/subalpine/alpine) defined for particular areas. Based on this comparative analysis we attempted to analyze and discuss general views on the altitudinal/biogeographical properties of nivicolous myxomycetes. Our study indicates that the altitudinal distribution of nivicolous myxomycetes extends over montane, subalpine and alpine belts. The most abundant records were found in the forest (montane) belt, while the alpine belt had the lowest number of occurrences. Although this picture might be biased to some extent by better average exploration of lower areas, it shows clearly that this ecological group—even though connected with mountainous habitats—does not form an alpine element. Therefore they should not be considered alpine species. Based on the available data it also could be hypothesized that nivicolous myxomycetes form a widely distributed biogeographical mountain element instead of an alpine or arctic-alpine element. Based on our conclusions we also emphasize the need for precise and cautious use of the notion of “alpines”, which appears to be confusingly overused in the myxomycete studies.

Key words: alpine ecology, biogeography, distribution patterns, geographical element, slime molds, species altitudinal ranges

INTRODUCTION

Spatial distribution patterns of organisms are shaped by a combination of numerous factors as environmental demands and adaptations, availability of ecological niches, dispersal abilities, history and

others (Gaston 2003). Understanding the biogeographical patterns of various biological groups has a great meaning for unravelling the processes that shape the biodiversity, composition of ecological assemblages and for predicting changes of ecosystems. However, while the biogeography of some taxonomical groups has been extensively studied and analyzed, even basic properties of many others remain hardly known. Myxomycetes (plasmodial slime molds) are phagotrophic eucariotic organisms that commonly occur in associations with decaying plant material in terrestrial ecosystems (Schnittler and Mitchell 2000, Stephenson et al 2008). They belong to kingdom Protozoa (Kirk et al 2001) and represent the class characterized by the highest level of organization within the phylum Myxomycota. One of most spectacular ecological groups of slime molds is formed by nivicolous myxomycetes. They occur often abundantly at the edge of spring-melting snow in mountainous areas. The diversity and taxonomical assessment of this group is a recently well developing field and data from various areas become available (see below). However very little is known on their general biogeographical properties both in terms of geographical occurrence and altitudinal distribution.

Although the first strictly nivicolous species, *Stemonitis cribrarioides* Fr. (currently *Lamproderma cribrarioides* [Fr.] R.E. Fr.) and *Physarum vernum* Sommerf. were described already in the first half of 19th century (Fries 1829), the research focused on nivicolous myxomycetes as an ecologically distinct group was initiated 80 y later (e.g. Meylan 1908, 1914a). Only recently they became a subject of more extensive studies in various regions of the world (e.g. Bozonnet 1984, Meyer 1986, 1987, Bozonnet et al 1991, Novozhilov and Schnittler 1996, Schnittler 1998, Tamayama 2000, Sánchez et al 2002, Moreno et al 2003a, b, Lado 2004, Lado et al 2005, Yajima et al 2006, Stephenson et al 2007, Ronikier and Ronikier 2007, Ronikier et al 2008, Lado and Ronikier 2008). This remarkable group of organisms inspires several basic biogeographical questions concerning their geographical and altitudinal distributions, shaped by specific ecological demands. Nivicolous myxomycetes often are considered and described as alpine species, occurring in the high altitudinal belts of the mountains and exclusively or the most frequently attached to the alpine belt (e.g. Lister 1911, Kowalski 1971, 1972, Mitchell and Chapman 1980, Nannenga-

Bremekamp 1991, Ing 1994, 1998, 1999, 2003, Moreno et al 2002, Stephenson and Shadwick 2005, Stephenson et al 2008). The term “alpine myxomycetes” appeared in literature at the beginning of the 20th century. One of the first to notice the affinity of nivicolous myxomycetes to mountainous environment was Fries (1906), who observed that some species recorded in the mountains of Jamtland were absent in the Swedish lowland. He compared known localities of these species from other regions of Europe and North America and noticed that all of them originated from mountainous elevations; in consequence he proposed a term “alpine myxomycetes” for these species (*Trichia alpina*, *Lepidoderma granuliferum*, *Diderma fallax*). Later on Kowalski (1971) recognized genus *Lepidoderma* as alpine, while Ing (1994) considered three genera, *Lamproderma*, *Lepidoderma* and *Diachoeopsis*, as “essentially alpine”. According to most authors, open high-mountain vegetation, such as alpine and subalpine meadows, represent the typical habitat for nivicolous myxomycetes, which thrive exclusively in such areas of the world (e.g. Moreno et al 2002, Lado 2004). Results of our recent study carried out in a low-altitude massif in the Carpathians (Ronikier et al 2008) indicated a considerable diversity of these species also within the forest belt, which was in accordance with several other studies from lower mountain regions devoid of alpine belt (e.g. Meylan 1908, 1910b, 1924, Tamayama 2000, Müller 2002, Yajima et al 2006). Data concerning the biogeographical and altitudinal distribution of nivicolous myxomycetes are dispersed in literature and to our knowledge no attempt of a comprehensive analysis has been undertaken to investigate the trends in the occurrence of this group. Stephenson et al (2000) in their biogeographical analysis of myxomycetes occurring in northern latitudes included also some records of nivicolous species, but no dedicated syntheses were approached so far. Basic biogeographical properties of nivicolous myxomycetes remain to be examined in a synthetic way to evaluate the existing data and to settle a basis for future focused research. The main aim of our present study therefore is to analyze available literature data with focus on vertical distribution of nivicolous myxomycetes and to verify the altitudinal preferences of this group.

Specific aims of this study are: (i) to verify whether nivicolous myxomycetes are essentially alpine species only occasionally found at lower altitudes; (ii) to test whether all nivicolous myxomycetes exhibit similar altitudinal distribution pattern or could different patterns be recognized; and (iii) to discuss whether nivicolous myxomycetes constitute a clear geographical element.

MATERIALS AND METHODS

Definitions—We define the term “nivicolous myxomycetes” as describing the distinct ecological group of myxomycetes requiring for development of their sporangia specific microenvironmental conditions that can be found under long persisting snow cover, at margins of such snow patches and in places where the snow cover has just disappeared. Due to most likely a specific combination of climatic factors, such as precipitation and temperature regimes, the center of their occurrence is placed in the mountains. Some myxomycetes form sporangia exclusively during the thawing of snow cover and this group of species often is termed “strictly nivicolous”. Several other species may be found both at snowbanks as well as later in the season. Our analysis is focused on the first group of species occurring exclusively in nivicolous locations.

We define the term “alpine species” following Körner (2003) as species restricted to the alpine belt or centered in the alpine belt and occasionally found at lower altitudes. The term “alpine belt” is relatively well defined and fairly uniformly understood worldwide although with some exceptions (e.g. Japanese mention of alpine belt, see Tsukada 1988, Yoshino 1978). It is herein defined following Löve (1970) and Körner (2003) as an area above the natural high altitude tree line and formed by treeless vegetation. Although alpine floras are considerably different in many mountain ranges at various latitudes and thus under various climatic conditions, similar life forms can be found here. This belt is populated by herbaceous and grassy vegetation, cushion and rosette plants, mosses, prostrate dwarf shrubs and ericoid plants (Billings 1973). We apply the term “alpine belt” to all alpine regions of the world, although other terms may be found in the literature, reflecting regional climatic particularities, for instance the terms “crioro-mediterranean” or “alti-mediterranean zone” used in the Mediterranean region (e.g. Quèzel 1981, Rivas-Martínez and Loidi Arregui 1999).

The term “subalpine belt” is much more ambiguous and variously interpreted by authors depending on “where geographically and to which school the discussant belongs” (Löve 1970). We follow the terminology accepted by Löve (1970) and Körner (2003) who define the “subalpine belt” as the forest-tundra ecotone, the transition zone between the upper limit of the closed montane forest and the beginning of the treeless alpine belt. This area usually is covered incoherently by various shrubs and dwarfed trees intermingled with subalpine meadows. Other terms applied for this belt are “Hudsonian zone” in North America (e.g. Jepson 1960) or “oro-mediterranean zone” in the Mediterranean region (e.g. Quèzel 1981, Rivas-Martínez and Loidi Arregui 1999). Some authors (e.g. Favarger 1995a, b, Ozenda 1985) include the zone of closed coniferous forests to the subalpine belt. We prefer to follow Dansereau (1957), Meusel et al (1965), Pawłowski (1969), Löve (1970) and recognize the area covered by closed forest in a montane vegetation belt. This belt is dominated by broad-leaf, mixed or coniferous forest built up of various trees.

Data analysis—Our analysis is based on data from 79 papers (see TABLE I) reporting localities of (strictly) nivicolous

myxomycetes from 22 mountain areas of the world (FIG. 1). Sixty-three such species are included in our analysis. They were selected on the basis of the list of nivicolous myxomycetes provided by Bozonnet et al (1991) and updated according to more recent data (new species described). Only published localities of nivicolous myxomycetes precise enough (i.e. containing name of massif/region and providing information on altitude above sea level) were taken into account for the analysis, therefore the list of species (TABLE I) does not include the full list of species ever reported from these regions but the species for which localities were accompanied by data on altitude or altitudinal ranges (the species taken for the analysis).

Most published localities of nivicolous myxomycetes were not provided with information on particular altitudinal belts or detailed descriptions of habitats. Thus it was necessary to assign the records to their most probable vegetation belts. Based on the literature data we have set the average altitudinal ranges of three main climatic-vegetation belts defined above: forest (montane) belt, subalpine belt and alpine belt, for every massif analyzed (TABLE II). Then we classified every published locality of a nivicolous myxomycete into one of the three climatic-vegetation belts defined for each massif (TABLE II) based exclusively on the altitude or altitudinal range. If the altitude of a given locality of a species was equal with the border value between two altitudinal belts (defined in TABLE II) we classified such a locality to the higher belt.

There is no common definition of a 'collection' or 'specimen' as well as of a single locality, therefore the literature data are often difficult to compare. Some authors provide only one collection per locality and treat other collections from the same population as duplicates, whereas other authors list many collections (with different herbarium numbers) originating from the same population or specimen. Counting these two kinds of records equally would lead to wrong conclusions. In addition in some papers one can find altitude at each sample whereas others list only of a great number of collections with collective altitude ranges for all of them. Therefore, to avoid unequal counting of differently defined collections and repeated counting of the same collection quoted in several publications, the record of a species in a given vegetation belt of a given massif was taken into account as one occurrence, regardless of how many collections and in how many papers the species was reported from this area. Therefore the records taken into account are qualitative and not quantitative data (taking into account the abundance would lead to a strong bias due to unequal data presentation in various papers). Each species may have a maximum three records (occurrences) from one massif: one from forest belt, one from subalpine belt and one from alpine belt. The records prepared as described above have served as a basis for the comparative analysis of the occurrence of nivicolous myxomycetes (percentage share) across the altitudinal belts on the level of (i) species, (ii) massifs and (iii) all records pooled.

Data taken for our analysis originate exclusively from literature and we could not revise the identity of reported species. Therefore we always took the published name of a

given species. The names *Comatricha alpina* and *Lamproderma carestiae* were excluded from the analysis because these species are treated variously in older literature and it was not always possible to verify their identity with certainty. *Lamproderma sauteri* ss. Kowalski (1970) is treated in a wide sense including *L. ovoideum*, therefore localities of this species given by this author were not included in our analysis. When a given specimen was revised by another author who corrected the identification we included it under the corrected name. For instance *Diacheopsis kowalskii* was described by Meyer and Poulain (1998) who revised Kowalski's material published earlier under the name *D. metallica* (Kowalski 1975). Here we included all revised collections under *D. kowalskii* while all other collections of *D. metallica* published by Kowalski (1975) are included by us under *D. metallica*.

We follow the nomenclature by Hernández-Crespo and Lado (2005). Because of several recent taxonomical and nomenclatural changes some species require comments. This treatment is used:

Lamproderma retirugisporum = *L. cribrarioides* ss. auct. pluribus, non Fr. (see Singer et al 2003), non Kowalski (1970)

Lamproderma cribrarioides = *L. atrosporum* var. *pseudocribrarioides* (see Singer et al 2003) = *L. cribrarioides* ss. Kowalski (1970)

Lamproderma carestiae = *L. atrosporum* (see Poulain et al 2003) = *L. cribrarioides* var. *carestiae* (see Sánchez et al 2007) ≠ *L. carestiae* ss. auct. pluribus

RESULTS

The map of included study sites outlines the general known distribution of nivicolous myxomycetes (FIG. 1). The assessment of vertical distribution of 63 nivicolous species resulted in gathering 415 records (occurrences). The analysis revealed that all but one species (recently described *Dianema inconspicuum*) have been reported from the forest belt. Forty-eight species also were found in the subalpine belt, and only 36 species had their localities within the alpine belt (FIG. 2). To eliminate the potential influence of approximate classification of records at the alpine/subalpine ecotone, similar assessment also was performed for the forest belt vs. subalpine plus alpine belts (FIG. 3). This analysis also revealed a lower overall contribution of sites from the two belts above timberline in the distribution of most taxa. Forest sites prevailed in 38 taxa (60%), while only 14 taxa had more occurrences above timberline (subalpine plus alpine belts) and 11 taxa were equally distributed above and below timberline. The tendency of prevalence of forest belt records also was confirmed by an overall analysis of all species/regions data pooled, where more than a half of occurrences (55%) were classified within the forest belt, 31% in the subalpine belt and only 14% in the alpine belt. Of interest, the large contribution of forest belt records

TABLE I. Analyzed records of (strictly) nivicolous myxomycetes from all studied mountain areas

| Species | Mountain massif | | | | | | | | | | | | | | | | | | | | | |
|--|---------------------------------|-------------------------------------|---------------------|----------------------|----------------------------|--------------------|------------------------|-------------------------|-------------------------------------|--------------------------------|---|------------------------------|---|--------------------------------------|-----------------------------------|-------------------------------------|---|-----------------------------|-----------------------------|------------------------------------|--|-------------------------------|
| | Scottish Highlands ¹ | Thuringian Forest ^{2,3,47} | Abisko ⁴ | Khibiny ⁵ | Carpathians ^{6,7} | Pirin ⁸ | Lefka Ori ⁹ | Alps ^{8,10-46} | Sierra Nevada (Spain) ⁴⁷ | Sierra de Gredos ⁴⁸ | Sierra de Guadarrama ^{36,39,41,44,49-52} | Pyrenees ^{49,53-56} | Jura ^{10-13,18,37,36,39,42,44,57-65} | Nordrhein-Westfalen ^{45,66} | Glerárdalur area ^{29,67} | mountains of Hokkaido ⁶⁸ | mountains of Honshu ^{37,42,69} | Southern Alps ⁷⁰ | Olympic ^{41,76-78} | Cascades ^{31,41,71,75-77} | Sierra Nevada (USA) ^{31,41,72-74,76-78} | Rocky Mountains ⁷⁰ |
| <i>Collaria nigricapillitia</i> | | | | | | | | + | + | + | + | | | | | | | | | | | |
| <i>Comatricha fusiformis</i> | | | | | | | | | | | | | | | | | | | | + | | |
| <i>Comatricha pseudoalpina</i> | | | | | | | | | | + | | | | | | | | | | | | |
| <i>Comatricha sinuatocolumellata</i> | | | | | | | | + | | + | | | | | | | | + | + | + | | |
| <i>Comatricha suksdorfii</i> | | | | | | | | | | + | + | + | | | | | | + | + | + | | |
| <i>Diacheopsis effusa</i> | | | | + | | | | | | | | | | | | | | | | | + | + |
| <i>Diacheopsis kowalskii</i> | | | | | | | | + | | + | | | | | | | + | | + | + | + | |
| <i>Diacheopsis metallica</i> | | | | | | | | + | | + | | + | | | | | + | + | + | + | + | |
| <i>Diacheopsis pauxilla</i> | | | | | | | | + | | | | | | | | | | | | | | |
| <i>Diacheopsis reticulospora</i> | | | | | | | | + | | | | | | | | | | | | | | |
| <i>Diacheopsis serpula</i> | | | | | | | | | | | | | | | | | | + | | | | |
| <i>Dianema aggregatum</i> | | | | | | | | | | | | | | | | | | | | | + | |
| <i>Dianema inconspicuum</i> | | | | | | | | + | | | | | | | | | | | | | | |
| <i>Dianema nivale</i> | + | | | | | | | + | | | | + | | | | | + | | | | | |
| <i>Dianema subretisporum</i> | | | | | | | | + | | | | | | | | | | | | | + | + |
| <i>Diderma alpinum</i> | + | + | | | + | + | + | + | + | + | + | + | + | + | | + | + | + | | | + | + |
| <i>Diderma brooksii</i> | | | | | | | | | | | | | | | | | | | | | + | + |
| <i>Diderma globosum var. europaeum</i> | | + | | | + | | | | | | + | | | | | + | + | | | | | |
| <i>Diderma fallax</i> | + | | | | | | | + | | + | + | + | | | | | | | | | | + |
| <i>Diderma meyeræ</i> | | + | | | | | | + | | + | | | | | | | | | | | | |
| <i>Diderma microcarpum</i> | | + | | | | | | + | | | | + | + | | | | | | | | | |
| <i>Diderma niveum</i> | + | + | + | + | + | + | + | + | + | + | + | + | + | + | | | | + | | | | |
| <i>Diderma peyerimhoffii</i> | | | | | | | | + | + | | | + | + | | | | | | | | | |
| <i>Didymium decipiens</i> | | | | | | | | | | | | + | | | | | | | | | | + |
| <i>Didymium nivicolum</i> | + | | | | | | | + | + | | + | | | | | | + | | | | | + |
| <i>Hemitrichia montana</i> | | | | | | | | + | | | | | | | | | | | | | | |
| <i>Hemitrichia montanoides</i> | | | | | | | | + | | | | | | | | | | | | | | |
| <i>Lamproderma acanthosporum</i> | | | | | | | | + | | | | | | | | | | | | | + | |
| <i>Lamproderma aeneum</i> | | | | | + | | | + | | | | + | | | | + | | | | | | |
| <i>Lamproderma cacographicum</i> | | | | | | | | + | | | | | | | + | | | | | | | |
| <i>Lamproderma carestiae</i> | + | + | | | + | | | + | + | + | + | + | + | + | | + | + | + | | + | + | + |
| <i>Lamproderma cribrarioides</i> | | + | | | + | + | | + | + | + | | | | | | | | + | + | + | + | + |
| <i>Lamproderma cristatum</i> | | | | | | | | + | | | | | + | | | | + | | | | | + |
| <i>Lamproderma cucumer</i> | | | | | | | | | | | + | | + | | | | + | | | | | |
| <i>Lamproderma disseminatum</i> | | | | | | | | | | | | | | | | | | | | | | + |
| <i>Lamproderma echinosporum</i> | | + | | | | | | + | + | + | | + | | | | + | + | + | + | + | + | + |
| <i>Lamproderma fuscatum</i> | | | | + | | | | + | | + | | + | | | | | + | + | + | + | + | + |
| <i>Lamproderma maculatum</i> | | | | | | | | + | + | + | + | + | | | | | | | + | + | + | + |
| <i>Lamproderma meyerianum</i> | | | | | | | | + | + | + | + | | | | | + | | | | | | |
| <i>Lamproderma ovoideoechinulatum</i> | | | | | + | | | + | | | | + | | | | + | + | | | | | |

TABLE I. Continued

| Species | Mountain massif | | | | | | | | | | | | | | | | | | | | | | |
|------------------------------------|---------------------------------|--------------------------------------|---------------------|----------------------|----------------------------|--------------------|------------------------|-------------------------|-------------------------------------|--------------------------------|---|------------------------------|---|--------------------------------------|-----------------------------------|-------------------------------------|---|-----------------------------|-----------------------------|------------------------------------|--|-------------------------------|---|
| | Scottish Highlands ¹ | Thuringian Forest ^{2,3,4,7} | Abisko ⁴ | Khibiny ⁵ | Carpathians ^{6,7} | Pirin ⁸ | Lefka Ori ⁹ | Alps ^{8,10-46} | Sierra Nevada (Spain) ⁴⁷ | Sierra de Gredos ⁴⁸ | Sierra de Guadarrama ^{36,39,41,44,49-52} | Pyrenees ^{49,53-56} | Jura ^{10-13,18,37,36,39,42,44,57-65} | Nordrhein-Westfalen ^{45,66} | Glerárdalur area ^{29,67} | mountains of Hokkaido ⁶⁸ | mountains of Honshu ^{37,42,69} | Southern Alps ⁷⁰ | Olympic ^{41,76-78} | Cascades ^{31,41,71,75-77} | Sierra Nevada (USA) ^{31,41,72-74,76-78} | Rocky Mountains ⁷⁹ | |
| <i>Lamproderma ovoideum</i> | | + | | | + | | | + | + | + | + | | | | | + | + | + | | | | | |
| <i>Lamproderma piriforme</i> | | | | | | | | | | | | | + | | | + | | | | | | | |
| <i>Lamproderma pseudomaculatum</i> | | | | | | | | + | | | | | | | | | + | | | | | | |
| <i>Lamproderma pulchellum</i> | | + | | | | | | + | | | | | | | | | | | | | | | |
| <i>Lamproderma pulveratum</i> | | | | | + | | | + | | | + | | | + | | | | | | | | | |
| <i>Lamproderma retirugisporum</i> | + | | | | | | | + | | + | + | | + | | | | | | | | | | |
| <i>Lamproderma sauteri</i> | | | + | + | + | | | + | + | + | + | + | + | | | | + | + | | | | | |
| <i>Lamproderma spinulosporum</i> | | | | | + | | | + | | | | | | | | | | | | | | | |
| <i>Lamproderma splendens</i> | | + | | | | | | + | | + | | | + | | | | + | + | + | + | + | + | + |
| <i>Lamproderma zonatum</i> | | | | | | | | + | | | | | + | | | | + | | | | | | |
| <i>Lepidoderma alpestroides</i> | | | | | | | | + | | | | | | | | + | | | | | | | |
| <i>Lepidoderma aggregatum</i> | + | + | | + | + | | | + | | | + | | | | | | | | + | + | | | |
| <i>Lepidoderma caestianum</i> | + | + | | | | | | + | | + | | + | + | | | | + | + | + | + | + | + | + |
| <i>Lepidoderma chailletii</i> | | | | | + | | | + | + | + | + | + | | | | | + | | | + | + | | + |
| <i>Lepidoderma crustaceum</i> | | | | | | | + | | | | | | | | | | + | | + | + | | + | + |
| <i>Lepidoderma granuliferum</i> | | | | + | | | | + | + | + | | | | | | + | + | + | + | + | + | + | + |
| <i>Lepidoderma perforarum</i> | | | | | | | + | | | | | | | | | | | | | | | | |
| <i>Physarum albescens</i> | + | | | | + | | | + | + | + | + | + | | | | + | + | + | | | | | + |
| <i>Physarum alpestre</i> | | | | | + | | | + | | + | + | + | + | | | + | + | + | | | | | |
| <i>Physarum alpinum</i> | | | + | | | | | + | + | | + | | + | | | | | + | | | | | + |
| <i>Physarum vernum</i> | | + | | | + | | | + | + | | + | + | + | | | | | | | | | | |
| <i>Trichia alpina</i> | | + | | + | + | | | + | | + | + | + | + | + | | | + | | | | | | + |
| <i>Trichia sordida</i> | | | | | | | | + | | + | + | + | | | | | | | | | | | |
| TOTAL: | 10 | 15 | 3 | 7 | 17 | 3 | 2 | 48 | 14 | 16 | 27 | 19 | 26 | 5 | 1 | 15 | 25 | 11 | 10 | 15 | 18 | 16 | |

¹Ing (1998), ²Schnittler (1998), ³Müller (2002), ⁴Schinner (1983), ⁵Novozhilov and Schnittler (1996), ⁶Wichanský (1962), ⁷Ronikier et al (2008), ⁸Ronikier and Ronikier (2007), ⁹Schnittler and Novozhilov (1999), ¹⁰Meylan (1921), ¹¹Meylan (1925), ¹²Meylan (1929), ¹³Meylan (1931), ¹⁴Meylan (1937), ¹⁵Poelt (1956), ¹⁶Döbbeler and Remler (1976), ¹⁷Schinner (1982), ¹⁸Mitchel et al (1986), ¹⁹Bozonnet (1984), ²⁰Meyer (1986), ²¹Neubert et al (1989), ²²Meyer and Poulain (1990), ²³Bozonnet et al (1990), ²⁴Bozonnet et al (1991), ²⁵Neubert et al (1993), ²⁶Meyer et al (1994), ²⁷Bozonnet et al (1995), ²⁸Neubert et al (1995), ²⁹Bozonnet et al (1997), ³⁰Castillo et al (1997), ³¹Meyer and Poulain (1998), ³²Neubert et al (2000), ³³Poulain et al (2000), ³⁴Singer et al (2001a), ³⁵Singer et al (2001b), ³⁶Moreno et al (2002), ³⁷Poulain et al (2002a), ³⁸Poulain et al (2002c), ³⁹Moreno et al (2003b), ⁴⁰Poulain et al (2003), ⁴¹Moreno et al (2004), ⁴²Poulain and Meyer (2005), ⁴³Kuhnt (2006), ⁴⁴Moreno et al (2006), ⁴⁵Kuhnt (2007), ⁴⁶Poulain and Meyer (2007), ⁴⁷Moreno et al (2003a), ⁴⁸Lado et al (2005), ⁴⁹Lado (1992), ⁵⁰Illana et al (1993), ⁵¹Sánchez et al (2002), ⁵²Sánchez et al (2007), ⁵³Gràcia (1986), ⁵⁴Gorris et al (1999), ⁵⁵Garcia-Porta and Llimona (2005), ⁵⁶Lado and Ronikier (2008), ⁵⁷Meylan (1908), ⁵⁸Meylan (1910a), ⁵⁹Meylan (1910b), ⁶⁰Meylan (1913), ⁶¹Meylan (1914b), ⁶²Meylan (1924), ⁶³Meylan (1927), ⁶⁴Meylan (1930), ⁶⁵Meylan (1935), ⁶⁶Kriegelsteiner (2000), ⁶⁷Göttsche (1984), ⁶⁸Yajima et al (2006), ⁶⁹Tamayama (2000), ⁷⁰Stephenson and Johnston (2003), ⁷¹Kowalski (1966), ⁷²Kowalski (1967a), ⁷³Kowalski (1967b), ⁷⁴Kowalski (1968a), ⁷⁵Kowalski (1968b), ⁷⁶Kowalski (1970), ⁷⁷Kowalski (1971), ⁷⁸Kowalski (1975), ⁷⁹Mitchel and Chapman (1980).



FIG. 1. Sites included in the comparative analysis of altitudinal distribution of nivicolous myxomycetes (numbers refer to TABLE II).

was observed not only in lower altitude mountain ranges but also in several high mountains where the alpine belt covers wide areas (Alps, American Sierra Nevada, Cascades, Rocky Mountains; FIG. 4).

The mountain regions included in the analysis differed largely with respect to the amount of data available. The number of species reported in particular areas varied from one to 48 (TABLE I), depending mainly on the degree and scale of scientific exploration. The highest number of species has been published so far for the European Alps, which represent the area where the nivicolous myxomycetes have been the most regularly studied for past 100 y. It can be assumed that the body of data available for the Alps reflects most reliably the distribution of nivicolous myxomycetes because it suffers the least from random and accidental character of observations. Moreover these mountains encompass all altitudinal belts including extensive areas of well developed alpine belt. We therefore performed a separate analysis for the Alps. This analysis showed a slightly altered proportion of altitudinal occurrences with higher contribution of the alpine belt. However still the highest number of records, amounting to 42%, originated from the forest belt. Subalpine and alpine belts had similar number of records (29% each).

DISCUSSION

Are nivicolous myxomycetes alpine species?—The term “alpine myxomycetes” has been applied commonly in the literature (see INTRODUCTION). It probably was introduced by Fries (1906) who noticed that all localities of some nivicolous species originated from high mountain elevations. It seems however that Fries (1906) either did not analyze details of the altitudinal distribution, because he quoted a locality from 5800 ft. a.s.l. (1770 m), below the alpine belt of the Alps, or used the term “alpine” in a wide sense not fitting its ecological meaning. Such an ambiguous terminology is common. For instance Ing (1998) in his paper titled *Alpine Myxomycetes in Scotland* states that nivicolous species occur in montane (forest) belt in Central Europe. Similarly Mitchell and Chapman (1980) write: “Most of our collections has been done in the montane and subalpine life zones of the mountains of central Colorado...” while at *Physarum albescens* they make a note: “This alpine, ‘snowbank’ slime mold...” Thus the term “alpine” often seems to be used automatically as synonymous with “nivicolous”.

Of note, the first extensive studies focused on nivicolous myxomycetes (e.g. Meylan 1908, 1910b,

1924) were carried out mainly in the Swiss Jura Mountains devoid of climatic subalpine/alpine habitats. The incorrect ecological definition of the group already has been pointed out by Tamayama (2000) in his analysis of Japanese records. Similarly Buyck (1982) reporting locality of *Diderma niveum* from the hills of Ardennes noticed that his finding contradicted the usual statement that this species was “considered to be confined to alpine regions.” Accidental findings in the lowland of the St Petersburg region (Novozhilov 1986) suggest that conditions necessary for persistence and development of nivicolous myxomycetes may occur exceptionally even outside mountain areas. Our comparative analysis providing a systematic overview of altitudinal occurrences of nivicolous species allows a first general assessment. Almost all species of nivicolous myxomycetes have been recorded within the forest belt, which clearly confirms the regional observations from lower elevation mountain areas (e.g. Tamayama 2000, Ronikier et al 2008). Although the present paper is based on analysis of altitudes only and aspect of specific microhabitats is not addressed here, it should be emphasized that the occurrence of nivicolous species in the forest belt is not driven by presence of anthropogenically induced open areas but that such species also can occur abundantly inside forest and among shrubs (Ronikier et al 2008, A. Ronikier and M. Ronikier unpubl data). Moreover forest belt records prevail over higher mountain occurrences in the majority of species (FIGS. 2, 3). Because the subalpine belt often is not covered extensively by shrubs or krummholz trees wide treeless areas may be present there. Therefore it sometimes is difficult to recognize the subalpine/alpine border in the field. Due to pastoral culture present on many massifs the tree line sometimes may be lowered considerably (e.g. in the Scottish Highlands [Poore and McVean 1951]). In such cases treeless vegetation covers directly an area up from timberline, serving physiographically similar sites for nivicolous myxomycetes. However even considering this, when comparing the presence of nivicolous species in the forested vs. joint subalpine/alpine belt, only 14 species (22%) had more records above timberline (FIG. 3).

Taking into account this evidence, we conclude that nivicolous myxomycetes should not be considered alpine or even most frequently attached to the alpine or subalpine mountains. Even though a collecting bias favoring lower belts may be suspected for many areas, it is not likely to change the general conclusion, as indirectly confirmed by a high share of forest records in the best studied range of the European Alps. Although data suggesting that the

ecological group of myxomycetes connected to melting snow can be found outside alpine environments were regularly reported (as reviewed above), a general evidence and the need for precision in ecological definition, especially in use of the strictly defined term of “alpine” environment, never has been explicitly discussed so far. We aim to emphasize particularly that this precision is indispensable to grasp properly the genuine ecological properties of nivicolous myxomycetes in future studies.

Are altitudinal preferences of nivicolous species diversified?—As concluded above nivicolous slime molds as a whole group should not be considered attached to alpine environments. However interesting questions are whether some species might have a more pronounced preference for open areas and higher elevations and especially whether a group of species occurring exclusively in the alpine belt exists. Our analysis demonstrates that only one of the nivicolous species was recorded exclusively in alpine or subalpine/alpine belts (the exception is *Dianema inconspicuum*, known so far from a single site in the subalpine area). However two species, namely *Didymium nivicolum* and *Lamproderma cacographicum*, have more records in the alpine belt than in the forest belt and *Collaria nigricapillitia* has more records in the subalpine belt than in the forest belt (FIG. 2). In addition the following species have more records above timberline (in subalpine plus alpine belt) than in the forest belt (FIG. 3): they are *Diacheopsis pauxilla*, *Diderma fallax*, *Diderma niveum*, *Lamproderma retirugisporum*, *Lamproderma sauteri*, *Lepidoderma granuliferum*, *Lepidoderma perforatum*, *Physarum albescens*, *Physarum alpinum* and *Trichia sordida*. It would be premature to claim that these patterns reflect ecological preferences for higher elevations (especially for species with few records). However it should be noted that these species (apart from *Diderma niveum* and *Physarum albescens*) have no records in most lower altitude massifs (TABLE I), and eight of them, *Collaria nigricapillitia*, *Dianema inconspicuum*, *Diacheopsis pauxilla*, *Didymium nivicolum*, *Lamproderma cacographicum*, *Lepidoderma granuliferum*, *Lepidoderma perforatum* and *Trichia sordida* never have been recorded in low altitude massifs without subalpine and alpine belts included in the analysis. It may be hypothesized that in such species the distribution of populations might be centered above timberline and these populations also could serve as source for downshifted occurrences in the forest belt, while no stable populations could persist in low altitude mountains.

Ing (1998) distinguished four groups of species occurring in different elevations in the Scottish

TABLE II. Altitudinal ranges of vegetation belts of all massifs included in the comparative analysis of altitudinal records in nivicolous myxomycetes

| No | Site (massif) | Location | Average altitudinal ranges of vegetation belts | | | Maximum elevation | Literature source |
|----|-----------------------|--|--|--|--|-------------------|---|
| | | | forest belt | subalpine belt | alpine belt | | |
| 1 | Scottish Highlands | Europe: United Kingdom | up to 640 m ^a | 640—1200 m | above 1200 m | 1344 m | Poore and McVean (1957), Pears (1968) |
| 2 | Thuringian Forest | Europe: Germany | up to top | — | — | 982 m | Schlüter (1964) |
| 3 | Abisko | Europe: Sweden | up to 600 m | 600—1000 m | above 1000 m | 1365 m | Carlsson et al (1999) |
| 4 | Khibiny | Europe: Russia | up to 400 m | 400—500 m | above 500 m | 1191 m | Novozhilov and Schnittler (1996) |
| 5 | Carpathians | Europe: Poland, Romania, Slovakia, Ukraine, | up to 1500 m | 1500—1800 m | above 1800 m | 2663 m | Mirek and Piękoś-Mirkowa 1992 |
| 6 | Pirin | Europe: Bulgaria | up to 2000 m | 2000—2300 m | above 2300 m | 2914 m | Simon (1958) |
| 7 | Lefka Ori | Europe: Greece | S-facing slopes: up to 1600 m N-facing slopes: up to 1750 m | S-facing slopes: above 1600 m N-facing slopes: above 1750 m | above 1600 m | 2453 m | Vogiatzakis et al (2003) |
| 8 | Alps | Europe: Austria, France, Germany, Italy, Switzerland | Central/W Alps: up to 1800 m E Alps: up to 1800 m | Central/W Alps: 1800—2000 m E Alps: 1800—1950 m | Central/W Alps: above 2000 m E Alps: above 1950 m | 4808 m | Ozenda (1985), Favarger (1995a, b) |
| 9 | Sierra Nevada | Europe: Spain | up to 1900 m | 1900—2800 m | above 2800 m | 3479 m | Molero Mesa (1999), Villalobos Megía (2001) |
| 10 | Sierra de Gredos | Europe: Spain | up to 1800 m | 1800—2300 m | above 2300 m | 2592 m | Luceño Garcés (1998) |
| 11 | Sierra de Guadarrama | Europe: Spain | up to 2000 m | 2000—2400 m | above 2400 m | 2428 m | Rivas-Martínez et al (1999) |
| 12 | Pyrenees | Europe: Andorra, France, Spain | up to 1800 m | 1800—2400 m | above 2400 m | 3404 m | Ozenda (1985), Lévy (1999) |
| 13 | Jura | Europe: France, Switzerland | up to top | — | — | 1723 m | Favarger (1995b) |
| 14 | Nordrhein-Westfalen | Europe: Germany | up to top | — | — | 843 m | Walter (1985) |
| 15 | Glerárdalur area | Europe: Northern Iceland | — | — | the whole area ^b | 1538 m | Walter (1985) |
| 16 | Mountains of Hokkaido | Asia: Japan | up to 1500 | above 1500 | — | 1365 m | Tsukada (1988), Wardle (1977) |
| 17 | Mountains of Honshu | Asia: Japan | Central Honshu: up to 2500 m N-E Honshu: up to 2000 m | Central Honshu: above 2500 m N-E Honshu: above 2000 m | — ^c | 3192 m | Tsukada (1988), Wardle (1977), Yoshino (1978) |

TABLE II. Continued

| No | Site (massif) | Location | Average altitudinal ranges of vegetation belts | | | Maximum elevation | Literature source |
|----|-----------------|--------------------------------------|---|---|--|-------------------|---|
| | | | forest belt | subalpine belt | alpine belt | | |
| 18 | Southern Alps | New Zealand: South Island | at latitude 41°S: up to 1200 m at latitude 45°S: up to 900 m | at latitude 41°S: 1200—1500 m at latitude 45°S: 900—1200 m | at latitude 41°S: above 1500 m at latitude 45°S: above 1200 m | 3754 m | Wardle (1965, 1973), Kuschel (1975) |
| 19 | Olympic | North America: United States | up to 1800 m | 1800—2000 m | above 2000 m | 2427 m | Fonda and Bliss (1969), Kuramoto and Bliss (1970) |
| 20 | Cascades | North America: Canada, United States | N Cascades: up to 1800 m S Cascades: up to 2400 m | N Cascades: 1800—2300 m S Cascades: 2400—2900 m | N Cascades: above 2300 m S Cascades: above 2900 m | 4392 m | Munz and Keck (1959), Abrams (1968), Douglas (1972) |
| 21 | Sierra Nevada | North America: United States | up to 2900 m | 2900—3200 m | above 3200 m | 4421 m | Munz and Keck (1959), Abrams (1968) |
| 22 | Rocky Mountains | North America: Canada, United States | Colorado: up to 2700 m | Colorado: 2700—3350 m | Colorado: above 3350 m | 4399 m | Weber (1972) |

^aThe upper limit of the forest belt (640 m) is the altitude of the highest natural forest limit (pine) defined by Poore and McVean (1957). The subalpine belt is a belt laying above the natural forest limit up to the upper limit of the lower alpine belt defined by Poore and McVean (1957). We include the lower alpine belt described by Poore and McVean (1957) into the subalpine belt, because the vegetation of this belt is composed of shrubs.

^bThe area of northern Iceland lays within arctic zone (Walter 1985) and it is treated as equivalent to the alpine belt of the mountains.

^cIn Japan the alpine belt is defined as an area including belts dominated by *Pinus pumila* (Tsukada 1988, Yoshino 1978) which according to definitions used by us belong to the subalpine belt. True alpine = treeless vegetation above shrubland belt is almost absent in Japan except the highest elevations of Mt. Fuji (Wardle 1977). There are no records of nivicolous myxomycetes from Mt. Fuji in our analysis

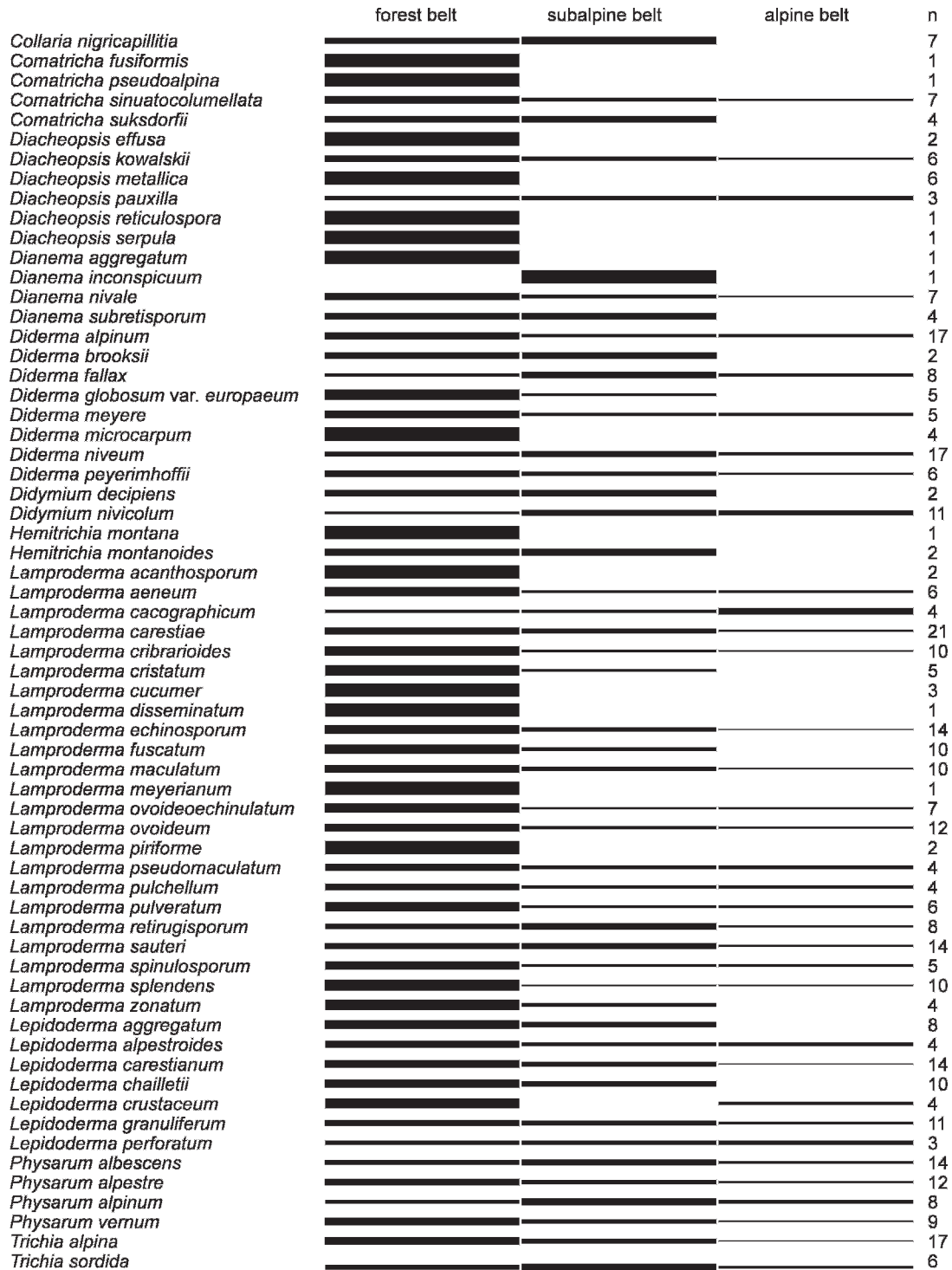


FIG. 2. Altitudinal distribution of 63 nivicolous species in three main vegetation belts (forest, subalpine, alpine). Thickness of bar represents the percentage share of a species records in the given belt. Numbers of records considered for each species are given in the right column (n); one record = occurrence in one belt of one massif. (See text for details.)

Highlands. In the highest areas *Diderma niveum* and *Diderma fallax* were found. In the Spanish mountains (Lado 2004) the group preferring the highest situations was composed of these species: *Diderma fallax*, *D. peyerimhoffii*, *Physarum vernum* and some

species of *Lamproderma*. *Diderma fallax* was mentioned by both authors as a species occurring in the highest elevations. Our analysis also confirms the preference of this species for higher mountain elevations (FIG. 3).

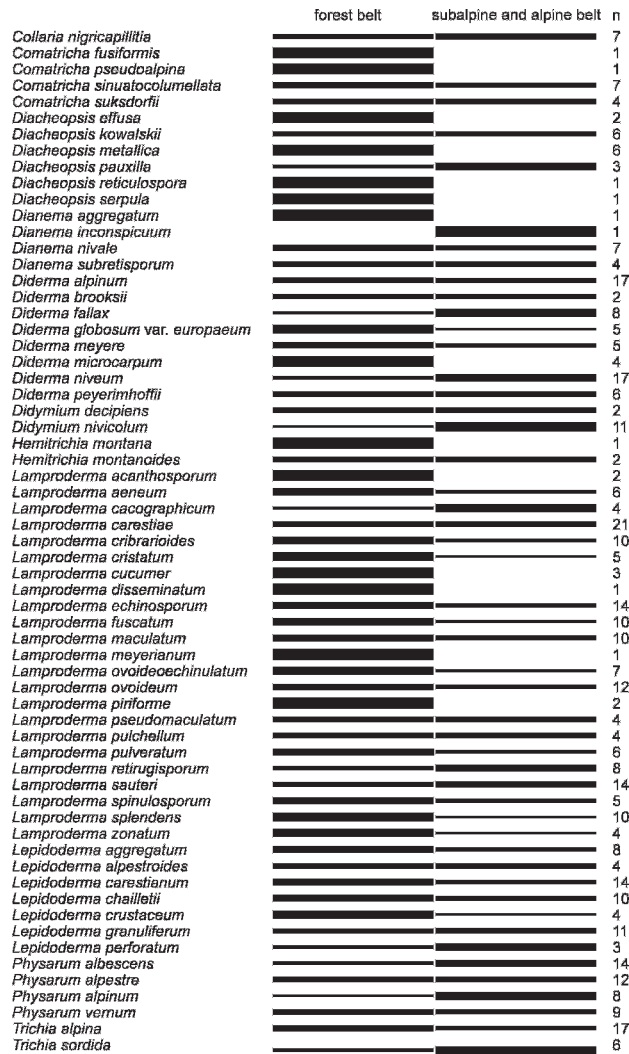


FIG. 3. Altitudinal distribution of 63 nivicolous species below and above timberline (in forest vs. subalpine plus alpine). Thickness of bar represents the percentage share of a species records in the given belt. Numbers of records considered for each species are given in the right column (n); one record = occurrence in one belt of one massif. (See text for details.)

Some attempts toward understanding the ecological preferences of nivicolous myxomycetes already have been done. Many factors influence their appearance and development. Already Meylan (1932) observed the importance of long winters with continuous snow cover preceding spring. Schinner (1982) emphasized the importance of these elements: (i) low temperatures at freezing point for induction of spore germination and/or fructification, (ii) fluctuation of stress factors (frost, warmth, draught, moist), (iii) long state of repose at low temperatures under snow and (iv) high concentration of water in substrate during vegetative stage. Novozhilov and Schnittler (1996) supplemented Schinner's (1982)

observations with these habitat requirements: (i) open areas, (ii) thick layer of herbaceous plant refuse, (iii) heavy snow cover in winter. Lado (2004) measured the air at nivicolous locations and noticed that the temperature at ground level was relatively high (about 20 C) and suitable for myxomycete development. He also pointed out the importance of buffer role of snow cover protecting developing plasmodia from temperatures below 0 C. Novozhilov and Schnittler (1996) based on the observations from the Khibiny Mountains (Kola Peninsula) recognized two ecological subgroups of "cryophilous-nivicole litter myxomycetes" on account of phenology and habitat requirements. The first subgroup of "true nivicole" species connected to open places counts *Diacheopsis effusa*, *Diderma niveum* and the *Lepidoderma* and *Lamproderma* species (with the exception of *L. sauteri*), whereas the second subgroup of "cryophilous species" comprises the myxomycetes growing in summer, under cool and wet conditions, on litter, especially in shady woodland. Apart from some nonnivicolous species the authors put here *Lamproderma sauteri* and *Trichia alpina*.

It seems therefore that the altitudinal distribution patterns might be diversified among nivicolous myxomycetes. Only comparative analysis of extensive datasets from altitudinal gradients from alpine to low mountain areas in comparable climatic regions, e.g. within the temperate European mountains, together with ecological observations further could help to seize more rigorously potential altitudinal and ecological preferences of nivicolous species.

Do nivicolous myxomycetes form an arctic-alpine geographical element?—When discussing the mountain character of nivicolous myxomycetes, it seems additionally useful to bring up the question of potential geographical element formed by this group. Ing (1994) discussed similarity between alpine regions of European and America and the Arctic, not only in occurrence of particular species of myxomycetes but also in species composition. Based on comparison of results from various alpine and Arctic regions he proposed a distinction of a group of "alpine and polar myxomycetes". However the basis for it seems to be moderately supported because in most works cited by this author information on only a few species in common can be found. Also Singer et al (2005) state that nivicolous species "can be found only in high mountain areas or within northern latitudes." Data available from high latitude regions however demonstrate that myxomycetes occurring in the arctic/subarctic situations have little in common with those found in the alpine locations. As already noted by Gøtzsche (1989) species diversity

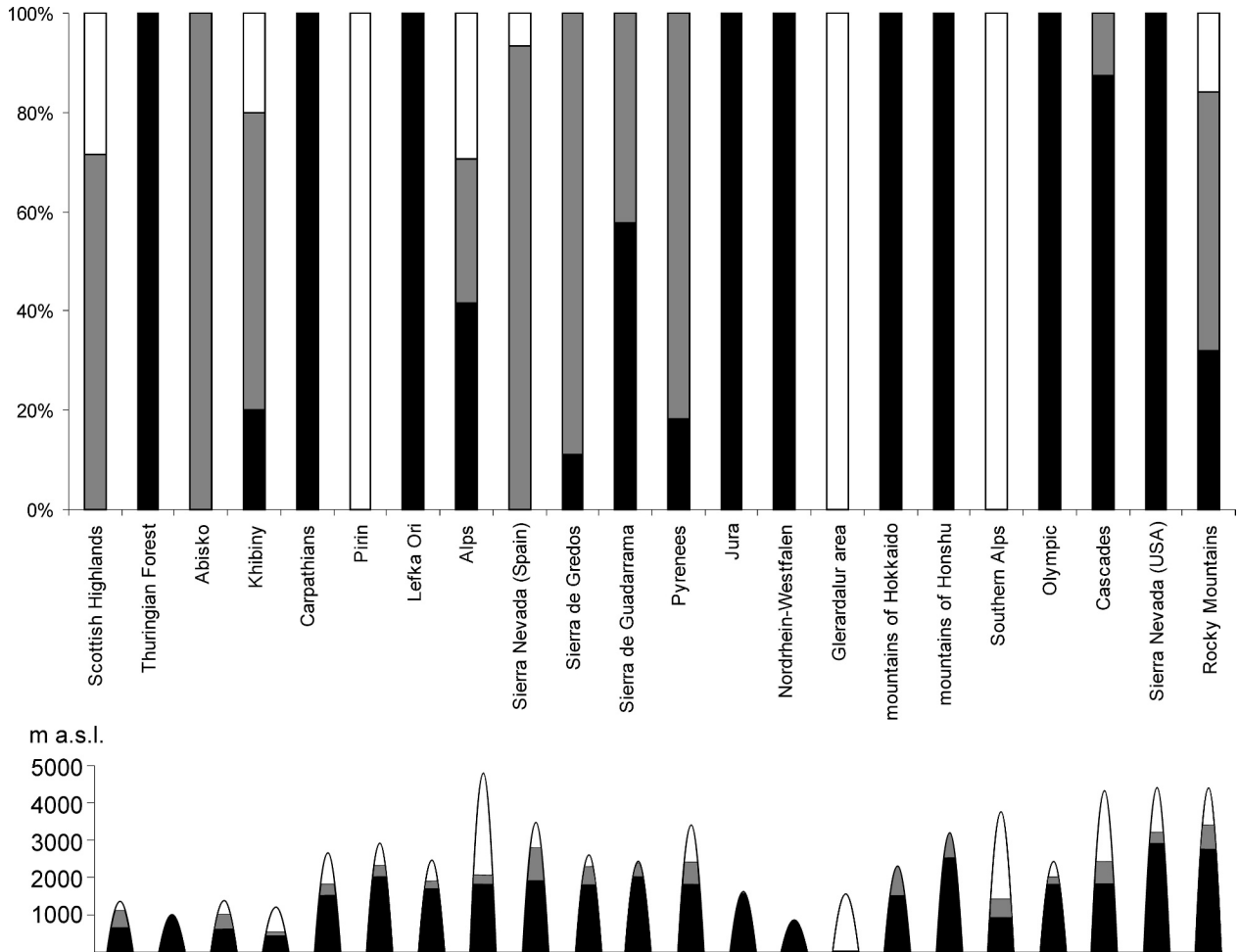


FIG. 4. Share of records of nivicolous myxomycetes in three main altitudinal belts across all studied mountain areas (black = forest, gray = subalpine, white = alpine). Schematic representation of maximum altitude and distribution of belts in the studied areas is shown at the bottom.

in Greenland is more similar to adjacent boreal. Stephenson et al (2000) published an extensive comparison of species diversity in high-latitude regions of the northern hemisphere, and they also pointed out the similarity of the myxomycete biota of these areas to temperate and boreal regions instead of alpine areas. Accordingly, most nivicolous species cited in that study were recorded in the mountains of arctic/subarctic regions (e.g. in the Khibiny Mountains) (see Novozhilov and Schnittler 1996).

Based on the available data it seems that it is difficult to define an arctic-alpine element in myxomycetes. The ecological group of nivicolous species does not dominate in arctic areas. Moreover the presence of nivicolous species in high latitude regions appears to be connected usually to the vicinity of snow in arctic/subarctic mountainous environments (see also Stephenson et al 2000), while they are almost absent from arctic lowland areas, alike in temperate regions. Therefore it seems more appropriate to treat

this group as a widely distributed mountain element instead of an arctic-alpine element.

CONCLUSIONS AND PERSPECTIVES

Our analysis clearly demonstrates that nivicolous myxomycetes should not be treated as a subalpine/alpine ecological group, as it is often stated in the literature. They occur abundantly also in lower areas including low mountain ranges with no contact to alpine belt and even exceptionally in lowland regions. No clear tendencies of differences in altitudinal preferences of species emerged, although a few species were encountered more often in higher areas suggesting that a group of more stenoecious high mountain species might exist.

Furthermore from the biogeographical point of view it seems that no arctic-alpine geographical element can be defined in myxomycetes and nivicolous slime molds most probably form a widely

distributed mountain element. Our synthesis based on literature data inevitably suffers from necessary assumptions in classification of unevenly collected and reported records. However it gives a foundation for understanding the essential altitudinal properties of nivicolous myxomycetes, breaks the hitherto dominating opinions and thus sets a good basis for further studies. Dedicated research on rigorous altitudinal gradients in low and high mountain ranges of similar climatic zones would be a promising approach to better seize the specific ecological properties of particular taxa. It is possible that deeper knowledge of the distribution, dynamics and ecology of this peculiar group might reveal these snow cover-dependent mountain organisms as useful, sensitive indicators for assessment of many general environmental trends affecting mountain ecosystems (e.g. those connected with climate change).

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