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RESEARCH ARTICLE

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Ellenberg *N* values of bryophytes in Central Europe*

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Abstract

We present a list of Ellenberg indicator values *N* values for Central European bryophytes and the methodology we used to obtain these values. Values are given for 6 hornworts, 255 liverworts, 35 peat mosses, and 772 mosses, i.e., for a total of 1,068 species. We ng the *N* values for different variables related to bryophyte morphology, taxonomy, Red List status, and ecology. Among the morphological and taxonomical groups, peat mosses, foliose hepatics, and species with porous leaves on average had the lowest *N* values, while no strong differentiation was found between Red List groups. Ecology and life span exhibited a strong differentiation, with lowest mean values for aquatic and indefinitely growing species, and highest mean values for ecologically rather unspecific and annual species. Furthermore, we compared the bryophyte *N* values with those of vascular plants and macromycetes from Central Europe.

KEYWORDS

foliose, indicator value, liverwort, moss, nitrogen, nutrient, peat moss, thallose

1 | INTRODUCTION

In studies dealing with the applied ecology of plant species mostly the species' realised niche is assessed (Diekmann, 2003; Smart et al., 2010). Typically, habitat characteristics such as substrate pH, air temperature, or water-holding capacity of the soil are measured directly. Other variables such as the substrate's content of specific nutrients or soil moisture and hydrology respectively are also often measured, although such data cover a limited range in space and time (Ellenberg, 2001; Simmel et al., 2017). In contrast, the concept of indicator values has been developed with the intention to integrate conditions over all seasons (Ellenberg, 2001), potentially offering a valuable additional tool for ecological assessments.

For Central Europe, Ellenberg (1974; 2001) and for Switzerland and the Alps, Landolt (1977; 2010) have developed sets of indicator values covering a broad range of environmental conditions such as properties of the soil/substrate, light and climate, water supply, and others. The concept of Ellenberg indicator values (EIVs), which was established for Central Europe including Germany, is the one most commonly used in this region. Both indicator value sets were originally compiled for vascular plants but subsequently both have been adopted for lichens and bryophytes (EIVs: Düll, 2001; Wirth, 2001; Landolt indicator values: Urmi, 2010; Vust, 2010). Hill et al. (2007) provide Ellenberg-style scores for the UK and Ireland; however, Hill et al. (2005) make clear that a comparison of their values for British and Irish bryophytes with corresponding values for, e.g., Central Europe, will not be meaningful due to considerable differences in climate and ecology. This accords with Hedwall et al. (2019), who have shown decreasing reliability of EIVs outside of Central Europe.

In his compilation of EIVs for bryophytes, Düll (2001) did not include values of *N*, which is the nine-level indicator that addresses nutrient availability of the substrate on which a plant grows. In contrast to vascular plants and lichens — and also macromycetes (Simmel et al., 2017) — there are, thus, no *N* values for bryophytes

*Dedicated to Dr. Hermann Muhle for his lifework on cryptogams and his enthusiasm to inspire other people for them.

elaborated in the Ellenberg system. This complicates comparative studies on these taxonomical groups and is unfortunate since bryophytes are important indicator organisms due to their sensitivity to environmental pollution and nitrogen deposition (Nash and Wirth, 1988; Mäkipää, 1995; Huber, 1998; Burton, 2008).

Against this background we addressed this gap and provide a first compilation of *N* values for bryophytes. We understand *N* values not as indicator values for demands for, or preferences of, nitrogen as such, but as indicators of the general nutrient status of the sites in which the species was found. This accords with the view of Ellenberg: in his last

TABLE 1 List of 77 species of bryophytes used as basis in the preparation of *N* values

Taxon	Species group	Taxon	Species group
Anthoceros agrestis	hepat+hornw	*Dicranum montanum*	acro moss
Anthoceros caucasicus	hepat+hornw	*Dicranum muehlenbeckii*	acro moss
Anthoceros neesii	hepat+hornw	*Dicranum polysetum*	acro moss
Anthoceros punctatus	hepat+hornw	*Dicranum scoparium*	acro moss
Barbula amplexifolia	acro moss	*Dicranum spadiceum*	acro moss
Barbula bicolor	acro moss	*Dicranum spurium*	acro moss
Barbula convoluta	acro moss	*Dicranum tauricum*	acro moss
Barbula crocea	acro moss	*Dicranum viride*	acro moss
Barbula enderesii	acro moss	*Eurhynchium angustirete*	pleur moss
Barbula unguiculata	acro moss	*Eurhynchium hians*	pleur moss
Brachythecium albicans	pleur moss	*Eurhynchium praelongum*	pleur moss
Brachythecium campestre	pleur moss	*Eurhynchium pulchellum*	pleur moss
Brachythecium collinum	pleur moss	*Eurhynchium pumilum*	pleur moss
Brachythecium curtum (= *B. oedipodium*)	pleur moss	*Eurhynchium schleicheri*	pleur moss
Brachythecium glaciale	pleur moss	*Eurhynchium speciosum*	pleur moss
Brachythecium glareosum	pleur moss	*Eurhynchium striatum*	pleur moss
Brachythecium latifolium	pleur moss	*Isothecium striatulum* (= *Eurhynchium striatulum*)	pleur moss
Brachythecium mildeanum	pleur moss	*Lophocolea bidentata*	hepat+hornw
Brachythecium oxycladon	pleur moss	*Lophocolea fragrans*	hepat+hornw
Brachythecium plumosum	pleur moss	*Lophocolea heterophylla*	hepat+hornw
Brachythecium populeum	pleur moss	*Lophocolea minor*	hepat+hornw
Brachythecium reflexum	pleur moss	*Pellia endiviifolia*	hepat+hornw
Brachythecium rivulare	pleur moss	*Pellia epiphylla*	hepat+hornw
Brachythecium rutabulum	pleur moss	*Pellia neesiana*	hepat+hornw
Brachythecium salebrosum (incl. *B. capillaceum*)	pleur moss	*Polytrichum alpinum*	acro moss
Brachythecium starkii	pleur moss	*Polytrichum commune*	acro moss
Brachythecium trachypodium	pleur moss	*Polytrichum formosum*	acro moss
Brachythecium turgidum	pleur moss	*Polytrichum juniperinum*	acro moss
Brachythecium velutinum	pleur moss	*Polytrichum longisetum*	acro moss
Dicranum bergeri	acro moss	*Polytrichum pallidisetum*	acro moss
Dicranum bonjeanii	acro moss	*Polytrichum piliferum* var. *piliferum*	acro moss
Dicranum brevifolium	acro moss	*Polytrichum sexangulare*	acro moss
Dicranum dispersum	acro moss	*Polytrichum strictum*	acro moss
Dicranum elongatum	acro moss	*Thuidium abietinum*	pleur moss
Dicranum flagellare	acro moss	*Thuidium delicatulum*	pleur moss
Dicranum flexicaule (*D. fuscescens* var. *congestum*)	acro moss	*Thuidium philibertii*	pleur moss
Dicranum fulvum	acro moss	*Thuidium recognitum*	pleur moss
Dicranum fuscescens	acro moss	*Thuidium tamariscinum*	pleur moss
Dicranum majus	acro moss		

Species groups: see Table 2.

edition of the publication of EIVs he emphasised that *N* numbers are reflecting total nutrient availability rather than nitrogen availability *as such* (Ellenberg 2001). Other authors therefore interpret the *N* numbers as reflecting general productivity rather than substrate nitrogen contents (Hill & Carey 1997; Wagner et al. 2007; see also Bartelheimer & Poschlod 2016). We used the species list of Düll (2001) as a basis for the new list of EIV *N* values. Furthermore, we explore if differences in species' morphology, life form, taxonomy, Red List status and ecology (substrate) can be explained by EIV *N* values.

2 | METHODS

The species list of bryophytes used in the present study is the list compiled by Düll (2001), gently updated for taxonomy and nomenclature according to Frey et al. (2006). In total, the list contains 1,068 taxa.

2.1 | Compilation and validation of *N* values

The *N* values (nutrient availability indicator values; see above) for bryophytes were established following the approach described by Simmel et al. (2017):

1. Compilation of a short list of species with well-known ecology, covering a broad range of habitat types and all growth forms (see Table 1)
2. Establishment of *N* values for the short list of species based on soil nutrient analyses (data not shown) and/or comparison with *N* values for vascular plants, lichens, and macromycetes co-occurring with these species. Further calibration during this step and the following two steps took place using ecological data from the literature (Daniels and Eddy, 1985; Huber, 1998; Nebel and Philippi, 2000; Nebel and Philippi, 2001; Nebel and Philippi, 2005; Frahm, 2001; Frahm and Frey, 2004; Frey et al., 2006)
3. Establishment of *N* values for the remaining species by comparison of the respective species' ecology with that of the species on the short list
4. Final evaluation and, when necessary, reworking of the *N* values by comparison of the values within groups of ecologically similar species

2.2 | Analyses of *N* values

The distribution of *N* values was explored by calculation of species numbers and mean values for groups of bryophyte species. We defined groups by the species' Red List status, taxonomy (major clades of bryophytes), ecology (different aquatic and terrestrial lifestyles; life span), and morphology (form groups; structure of leaf surface). Ecological and morphological characteristics were selected with the purpose of accounting for differences in nutrient uptake in bryophytes.

TABLE 2 List of *N* values for 1,068 Central European bryophyte species

Taxon	Species group	*N* value
Acaulon casasianum	acro moss	4
Acaulon muticum	acro moss	4
Acaulon triquetrum	acro moss	4
Aloina aloides	acro moss	3
Aloina ambigua	acro moss	5
Aloina brevirostris	acro moss	6
Aloina obliquifolia	acro moss	3?
Aloina rigida	acro moss	4
Amblyodon dealbatus	acro moss	3
Amblystegium humile	pleur moss	5
Amblystegium radicale (*A. saxatile*)	pleur moss	3
Amblystegium riparium	pleur moss	7
Amblystegium serpens var. *serpens*	pleur moss	6
Amblystegium serpens var. *juratzkanum*	pleur moss	5
Amblystegium varium	pleur moss	6
Amphidium lapponicum	acro moss	3
Amphidium mougeotii	acro moss	4
Anacamptodon splachnoides	pleur moss	3
Anastrepta orcadensis	folios hepat	3
Anastrophyllum hellerianum	folios hepat	3
Anastrophyllum michauxii	folios hepat	3
Anastrophyllum minutum	folios hepat	4
Anastrophyllum saxicola	folios hepat	3
Andreaea crassinervia	acro moss	3?
Andreaea heinemannii	acro moss	4
Andreaea rothii	acro moss	2
Andreaea rupestris	acro moss	4
Aneura pinguis	thall hepat	5
Anoectangium aestivum	acro moss	4
Anoectangium hornschuchianum (incl. *A. sendtnerianum* and *A. tenuinerve*)	acro moss	3
Anomobryum julaceum	acro moss	3
Anomodon attenuatus	pleur moss	6
Anomodon longifolius	pleur moss	5
Anomodon rostratus	pleur moss	4
Anomodon rugelii	pleur moss	4
Anomodon viticulosus	pleur moss	7
Anthelia julacea	folios hepat	3?
Anthelia juratzkana	folios hepat	2
Anthoceros agrestis	hornwort	5
Anthoceros caucasicus	hornwort	4
Anthoceros neesii	hornwort	5
Anthoceros punctatus	hornwort	4
Antitrichia curtipendula	pleur moss	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Aongstroemia longipes	acro moss	2?
Aphanorhegma patens (*Physcomitrella patens*)	acro moss	6
Apometzgeria pubescens	thall hepat	4
Archidium alternifolium	acro moss	4
Arnellia fennica	folios hepat	?
Asterella gracilis	thall hepat	4
Asterella lindenbergiana	thall hepat	4?
Asterella saccata	thall hepat	2
Athalamia hyalina	thall hepat	2
Atrichum angustatum	acro moss	3
Atrichum haussknechtii	acro moss	3
Atrichum tenellum	acro moss	4
Atrichum undulatum	acro moss	4
Aulacomnium androgynum	acro moss	3
Aulacomnium palustre	acro moss	3
Barbilophozia atlantica	folios hepat	?
Barbilophozia attenuata	folios hepat	3
Barbilophozia barbata	folios hepat	4
Barbilophozia floerkei	folios hepat	3
Barbilophozia hatcheri	folios hepat	4
Barbilophozia kunzeana	folios hepat	2
Barbilophozia lycopodioides	folios hepat	5
Barbilophozia quadriloba	folios hepat	?
Barbula amplexifolia	acro moss	?
Barbula bicolor	acro moss	3
Barbula convoluta	acro moss	5
Barbula crocea	acro moss	4
Barbula enderesii	acro moss	3
Barbula unguiculata	acro moss	6
Bartramia halleriana	acro moss	2
Bartramia ithyphylla	acro moss	3
Bartramia pomiformis	acro moss	3
Bartramia stricta	acro moss	3
Bazzania flaccida	folios hepat	3
Bazzania tricrenata	folios hepat	3
Bazzania trilobata	folios hepat	4
Blasia pusilla	thall hepat	4
Blepharostoma trichophyllum	folios hepat	3
Blindia acuta	acro moss	3
Blindia caespiticia	acro moss	4?
Brachydontium trichodes	acro moss	4
Brachythecium albicans	pleur moss	4
Brachythecium campestre	pleur moss	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Brachythecium collinum	pleur moss	?
Brachythecium curtum (*oedipodium*)	pleur moss	3
Brachythecium glaciale	pleur moss	4
Brachythecium glareosum	pleur moss	5
Brachythecium latifolium	pleur moss	?
Brachythecium mildeanum	pleur moss	4
Brachythecium oxycladon	pleur moss	5
Brachythecium plumosum	pleur moss	4
Brachythecium populeum	pleur moss	5
Brachythecium reflexum	pleur moss	4
Brachythecium rivulare	pleur moss	7
Brachythecium rutabulum	pleur moss	8
Brachythecium salebrosum (incl. *B. capillaceum*)	pleur moss	6
Brachythecium starkii	pleur moss	3
Brachythecium trachypodium	pleur moss	4
Brachythecium turgidum	pleur moss	2
Brachythecium velutinum	pleur moss	5
Breutelia chrysocoma	acro moss	4?
Brotherella lorentziana	pleur moss	4
Bruchia vogesiaca	acro moss	3?
Bryoerythrophyllum ferruginascens	acro moss	4
Bryoerythrophyllum recurvirostrum	acro moss	4
Bryoerythrophyllum rubrum	acro moss	3
Bryum algovicum	acro moss	3
Bryum alpinum	acro moss	3
Bryum arcticum (incl. *B. imbricatum*, *B. luridum*, *B. purpurascens*)	acro moss	?
Bryum argenteum	acro moss	7
Bryum barnesii	acro moss	5
Bryum bicolor (incl. *B. dunense*)	acro moss	5
Bryum bimum (*B. pseudotriquetrum* var. *bimum*)	acro moss	4
Bryum bornholmense	acro moss	2
Bryum caespiticium	acro moss	4
Bryum calophyllum	acro moss	5?
Bryum capillare (incl. *B. flaccidum und B. laevifilum*)	acro moss	4
Bryum creberrimum (incl. *B. lonchocaulon*)	acro moss	4
Bryum cyclophyllum	acro moss	4
Bryum demaretianum	acro moss	4?
Bryum elegans (incl. *B. stirtonii*)	acro moss	3
Bryum funkii	acro moss	3
Bryum gemmiferum	acro moss	3

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Bryum gemmilucens	acro moss	4
Bryum gemmiparum	acro moss	5
Bryum inclinatum (*B. imbricatum*, incl. *B. archangelicum*)	acro moss	3
Bryum intermedium	acro moss	3
Bryum klinggraeffii	acro moss	5
Bryum knowltonii	acro moss	3?
Bryum kunzei	acro moss	4
Bryum longisetum	acro moss	2
Bryum marratii	acro moss	5
Bryum microerythrocarpum	acro moss	4
Bryum mildeanum (incl. *B. reyeri*)	acro moss	4
Bryum muehlenbeckii	acro moss	3
Bryum neodamense	acro moss	2
Bryum oblongum	acro moss	3?
Bryum pallens (incl. *B. rutilans*)	acro moss	4
Bryum pallescens	acro moss	3
Bryum pseudotriquetrum (var. *pseudotriquetrum*)	acro moss	5
Bryum radiculosum	acro moss	3
Bryum rubens	acro moss	5
Bryum ruderale	acro moss	3
Bryum salinum	acro moss	3
Bryum schleicheri var. *schleicheri*	acro moss	4
Bryum schleicheri var. *latifolium*	acro moss	3
Bryum subneodamense	acro moss	2?
Bryum tenuisetum	acro moss	4
Bryum torquescens	acro moss	3
Bryum turbinatum	acro moss	4
Bryum uliginosum	acro moss	4
Bryum versicolor (incl. *B. gerwigii*)	acro moss	4
Bryum violaceum	acro moss	3
Bryum warneum (incl. *B. mamillatum*)	acro moss	4
Bryum weigelii	acro moss	5
Buxbaumia aphylla	acro moss	2
Buxbaumia viridis	acro moss	3
Callicladium haldanianum	pleur moss	3
Calliergon cordifolium	pleur moss	5
Calliergon giganteum	pleur moss	4
Calliergon megalophyllum	pleur moss	3?
Calliergon richardsonii	pleur moss	3
Calliergon sarmentosum	pleur moss	3
Calliergon stramineum	pleur moss	2
Calliergon trifarium	pleur moss	2
Calliergonella cuspidata	pleur moss	6

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Calypogeia arguta	folios hepat	3
Calypogeia azurea	folios hepat	3
Calypogeia fissa	folios hepat	4
Calypogeia integristipula	folios hepat	3
Calypogeia muelleriana	folios hepat	3
Calypogeia neesiana	folios hepat	3
Calypogeia sphagnicola	folios hepat	1
Calypogeia suecica	folios hepat	4
Campylium calcareum	pleur moss	4
Campylium chrysophyllum	pleur moss	3
Campylium decipiens	pleur moss	5
Campylium elodes	pleur moss	2
Campylium halleri	pleur moss	3
Campylium polygamum	pleur moss	4
Campylium stellatum (incl. *C. protensum*)	pleur moss	4
Campylopus brevipilus	acro moss	2
Campylopus flexuosus	acro moss	2
Campylopus fragilis	acro moss	3
Campylopus introflexus	acro moss	3
Campylopus pyriformis	acro moss	2
Campylopus schwarzii	acro moss	2
Campylopus subulatus	acro moss	2
Campylostelium saxicola	acro moss	4
Catoscopium nigritum	acro moss	4
Cephalozia ambigua	folios hepat	5
Cephalozia bicuspidata var. *bicuspidata*	folios hepat	2
Cephalozia bicuspidata var. *lammersiana*	folios hepat	2
Cephalozia catenulata	folios hepat	3
Cephalozia connivens	folios hepat	2
Cephalozia lacinulata	folios hepat	4
Cephalozia leucantha	folios hepat	4
Cephalozia loitlesbergeri	folios hepat	1
Cephalozia lunulifolia	folios hepat	4
Cephalozia macrostachya	folios hepat	1
Cephalozia pleniceps	folios hepat	4
Cephaloziella divaricata	folios hepat	3
Cephaloziella elachista	folios hepat	1
Cephaloziella elegans	folios hepat	3
Cephaloziella grimsulana	folios hepat	3
Cephaloziella hampeana var. *hampeana*	folios hepat	4
Cephaloziella hampeana var. *subtilis*	folios hepat	1
Cephaloziella integerrima	folios hepat	4?
Cephaloziella rubella var. *pulchella*	folios hepat	2

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Cephaloziella rubella var. *r.* (incl. var. *bifida*)	folios hepat	3
Cephaloziella rubella var. *sullivantii*	folios hepat	3
Cephaloziella stellulifera (incl. var. *limprichtii*)	folios hepat	3
Cephaloziella subdentata (*C. spinigera*)	folios hepat	1
Cephaloziella varians (incl. var. *arctica und C. uncinata*)	folios hepat	4
Ceratodon conicus	acro moss	?
Ceratodon purpureus	acro moss	×
Chiloscyphus pallescens	folios hepat	6
Chiloscyphus polyanthos	folios hepat	5
Cinclidium arcticum	acro moss	?
Cinclidium stygium	acro moss	2
Cinclidotus aquaticus	acro moss	4
Cinclidotus danubicus	acro moss	7
Cinclidotus fontinaloides	acro moss	6
Cinclidotus riparius	acro moss	6
Cirriphyllum cirrosum	pleur moss	3
Cirriphyllum crassinervium (*Eurhynchium crassinervium*)	pleur moss	5
Cirriphyllum piliferum	pleur moss	7
Cirriphyllum reichenbachianum (*C. flotowianum, Eurhynchium flotowianum*)	pleur moss	4
Cirriphyllum tommasinii (*C. tenuinerve*, incl. *C. germanicum*)	pleur moss	5
Cladopodiella fluitans	folios hepat	1
Cladopodiella francisci	folios hepat	2
Clasmatodon parvulus	pleur moss	?
Climacium dendroides	pleur moss	4
Cnestrum schistii	acro moss	4
Cololejeunea calcarea	folios hepat	4
Cololejeunea minutissima	folios hepat	2
Cololejeunea rossettiana	folios hepat	3
Conardia compacta	pleur moss	5
Conocephalum conicum	thall hepat	6
Coscinodon cribrosus	acro moss	2
Cratoneuron commutatum (excl. var. *sulcatum*)	pleur moss	5
Cratoneuron commutatum var. *sulcatum* (*Cratoneuron sulcatum*)	pleur moss	4
Cratoneuron curvicaule	pleur moss	3
Cratoneuron decipiens	pleur moss	3
Cratoneuron filicinum	pleur moss	6
Crossidium aberrans	acro moss	4
Crossidium crassinerve	acro moss	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Crossidium squamiferum	acro moss	4
Cryphaea heteromalla	pleur moss	7
Cryptothallus mirabilis (*Aneura mirabilis*)	thall hepat	×?
Ctenidium molluscum (incl. var. *condensatum*)	pleur moss	4
Ctenidium procerrimum	pleur moss	3
Cynodontium bruntonii (*Oreoweisia bruntonii*)	acro moss	3
Cynodontium fallax	acro moss	2
Cynodontium gracilescens	acro moss	2
Cynodontium jenneri	acro moss	?
Cynodontium polycarpon	acro moss	2
Cynodontium tenellum	acro moss	2
Cyrtomnium hymenophylloides	acro moss	2
Desmatodon cernuus	acro moss	4
Desmatodon guepinii	acro moss	4
Desmatodon heimii	acro moss	5
Desmatodon latifolius	acro moss	4
Desmatodon laureri	acro moss	4?
Desmatodon leucostoma	acro moss	3?
Desmatodon systylius	acro moss	?
Desmatodon wilczekii	acro moss	?
Dialytrichia mucronata (*Cinclidotus mucronatus*)	acro moss	7
Dichelyma capillaceum	pleur moss	?
Dichodontium flavescens	acro moss	6?
Dichodontium pellucidum	acro moss	6
Dicranella cerviculata	acro moss	2
Dicranella crispa	acro moss	4
Dicranella grevilleana	acro moss	2?
Dicranella heteromalla	acro moss	3
Dicranella howei	acro moss	4
Dicranella humilis	acro moss	4
Dicranella palustris	acro moss	4
Dicranella rufescens	acro moss	4
Dicranella schreberiana	acro moss	5
Dicranella staphylina	acro moss	4
Dicranella subulata	acro moss	2
Dicranella varia	acro moss	5
Dicranodontium asperulum	acro moss	2
Dicranodontium denudatum	acro moss	3
Dicranodontium uncinatum	acro moss	3
Dicranoweisia cirrata	acro moss	3
Dicranoweisia crispula var *crispula*	acro moss	2
Dicranoweisia crispula var. *compacta*	acro moss	2

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Dicranum bergeri	acro moss	1
Dicranum bonjeanii	acro moss	3
Dicranum brevifolium	acro moss	4
Dicranum dispersum	acro moss	4
Dicranum elongatum	acro moss	4
Dicranum flagellare	acro moss	3
Dicranum fulvum	acro moss	2
Dicranum fuscescens	acro moss	3
Dicranum flexicaule (*D. fuscescens* var. *congestum*)	acro moss	3
Dicranum majus	acro moss	5
Dicranum montanum	acro moss	2
Dicranum muehlenbeckii	acro moss	3
Dicranum polysetum	acro moss	2
Dicranum scoparium	acro moss	4
Dicranum spadiceum	acro moss	2
Dicranum spurium	acro moss	1
Dicranum tauricum	acro moss	3
Dicranum viride	acro moss	3
Didymodon acutus (incl. *D. icmadophilus*)	acro moss	4
Didymodon asperifolius	acro moss	3
Didymodon cordatus	acro moss	5
Didymodon fallax	acro moss	6
Didymodon ferrugineus	acro moss	5
Didymodon glaucus (incl. *D. verbanus*)	acro moss	3
Didymodon luridus	acro moss	5
Didymodon nicholsonii	acro moss	6
Didymodon rigidulus	acro moss	4
Didymodon sinuosus	acro moss	6
Didymodon spadiceus	acro moss	5
Didymodon subandreaeoides	acro moss	3
Didymodon tophaceus	acro moss	5
Didymodon umbrosus (*Trichostomopsis* [*australasiae* ssp.] *umbrosa*)	acro moss	?
Didymodon validus	acro moss	4?
Didymodon vinealis (incl. *D. insulanus und D. tomaculosus*)	acro moss	5
Diphyscium foliosum	acro moss	3
Diplophyllum albicans	folios hepat	3
Diplophyllum obtusifolium	folios hepat	2
Diplophyllum taxifolium	folios hepat	2
Discelium nudum	acro moss	5
Distichium capillaceum	acro moss	4
Distichium inclinatum	acro moss	4
Distichophyllum carinatum	pleur moss	3?

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Ditrichum cylindricum	acro moss	4
Ditrichum flexicaule	acro moss	3
Ditrichum heteromallum	acro moss	2
Ditrichum lineare (incl. *D. plumbicola*)	acro moss	2
Ditrichum pallidum	acro moss	3
Ditrichum pusillum	acro moss	3
Ditrichum zonatum	acro moss	2
Douinia ovata	folios hepat	3
Drepanocladus aduncus (incl. *D. polycarpus und D. stagnatus*)	pleur moss	6
Drepanocladus capillifolius	pleur moss	5
Drepanocladus cossonii	pleur moss	3
Drepanocladus exannulatus (*Warnstorfia exannulata*)	pleur moss	3
Drepanocladus fluitans (*Warnstorfia fluitans*)	pleur moss	3
Drepanocladus lapponicus (*Hamatocaulis lapponicus*)	pleur moss	4
Drepanocladus lycopodioides	pleur moss	4
Drepanocladus pseudostramineus (*Warnstorfia pseudostraminea*)	pleur moss	4
Drepanocladus revolvens	pleur moss	3
Drepanocladus sendtneri (incl. *D. sordidus*)	pleur moss	3
Drepanocladus vernicosus (*Hamatocaulis vernicosus*)	pleur moss	4
Dryptodon patens	acro moss	3
Encalypta affinis	acro moss	3
Encalypta alpina	acro moss	3
Encalypta ciliata	acro moss	3
Encalypta longicollis	acro moss	4
Encalypta microstoma	acro moss	?
Encalypta rhaptocarpa agg.	acro moss	3
Encalypta spathulata	acro moss	3
Encalypta streptocarpa	acro moss	5
Encalypta vulgaris	acro moss	4
Entodon concinnus	pleur moss	4
Entodon schleicheri	pleur moss	5
Entosthodon fascicularis	acro moss	4
Entosthodon hungaricus	acro moss	5
Entosthodon obtusus	acro moss	3
Ephemerum cohaerens	acro moss	4
Ephemerum minutissimum (*E. serratum* var. *minutissimum*)	acro moss	4
Ephemerum recurvifolium	acro moss	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Ephemerum serratum (incl. *E. rutheanum und E. spinulosum*)	acro moss	5
Ephemerum sessile	acro moss	5
Ephemerum stellatum	acro moss	?
Eremonotus myriocarpus	folios hepat	4
Eucladium verticillatum	acro moss	5
Eurhynchium angustirete	pleur moss	4
Eurhynchium hians	pleur moss	5
Eurhynchium praelongum	pleur moss	7
Eurhynchium pulchellum	pleur moss	5
Eurhynchium pumilum	pleur moss	6
Eurhynchium schleicheri	pleur moss	5
Eurhynchium speciosum	pleur moss	6
Eurhynchium striatum	pleur moss	6
Fabronia pusilla	pleur moss	3
Fissidens adianthoides	acro moss	4
Fissidens arnoldii	acro moss	5
Fissidens bambergeri	acro moss	3
Fissidens bryoides var. *bryoides*	acro moss	5
Fissidens crassipes	acro moss	6
Fissidens cristatus	acro moss	3
Fissidens dubius	acro moss	4
Fissidens exiguus	acro moss	4
Fissidens exilis	acro moss	5
Fissidens gracilifolius	acro moss	4
Fissidens grandifrons	acro moss	4
Fissidens gymnandrus (*F. bryoides* var. *gymnandrus*)	acro moss	6
Fissidens incurvus	acro moss	4
Fissidens monguillonii	acro moss	?
Fissidens osmundoides	acro moss	3
Fissidens pusillus	acro moss	3
Fissidens rivularis	acro moss	5
Fissidens rufulus	acro moss	4
Fissidens taxifolius	acro moss	6
Fissidens viridulus var. *viridulus*	acro moss	3
Fontinalis antipyretica	pleur moss	6
Fontinalis hypnoides	pleur moss	6
Fontinalis squamosa	pleur moss	5
Fossombronia foveolata	folios hepat	3
Fossombronia incurva	folios hepat	2
Fossombronia pusilla	folios hepat	4
Fossombronia wondraczekii	folios hepat	5
Frullania dilatata	folios hepat	4
Frullania fragilifolia	folios hepat	3

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Frullania jackii	folios hepat	4
Frullania tamarisci	folios hepat	3
Funaria hygrometrica	acro moss	8
Funaria muhlenbergii	acro moss	3
Funaria pulchella	acro moss	4
Geheebia gigantea	acro moss	3
Geocalyx graveolens	folios hepat	2
Grimmia affinis (*G. longirostris*)	acro moss	4
Grimmia alpestris	acro moss	3?
Grimmia anodon	acro moss	4
Grimmia anomala	acro moss	4?
Grimmia caespiticia	acro moss	4
Grimmia crinita	acro moss	4
Grimmia decipiens	acro moss	3
Grimmia dissimulata	acro moss	4
Grimmia donniana (incl. var. *curvula* [= *G. arenaria*])	acro moss	3
Grimmia elatior	acro moss	3
Grimmia elongata	acro moss	3
Grimmia funalis	acro moss	3
Grimmia hartmanii	acro moss	3
Grimmia incurva	acro moss	3
Grimmia laevigata	acro moss	3
Grimmia limprichtii	acro moss	4?
Grimmia lisae	acro moss	4
Grimmia montana	acro moss	3
Grimmia orbicularis	acro moss	5
Grimmia ovalis	acro moss	4
Grimmia plagiopodia	acro moss	5
Grimmia pulvinata (incl. var. *africana*)	acro moss	7
Grimmia sessitana	acro moss	4
Grimmia teretinervis	acro moss	3
Grimmia tergestina	acro moss	4
Grimmia torquata	acro moss	3
Grimmia trichophylla (incl. var. *meridionalis* and var. *brachycarpa*)	acro moss	4
Grimmia trichophylla var. *tenuis* (*G. muehlenbeckii*)	acro moss	4
Grimmia unicolor	acro moss	3?
Gymnocolea acutiloba	folios hepat	2
Gymnocolea inflata	folios hepat	2
Gymnomitrion concinnatum	folios hepat	2
Gymnomitrion corallioides	folios hepat	1
Gymnomitrion obtusum	folios hepat	3
Gymnostomum aeruginosum	acro moss	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Gymnostomum calcareum	acro moss	4
Gymnostomum viridulum	acro moss	4
Gyroweisia tenuis	acro moss	4
Habrodon perpusillus	pleur moss	?
Haplomitrium hookeri	folios hepat	2
Harpanthus flotovianus	folios hepat	3
Harpanthus scutatus	folios hepat	2
Hedwigia ciliata var. *ciliata*	acro moss	3
Hedwigia ciliata var. *leucophaea*	acro moss	4
Hedwigia stellata	acro moss	3
Helodium blandowii	pleur moss	3
Herzogiella seligeri	pleur moss	3
Herzogiella striatella	pleur moss	3
Heterocladium dimorphum	pleur moss	4
Heterocladium heteropterum var. *flaccidum*	pleur moss	4
Heterocladium heteropterum var. *heteropterum*	pleur moss	3
Heterophyllium affine	pleur moss	?
Homalia trichomanoides	pleur moss	6
Homalothecium geheebii	pleur moss	4
Homalothecium lutescens	pleur moss	3
Homalothecium nitens (*Tomentypnum n.*)	pleur moss	3
Homalothecium philippeanum	pleur moss	4
Homalothecium sericeum	pleur moss	5
Homomallium incurvatum	pleur moss	5
Hookeria lucens	pleur moss	5
Hygroamblystegium fluviatile (*Amblystegium f.*)	pleur moss	5
Hygroamblystegium tenax (*Amblystegium t.*)	pleur moss	6
Hygrobiella laxifolia	folios hepat	5
Hygrohypnum alpestre	pleur moss	?
Hygrohypnum duriusculum	pleur moss	3
Hygrohypnum eugyrium	pleur moss	3
Hygrohypnum luridum	pleur moss	6
Hygrohypnum ochraceum	pleur moss	5
Hygrohypnum smithii	pleur moss	3
Hylocomium brevirostre	pleur moss	4
Hylocomium pyrenaicum	pleur moss	3
Hylocomium splendens	pleur moss	4
Hylocomium umbratum	pleur moss	3
Hymenostylium recurvirostrum	acro moss	4
Hyocomium armoricum	pleur moss	4
Hyophila involuta	acro moss	5

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Hypnum bambergeri	pleur moss	3
Hypnum callichroum	pleur moss	4
Hypnum cupressiforme var. *cupressiforme* (var. *uncinatum*, incl. mod. *filiforme*)	pleur moss	5
Hypnum cupressiforme var. *lacunosum*	pleur moss	3
Hypnum cupressiforme var. *resupinatum*	pleur moss	6
Hypnum cupressiforme var. *subjulaceum*	pleur moss	4
Hypnum fertile	pleur moss	3
Hypnum hamulosum	pleur moss	3?
Hypnum heseleri	pleur moss	6
Hypnum imponens	pleur moss	2
Hypnum jutlandicum	pleur moss	2
Hypnum lindbergii	pleur moss	4
Hypnum mamillatum (*H. andoi*)	pleur moss	3
Hypnum pallescens	pleur moss	3
Hypnum pratense	pleur moss	3
Hypnum recurvatum	pleur moss	3
Hypnum reptile	pleur moss	2
Hypnum revolutum var. *revolutum*	pleur moss	4
Hypnum revolutum var. *dolomiticum*	pleur moss	4?
Hypnum sauteri	pleur moss	4
Hypnum vaucheri	pleur moss	4
Isopterygiopsis muelleriana	pleur moss	3?
Isopterygium elegans (*Pseudotaxiphyllum elegans*)	pleur moss	3
Isopterygium pulchellum (*Isopterygiopsis pulchella*, incl. var. *nitidulum*)	pleur moss	3
Isothecium alopecuroides	pleur moss	4
Isothecium holtii	pleur moss	3
Isothecium myosuroides	pleur moss	4
Isothecium striatulum (*Eurhynchium striatulum*)	pleur moss	3
Jamesoniella autumnalis	folios hepat	2
Jamesoniella undulifolia	folios hepat	3
Jungermannia atrovirens	folios hepat	4
Jungermannia borealis	folios hepat	4?
Jungermannia caespiticia	folios hepat	3
Jungermannia confertissima	folios hepat	4
Jungermannia exsertifolia ssp. *cordifolia*	folios hepat	5
Jungermannia gracillima	folios hepat	2
Jungermannia hyalina	folios hepat	3
Jungermannia leiantha	folios hepat	3
Jungermannia obovata	folios hepat	3
Jungermannia paroica	folios hepat	3?
Jungermannia polaris	folios hepat	3?
Jungermannia pumila	folios hepat	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Jungermannia sphaerocarpa	folios hepat	4
Jungermannia subelliptica	folios hepat	5
Jungermannia subulata	folios hepat	3
Kiaeria blyttii	acro moss	3
Kiaeria falcata	acro moss	3
Kiaeria starkei	acro moss	4
Kurzia pauciflora	folios hepat	1
Kurzia sylvatica	folios hepat	2
Kurzia trichoclados	folios hepat	2
Lejeunea cavifolia	folios hepat	5
Lejeunea lamacerina	folios hepat	4
Lejeunea ulicina (*Microlejeunea ulicina*)	folios hepat	3
Lepidozia cupressina	folios hepat	3
Lepidozia reptans	folios hepat	4
Leptobarbula berica	acro moss	3
Leptobryum pyriforme	acro moss	6
Leptodon smithii	pleur moss	?
Leptodontium flexifolium	acro moss	2
Leptodontium gemmascens	acro moss	2
Leptodontium styriacum	acro moss	3?
Lescuraea incurvata (*Pseudoleskea incurvata*)	pleur moss	3
Lescuraea mutabilis	pleur moss	4
Lescuraea patens (*Pseudoleskea patens*)	pleur moss	3?
Lescuraea plicata (*Ptychodium plicata*)	pleur moss	3
Lescuraea radicosa (*Pseudoleskea radicosa*)	pleur moss	3?
Lescuraea saxicola	pleur moss	3
Leskea polycarpa	pleur moss	6
Leucobryum glaucum	acro moss	2
Leucobryum juniperoideum	acro moss	3
Leucodon sciuroides	pleur moss	6
Lophocolea bidentata	folios hepat	6
Lophocolea fragrans	folios hepat	3
Lophocolea heterophylla	folios hepat	4
Lophocolea minor	folios hepat	4
Lophozia ascendens	folios hepat	3
Lophozia badensis	folios hepat	3
Lophozia bantriensis (*Leiocolea bantriensis*)	folios hepat	2
Lophozia bicrenata	folios hepat	2
Lophozia capitata	folios hepat	2
Lophozia collaris (*Leiocolea alpestris*)	folios hepat	4
Lophozia excisa	folios hepat	3
Lophozia gillmanii	folios hepat	?

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Lophozia grandiretis	folios hepat	?
Lophozia guttulata	folios hepat	3
Lophozia heterocolpos	folios hepat	4
Lophozia incisa	folios hepat	3
Lophozia laxa	folios hepat	1
Lophozia longidens	folios hepat	4
Lophozia longiflora	folios hepat	2
Lophozia obtusa	folios hepat	3
Lophozia perssonii	folios hepat	5
Lophozia rutheana (*Leiocolea rutheana*)	folios hepat	4?
Lophozia sudetica	folios hepat	2
Lophozia turbinata	folios hepat	3
Lophozia ventricosa	folios hepat	3
Lophozia wenzelii	folios hepat	2
Lunularia cruciata	thall hepat	8
Mannia fragrans	thall hepat	3
Mannia pilosa	thall hepat	?
Mannia triandra	thall hepat	3
Marchantia alpestris	thall hepat	4
Marchantia polymorpha var. *aquatica* (*M. aquatica*, *M. polymorpha* ssp. *polymorpha*)	thall hepat	5
Marchantia polymorpha var. *ruderalis* (*M. polymorpha* var. *polymorpha*, *M. polymorpha* ssp. *ruderalis*)	thall hepat	9
Marsupella adusta	folios hepat	2?
Marsupella alpina	folios hepat	2
Marsupella badensis	folios hepat	3
Marsupella brevissima	folios hepat	2?
Marsupella emarginata	folios hepat	3
Marsupella funckii	folios hepat	2
Marsupella ramosa	folios hepat	2
Marsupella sparsifolia	folios hepat	3
Marsupella sphacelata	folios hepat	2
Marsupella sprucei	folios hepat	2
Meesia hexasticha	acro moss	3?
Meesia longiseta	acro moss	2
Meesia triquetra	acro moss	2
Meesia uliginosa	acro moss	3
Metzgeria conjugata	thall hepat	5
Metzgeria fruticulosa	thall hepat	3
Metzgeria furcata	thall hepat	3
Metzgeria temperata	thall hepat	3
Metzleria alpina (*Atractylocarpus alpinus*)	acro moss	?
Micromitrium tenerum	acro moss	5
Mielichhoferia mielichhoferiana	acro moss	2

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Mnium ambiguum	acro moss	4
Mnium hornum	acro moss	2
Mnium marginatum	acro moss	3
Mnium spinosum	acro moss	5
Mnium spinulosum	acro moss	3
Mnium stellare	acro moss	3
Mnium thomsonii	acro moss	4
Moerckia blyttii	thall hepat	3
Moerckia hibernica	thall hepat	4
Mylia anomala	folios hepat	1
Mylia taylorii	folios hepat	2
Myurella julacea	pleur moss	4
Myurella sibirica	pleur moss	4
Myurella tenerrima	pleur moss	4
Nardia breidleri	folios hepat	?
Nardia compressa	folios hepat	3
Nardia geoscyphus	folios hepat	2
Nardia insecta	folios hepat	3
Nardia scalaris	folios hepat	2
Neckera besseri	pleur moss	4
Neckera complanata	pleur moss	6
Neckera crispa	pleur moss	5
Neckera menziesii	pleur moss	4
Neckera pennata	pleur moss	4
Neckera pumila	pleur moss	4
Notothylas orbicularis	hornwort	5
Nowellia curvifolia	folios hepat	3
Octodiceras fontanum	acro moss	7
Odontoschisma denudatum	folios hepat	3
Odontoschisma elongatum	folios hepat	4?
Odontoschisma macounii	folios hepat	3
Odontoschisma sphagni	folios hepat	2
Oligotrichum hercynicum	acro moss	2
Oncophorus virens	acro moss	3
Oncophorus wahlenbergii	acro moss	3
Oreoweisia torquescens	acro moss	3
Orthodontium lineare	acro moss	3
Orthothecium intricatum (incl. *O. chryseon* and *O. strictum*)	acro moss	3
Orthothecium rufescens	acro moss	3
Orthotrichum acuminatum	acro moss	5?
Orthotrichum affine	acro moss	7
Orthotrichum alpestre	acro moss	6
Orthotrichum anomalum	acro moss	6

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Orthotrichum consimile (*O. winteri*)	acro moss	6?
Orthotrichum cupulatum var. *cupulatum*	acro moss	5
Orthotrichum cupulatum var. *riparium* (*O. nudum*)	acro moss	6?
Orthotrichum diaphanum	acro moss	8
Orthotrichum gymnostomum	acro moss	5
Orthotrichum lyellii	acro moss	6
Orthotrichum obtusifolium	acro moss	7
Orthotrichum pallens	acro moss	7
Orthotrichum patens	acro moss	6
Orthotrichum pulchellum	acro moss	5
Orthotrichum pumilum (incl. *O. schimperi*)	acro moss	6
Orthotrichum rivulare	acro moss	4
Orthotrichum rogeri	acro moss	5
Orthotrichum rupestre	acro moss	3
Orthotrichum scanicum	acro moss	5
Orthotrichum speciosum	acro moss	6
Orthotrichum sprucei	acro moss	4?
Orthotrichum stellatum	acro moss	5
Orthotrichum stramineum	acro moss	6
Orthotrichum striatum	acro moss	7
Orthotrichum tenellum	acro moss	6
Orthotrichum urnigerum	acro moss	3
Oxystegus tenuirostris (*O. cylindricus*)	acro moss	3
Paludella squarrosa	pleur moss	4
Paraleucobryum enerve	acro moss	2
Paraleucobryum longifolium	acro moss	2
Paraleucobryum sauteri	acro moss	3
Pedinophyllum interruptum	folios hepat	4
Pellia endiviifolia	thall hepat	6
Pellia epiphylla	thall hepat	4
Pellia neesiana	thall hepat	4
Phaeoceros carolinianus	hornwort	5
Phascum curvicolle	acro moss	4
Phascum cuspidatum (excl. var. *piliferum*)	acro moss	5
Phascum cuspidatum var. *piliferum*	acro moss	3
Phascum floerkeanum	acro moss	5
Phascum leptophyllum (*Tortula rhizophylla*)	acro moss	4
Philonotis caespitosa	acro moss	4
Philonotis calcarea	acro moss	3
Philonotis capillaris (*Ph. arnellii*)	acro moss	2
Philonotis fontana	acro moss	4
Philonotis marchica	acro moss	3

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Philonotis seriata	acro moss	3
Philonotis tomentella	acro moss	3
Physcomitrium eurystomum	acro moss	7
Physcomitrium pyriforme	acro moss	7
Physcomitrium sphaericum	acro moss	5
Plagiobryum demissum	acro moss	?
Plagiobryum zierii	acro moss	3
Plagiochila asplenioides	folios hepat	6
Plagiochila porelloides	folios hepat	3
Plagiochila punctata	folios hepat	?
Plagiomnium affine	acro moss	5
Plagiomnium cuspidatum	acro moss	5
Plagiomnium elatum	acro moss	2
Plagiomnium ellipticum	acro moss	3
Plagiomnium medium	acro moss	6
Plagiomnium rostratum	acro moss	5
Plagiomnium undulatum	acro moss	7
Plagiopus oederianus	acro moss	3
Plagiothecium cavifolium	pleur moss	4
Plagiothecium curvifolium (*P. laetum* var. *curvifolium*)	pleur moss	3
Plagiothecium denticulatum	pleur moss	3
Plagiothecium laetum	pleur moss	3
Plagiothecium latebricola	pleur moss	3
Plagiothecium neckeroideum	pleur moss	2?
Plagiothecium nemorale	pleur moss	5
Plagiothecium platyphyllum	pleur moss	4
Plagiothecium ruthei	pleur moss	4
Plagiothecium succulentum	pleur moss	4
Plagiothecium undulatum	pleur moss	3
Platydictya confervoides (*Amblystegiella confervoides*, *Amblystegium confervoides*)	pleur moss	4
Platydictya jungermannoides	pleur moss	4
Platydictya subtilis (*Amblystegiella subtilis*, *Amblystegium subtile*)	pleur moss	4
Platygyrium repens	pleur moss	5
Pleuridium acuminatum	acro moss	4
Pleuridium palustre	acro moss	5
Pleuridium subulatum	acro moss	4
Pleurochaete squarrosa	acro moss	2
Pleurocladula albescens (*Fuscocephaloziopsis albescens*)	folios hepat	4
Pleurozium schreberi	pleur moss	2
Pogonatum aloides	acro moss	2
Pogonatum nanum	acro moss	2
Pogonatum urnigerum	acro moss	2
Pohlia acuminata	acro moss	3?
Pohlia andalusica	acro moss	4
Pohlia andrewsii	acro moss	?
Pohlia annotina	acro moss	4
Pohlia bulbifera	acro moss	5
Pohlia camptotrachela	acro moss	5
Pohlia cruda	acro moss	4
Pohlia drummondii	acro moss	5
Pohlia elongata (incl. *P. ambigua* and *P. polymorpha*)	acro moss	3
Pohlia filum	acro moss	3
Pohlia lescuriana	acro moss	4
Pohlia longicolla	acro moss	4
Pohlia ludwigii	acro moss	2?
Pohlia lutescens	acro moss	4
Pohlia marchica	acro moss	2
Pohlia melanodon	acro moss	5
Pohlia muyldermansii (*P. flexuosa*)	acro moss	2?
Pohlia nutans (incl. *P. schimperi*)	acro moss	3
Pohlia obtusifolia	acro moss	3
Pohlia proligera	acro moss	3
Pohlia sphagnicola	acro moss	2
Pohlia tundrae	acro moss	3?
Pohlia wahlenbergii	acro moss	5
Polytrichum alpinum	acro moss	2
Polytrichum commune	acro moss	2
Polytrichum formosum	acro moss	3
Polytrichum juniperinum	acro moss	3
Polytrichum longisetum	acro moss	1
Polytrichum pallidisetum	acro moss	2
Polytrichum piliferum var. *piliferum*	acro moss	1
Polytrichum sexangulare	acro moss	2
Polytrichum strictum	acro moss	2
Porella arboris–vitae	folios hepat	3
Porella cordaeana	folios hepat	4
Porella platyphylla	folios hepat	4
Pottia bryoides	acro moss	4
Pottia caespitosa	acro moss	3
Pottia conica	acro moss	5
Pottia davalliana	acro moss	6
Pottia intermedia	acro moss	5
Pottia lanceolata	acro moss	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Pottia mutica	acro moss	4
Pottia recta	acro moss	3
Pottia starckeana	acro moss	5
Pottia truncata	acro moss	6
Preissia quadrata	thall hepat	4
Pseudephemerum nitidum	acro moss	6
Pseudobryum cinclidioides	acro moss	4
Pseudocrossidium hornschuchianum	acro moss	4
Pseudocrossidium revolutum	acro moss	5
Pseudoleskeella catenulata (var. *catenulata*)	pleur moss	4
Pseudoleskeella nervosa	pleur moss	5
Pseudoleskeella rupestris (*P. catenulata* var. *sibirica*)	pleur moss	4?
Pseudoleskeella tectorum	pleur moss	6?
Pterigynandrum filiforme	pleur moss	4
Pterogonium gracile	pleur moss	4
Pterygoneurum lamellatum	acro moss	4
Pterygoneurum ovatum	acro moss	4
Pterygoneurum papillosum	acro moss	4
Pterygoneurum subsessile	acro moss	5
Ptilidium ciliare	folios hepat	2
Ptilidium pulcherrimum	folios hepat	3
Ptilium crista-castrensis	pleur moss	3
Ptychomitrium polyphyllum	acro moss	4
Pylaisia polyantha	pleur moss	6
Pyramidula tetragona	acro moss	4
Racomitrium aciculare	acro moss	5
Racomitrium affine	acro moss	3
Racomitrium aquaticum	acro moss	3
Racomitrium canescens ssp. *canescens*	acro moss	2
Racomitrium elongatum	acro moss	2
Racomitrium ericoides	acro moss	3
Racomitrium fasciculare	acro moss	2
Racomitrium heterostichum	acro moss	2
Racomitrium lanuginosum	acro moss	3
Racomitrium macounii (ssp. *alpinum*)	acro moss	3?
Racomitrium microcarpum	acro moss	3
Racomitrium obtusum	acro moss	3?
Racomitrium sudeticum	acro moss	3
Radula complanata	folios hepat	5
Radula lindenbergiana	folios hepat	3
Reboulia hemisphaerica	thall hepat	4
Rhabdoweisia crenulata	acro moss	3

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Rhabdoweisia crispata	acro moss	3
Rhabdoweisia fugax	acro moss	2
Rhizomnium magnifolium	acro moss	4
Rhizomnium pseudopunctatum	acro moss	5
Rhizomnium punctatum	acro moss	6
Rhodobryum ontariense	acro moss	5
Rhodobryum roseum	acro moss	5
Rhynchostegiella curviseta	pleur moss	6
Rhynchostegiella litorea	pleur moss	5
Rhynchostegiella tenella	pleur moss	4
Rhynchostegiella teneriffae (*Rh. jacquinii*, *Rh. teesdalii*)	pleur moss	4
Rhynchostegium alopecuroides	pleur moss	5
Rhynchostegium confertum	pleur moss	5
Rhynchostegium megapolitanum	pleur moss	4
Rhynchostegium murale	pleur moss	5
Rhynchostegium riparioides	pleur moss	6
Rhynchostegium rotundifolium	pleur moss	6
Rhytidiadelphus loreus	pleur moss	3
Rhytidiadelphus squarrosus	pleur moss	6
Rhytidiadelphus subpinnatus	pleur moss	5
Rhytidiadelphus triquetrus	pleur moss	5
Rhytidium rugosum	pleur moss	2
Riccardia chamaedryfolia	thall hepat	2
Riccardia incurvata	thall hepat	3
Riccardia latifrons	thall hepat	3
Riccardia multifida	thall hepat	4
Riccardia palmata	thall hepat	3
Riccia beyrichiana	thall hepat	4
Riccia bifurca	thall hepat	6
Riccia canaliculata	thall hepat	3
Riccia cavernosa	thall hepat	5
Riccia ciliata	thall hepat	5
Riccia ciliifera (incl. *R. gougetiana*)	thall hepat	2
Riccia crozalsii	thall hepat	4
Riccia fluitans	thall hepat	6
Riccia glauca	thall hepat	4
Riccia gothica	thall hepat	6
Riccia huebeneriana	thall hepat	4
Riccia intumescens (*R. trichocarpa*)	thall hepat	2
Riccia papillosa	thall hepat	3
Riccia rhenana	thall hepat	6?
Riccia sorocarpa	thall hepat	4
Riccia subbifurca sensu Nebel & Philippi	thall hepat	4

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Riccia warnstorfii	thall hepat	5
Ricciocarpos natans	thall hepat	6
Saelania glaucescens	acro moss	4
Sanionia uncinata	pleur moss	4
Sauteria alpina	thall hepat	2
Scapania aequiloba	folios hepat	4
Scapania apiculata	folios hepat	3
Scapania aspera	folios hepat	4
Scapania calcicola	folios hepat	4
Scapania carinthiaca	folios hepat	3
Scapania compacta	folios hepat	2
Scapania curta	folios hepat	2
Scapania cuspiduligera	folios hepat	3
Scapania degenii	folios hepat	3?
Scapania glaucocephala	folios hepat	3
Scapania gymnostomophila	folios hepat	4
Scapania helvitica	folios hepat	2
Scapania irrigua	folios hepat	3
Scapania lingulata	folios hepat	4
Scapania massalongi	folios hepat	3
Scapania mucronata	folios hepat	3
Scapania nemorea	folios hepat	3
Scapania obscura	folios hepat	3
Scapania paludicola	folios hepat	3
Scapania paludosa	folios hepat	2
Scapania parvifolia	folios hepat	?
Scapania praetervisa	folios hepat	4?
Scapania scandica	folios hepat	3
Scapania subalpina	folios hepat	3
Scapania uliginosa	folios hepat	2
Scapania umbrosa	folios hepat	3
Scapania undulata	folios hepat	3
Schistidium apocarpum s. lat.	acro moss	×
Schistidium maritimum	acro moss	3?
Schistidium rivulare s. lat., excl. ssp. *latifolium*	acro moss	4
Schistidium rivulare ssp. *latifolium* (*S. platyphyllum*)	acro moss	6
Schistostega pennata	acro moss	1
Scleropodium cespitans	pleur moss	5
Scleropodium purum	pleur moss	6
Scleropodium touretii	pleur moss	5
Scopelophila cataractae	acro moss	4?
Scorpidium scorpioides	pleur moss	2
Scorpidium turgescens	pleur moss	3
Scorpiurium circinatum	pleur moss	3
Seligera acutifolia	acro moss	4
Seligera brevifolia	acro moss	3?
Seligera calcarea	acro moss	4
Seligera campylopoda	acro moss	3
Seligera donniana	acro moss	3
Seligera irrigata	acro moss	?
Seligera patula	acro moss	3?
Seligera pusilla	acro moss	5
Seligera recurvata var. *recurvata*	acro moss	3
Seligera trifaria (incl. *S. alpestris* and *S. austriaca*)	acro moss	4
Sematophyllum demissum	pleur moss	2
Sematophyllum micans	pleur moss	4
Sphaerocarpos michelii	thall hepat	7
Sphaerocarpos texanus	thall hepat	7
Sphagnum angustifolium	Torf/Sphag	3
Sphagnum auriculatum	Torf/Sphag	2
Sphagnum balticum	Torf/Sphag	2
Sphagnum capillifolium	Torf/Sphag	2
Sphagnum centrale	Torf/Sphag	5
Sphagnum compactum	Torf/Sphag	2
Sphagnum contortum	Torf/Sphag	5
Sphagnum cuspidatum	Torf/Sphag	2
Sphagnum fallax	Torf/Sphag	3
Sphagnum fimbriatum	Torf/Sphag	4
Sphagnum flexuosum	Torf/Sphag	4
Sphagnum fuscum	Torf/Sphag	1
Sphagnum girgensohnii	Torf/Sphag	3
Sphagnum imbricatum	Torf/Sphag	1
Sphagnum inundatum	Torf/Sphag	3
Sphagnum lindbergii	Torf/Sphag	2
Sphagnum magellanicum	Torf/Sphag	1
Sphagnum majus	Torf/Sphag	2
Sphagnum molle	Torf/Sphag	1
Sphagnum obtusum	Torf/Sphag	4
Sphagnum palustre	Torf/Sphag	5
Sphagnum papillosum	Torf/Sphag	2
Sphagnum platyphyllum	Torf/Sphag	6
Sphagnum pulchrum	Torf/Sphag	1
Sphagnum quinquefarium	Torf/Sphag	3
Sphagnum riparium	Torf/Sphag	3
Sphagnum rubellum	Torf/Sphag	1
Sphagnum russowii	Torf/Sphag	3

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Sphagnum squarrosum	Torf/Sphag	4
Sphagnum strictum	Torf/Sphag	2
Sphagnum subnitens	Torf/Sphag	3
Sphagnum subsecundum	Torf/Sphag	3
Sphagnum tenellum	Torf/Sphag	2
Sphagnum teres	Torf/Sphag	5
Sphagnum warnstorfii	Torf/Sphag	4
Splachnum ampullaceum	acro moss	8
Splachnum sphaericum	acro moss	8
Splachnum vasculosum	acro moss	?
Stegonia latifolia	acro moss	4
Targionia hypophylla	thall hepat	4
Taxiphyllum wissgrillii	pleur moss	5
Tayloria acuminata	acro moss	?
Tayloria froelichiana	acro moss	4
Tayloria lingulata	acro moss	5?
Tayloria rudolphiana	acro moss	8
Tayloria serrata	acro moss	9
Tayloria splachnoides	acro moss	9
Tayloria tenuis	acro moss	5
Tetralophozia setiformis	folios hepat	3
Tetraphis pellucida	pleur moss	3
Tetraplodon angustatus	acro moss	9
Tetraplodon mnioides	acro moss	9
Tetraplodon urceolatus	acro moss	8
Tetrodontium brownianum	acro moss	2
Tetrodontium ovatum	acro moss	2
Tetrodontium repandum	acro moss	2
Thamnobryum alopecurum	pleur moss	5
Thuidium abietinum	pleur moss	2
Thuidium delicatulum	pleur moss	5
Thuidium philibertii	pleur moss	4
Thuidium recognitum	pleur moss	2
Thuidium tamariscinum	pleur moss	5
Timmia austriaca	acro moss	4
Timmia bavarica (*T. megapolitana* var. *bavarica*)	acro moss	3
Timmia megapolitana	acro moss	4?
Timmia norvegica	acro moss	4
Tortella bambergeri	acro moss	3
Tortella densa	acro moss	4
Tortella flavovirens	acro moss	2
Tortella fragilis	acro moss	4
Tortella humilis	acro moss	3

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Tortella inclinata	acro moss	3
Tortella inflexa	acro moss	3
Tortella tortuosa	acro moss	3
Tortula aestiva	acro moss	6
Tortula atrovirens	acro moss	2
Tortula brevissima	acro moss	4
Tortula calcicolens	acro moss	4
Tortula canescens	acro moss	3
Tortula cuneifolia	acro moss	4
Tortula inermis	acro moss	3
Tortula intermedia (*T. crinita*)	acro moss	5
Tortula laevipila	acro moss	7
Tortula latifolia	acro moss	6
Tortula lingulata	acro moss	4?
Tortula marginata	acro moss	5
Tortula mucronifolia	acro moss	3
Tortula muralis	acro moss	7
Tortula norvegica	acro moss	?
Tortula obtusifolia	acro moss	5
Tortula pagorum	acro moss	6
Tortula papillosa	acro moss	5
Tortula papillosissima var. *submamillosa*	acro moss	4
Tortula princeps	acro moss	4
Tortula revolvens	acro moss	2
Tortula ruraliformis	acro moss	3
Tortula ruralis	acro moss	7
Tortula subulata	acro moss	5
Tortula vahliana	acro moss	5?
Tortula virescens	acro moss	6
Trematodon ambiguus	acro moss	4
Trichocolea tomentella	folios hepat	5
Trichostomum brachydontium	acro moss	3
Trichostomum crispulum (incl. var. *viridulum*)	acro moss	4
Tritomaria exsecta	folios hepat	4
Tritomaria exsectiformis	folios hepat	4
Tritomaria polita	folios hepat	2
Tritomaria quinquedentata	folios hepat	3
Tritomaria scitula	folios hepat	2
Trochobryum carniolicum	acro moss	?
Ulota bruchii	acro moss	5
Ulota coarctata	acro moss	5
Ulota crispa	acro moss	6
Ulota curvifolia	acro moss	?

(Continues)

TABLE 2 (Continued)

Taxon	Species group	*N* value
Ulota drummondii	acro moss	4
Ulota hutchinsiae	acro moss	3
Ulota macrospora	acro moss	4
Ulota phyllantha	acro moss	5
Ulota rehmannii	acro moss	5?
Weissia brachycarpa (incl. var. *microstoma* [= *W. brachycarpa* var. *obliqua*])	acro moss	5
Weissia condensa	acro moss	5
Weissia controversa (incl. var. *densifolia*)	acro moss	4
Weissia fallax	acro moss	3
Weissia longifolia	acro moss	4
Weissia rostellata	acro moss	4?
Weissia rutilans	acro moss	4
Weissia squarrosa	acro moss	5
Weissia triumphans (*Trichostomum triumphans*)	acro moss	3
Weissia wimmeriana (incl. var. *gymnostoma* [= *W. muralis*])	acro moss	3
Zygodon conoideus	acro moss	7
Zygodon dentatus	acro moss	6
Zygodon forsteri	acro moss	6?
Zygodon gracilis	acro moss	?
Zygodon rupestris	acro moss	5
Zygodon viridissimus (incl. *Z. stirtonii*)	acro moss	6

Species groups: acro mos = acrocarpous mosses; pleur moss = pleurocarpous mosses; folios hepat = foliose hepatics; thall hepat = thallose hepatics; hornworts.

In contrast to most vascular plants, bryophytes take up nutrients not only from the substrate but also directly from precipitation water as well as from airborne dust and aerosols (Frahm, 2001; Vanderpoorten and Goffinet, 2009). Therefore, uptake occurs, besides via mycorrhizal connections and the rhizoidosphere, by means of their complete gametophyte (and probably also sporophyte) surface (Raven et al., 1998; Frahm, 2001; Vanderpoorten and Goffinet, 2009). This way of nutrient uptake is promoted by a high extra- and intracellular cation exchange and ion-binding capacity (Smith, 1982; Daniels and Eddy, 1985; Frahm, 2001; Vanderpoorten and Goffinet, 2009).

Statistical analyses were performed in SPSS (Version 17. SPSS Inc., Chicago, IL, USA). Median values were compared by the Wilcoxon–Mann–Whitney *U* test (MacFarland and Yates 2016) with Bonferroni correction (using the number of pairwise tests; Shaffer 1995).

3 | RESULTS

In total, we compiled *N* values for 1,068 bryophyte taxa: 6 hornworts, 255 liverworts, 35 peat mosses, and 772 mosses (Table 2; Figures 1 and 2). The *N* values showed a clear unimodal distribution. A total of 41 species (3.8%) were classified as indifferent (×; Figure 1). The most frequent *N* values were 3 (316 species) and 4 (284 species), while the mean of *N* values for all species was 3.76.

Grouped by morphology and taxonomy, peat mosses, foliose hepatics, and species with porous leaves (*Sphagnum* sp., *Leucobryum* sp.) had the lowest *N* values (Figures 2–4). No strong differentiation between groups according to Red List status was found (Figure 5). With respect to ecological groups, the lowest *N* values were found for species from aquatic to wet sites and the highest *N* values were obtained for species with "unspecific" ecological requirements (Figure 6). Annual species had the highest and species with indefinite growth the lowest *N* values (Figure 7).

4 | DISCUSSION

The distribution of *N* values for bryophytes along the gradient (Figure 1) differs from that of vascular plants (Ellenberg, 2001) and macromycetes (Simmel et al., 2017). For vascular plants, the largest proportion of species have a nutrient indicator value 2 and the graph

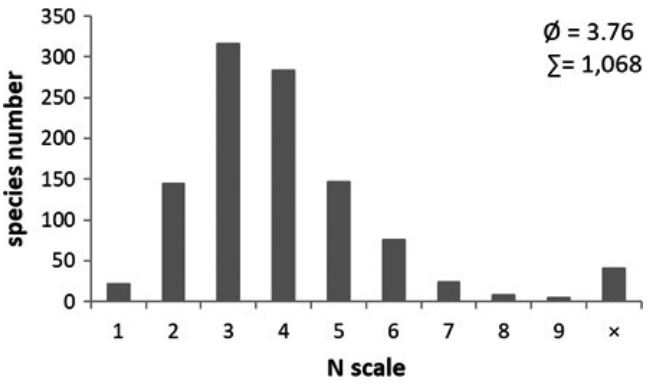

FIGURE 1 Numbers of bryophyte species by *N* values and number of species classified as indifferent (×)

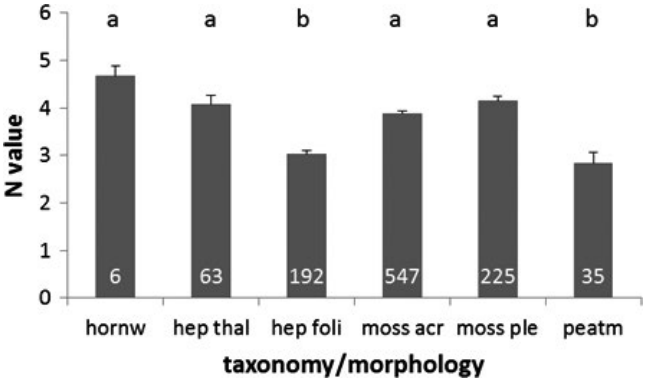

FIGURE 2 Mean *N* values ± *SE* and species numbers of bryophytes grouped by taxonomic or morphologic criteria, i.e., into hornworts, thallose hepatics, foliose hepatics, acrocarpous mosses, pleurocarpous mosses, and peat mosses. Different letters indicate significant differences (Wilcoxon–Mann–Whitney *U* test with Bonferroni correction; $p < 0.0033$)

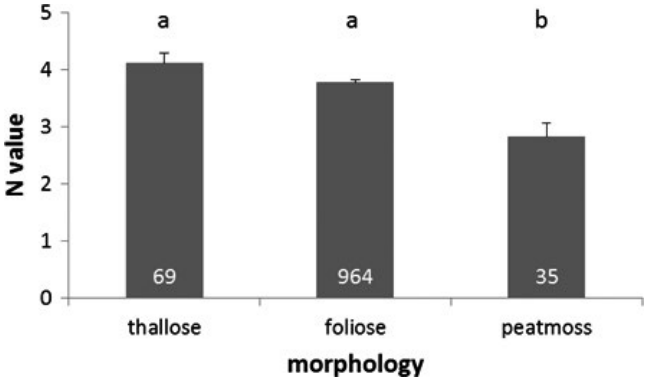

FIGURE 3 Mean *N* values ± *SE* and species numbers of bryophytes grouped by morphologic criteria, i.e., into thallose (hornworts and hepatics), foliose (hepatics and mosses), and peat moss species. Different letters indicate significant differences (Wilcoxon–Mann–Whitney *U* test with Bonferroni correction; $p < 0.0167$)

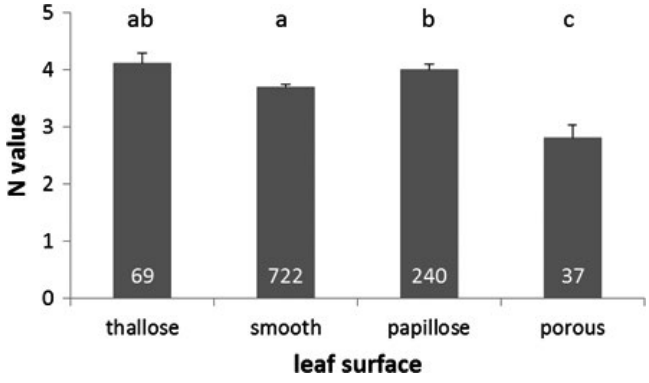

FIGURE 4 Mean *N* values ± SE and numbers of bryophyte species grouped by leaf surface criteria into thallose species and foliose species with smooth, papillose to mamillose, or porous (hyalocysts with pores) leaf surfaces. Different letters indicate significant differences (Wilcoxon–Mann–Whitney *U* test with Bonferroni correction; $p < 0.0083$)

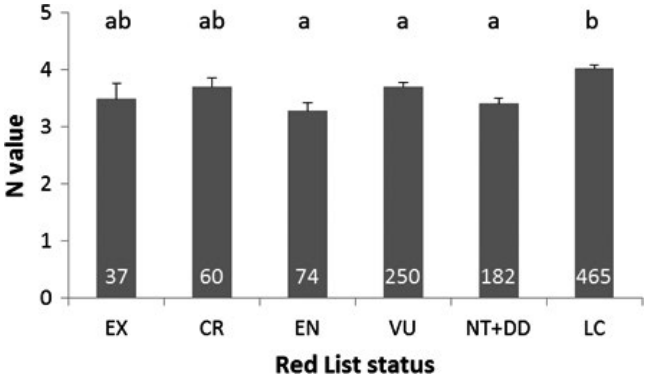

FIGURE 5 Mean *N* values ± *SE* and species numbers of bryophyte species grouped by Red List status into EX (extinct), CR (critically endangered), EN (endangered), VU (vulnerable), NT + DD (not threatened, data deficient) and LC (least concern). Different letters indicate significant differences (Wilcoxon–Mann–Whitney *U* test with Bonferroni correction; $p < 0.0033$)

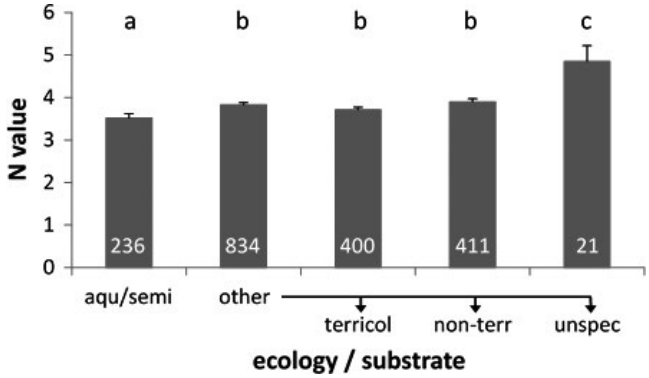

FIGURE 6 Mean *N* values ± *SE* and numbers of bryophyte species grouped by ecology/substrate into (i) species of aquatic to semiterrestric habitats or (ii) other, drier habitats; the latter divided into terricolous, non-terricolous (rock, bark, dead wood, dung, etc.), hypogeic (not shown; only comprising *Cryptothallus mirabilis*, classified as ×), and ecologically unspecific species. Different letters indicate significant differences [Wilcoxon–Mann–Whitney *U* test; (i) $p < 0.05$; (ii) with Bonferroni correction, $p < 0.0083$]

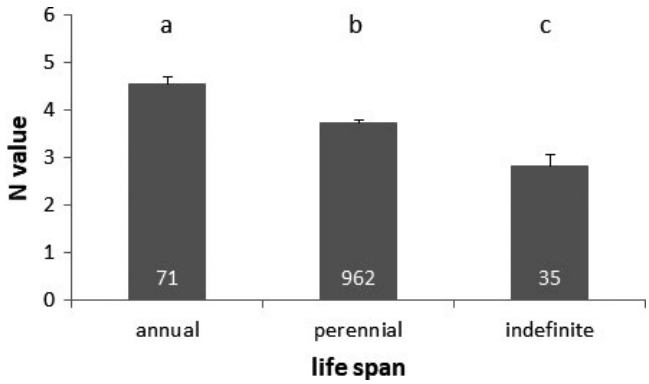

FIGURE 7 Mean *N* values ± *SE* and species numbers of bryophytes grouped by life span, i.e., into winter or summer annual, pauci- to pluriennial or indefinite, and rhizoidlessly tip-growing (*Sphagnum* spec.). Different letters indicate significant differences (Wilcoxon-Mann-Whitney *U* test with Bonferroni correction; $p < 0.0167$)

shows a clear positive skew, whereas for macromycetes, the largest number of species occurs for a *N* value of 6 and the graph shows a more even distribution. The distribution of values for bryophytes is somewhere in between these extremes, with its largest species number at 3 and a clearly unimodal shape.

The comparison of taxonomical and morphological groups (Figures 2, 3, 4) shows that *N* values for the hornwort, thallose liverwort, and moss groups are similar, while values for peat mosses and foliose liverworts are significantly lower. For species of *Sphagnum* and, to a lesser extent, *Leucobryum*, this is due to their adaptation to extremely nutrient-poor habitats with the porous hyaline cells of their leaves in combination with highly effective cation exchange mechanisms (Smith, 1982; Andrus, 1986; Hölzer, 2010; Simmel and Poschlod, 2017). Foliose liverworts lack such adaptations and the species of this group occur over a wide range

of substrates in various habitats. This group may tend to avoid interaction with other plants and prefer colder sites with a relatively short vegetation period (cf. Vanderpoorten and Goffinet, 2009) rather than avoid nutrient-richer substrates as such. This topic warrants further studies.

Interestingly, and contrary to our expectations, we find no strong differentiation of mean *N* among Red List categories (Figure 5). Even though the species of least concern (LC) on average have the highest *N* values, the mean value of LC species does not differ significantly from that of species classified as extinct or critically endangered. Nutrient availability thus does not itself seem to be the (main) driver of threat to bryophytes, although Vanderpoorten and Goffinet (2009) emphasise the importance of degradation and loss of actual and potential habitats (which is, of course, also influenced by anthropogenic nutrient input to ecosystems).

With respect to substrate preferences (Figure 6), aquatic species have on average the lowest and indifferent species the highest *N* values. Among life forms (Figure 7), the highest mean *N* value is found for annual species. The low *N* value for aquatic species most likely results from the permanently wet conditions and, thus, the constant supply of nutrients from the surrounding water in combination with a markedly prolonged vegetation period; both allow for a continuous nutrient uptake but at low rates, while species from drier habitats have to take up nutrients during the short(er) times of turgescence. Furthermore, by their ability to colonise rather nutrient-poor water bodies, aquatic bryophytes can avoid interactions with vascular plants. This accords with the high mean *N* value found for the unspecific species, which have to cope with very different conditions regarding water availability, competition, and substrate composition (Frahm, 2001; Vanderpoorten and Goffinet, 2009). The life-form analysis conceals the fact that a large share of bryophyte species (and not only *Sphagnum* species which were treated separately in the analyses due to their specific morphological characteristics, including lack of rhizoids) can grow indefinitely old by means of their protonema and/or their thallus. Nevertheless, it demonstrates a clear correlation between maximum age and nutrient requirements which most likely is brought about by annual species having to produce gameto- and sporophytes within a very short time and hence have a larger demand for nutrients in this period, whereas long-living species can maintain life by lower growth rates and, hence, with lower demands on nutrients.

The EIV concept has repeatedly been criticised for the predominantly subjective assignment of values to species and for some potential pitfalls in the application and analyses of EIV values (Böcker et al. 1983; Kowarik and Seidling 1989; Diekmann 2003). Although the EIV values are obtained by a combination of actual measurements and expert judgements (or by expert judgements only) the unique quality of the EIV concept is to integrate information about the species' relationship to its surroundings over geographical ranges, habitats and time periods. Such integration is hardly possible in other ways. Furthermore, indicator systems like the one named after Ellenberg have been underpinned by strong correlations between EIVs and actual measurements — see the literature references and discussions in Ellenberg et al. (2001), Diekmann (2003) and Simmel et al. (2017). This is why EIV values are regarded as a valuable tool and widely used in applied ecology (e.g. Bratli et al., 2006; Chytrý et al., 2009; Bartelheimer and Poschlod, 2016), also outside of Central Europe (Shipley et al., 2017; Hedwall et al., 2019).

With respect to nutrient requirements of bryophytes it is important to distinguish between the qualitative and quantitative needs. Bryophytes have been shown to have, qualitatively, nutrient requirements that are very similar to those of vascular plants, both with respect to macronutrients such as nitrogen and phosphorus, and micronutrients such as sulphur (Frahm, 2001; Vanderpoorten and Goffinet, 2009). However, regarding quantitative nutrient requirements, previous studies have come to largely different results and conclusions. While many studies show that excess nutrient supplies hinder growth or even have harmful or lethal effects, a variety of patterns have been shown for growth rate, nutrient uptake, and potential effects of interaction with taller (i.e., mostly vascular) plants (e.g. Smith, 1982; Bates and Bakken, 1998; Bergamini and Pauli, 2001; Aude and Ejrnaes, 2005; Ingerpuu et al., 2005; van der Wal et al., 2005; Botting and Fredeen 2006; Vanderpoorten and Goffinet, 2009). As a consequence, bryophytes' growth as well as their interaction with vascular plants may be affected by nutrient levels in many different ways. Moreover, most studies have addressed effects of nitrogen and fertiliser mixtures with macronutrients, not the effects of micronutrients alone. Accordingly, in line with observations and considerations in the literature (e.g. Ellenberg, 2001; Wirth, 2001; Landolt, 2010; Simmel et al., 2017), we consider the *N* values for bryophytes provided in this paper as expressions of the species' response to the availability of the sum of nutrients, and not to one single nutrient (such as, e.g., nitrogen).

These *N* values should be considered a first approach to this end. Accordingly, corrections and contributions will be greatly appreciated.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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REFERENCES

Andrus, R.E. (1986) Some aspects of Sphagnum ecology. *Canadian Journal of Botany*, 64, 416–426. https://doi.org/10.1139/b86-057

Aude, E. & Ejrnaes, R. (2005) Bryophyte colonisation in experimental microcosms: the role of nutrients, defoliation and vascular vegetation. *Oikos*, 109, 323–330. https://doi.org/10.1111/j.0030-1299.2005.13268.x

Bartelheimer, M. & Poschlod, P. (2016) Functional characterizations of Ellenberg Indicator Values – a review on ecophysiological determinants. *Functional Ecology*, 30, 506–516. https://doi.org/10.1111/1365-2435.12531

Bates, J.W. & Bakken, S. (1998) Nutrient retention, desiccation and redistribution in mosses. In: Bates, J.W., Ashton, N.W. and Duckett, J.G. (Eds.) *Bryology for the twenty-first century*. Boca Raton, London: CRC Press and the British Bryological Society, pp. 293–304.

Bergamini, A. & Pauli, D. (2001) Effects of increased nutrient supply on bryophytes in montane calcareous fens. *Journal of Bryology*, 23, 331–339. https://doi.org/10.1179/jbr.2001.23.4.331

Böcker, R., Kowarik, I. & Bornkamm, R. (1983) Studies on the application of Ellenberg indicator values (German). *Verhandlungen der Gesellschaft für Ökologie*, 11, 35–56.

Botting, R.S. & Fredeen, A.L. (2006) Contrasting terrestrial lichen, liverwort, and moss diversity between old-growth and young second-growth forest on two soil textures in central British Columbia. *Canadian Journal of Botany*, 84, 120–132. https://doi.org/10.1139/b05-146

Bratli, H., Økland, T., Økland, R.H., Dramstad, W.E., Elven, R., Engan, G., Fjellstad, W., Heegaard, E., Pederson, O. & Solstad, H. (2006) Patterns of variation in vascular plant species richness and composition in SE Norwegian agricultural landscapes. *Agriculture, Ecosystems & Environment*, 114(2–4), 270–286. https://doi.org/10.1016/j.agee.2005.10.022

Burton, M.A.S. (2008) Terrestrial and aquatic bryophytes as monitors of environmental contaminants in urban and industrial habitats. *Botanical Journal of the Linnean Society*, 104, 267–280. https://doi.org/10.1111/j.1095-8339.1990.tb02222.x

Chytrý, M., Hejcman, M., Henneksen, S.M. & Schellberg, J. (2009) Changes in vegetation types and Ellenberg indicator values after 65 years of fertilizer application in the Rengen Grassland Experiment, Germany. *Applied Vegetation Science*, 12, 167–176. https://doi.org/10.1111/j.1654-109X.2009.01011.x

Daniels, R.E. & Eddy, A. (1985) *Handbook of European Sphagna*. Huntingdon: Institute of Terrestrial Ecology.

Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology*, 4, 493–506. https://doi.org/10.1078/1439-1791-00185

Düll, R. (2001) Indicator values of mosses and liverworts (German). In: Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. and Werner, W. (Eds.) *Indicator values of plants in Central Europe (German)*. Erich Goltze: Göttingen, pp. 175–220.

Ellenberg, H. (1974) *Indicator Values of the Vascular Plants of Central Europe (German)*. Göttingen: Erich Goltze.

Ellenberg, H. (2001) Indicator values of vascular plants (except *Rubus*) (German). In: Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. and Werner, W. (Eds.) *Indicator Values of Plants in Central Europe (German)*. Erich Goltze: Göttingen, pp. 9–166.

Frahm, J.-P. (2001) *Biology of Bryophytes (German)*. Heidelberg, Berlin: Spektrum Akademischer Verlag.

Frahm, J.-P. & Frey, W. (2004) *Bryophyte flora (German)*, 4th edition. Stuttgart: Ulmer.

Frey, W., Frahm, J.-P., Fischer, E. & Lobin, W. (Eds) (2006) *The Liverworts, Mosses and Ferns of Europe*. Martins, Great Horkesley: Colchester Harley: Books.

Hedwall, P.-O., Brunet, J. & Diekmann, M. (2019) With Ellenberg indicator values towards the north: Does the indicative power decrease with distance from Central Europe? *Journal of Biogeography*, 46, 41–53. https://doi.org/10.1111/jbi.13565

Hill, M.O. & Carey, P.D. (1997) Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. *Journal of Vegetation Science*, 8, 579–586. https://doi.org/10.2307/3237210

Hill, M.O., Preston, C.D., Bosanquet, S.D.S. & Roy, D.B. (2007) *BRYOATT – Attributes of British and Irish Mosses, Liverworts and Hornworts*. Peterborough: NERC, Centre for Ecology & Hydrology.

Hill, M.O., Roy, D.B. & Preston, C. (2005) Appendix 10: Development of environmental indices (Ellenberg-style scores) for British bryophytes. In: Smart, S., Evans, C., Rowe, E., Wamelink, W., Wright, S., Scott, A., Roy, D., Preston, C., Hill, M., Rothery, P., Bullock, J., Moy, I., Emmett, B. and Maskell, L. (Eds.) *Final report to Department of the Environment, Food and Rural Affairs, Joint Nature Conservation Committee and English Nature*. pp. 116–123.

Hölzer, A. (2010) *The peatmosses of southern Germany and adjacent regions (German)*. Jena: Weissdorn-Verlag.

Huber, A. (1998) The bryophytes of the area of Regensburg and how they can be used as bio-indicators of radiocesium (German). *Hoppea*, 59, 1–704.

Ingerpuu, N., Liira, J. & Pärtel, M. (2005) Vascular plants facilitated bryophytes in a grassland experiment. *Plant Ecology*, 180, 69–75. https://doi.org/10.1007/s11258-005-2508-0.

Kowarik, I. & Seidling, W. (1989) Computing of Ellenberg indicator values – on problems and limitations of a meaningful method (German). *Landschaft und Stadt*, 21, 132–143.

Landolt, E. (Ed.) (2010) *Flora Indicativa. Ecological indicator Values and Biological Traits of the Flora of Swiss and the Alps (German)*. Bern: Haupt.

Landolt, E. (1977) *Ecological Indicator Values of the Swiss Flora (German)*. Zürich: Geobotanisches Institut der ETH, Stiftung Rübel.

MacFarland, T.W. & Yates, J.M. (2016) Mann-Whitney U test. In: MacFarland, T.W. and Yates, J.M. (Eds.) *Introduction to Nonparametric Statistics for the Biological Sciences Using R*. Cham: Springer: pp. 103–132. https://doi.org/10.1007/978-3-319-30634-6_4.

Mäkipää, R. (1995) Sensitivity of forest-floor mosses in boreal forests to nitrogen and sulphur deposition. *Water, Air, and Soil Pollution*, 85, 1239–1244. https://doi.org/10.1007/BF00477151.

Nash, III T.H. & Wirth, V. (Eds) (1988) *Lichens, Bryophytes and Air Quality*. Stuttgart: Schweizerbart.

Nebel, M. & Philippi, G. (Eds) (2000) *The bryophytes of Baden-Württemberg*, Vol. 1 (German). Stuttgart: Ulmer.

Nebel, M. & Philippi, G. (Eds) (2001) *The bryophytes of Baden-Württemberg*, Vol. 2 (German). Stuttgart: Ulmer.

Nebel, M. & Philippi, G. (Eds) (2005) *The bryophytes of Baden-Württemberg*, Vol. 3 (German). Stuttgart: Ulmer.

Raven, J.A., Griffiths, H., Smith, E.C. & Vaughn, K.C. (1998) New perspectives in the biophysics and physiology of bryophytes. In: Bates, J.W., Ashton, N.W. and Duckett, J.G. (Eds.) *Bryology for the Twenty-First Century*. Boca Raton, London: CRC Press and the British Bryological Society, pp. 261–275.

Shaffer, J.P. (1995) Multiple hypothesis testing. *Annual Review of Psychology*, 46, 561–584.

Shipley, B., Belluau, M., Kühn, I., Soudzilovskaia, N.A., Bahn, M., Penuelas, J., Kattge, J., Sack, L., Cavender-Bares, J., Ozinga, W.A., Blonder, B., van Bodegom, P.M., Manning, P., Hickler, T., Sosinski, E., De Patta Pillar, V., Onipchenko, V. & Poschlod, P. (2017) Predicting habitat affinities of plant species using commonly measured functional traits. *Journal of Vegetation Science*, 28, 1082–1095. https://doi.org/10.1111/jvs.12554

Simmel, J., Bässler, C. & Poschlod, P. (2017) Ellenberg indicator values for macromycetes – a methodological approach and first applications. *Fungal Ecology*, 27, 202–212. https://doi.org/10.1016/j.funeco.2016.09.004

Simmel, J. & Poschlod, P. (2017) Contributions on the ecology of Central European *Leucobryum* taxa and their determination (German). *Herzogia*, 30, 397–411.

Smart, S.M., Scott, W.A., Whitaker, J., Hill, M.O., Roy, D.B., Critchley, C.N., Marini, L., Evans, C., Emmett, B.A., Rowe, E.C., Crowe, A., Le Duc, M. & Marrs, R.H. (2010) Empirical realised niche models for British higher and lower plants – development and preliminary testing. *Journal of Vegetation Science*, 21, 643–656. https://doi.org/10.1111/j.1654-1103.2010.01173.x

Smith, A.J.E. (1982) *Bryophyte Ecology*. London, New York: Chapman and Hall.

Urmi, E. (2010) Bryophyta. In Landolt, E. (Ed), *Flora Indicativa. Ecological indicator values and biological traits of the flora of Swiss and the Alps (German)*. Bern: Haupt, pp. 283–310.

Vanderpoorten, A. & Goffinet, B. (2009) *Introduction to Bryophytes*. Cambridge: Cambridge University Press.

Vust, M. (2010) Lichenes. In E. Landolt (Ed.), *Flora Indicativa. Ecological Indicator Values and Biological Traits of the Flora of Swiss and the Alps (German)*. Bern: Haupt, pp. 311–320.

van der Wal, R., Pearce, I.S.K. & Brooker, R.W. (2005) Mosses and the struggle for light in a nitrogen-polluted world. *Oecologia*, 142, 159–168. https://doi.org/10.1007/s00442-004-1706-0

Wagner, M., Kahmen, A., Schlumprecht, H., Audorff, V., Perner, I., Buchmann, N. & Weisser, W. (2007) Prediction of herbage yield in grassland: how well do Ellenberg N-values perform? *Applied Vegetation Science*, 10, 15–24. https://doi.org/10.1111/j.1654-109X.2007.tb00499.x

Wirth, V. (2001) Indicator values of lichens (German). In: Ellenberg, H., Weber, H.E., Düll, R., Wirth, V. and Werner, W. (Eds.) *Indicator Values of Plants in Central Europe (German)*. Erich Goltze: Göttingen, pp. 221–243.

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