



Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia

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Dead wood is an important habitat feature for lichens in forest ecosystems, but little is known about how many and which lichens are dependent on dead wood. We reviewed substrate use by epiphytic lichens in the combined floras of Fennoscandia and the Pacific Northwest of North America based on literature and herbarium data and analyzed substrate affinity relative to life form, reproductive mode and major phylogenetic group within the floras. A total of 550 (43%) of the 1271 epiphytic species in the combined floras use wood, and 132 species (10%) are obligately associated with dead wood in one or both regions. Obligate and facultative wood-dwelling guilds in the two floras were strongly similar in terms of internal guild structure in each region, but differ somewhat in species composition, while the bark-dwelling guild differs strongly in both. Most obligate dead wood users are sexually reproducing crustose lichens. The largest numbers of species are associated with forest structural features such as logs and snags that have been greatly reduced by forest practices. Conservation of lichens inhabiting wood requires greater attention to crustose lichen species and the development of conservation strategies that look beyond numbers and volumes of dead wood and consider biologically meaningful dead wood structure types.

Dead wood is a primary habitat for many organisms, including invertebrates (Berg et al. 1994, Grove 2002), macrofungi (Bader et al. 1995, Ódor et al. 2006), myxomycetes (Ing 1994), bryophytes (Söderström 1988, Anderson and Hytteborn 1991) and lichens (Löhmus and Löhmus 2001). Forest practices have significantly reduced amounts of dead wood over large areas of nemoral and boreal forests (Angelstam 1997, Linder and Östlund 1998, Wilhere 2003). Many researchers have found a link between reduction in dead wood and declines in wood-dependent species, particularly those dependent on wood of certain size or decay classes (Warren and Key 1991, Amaranthus et al. 1994, Siitonen 2001). More recently, there has been increased investment in developing forestry methods that take habitat structure of these organisms into consideration (Rosenvald and Löhmus 2008), especially for snag-dependent birds (Walter and Maguire 2005, Hutto 2006) and invertebrates (Hyvärinen et al. 2006, Tero and Kotiaho 2007, Davies et al. 2008). There have been few such studies for lichens, concentrating mainly on logs (Bunnell et al. 2008) and stumps (Caruso et al. 2008). Concerns about impacts of forest practices on lichens have instead focused more on the value of old-growth forests (Rose 1992, Tibell

1992, Goward 1994). As the pressure increases to extract dead wood for salvage or as a source of energy, all organisms relying on it will be impacted. The number of lichen species potentially affected is unknown.

Lignicolous (wood-dwelling or saproxylic) lichens are often overlooked in reviews of dead wood as habitat (e.g. Harmon et al. 1986). Dependence of some lichen species on dead wood is well established (Darbishire 1914, Räsänen 1927), but the number of species and types of specific habitat affinities are unknown. Data on lignicolous lichens must be gleaned from anecdotal accounts scattered throughout the taxonomic and floristic literature, or from broader, forest stand-level ecological studies. In most, lignicolous lichens are treated among other epiphytic species. Most ecological research specific to lignicolous lichens and their substrate has been limited to regional case studies, almost all from northern Europe. These studies have documented the richness of lichens on dead wood in forest environments (Forsslund and Koffman 1998, Krüys et al. 1999, Jansová and Soldán 2006, Nascimbene et al. 2008) or on secondary, anthropogenic wood substrates such as barns (Svensson et al. 2005) as well as differences between various types of dead wood (Löhmus and Löhmus 2001). To date, however,

a comprehensive review of dead wood-dependent lichens has not been published for any larger geographic area.

Our intent is to provide an overview of lignicolous lichens as an aid in circumscribing them as a group for conservation, research and management. Using two well studied northern epiphytic lichen floras, that of the Pacific Northwest of North America (hereafter PNW) and Fennoscandia (FS), we a) assess how many species are facultatively and obligately dependent on wood; b) characterize the biology of these species based on life form, reproductive strategy and phylogenetic group; and c) catalog what is known about different dead wood microsites they use. Finally we examine the relevance of our findings in light of current conservation and management approaches.

Materials and methods

Study areas and species included

Our decision to base analysis of species on the PNW and Fennoscandia was based on two considerations: 1) the knowledge of the lichen flora of both regions is relatively good in terms of both species and substrates used; and 2) both regions are large enough to provide a comprehensive overview. The PNW as defined here includes British Columbia, Washington, Oregon, California north of 37°N, Idaho and western Montana, an area of ca 1.89 million km². Fennoscandia has a total area of ca 1.17 million km² and is defined here as including Norway, Sweden and Finland. Both regions occupy large areas on the eastern side of large oceans and are mountainous, but also have broad differences. The PNW includes large areas of nemoral vegetation and Mediterranean climate, with a humidity gradient from arid to rain forest. Fennoscandia is arctic-boreal with only minor areas of nemoral vegetation that has been heavily impacted by humans and no arid land. Nearly all of Fennoscandia was glaciated in the last glacial period, whereas areas of the PNW south of about 47°N were not. Partly because of their different glacial histories, the number of tree species is much higher in the PNW. We included all lichenized fungi as well as non-lichenized calicioid fungi traditionally studied by lichenologists (hereafter “lichens”). Non-calicioid lichenicolous fungi are not included.

Data set

We initially assessed two parallel databases of lichen-substrate affinities, one for the PNW and one for Fennoscandia. Lacking a consolidated regional checklist for the PNW, we assembled our database from a variety of sources: for macrolichens Goward et al. (1994), McCune and Geiser (1997), and Goward (1999) and recent articles; for calicioid fungi Goward (1999) and Rikkinen (2003a, b, c); and for crustose species Spribille (2006) and subsequent publications (Spribille and Björk 2008, Spribille et al. 2009). The PNW database contained 866 species. For Fennoscandia, the database was derived from Santesson et al. (2004) and recent updates (Svensson 2007); *Xylographa corrugans* will soon be reported as occurring in Fennoscandia and is therefore included. A total of 900

species were included in the latter database. The two databases were subsequently combined.

Substrate data specific to each of the two regions were derived from a review of the literature and herbarium specimens. In the course of developing lichen floras for the PNW, three of us (TS, CB and TG) had a large amount of published and unpublished substrate data at our disposal. For Fennoscandian species, literature data on substrate were derived from Foucard (2001), Santesson et al. (2004) and unpublished data (GT). All epiphytic species were noted as occurring on one or more of five substrates: wood, bark, resin, conifer needles or other lichens; rock- and soil-dwelling species with <1% of their occurrences on any one of those substrates were excluded. Using these assignments, we classified epiphytic lichens into three substrate guilds for each region: 1) “obligate lignicoles” (species with >99% of their occurrences on wood in at least one region); 2) “facultative lignicoles” (defined as all other species found on wood plus other substrates such as rock and/or soil and/or bark); and 3) “corticoles” (defined as all remaining epiphyte species, including both obligate and facultative corticoles). To take into account species common to both regions but with different guild assignments in each, guild numbers and ratios were calculated individually for each region or, when considering ratios of the combined floras, guild assignments were calculated sequentially as all species obligately lignicolous in one or both regions; then all species facultatively lignicolous in one or both regions. All remaining species are thus corticolous in one or both regions.

For obligate lignicoles, we also identified specific habitat microsite types wherever possible based on available literature, herbarium data and our own field experience (microsite types with <1% of the occurrences are not included). All obligately lignicolous species were furthermore assigned as occurring on conifers (C) and/or angiosperms (A) using a minimum 1% occurrence threshold.

Data analysis

To examine patterns underlying lignicole biology, we analyzed guild assemblage structure based on three species characteristics. First, we examined the relative proportions of three different lichen life forms: 1) macrolichens (species with three-dimensional aerial thalli, including all foliose, fruticose and squamulose species; Goward et al. 1994, Goward 1999, except for *Hypocenomyce*, which is treated as a microlichen in accordance with Fennoscandian traditions); and 2) microlichens (species with thalli so closely attached that their removal requires lifting of the substrate), subdivided for the purposes of analysis into a) calicioid crusts (hereafter “calicioids”; species bearing either stalked fruiting structures and/or loose spore masses; Tibell and Wedin 2000); and b) non-calicioid crustose lichens (hereafter “crusts”). Macrolichens, calicioids and crusts each have a distinctly different gross morphology, and thus can be thought of as functional groups. None, however, represents a natural monophyletic group.

Our second analysis examined whether certain reproductive modes occur more often among lignicoles than in

other guilds. We recognized four reproductive modes: 1) sexual, reproducing via spores (*Cheiromycina* and *Szczawinskia*, two small genera reproducing by conidia, are lumped in here for convenience); 2) asexual via soredia or gonocysts (e.g. *Micarea bedlundii*) (hereafter “soredia”); 3) asexual via isidia; and 4) asexual via coarse thallus fragments. Species that reproduce both by spores and asexual reproductive structures were assigned to the species’ main reproductive strategy.

The third analysis examined substrate affinity by higher level taxonomic grouping. Each species was assigned to its taxonomic order, where known. Although 15 orders are represented, the large majority of epiphytic lichens belong to a single order, Lecanorales. To improve the resolution of our analysis we analyzed members of Lecanorales additionally at the level of family. All taxonomic assignments follow Lumbsch and Huhndorf (2007) and subsequent phylogenetic revisions (Lumbsch et al. 2008).

Statistical analyses were restricted to chi-squared tests of relative distributions of features of the lichen flora in the two areas. Tests employed numbers of species, not percentages.

Results

Species pool

Combining the epiphytic floras of the Pacific Northwest and Fennoscandia yields a pool of 1271 species, including 531 species (42%) found in both regions (Table 1). Of the combined floras, a total of 550 species (43%) are found on wood, 132 (10%) of them as obligate lignicoles in at least one of the two regions and 418 as facultative lignicoles. The remaining 721 species (57%) of the pooled flora are corticoles (Table 1). The high percentage of species on dead wood (facultative and obligate lignicoles) is reflected in each flora individually: a total of 349 species have been recorded on dead wood in the PNW and 378 in Fennoscandia. There are 67 species of obligate lignicoles in the PNW of which 18 are unique to the PNW. Fennoscandia has 97 species of obligate lignicoles; 49 of these are unique to Fennoscandia (Table 1 and Supplementary material, Appendix 1). In terms of the relative numbers of obligate lignicoles, facultative lignicoles and

corticoles, the two floras do not differ significantly ($\chi^2 = 4.86$, 2 DF, $p = 0.088$).

The lignicolous lichen floras of the PNW and Fennoscandia are more similar to each other than are the corticole floras. Of the 132 species identified as obligate lignicoles in the pooled data set, a total of 65 (50%) are shared by both floras: 33 as obligate lignicoles in only one of the two regions, 32 as obligate lignicoles in both (Supplementary material, Appendix 1). Among facultative lignicoles, the percentage of shared species is similar (62%, 261 species); the combined total of facultative and obligate lignicoles common to the two floras is 326 species, or 59%. This stands in contrast to the corticole flora: of the 721 corticole species in the pooled floras, only 205 (28%) are found in both regions (Table 1).

Guild assemblage structure

Although relative numbers of obligate and facultative lignicoles and corticoles do not differ overall between the two regions, life forms are represented differently. The majority of obligate lignicoles are microlichens, including crusts (PNW 61%; FS 77% of lignicole species) and calicioids (PNW 33%; FS 16%; Fig. 1). There are only few obligately lignicolous macrolichens, all of them from the genus *Cladonia*. In the two other guilds, by contrast, macrolichens constitute a greater proportion of species: 25% (PNW) and 30% (FS) of facultative lignicoles are macrolichens, as well as 25% of corticoles in Fennoscandia and 50% in the PNW. Crusts are likewise well represented with 62% (PNW) and 58% (FS) of facultative lignicoles and 45% (PNW) and 71% (FS) of corticoles. Calicioids comprise a similar number of species in each guild, but they are proportionally better represented among obligate lignicoles (see above) than among facultative lignicoles (PNW 13%; FS 12%) and corticoles (PNW 5%; FS 4%; Fig. 1). The comparative macrolichen/crust/calicioid ratios differ significantly when the two epiphytic floras are compared as a whole ($\chi^2 = 44.1$, DF = 2, $p = 0.001$). Within guilds there is a significant difference in the ratios of the three life forms between regions for corticoles ($\chi^2 = 71.4$, 2 DF, $p < 0.001$) but not for facultative lignicoles ($p = 0.32$) and marginally for obligate lignicoles ($\chi^2 = 6.0$, DF = 2, $p = 0.05$).

Table 1. Numbers of lichen species by guild in the Pacific Northwest (PNW) and Fennoscandia (FS) and their percentages of each line category (in parentheses).

	A – Obligate lignicoles	B – Facultative lignicoles	C – Total wood users (A+B)	D – Corticoles	E – Total number of epiphytes (A+B+D)
Individual floras					
1) Total PNW flora	67 (7.7)	282 (32.6)	349 (40.3)	517 (59.7)	866
2) Total FS flora	97 (10.8)	281 (31.2)	378 (42.0)	522 (58.0)	900
Combined floras					
3) Species found only in PNW	18 (5.2)	81 (23.5)	99 (28.8)	245 (71.2)	344
4) Species found only in Fennoscandia	49 (12.4)	76 (19.2)	125 (31.6)	271 (68.4)	396
5) Species found in both regions: combined guild assignments*	65 (12.2)	261 (49.2)	326 (61.4)	205 (38.6)	531
6) Total combined floras [(3)+(4)+(5)]	132 (10.4)	418 (32.9)	550 (43.3)	721 (56.7)	1271

*guild assignments are calculated sequentially as all species obligately lignicolous in one or both regions, then all facultatively lignicolous species in one or both regions; all remaining species are corticolous in one or both regions.

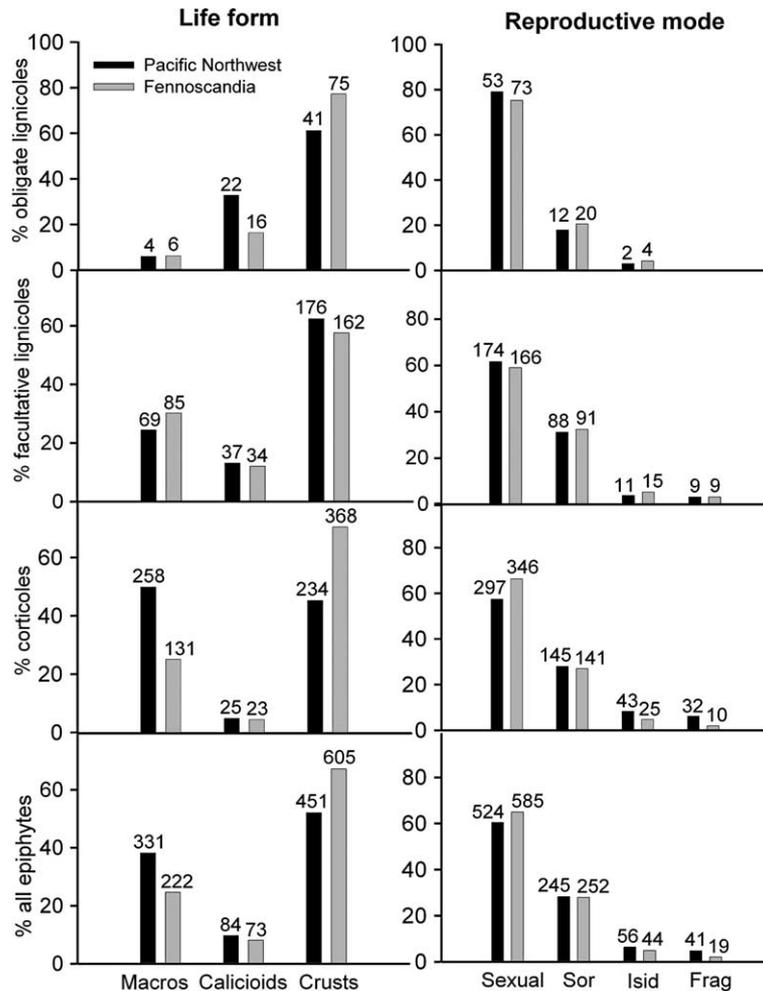


Figure 1. Proportions of life forms and reproductive modes by guild. Numbers above bars represent absolute species numbers. Reproductive mode abbreviations: sexual = spore dispersal; sor = sorediate; isid = isidiate; frag = fragmenting.

Sexually reproducing species account for over 75% of the obligate lignicole flora (Fig. 1). This is substantially more than among facultative lignicoles and corticoles, in which proportions of sexually reproducing species vary from 57 to 66%. It follows that species reproducing asexually by means of soredia, isidia or fragmentation are poorly represented among obligate lignicoles (sorediate spp. PNW 18%, FS 21%; isidiate spp. PNW 3%, FS 4%) but proportionally greater among facultative lignicoles (sorediate spp. PNW 31%, FS 32%, isidiate spp. PNW 4%, FS 5%) and corticoles (sorediate spp. PNW 28%, FS 27%, isidiate spp. PNW 8%, FS 5%). Of the three modes of asexual reproduction within the pooled floras of the two regions, by far the most disperse by soredia; species that reproduce by isidia constitute only just under 6% of the pooled floras (75 species) and are most numerous among corticoles. An even smaller percentage (4%, 46 species) reproduce by fragmentation, mainly macrolichen species of the genera *Bryoria*, *Cladonia* and *Usnea*. The ratios of the four reproductive modes differ between the two regions ($\chi^2 = 12.3$, DF = 3, $p = 0.006$), with Fennoscandia having more sexual and fewer asexually reproducing species. Within obligate and facultative lignicoles there is no significant difference in the relative proportions of repro-

ductive modes between the two regions ($p = 0.83$ and 0.84 , respectively). Within corticoles, sexual reproduction is more strongly represented in Fennoscandia ($\chi^2 = 20.1$, DF = 3, $p < 0.001$).

The obligate lignicole flora includes species from eight taxonomic orders as well as numerous calicioid lichen taxa of uncertain taxonomic position (Supplementary material, Appendix 1). Of the taxonomic groups analyzed, the families Cladoniaceae and Pilocarpaceae and the order Baecomycetales are more species-rich in the obligate lignicole and facultative lignicole guilds than in the corticole guild. The families Parmeliaceae and Ramalinaceae and orders Arthoniales, Peltigerales and Pertusariales, by contrast, are species-rich among corticoles and facultative lignicoles and nearly absent among obligate lignicoles (Fig. 2). The order Teloschistales and family Lecanoraceae are well represented in all guilds. When Lecanorales (including smaller families not shown in Fig. 2) are analyzed as one group alongside the seven other major taxonomic orders, there are no significant differences between regions in ratios of taxonomic groups for obligate or facultative lignicoles ($p = 0.41$ and 0.98 , respectively), corticoles ($p = 0.49$) or the two floras taken as a whole ($p = 0.53$). However, if major families of the Lecanoraceae are analyzed alone there are significant

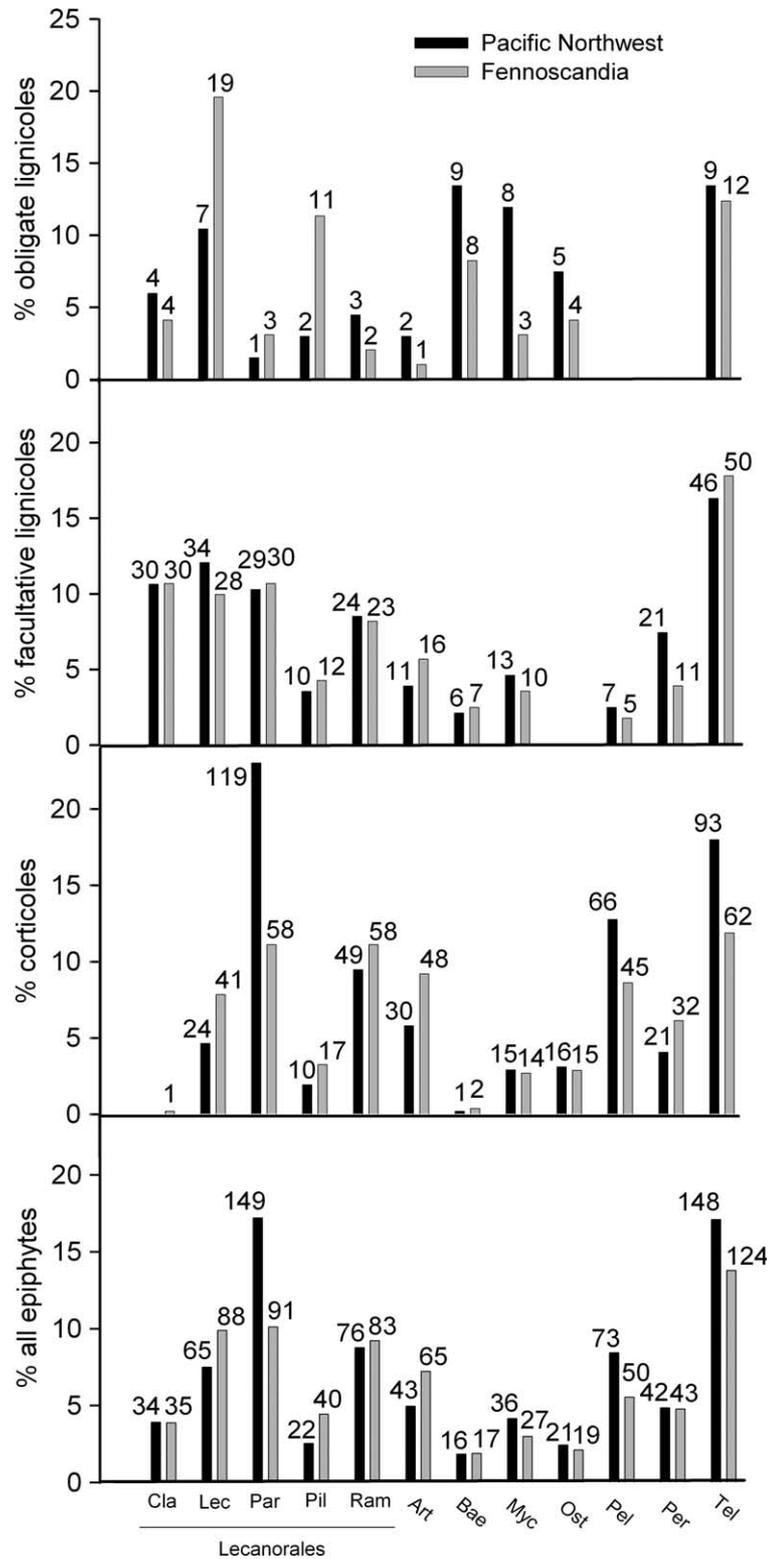


Figure 2. Proportions of selected taxonomic groups by guild. Numbers above bars represent absolute species numbers. Major families of Lecanorales: Cla = Cladoniaceae; Lec = Lecanoraceae; Par = Parmeliaceae; Pil = Pilocarpaceae; Ram = Ramalinaceae. Other orders: Art = Arthoniales; Bae = Baecomycetales; Myc = Mycocaliciales; Ost = Ostropales; Pel = Peltigerales; Per = Pertusariales; Tel = Teloschistales.

differences between the two regions for corticoles ($\chi^2 = 24.6$, DF = 4, $p < 0.001$) and the combined flora ($\chi^2 = 22.4$, DF = 4, $p < 0.001$), primarily because of the greater

representation of Parmeliaceae in the PNW. In the same analysis, there are no significant differences for obligate or facultative lignicoles ($p = 0.55$ and 0.95 , respectively).

Our analysis shows some groups notably more species-rich in the PNW than Fennoscandia (e.g. Parmeliaceae, Mycocaliciales, Teloschistales) and some vice versa (e.g. Lecanoraceae, Arthoniales). The largest genera of obligate lignicoles are *Lecanora* (15 spp.), *Lecidea* s.lat. (13 spp.), *Micarea* (13 spp.) and *Xylographa* (6 spp.) (Supplementary material, Appendix 1). Five genera (*Brucea*, *Elixia*, *Lignoscripta*, *Mycocalicium*, and *Xylographa*) are completely restricted to wood.

Microsite types

Current data are sufficient to broadly characterize the type of dead wood used by 121 of the 132 obligate lignicoles in our two study areas (Supplementary material, Appendix 1). A total of 109 species were identified as occurring on conifer wood, while only 24 obligate lignicoles have been recorded on angiosperm wood. We furthermore differentiated ten microsite types used by obligate lignicoles. According to present data, the largest number of species were found on stumps (53), logs (48), and snags (47), followed by anthropogenic wood substrates such as fenceposts and old barns (32), decorticated branches and twigs (21), burned wood (7) and dead wood scars of living trees (6 species). Microsite types used by fewer species were maritime driftwood (5), freshwater driftwood (2) and beaver scars (1). Microsite type could not be determined for 20 species.

Discussion

Patterns in the lignicole floras

The epiphytic lichen floras of the Pacific Northwest and Fennoscandia count among the best known within the circumboreal coniferous forest zone. The histories and scientific traditions in lichenology differ, however, in the two regions. In Fennoscandia, nearly three centuries of floristic tradition have made its lichen flora one of the most intensely researched in the world. Notwithstanding the similarity in the number of recorded epiphyte species, the PNW is less thoroughly explored, and the knowledge of its flora is highly dynamic: a large portion of the epiphytic lichen flora was only first reported in the last 20 yr (Spribille 2006). We acknowledge that epiphytic lichen numbers will continue to increase in the PNW and Fennoscandia with the exploration of remote areas. Future research will show what effect this may have on ratios reported here.

The cause of obligate dead wood affinity in lichens is poorly understood. For a minority of obligate lignicoles, mostly members of the order Mycocaliciales, close association with wood can be attributed to saprophytic as opposed to lichenized nutritional mode (Tibell and Wedin 2000). Facultative saprophytism, in which a single fungal species may occur as either a saprophyte or a lichen in different settings, has been proposed for *Chaenotheca* (Tibell 1997) and *Stictis* (Wedin et al. 2004) and should be explored in the Baeomycetales. However, saprophytism is not currently believed to play a role in the biology of most lignicolous lichens. For these species, other forms of

niche specialization may be involved. Our data suggest close affinity for dead wood is aligned with both functional traits and phylogeny. As noted by Forslund and Koffman (1998), most obligately lignicolous lichens are crustose and reproduce sexually, although these traits are by no means unique to lignicoles. Macrolichens and asexually reproducing species, by contrast, are largely absent from the obligate lignicole guild, though they are common among facultative lignicoles and corticoles. It is possible that low biomass and presumably rapid sexual reproduction among obligate lignicoles are an adaptation to their relatively ephemeral substrate and place species at a competitive disadvantage when establishing on more stable substrates. Discrimination against macrolichens would eliminate most Parmeliaceae and Peltigerales from the pool of obligate lignicoles, but does not explain the lack of obligately lignicolous members of the Pertusariales.

The highly similar proportions of life forms, reproductive modes and taxonomic groups among obligate and facultative lignicoles between the two floras could plausibly be attributed to substantial species overlap in these guilds (59%). This however implies that a species found in both regions maintains a fixed ecological envelope. Although this is clearly the case for some species (e.g. *Xylographa* spp.), numerous others do not espouse the same microsite adaptations in both study areas (Supplementary material, Appendix 1). This apparent niche drift may be related to genetic variability. Evidence is increasing for divergence of Old and New World lichen populations in pre-Pleistocene times and low or non-existent gene flow since then (Printzen et al. 2003, Palice and Printzen 2004). If the low gene flow trend holds, the ecological envelopes of disjunct, long-isolated species could make for an interesting case study in phylogenetic niche conservatism (Wiens 2004).

Even if every species found in both floras were to have a fixed ecology across its range, it remains that almost 40% of the combined lignicole species pool is not shared. That the proportional make-up of lichen life forms, reproductive strategies and taxonomic groups is nonetheless largely congruent in the two regions is particularly striking. There would theoretically have been plenty of opportunity for proportions to diverge given disjunct area with distinct species composition and hundreds of thousands of years to do it. The fact that this did not happen suggests the existence of common underlying mechanisms that lead to similar functional group assemblages occupying homologous microsities in disjunct regions. The pattern bears resemblance to taxonomic and functional group proportionality in other organism groups, e.g. fish and corals (Bellwood and Hughes 2001), leading some to suggest the existence of regional level assembly rules related to function and taxonomic group. Assessing whether or not assembly rules are at play in lignicolous lichens will require data on species composition from other regions and the parsing out of the species overlap effect. Within the circumboreal realm, regional-scale data of sufficient resolution are currently available only for the two regions treated here.

An intriguing by-product of our analysis is the observation that the corticolous lichen floras of the two regions are substantially more dissimilar than the lignicole floras. Arguably the greater latitudinal spread of the PNW

compared to Fennoscandia could mean more temperate species are included in the PNW flora. However, even in Parmeliaceae, the group with the largest single difference between the two floras, only 27 of 149 species in the PNW are restricted to areas south of 50°N, suggesting that differences hold up even at higher latitudes. The strong endemism among PNW corticolous macrolichens was already recognized by Goward and Ahti (1992), who suggested evolutionary isolation of the PNW as an explanation. We additionally found that the two corticole floras differ significantly in their internal life form, reproductive mode and taxonomic group proportions. Much as the congruencies discussed for lignicoles might be ascribed to high species overlap, incongruencies among corticoles could be attributed to low overlap. However, here too we suspect that the root causes are more nuanced. Bark generally contains higher concentrations of secondary metabolites than wood (Obst 1998). We hypothesize that the richness of tree species and bark chemistries offered a more varied substrate landscape over evolutionary time than the chemically more neutral wood substrate.

Inventory and monitoring of lignicolous lichens

Our analysis of substrate use shows that a similar percentage of epiphytic lichen species in both floras use dead wood, and approximately one in ten species are completely dependent on it. The latter, listed in their entirety in Supplementary material, Appendix 1, include several species of epiphytic lichens under threat, not only on account of the worldwide decline of dead wood in managed forests, but also because in many regions these species and their habitats have not yet been flagged for conservation concern.

A large number of obligate lignicoles are poorly known in terms of their taxonomy, ecology and distribution. This is especially true of genera such as *Absoconditella*, *Lecanora*, *Lecidea*, *Micarea* and *Verrucaria*. The genera *Lecanora* and *Lecidea* s.lat. contain six species – *Lecanora apochroeooides*, *L. dovrensis*, *L. pseudohypopta*, *Lecidea consimilis* and *L. subhumida* from Fennoscandia and *Lecidea pullula* from the Pacific Northwest – that have not been recorded since their description in the late 1800s (1934 in the case of *L. subhumida*). Another species, *Lecidea scabridula*, was only recently rediscovered after having not been recorded since the 19th century. The state of baseline knowledge is exemplified by the genus *Xylographa*, which despite being one of the most common and easily recognized of obligate lignicole genera in the PNW, has only been reported a few times (Spribille 2006).

One reason for the inventory deficit in lignicolous lichens is the common emphasis by ecologists on macrolichens. It follows from life form ratios among facultative and obligate lignicoles that studies of dead wood in forest ecosystems based on macrolichens will miss the majority of species and thus fine-scale assemblage structure. This has been borne out by substrate inventories that included crusts (Forsslund and Koffman 1998, Bunnell et al. 2008, see also Ellis and Coppins 2006). Although macrolichens have been advanced as a stand-level surrogate for overall biodiversity (Negi and Gadgil 2002) or overall lichen richness (Bergamini et al. 2007), there are no data to suggest that

macrolichens are indicative of richness patterns in different wood microsites. Indeed, given the absence of macrolichens in many dead wood microsites, this is unlikely.

Emphasis on macrolichens has been particularly strong in the PNW. Red-listing and “Survey and Manage” tracking of lichens in the PNW focuses on macrolichens (USDA 2001, COSEWIC 2005); only one obligately lignicolous microlichen, *Calicium abietinum*, is currently tracked in the PNW (Supplementary material, Appendix 1). The lack of region-specific taxonomic treatments and keys for crustose lichens has meant that complete species inventories are difficult and often necessarily digress into systematic studies. The launching of an epiphytic crustose lichen flora project for British Columbia will improve the availability of identification literature in the PNW in future (Spribille 2006). In Fennoscandia the situation is better owing to availability of a checklist and floras (Foucard 2001, Santesson et al. 2004). Within the project “Signal species” (Nitare 2000) initiated by the Swedish Forest Agency, and now also in use in Finland, Norway and the Baltic states, the majority of lichens used are crustose. In Europe in general, crustose lichens are assuming increasing importance in studies of old forest and landscape habitat structures (Rose 1992, Kruys and Jonsson 1997, Berglund and Jonsson 2001, 2005, Ellis and Coppins 2006).

Lignicolous lichens and forest management

Our review of microsite affinities (Supplementary material, Appendix 1) shows that the largest numbers of obligate lignicoles occur on stumps, logs and snags. Although these are the most commonly studied structural types in dead wood studies (Berg et al. 1994, Forsslund and Koffman 1998, Löhmus and Löhmus 2001, Jansová and Soldán 2006, Bunnell et al. 2008), it is not clear that they translate to biologically meaningful environmental envelopes. Bunnell et al. (2008) found significant differences in the lichen flora between hard and soft logs assigned to the same decay class using regionally standard down wood classification protocols. Similarly, Goward et al. (unpubl.) and Svensson et al. (2005) found significant differences in the lichen flora between the exposed and shaded sides of snags and/or between hard/erect and soft/leaning snags. Stumps are a common result of forest practices, but are infrequently sampled. In general, wherever an effort is made to further discriminate lichen habitats, numerous microsites have been recognized (Räsänen 1927, Rikkinen 2003b), corroborating what is known for basidiomycetes and saproxylic insects. Improved methods are needed for randomized sampling of lignicoles that reassess current notions of sampling unit and plot size and discriminate structural types more closely fitting to the ecological behaviour of wood-dependent species.

Down wood generally is recognized as being one of the critical habitat elements in the maintenance of forest biodiversity (Berg et al. 1994, Humphrey et al. 2002). Forest practices have long discriminated against coarse dead wood. While modern silvicultural approaches increasingly recognize its value (Bunnell et al. 2002, Beese et al. 2003), overall levels of coarse dead wood in forests have fallen to a fraction of what they once were. Managed forests of today

in Fennoscandia contain only 2–10% of the coarse woody debris (diameter >10 cm) once found in natural forests (Linder and Östlund 1998, Fridman and Walheim 2000, Jonsson et al. 2005). Dramatic rates of decline also have been projected for parts of the PNW (Maser and Trappe 1984, Spies et al. 1988). We cannot rule out that many lignicolous lichens have experienced concomitant declines. In Fennoscandia, *Cyphelium notarisii* (Areskoug and Thor 2005) and *C. trachyloides* (Arup 1999), both associated with dry, weathered wood, may be such species.

The obligate relationship of some lignicoles to their substrate means they are directly threatened by activities that reduce amounts of coarse dead wood. Many bryophytes, unlichenized fungi and invertebrates reliant on dead wood are likewise threatened. Indiscriminate conservation of dead wood by volume may not be sufficient to meet the objectives of maintaining viable populations of microsite specialists. Dead wood habitats often have been treated as inextricable components of unmanaged forests, but recent studies suggest that structural features retained at timber harvest (slash, fallen snags, pre-existing fallen logs) help to sustain the flora otherwise found in unmanaged stands (Hazell and Gustafsson 1999, Bunnell et al. 2007, 2008, Caruso et al. 2008). Development of conservation strategies that look beyond numbers and volumes and consider biologically meaningful dead wood structure types is necessary to ensure that specific habitats are accounted for in forest management practices (Jonsson et al. 2005).

Concluding remarks

Lichen-substrate relationships are still a little-researched topic, and there is accordingly much work to do. At a regional level, it will be important for lichenologists to work together with conservation planners to identify flagship and indicator species for survey and monitoring. Regional identification guides such as Foucard (2001) play an important role in enabling inventory and can be developed outside Fennoscandia. At the level of ecosystem management, stand-level planning and reserve design approaches need to be refined to take into account habitat distribution at smaller spatial scales. A biologically informed approach to classifying dead wood types will be instrumental to the development of forest management approaches such as retention silviculture and ensure better results for securing populations of rare and/or declining species. On a macro-ecological scale, species-substrate relationships show promise for shedding light on long-term lichen diversification patterns as more insight is gained into the role of function and phylogeny in niche adaptation.

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