

Effect of patch size on species richness and distribution of sub-alpine saxicolous lichens

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ABSTRACT

Understanding how communities respond to environmental pressures is important for conservation planning and management. In this observational study, we examined the SLOSS debate and the ecological concept of nestedness in respect to how saxicolous lichen communities in sub-alpine habitats are structured. We analyzed the effects of patch size on the species richness and distribution of saxicolous lichen. We surveyed 242 granitic rocks in the White Mountains, California, and collected data on the different taxa found. Our results showed that there was greater species richness per m² on small rocks, supporting the “Several Small” side of the SLOSS debate. Additionally, we found that there was a high degree of nestedness in our study system. Saxicolous lichen provide a manageable scale to test community-level ecological concepts and allow us to better define the boundaries of their applications.

Keywords: saxicolous lichen, community ecology, SLOSS, nestedness, sub-alpine

INTRODUCTION

Investigation into how ecological concepts can be used to determine community responses to environmental pressures may help inform conservation planning and management of biotic assemblages (Will-wolf et al. 2006). Application of these models can vary among taxa and defining their boundaries can increase confidence in their use. The Single Large or Several Small (SLOSS) debate was first derived from the Island Biogeography Theory in 1976, and is used in conservation planning to determine if several small habitats or fewer large habitats are best for conserving biodiversity (Simberloff and Abele 1976). SLOSS

addresses species richness within a confined habitat, but overlooks species composition and distribution across habitats, and is therefore often supplemented with the ecological concept of nestedness. Nestedness is a measure of structure in the distribution of species across habitats. Systems with high nestedness would demonstrate that species-poor habitats contain a subset of the taxa in species-rich habitats (Patterson and D. 1987). In practice, this often results in rare species being confined to species-rich sites, and species found in species-poor sites being common in every habitat. Generally, systems that are strongly nested have more species on fewer large sites than on several smaller sites of

the same area (Wright and Reeves 1992). However, natural systems are rarely perfectly nested (Berglund and Jonsson 2003). A review examining nestedness on archipelagoes found that although 89% demonstrated a high degree of nestedness, zero exhibited perfect nestedness (Boecklen 1997). This was explained by variation in life history of organisms, including colonization, extinction rates, and behavioral plasticity in response to environmental shifts. Sessile organisms have relatively consistent habitats, due to slow migration rates, that offer a simplified model to study these ecological concepts.

Lichens are complex composite organisms that blur the boundary between the archaea, plantae, and fungi kingdoms (Nash III 2008). Touted in textbooks as a classic example of symbiosis, these organisms consist of a mycobiont (the fungal contributor) and a photobiont, which can be composed of one or multiple cyanobacteria or algae (Nash III 2008). Their contribution to biological weathering, soil production, and development of living soil crusts makes them important players in ecological resource cycling (Will-wolf et al. 2006). In addition, their sensitivity to air quality have made them useful as bioindicators for pollution (Conti and Cecchetti 2001). Their persistence in harsh habitats has contributed to their expansive colonization, with lichens making up approximately 8% of the Earth's surface (Ahmadjian 1995).

Lichens occupy a wide range of habitats globally, from the tropics to the arctic (Determeyer-Wiedmann et al. 2019). Lichen living in sub-alpine habitats are exposed to a number of harsh environmental conditions, such as low water availability, high UV

radiation, and frequent disturbances (Heber et al. 2000, Leavitt et al. 2021). Lichens living in such environments are often tolerant to these stressors, and although they are slow growing, they have adaptations that allow them to recover photosynthetic capabilities after desiccation and grow quickly following snow melt (Anstett and Coiner 2010). Saxicolous lichens, which grow on rocks, experience abiotic habitat stability as their substrates are relatively unchanging compared to biotic substrates. Developing an understanding of how lichens may respond to variation in habitat patch size and relative species richness could help predict how alpine lichens may respond to large-scale habitat disturbances, such as habitat fragmentation and reduction of precipitation due to anthropogenic climate change (Rodriguez et al. 2017).

Previous research examining the SLOSS debate has found that larger, continuous habitats are better for habitat conservation of predators (Soulé and Simberloff 1986), whereas in marine environments, several small habitats of seagrass beds were observed to increase species richness for fish and macro invertebrates (McNeill and Fairweather 1993). However, the SLOSS debate and nestedness theory has proven more nuanced regarding sessile species. One study focused on epixylic lichen, or those living on the surfaces of wood, found no relationship between the number of species and the tree size (Schei et al. 2013). This debate merits the exploration of how saxicolous sub-alpine lichens may respond to varying habitat patch size in order to determine which model is best applied to these unique organisms.

In this study, we examined how patch size contributes to saxicolous lichen species richness and distribution. We hypothesized that lichen richness per unit area would not be determined by habitat size, due to their sessile nature and previous research on epixylic lichen that found no relationship (Schei et al. 2013). However, we predicted we would see ecological nestedness because although there is often a relationship between habitat area and species richness, nestedness does not evaluate richness with respect to area (Cook 2008).

METHODS

2.1 Site Selection

We conducted our study at the University of California Natural Reserve System's White Mountain Research Center at the Sage Hen Flats (37°29'42"N, 118°10'06"W) on August 4-6, 2021. The clearing, located between Blanco and Campito Mountains, sits at a relatively level 3200 meters of elevation. Temperature data collected at the nearby Cooked Creek Station measure an average temperature of 13.5°C, an average humidity of 39%, and negligible amount of precipitation during the early-August timeframe of our study. Rock type in the area is primarily granitic, with dolomite, sandstone, and quartzite rocks being common fixtures of the terrain (Mooney et al. 1962). We chose to sample only granitic rocks, as they uniquely harbor a high diversity of lichen types, including crustose, umbilicate, fruticose and foliose lichen (Wolseley et al. 2006).

2.2 Observational Survey

We surveyed lichen species on 242 rocks and boulders to discover potential patterns in their distributions. Individual boulders were haphazardly chosen within a 150 m by 150 m area to standardize locational effects. An effort was made to exhaustively survey the rocks in the study area. Boulders with a calculated surface area below .025 m² or above 50 meters squared were omitted from our study for practical reasons. To calculate surface area, we treated each boulder as a rectangular prism. The height, width, and lengths of each boulder was calculated by measuring the most extreme point of each axis with transect tape. The bottom surface of the rectangular prism buried in the ground was omitted from the calculated surface area to make our measurement of surface area more representative of substrates suitable for lichen colonization. Each boulder was measured for species richness by counting and recording the number of different species of lichens. We identified lichen morphologically to the nearest taxonomic certainty, noting species and/or genus when positive species identification was not possible without the use of chemistry.

2.3 Statistical Analysis

We used JMP version 16.0.0 to perform all statistical analyses. We used logistic regressions to evaluate the effect of rock surface area on three factors: the total number of lichen species per m², the total number of lichen species per rock, and the presence of each lichen species. Additionally, we used the NeD online software to test the nestedness of the lichen

community with the NODF (nestedness based on overlap and decreasing fill) metric (Strona et al. 2014).

RESULTS

We identified seventeen taxa of lichen. Seven lichen taxa were identified to genus-level, and ten were identified to species-level. Thirteen were crustose, three were foliose, and one was fruticose. As rock surface area increased, there was an increase in the number of lichen taxa per rock (N=242, F=17.11, P<0.0001; Figure 1). However, lichen richness per meter squared decreased greatly as rock surface area increased, which suggests that there was greater species richness per meter squared on small rocks (N=242, F=9.75, P<0.0001; Figure 2). No lichen was found to be specialized on small rocks; each was found across the range of rock sizes or mostly found on larger rocks (Table 1). The lichen community exhibited nestedness, where the taxa on rocks with lower richness were a subset of the species on rocks with higher richness (N=242, NODF=77.957, P<0.001; Figure 3).

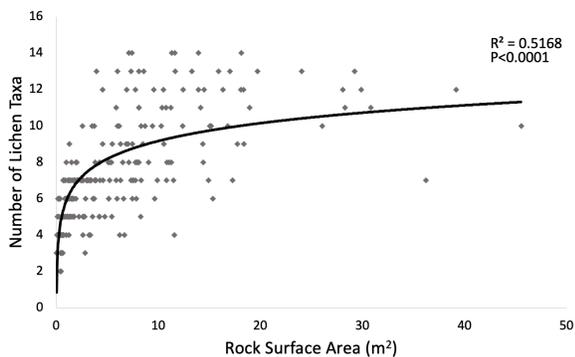


Figure 1. Effect of rock surface area on number of lichen taxa. As rock surface area increased, the number of lichen taxa found on each rock increased (N=242, F=17.11, P<0.0001).

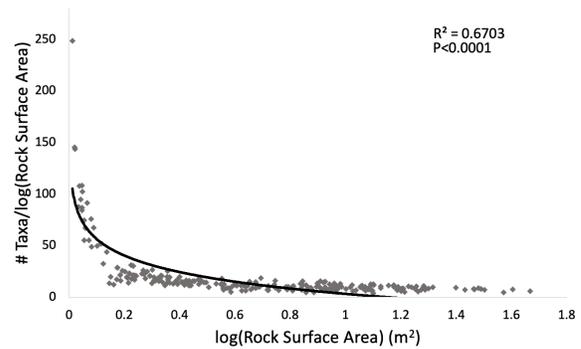


Figure 2. Effect of rock surface area on the number of lichen taxa per meter squared. As the surface area of the rocks increased, the number of taxa per meter squared decreased (N=242, F=9.75, p<0.0001). As the logarithm of the surface area reaches about 0.2 m² the effect is less distinct.

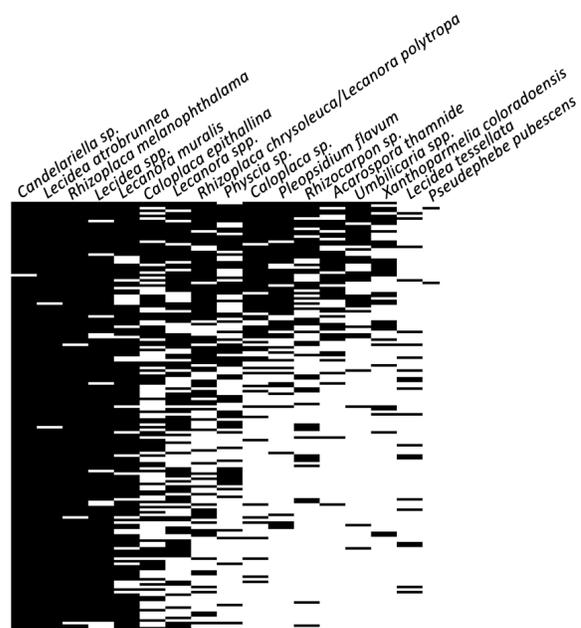


Figure 3. Nested matrix of lichen taxa. Each column corresponds with a specific lichen taxon, and each row correlates with rocks that were sampled by order of lichen richness. The black segments represent species presence, and the white lines represent species absence. The most abundant taxa were found on different sized rocks while rarer taxa were mostly found on larger rocks (N=242, NODF= 77.957, p<0.001).

Table 1. Lichen taxa and surface area. Thirteen lichen taxa were more commonly found on rocks with a larger surface area while four species were found on rocks with varying surface areas.

Lichen Taxa	N	χ^2	P
<i>Candelariella sp.</i>	239	0.26	0.6068
<i>Lecidea atrobrunnea</i>	232	7.39	0.0065
<i>Rhizoplaca melanophthalama</i>	219	19.51	<0.0001
<i>Lecidea spp.</i>	212	0.00	0.9943
<i>Lecanora muralis</i>	178	18.48	<0.0001
<i>Caloplaca epithallina</i>	110	0.67	0.4137
<i>Lecanora spp.</i>	104	27.40	<0.0001
<i>Rhizoplaca chrysoleuca/Lecanora polytropa</i>	92	42.03	<0.0001
<i>Physcia sp.</i>	71	20.45	<0.0001
<i>Caloplaca sp.</i>	68	53.27	<0.0001
<i>Pleopsidium flavum</i>	60	49.70	<0.0001
<i>Rhizocarpon sp.</i>	54	50.91	<0.0001
<i>Acarospora thamnide</i>	46	42.12	<0.0001
<i>Umbilicaria spp.</i>	37	32.70	<0.0001
<i>Xanthoparmelia coloradoensis</i>	35	24.42	<0.0001
<i>Lecidea tessellata</i>	23	0.99	0.3195
<i>Pseudephebe pubescens</i>	2	4.19	0.0407

DISCUSSION

We observed that as rock size increased, species richness increased, consistent with the species-area relationship. However, we found evidence that for sub-alpine saxicolous lichens, smaller rocks have a larger species richness per unit area within the scale we examined, which supports the “several small” position of the SLOSS debate. This conclusion does not agree with our initial hypothesis, which was that the lichen community would not tend towards occupying either “single large” or “several small” habitats. Our result could be explained by species saturation occurring at the largest rocks, in which we observed a plateau of species richness when the maximum number of species in the environment were accounted for.

A high degree of nestedness was observed within our study system, which supports our initial prediction. Lichens such as

Candelariella sp., *Lecidea atrobrunnea*, *Rhizoplaca melanophthalma*, and *Lecidea spp.* appear to grow ubiquitously in every size of habitat. However, rarer species such as *Umbilicaria spp.*, *Xanthoparmelia coloradoensis*, and *Pseudephebe pubescens* occurred mostly on larger, species-rich sites. This is consistent with the work of Wright et al., who argued that species with large area requirements tend to be found in large habitat patches, while species that can survive even in the smallest patches are likely to be found everywhere (1992).

Consistent with previous research, our pattern of nestedness was not perfect. One of the species observed to deviate from a nested pattern was *Caloplaca epithallina*. *C. epithallina* is a parasitic species with a broad range of lichen hosts. Previous research has revealed that *C. epithallina* commonly parasitize *Rhizoplaca melanophthalama* and *Lecanora muralis*, two species found almost

ubiquitously in our study (Søchting et al. 2008). The common presence of these hosts explains the near-random distribution of *C. epithallina* and presents a case that their distribution is more likely reflective of successful dispersal of its propagules, rather than any sort of habitat preference.

Our study did not account for microsite characteristics and rock quality, such as presence of certain lichen species with respect to crevices, aspect, wind, and light exposure. Species composition of lichen have been found to be affected by the differences in precipitation and sunlight exposure that comes with changes in aspect directionality (Fodor 2016). Microsite characteristics that maximize photosynthetic capabilities, such as low wind exposure while maintaining high light availability, may be more important for some species of lichens (Anstett and Coiner 2010). These microsites may provide refuges for rare species, and therefore increase overall diversity. Additionally, our study only looked at lichen on granitic rocks. It might be worthwhile to look at other types of rocks such as dolomite and shale to examine the SLOSS debate further and to test for nestedness, as we know that different species exhibit preferences for different substrates (Skorepa et al. 1979).

Nestedness is an important concept to study because it provides knowledge into the distribution of rare species, which in turn can provide insights on how these organisms may respond to habitat fragmentation (Berglund and Jonsson 2003). The SLOSS debate does not have a consistent answer for every study system, and it must be further researched in order to determine which habitat configuration is best for

conservation of various taxa. Understanding the extent to which ecological concepts can be applied, such as scale and taxa, can help in determining conservation planning and gain predictive power to how these systems may respond to ecosystem changes induced by climate change.

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