

Testing the competition–colonization trade-off with a 32-year study of a saxicolous lichen community

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Abstract. Competition–colonization trade-offs are theorized to be a mechanism of coexistence in communities structured by environmental fluctuations. But many studies that have tested for the trade-off have failed to detect it, likely because a spatiotemporally structured environment and many species assemblages are needed to adequately test for a competition–colonization trade-off. Here, we present a unique 32-year study of rock-dwelling lichens in New Mexico, USA, in which photographs were used to quantify lichen life history traits and interactions through time. These data allowed us to determine whether there were any trade-offs between traits associated with colonization and competition, as well as the relationship between diversity and disturbance in the community. We did not find evidence for a trade-off between competitive ability and colonization rate or any related life history traits. Interestingly, we did find a peak in all measures of species diversity at intermediate levels of disturbance, consistent with the intermediate disturbance hypothesis pattern. We suggest that the coexistence of the dominant species in this system is regulated by differences in persistence and growth rate mediating overgrowth competition rather than a competition–colonization trade-off.

Key words: *coexistence; disturbance; diversity; Hill's diversity index; intermediate disturbance hypothesis; life history trade-off.*

INTRODUCTION

Despite decades of research, the mechanisms that promote coexistence between competing species remain contentious. Theory suggests that, for species to coexist, they must have differential responses to spatial or temporal heterogeneity, to predation, or in resource acquisition (Chesson 2000, Amarasekare 2003). The competition–colonization trade-off is a hypothesized mechanism of spatiotemporal niche partitioning that is of particular interest (Levins and Culver 1971, Tilman 1994). Coexistence is maintained because species that are particularly good at colonizing empty patches of habitat are poor competitors, and vice versa. When patches become available, the good colonizers arrive first, but are eventually outcompeted by better competitors that arrive later.

In cases where competition is not perfectly asymmetric or preemptive, the validity of the competition–colonization trade-off as a mechanism of coexistence has been called into question (Yu and Wilson 2001, Levine and Rees 2002), but this mechanism has since been revitalized by models that allow the degree of competitive asymmetry and preemption in a community to occur on a continuum (Calcagno et al. 2006, Figueiredo

and Connolly 2012). Despite this recent theoretical activity, the empirical evidence for such a trade-off remains surprisingly sparse.

Many studies that have looked for a trade-off have instead found no relationship between traits associated with competition and colonization (e.g., Yu et al. 2004, Limberger and Wickham 2011, Kneitel 2012). Studies that have found trade-offs among only two or three species (e.g., Stanton et al. 2002, Hunt and Bonsall 2009) are inherently limited by statistical power. Documented evidence of competition–colonization trade-offs in multispecies assemblages include a trade-off between competition and dispersal ability in birds (Rodríguez et al. 2007), and a trade-off between colonization and competitive ability in laboratory cultures of protozoa (Cadotte et al. 2006). Though the latter study was not conducted in a natural setting, it does provide evidence of a genetic constraint for such a trade-off. However, subsequent studies using natural assemblages of protozoa have not found a competition–colonization trade-off (Limberger and Wickham 2011, Kneitel 2012).

The competition–colonization trade-off is also of interest due to its potential to explain diversity patterns over a disturbance gradient. For example, a peak in diversity at intermediate levels of disturbance is often hypothesized to be due to a trade-off between competitive abilities and colonization rates, conventionally thought of as the intermediate disturbance hypothesis (IDH; Grime 1973, Connell 1978). Though the IDH has

Manuscript received 6 February 2014; 3 July 2013; accepted 11 July 2013. Corresponding Editor: P. B. Adler.

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recently lost favor due to weak empirical support (reviewed in Mackey and Currie 2001, Hughes et al. 2007), under certain conditions, a competition–colonization trade-off is expected to generate the IDH pattern (Cadotte 2007, Fox 2012).

Here we present a pair of studies, one observational and one experimental, of a saxicolous lichen community in New Mexico, USA, intended to determine whether a competition–colonization trade-off exists among several species (or species complexes) in a natural community and to describe the relationship between disturbance and diversity. Saxicolous lichens are an amenable system for such an investigation and have been used to study community patterns in a number of other studies (e.g., Armstrong 2002, Armstrong and Welch 2007, Gjerde et al. 2012). Because, at our site, the main resource lichens compete for its space on rocks, and they rarely experience predation (T. E. Miller, *personal observation*), coexistence among species can be reduced to two possible axes of niche differentiation: space and time. These lichens are clearly affected by disturbance: Shards of the rock surface regularly flake away, patchily removing lichen thalli. This creates a spatiotemporal structure in this system, which makes it a good candidate for coexistence mediated by a competition–colonization trade-off.

The first study, conducted in 1978, consisted of a census of lichen diversity across a wide range of estimated disturbance rates. These data reveal an IDH-like pattern and can also be used to quantify the relationships between disturbance and abundance for each lichen species. If the mechanism generating an intermediate peak in diversity is a trade-off between colonization and competition, then, from these data, we should also be able to predict which species are better competitors (those successful at low disturbance rates) and which are better colonizers (those successful at high disturbance rates).

The second study was designed to quantify colonization and competition rates of each species in order to test for a trade-off. This ongoing study consists of disturbed and undisturbed plots photographed every one to five years from 1978 to 2009. The photographic record makes this study unique in its ability to measure competitive ability of individual lichen thalli over long timescales and colonization rates of each species, rather than proxies for these traits. We have used the first 32 years of data to (1) determine the relationship between disturbance and diversity in the area, and (2) test for a trade-off in competitive ability and colonization rate for seven lichen species.

METHODS

Study site

This study was conducted in the Gila National Forest, north of Pinos Altos, New Mexico, in an area of lichen-covered rocks on a slight northwest-facing slope (32°54'06" N, 108°14'23" W). The site is at an elevation of 2100 m and consists of a sparse forest of *Juniperus*

depeana, *Pinus edulis*, *P. ponderosa*, and *Quercus* spp. divided by areas of exposed flat rock surfaces, many quite large (>10 m²). The rock is an ash-flow tuff that is subject to regular exfoliation, in which thin sections, usually ranging in size from 5 to 100 cm², flake off of the surface, removing attached lichen occupants and leaving new bare rock surfaces.

A primary assumption of this study is that rock surfaces not covered by lichens reflects recent exfoliation, such that the percentage of open surface can be used as an estimate of disturbance rate. This assumption is reasonable, given that, we frequently saw exfoliation on or near our plots, lichen cover at the 1-m² scale frequently approached 100%, and the area on and around these rocks contains many thin rock fragments from past gradual exfoliation. Because there is some stochasticity in colonization and variation in rock texture, there is also variation in the rate of colonization and exfoliation of lichens, so percent lichen cover is only an approximation of disturbance rate. However, for the purposes of this study, we feel that percent bare rock is a good proxy for disturbance rate.

Lichen identification

By convention, lichens take the same name as their fungal component; however, because it involves a mutualism, lichen taxonomy is inherently challenging and even contentious (e.g., Ekman et al. 2008). We initially used traditional characteristics of color, growth form, and a simple thallus spot test for KOH response in the field in 1978 to differentiate among morphotypes (Hale 1969). Photographs were taken from representatives of each morphotype for later determination of species identities. Identifications of morphotypes were confirmed by genetic analysis of the fungal components of samples from lichen covered rocks collected adjacent to experimental plots in 2011 for all but two species. From two to nine thalli of each species were carefully removed from rocks and freeze-dried with liquid nitrogen. Fungal genetic material was extracted with the DNeasy Plant Mini kit (Qiagen, Hilden, Germany). The internal transcribed spacer (ITS) region of the DNA was amplified with ITS1 and ITS4 primers (White et al. 1990). Polymerase chain reaction (PCR) amplifications were performed with ReadyMix (Sigma, St. Louis, Missouri, USA) and purified with ExoSAP-IT (Affymetrix, Santa Clara, California, USA) according to the manufacturers' protocols. Products were sequenced with the Sanger method at the Florida State University (FSU, Tallahassee, Florida, USA) core facilities. Phylograms were visually inspected, and contiguous sequences were assembled in Sequencher (Gene Codes Corporation, Ann Arbor, Michigan, USA; GenBank accession numbers are KC990268–KC990385).

Contiguous sequences were compared to the GenBank database by means of a BLAST search to identify similar species (Benson et al. 2006). The genetic structure of the green, foliose lichens in the genus

Xanthoparmelia is currently under debate, and cryptic species can occur in sympatry (Leavitt et al. 2011). To determine if we had multiple species of *Xanthoparmelia*, we aligned the gene sequences of seven specimens with MAFFT (Katoh et al. 2002) using the Cipres Science gateway (Miller et al. 2010), and we calculated the nucleotide diversity using Arlequin v 3.5 (Excoffier and Lischer 2010).

In general, species in this study displayed typical growth and reproduction for saxicolous lichens, with radial growth consisting of an expanding leading edge, and an inner zone of thalli producing apothecia or other reproductive structures, often followed by senescence of the reproductive tissue. All of these species can reproduce and disperse sexually via ascospores, with *Acarospora fuscata*, *Acarospora rosulata*, and *Circinaria contorta* reproducing almost exclusively sexually. All other species can reproduce asexually as well via pycnidia (in *Candelariella rosulans*, *Lecidea tessellata*, and *Lecanora muralis*). Additionally, *L. muralis* and *Xanthoparmelia* can reproduce asexually via fragmentation of the thallus (Consortium of North American Lichen Herbaria [CNALH]; available online).⁵ Mode of reproduction can contribute to the dispersal ability of lichens, which is an important component of a species' colonization rate (Löbel et al. 2009, Johansson et al. 2012). In this study, we did not directly account for differences in the mode of dispersal between species, as colonization rate is the compounded effects of dispersal ability and establishment success.

Census of lichen communities in 1978

Flat (<5° slope) areas of continuous rock surface were censused in the summer of 1978 using a 1-m² quadrat. Sites ($n = 94$) were chosen across a wide range of lichen cover with no immediate tree cover, and were separated from one another by at least 5 m. Each quadrat contained a 10 × 10 grid of points and the lichen species (or bare ground) under each point was recorded to estimate percent cover. Plots with more bare rock points were assumed to be more recently disturbed, allowing us to estimate disturbance rate as inversely related to percent lichen cover.

The relationship between percent lichen cover and species diversity was quantified with Hill's general diversity indices (Hill 1973) as

$$D_a = \left(\sum_{i=1}^s p_i^a \right)^{\frac{1}{1-a}}$$

where p_i is the relative proportion of the community made up by species i , and a was evaluated at 0, 1, and 2, resulting in three common measures of diversity. The value of a determines the contribution of species abundances for each measure of diversity (e.g., larger

values of a mean that more weight is given to abundant species). When $a = 0$, D_0 reduces to species richness; all species are weighted equally. When $a = 1$, D_1 is the antilog of the Shannon-Weiner index. When $a = 2$, D_2 is the reciprocal of Simpson's index; dominant species have a relatively high weight. Hill's indices are a particularly valuable approach for quantifying diversity, because analyzing the same data with different measures of a permits separation of the relative contributions of species richness and species evenness within the same mathematical framework (Ellison 2010).

First- and second-order generalized linear models were fitted to the data for each value of a to determine the relationship between D_a and percent lichen cover as a proxy for disturbance rate, and ΔAIC_c values were calculated for model comparisons. Second-order models were assessed to determine if they were concave down and, if the maximum value fell within the range of 0 to 100 for percent lichen cover. A log-link function was used for $a = 0$, which has Poisson-distributed residuals. We tested the relationship between individual species and relative percent cover by determining Spearman correlation coefficients on the ranked values for relative percent cover.

Long-term experiments of colonization and competition traits

Immediately after the census, 10 sets of paired plots (10 × 10 cm) were established on nearby flat rock faces. Each plot contained numerous thalli, usually of several different species, making this the appropriate scale to study interactions between thalli. Paired plots were within 1 m of each other, but were separated from all other pairs by at least 5 m. In order to follow these plots through time, they were each marked with short brass rods inserted into ~2-cm holes drilled into the rock and extending ~2 cm above the rock surface; these rods do not seem to have subsequently affected the rate of rock exfoliation over the study period. For each pair of plots, we randomly selected one plot and removed the entire surface of the rock face with a chisel to an average depth of 2–3 mm to simulate natural disturbance. This depth was similar to the thickness of the natural exfoliation shards found commonly around the area. We found some evidence of thalli reemerging from locations they inhabited before chipping, indicating that some species could grow from hyphae that penetrated the rocks, or thalli that grew in crevices deeper than the exfoliation. Though rare in our study, this regrowth is likely a natural form of colonization for saxicolous lichens. The other plot in each pair was not chipped, and served as a control.

Since 1979, all pairs were photographed at irregular, one- to five-year intervals (one plot was not located from 1982 to 2004, and so is not included in the analyses). Because of changes in technology during the study, some of the photos are on Ektachrome or Kodachrome slides, whereas more recent photos were taken with different

⁵ <http://lichenportal.org/portal/index.php>

digital cameras. All the slides have been scanned (Morphbank Biological Imaging, Florida State University, Department of Scientific Computing, Tallahassee, Florida, USA; images are *available online*).⁶ All photos were then resized and rotated as necessary to allow comparisons of the same plots across years (representative picture sequences are shown in Appendix A). Some photos are missing, either because the plot was not found that year or because of poor quality photography. The result is from 11 to 19 photographs between 1978 and 2009 for each of the 18 plots; a total of 268 photographs were analyzed. In 1981, identifications from photographs were compared against measurements taken in the field to verify that photographs detected all thalli present.

The disturbed plots were used to quantify the total colonization rate for each lichen species. Digitized photos of each plot through time were overlaid and used to determine when a new lichen thallus appeared in the plot during the course of the study. The resolution of detection for small lichen thalli from the photographs was 0.06 cm. Total colonization rates for each species complex were determined separately for each plot as the average number of new thalli to appear in a plot per year (not including thalli that grew in from the plot edges), and then averaged across plots for each species ($n = 9$). In order to account for species abundances' effect on colonization rate, we approximated a per-abundance colonization rate of each species by assuming that the average percent cover of each species on control plots over the course of the study represented the source of new colonists. A per-abundance colonization rate was then calculated by dividing the number of colonizations per year by the average percent cover of each species.

Digitized photographs of the control plots were similarly used to quantify competitive abilities for each lichen species. A 10×10 digital grid was placed over each photo (positioned consistently from year to year using the brass rods and recognizable rock features) with Microsoft PowerPoint, which allowed us to make a 32-year time-lapse series of lichen growth for each of the 18 plots. To estimate competitive ability, we assumed that, if one species was replaced by another species at any given grid point between sequential photographs, then the second species was the "winner" in competition for that space. The lichen species at each grid point on each control plot in each year was identified, and the transitions evident in the subsequent photographs were used to estimate competitive ability. We quantified competitive ability, C_i , of a lichen species i as

$$C_i = \frac{\sum_{j=1}^n T_{ij}}{\sum_{j=1}^n T_{ij} + \sum_{j=1}^n T_{ji}}$$

⁶ <http://www.morphbank.net/?id=828511>

where T_{ij} is the number of instances in which the species at a grid point transitioned from j to i , for the total number of species, n (Connell et al. 2004). *Candelariella rosulans* did not occur on the long-term plots; no colonization or competition traits were measured for this species.

We determined average maximum growth rates by measuring the surface areas of between one and nine randomly chosen thalli (depending on availability) of each species on each disturbed plot from digitized photographs at three- to five-year intervals, using Image J software (NIH, Bethesda, Maryland, USA). Change in area between successive photographs was calculated for several intervals, and then the maximum growth rate was taken as the largest increase in area per year measured for each thallus. To avoid problems of the nonlinear scaling of area measurements, we standardized measurements by calculating the radius of a circle of equivalent area for each thallus to generate a linear metric of growth.

On control plots, persistence was calculated as the average number of years a point on the 10×10 grid was continuously held by one thallus of a species either from the beginning of the time series or from the first occurrence of the species until a return to bare space (i.e., how long a thallus remains adhered to the rock). On occasion, we observed *Xanthoparmelia* overgrow *C. contorta*, but when *Xanthoparmelia* flaked away, the original *C. contorta* thallus was intact, having apparently persisted under *Xanthoparmelia*. Thus, we assumed that, at points where *C. contorta* and *Xanthoparmelia* alternated over time, *C. contorta* occurred continuously and counted the number of years of persistence accordingly.

Trait data analysis

Shapiro tests were used to test for normal, or log-normal residuals. For parametric data (competitive ability and log-transformed maximum growth rates), we used analysis of variance followed by Tukey's HSD post hoc tests to look for difference in the trait values between species. For nonparametric data (total colonization rate, per-abundance colonization rate, and persistence), we used Kruskal-Wallis tests. We also ran Spearman rank correlation tests on all pairs of traits to find evidence for pairwise trade-offs between traits. For the correlation tests, Bonferroni corrections were applied.

Potential effects of climate change

Over the 32 years of this study, the climate of the area has become warmer and lichens are well known to respond quickly to environment change (e.g., van Hark et al. 2002). The average temperature near our study site has increased $\sim 2^\circ\text{C}$, while the rainfall has remained fairly constant (data for Fort Bayard, New Mexico, Western Regional Climate Center; Cooperative Clima-

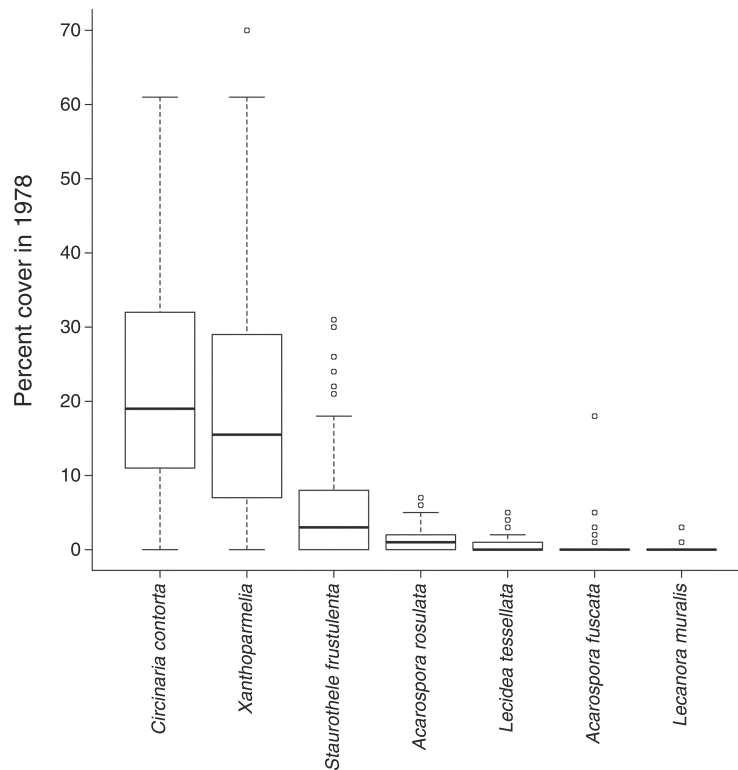


FIG. 1. Percent cover contributed by seven lichen species on 94 1-m² natural plots censused in the Gila National Forest, New Mexico, USA, in 1978. Boxes include 50% of the central values, and the broad bars in the boxes are median abundance values of each species. “Whiskers” give largest and smallest values, excluding outliers. Outliers are shown as points outside the whiskers. Species are ranked from highest to lowest median values.

tological Data Summaries; data *available online*).⁷ We investigated the effects of climate change with a regression of the thallus growth rate over time as a function of annual mean temperature and rainfall, using thalli from the *Xanthoparmelia* species complex, a commonly used genus in the study of climate change effects on lichens (Armstrong and Bradwell 2011). To determine growth rates, we measured the expansion of one thallus in one direction per control plot ($n = 9$), per sample date in the absence of interacting thalli. Mean annual temperature and precipitation were averaged over the interval prior to each sample date.

Unless otherwise noted, all analyses were conducted using the R statistical program (R Development Core Team 2013) and the vegan package (Oksanen et al. 2010).

RESULTS

Species identities

All four samples of the abundant gray, crustose lichen had the best match in the GenBank BLAST search with *Circinaria contorta* with a maximum identity ranging from 94% to 97%. These four samples had nucleotide

⁷ <http://www.wrcc.dri.edu/climatedata/climsum/>

diversity of 0.041 ± 0.028 (mean \pm SD) substitutions per site (s/s). The other dominant morphotype consisted of green, foliose thalli in the genus *Xanthoparmelia*. Species delimitation of this genus is currently uncertain in western North America (Leavitt et al. 2011). Del-Prado et al. (2010) proposed a threshold for intraspecific variation in the *Parmeliaceae* of 0.015–0.017 s/s. At our study site, we found the nucleotide diversity of this species complex to be 0.034 ± 0.020 s/s, indicating that we may have sampled multiple species of *Xanthoparmelia*; however, this diversity is well below the average interspecific variability of 0.103 ± 0.040 s/s of *Xanthoparmelia* (Del-Prado et al. 2010). As we cannot distinguish species either in the field or from photographs, we treated all *Xanthoparmelia* as a species complex. Even if multiple species of *Xanthoparmelia* are represented in our study, they diverged recently, have very similar growth forms, and are likely to have very similar life history traits. Thus, in our analyses, we treat *Xanthoparmelia* as a single species.

Other species with 0.5% or higher mean cover on original census plots were: *Staurothele frustulenta*, *Candelariella rosulans*, *Acarospora rosulata*, and *Lecidea tessellata* (Fig. 1). Two species, *Acarospora fuscata* and *Lecanora muralis*, were rare (<0.5% cover) on these plots and were not included in the correlation analyses.

Except for *Xanthoparmelia*, we will refer to species by abbreviating the genus. For all of these species, BLAST identified similar species with maximum identity of the top hit ranging from 91% to 98%, with the exception of *C. rosulans*, and *A. fuscata*, which we were unable to sequence due to insufficient thallus samples.

Census of lichen communities in 1978

Average total lichen cover in the 1978 census was 52% and ranged from 3% to 97%. Eight different lichen species were identified from the plots, and two species, the foliose *Xanthoparmelia* complex and the crustose *C. contorta*, were particularly abundant (Fig. 1). For all values of a , a quadratic model of the relationship between percent lichen cover and Hill's diversity index was a better fit to the data than a linear model (Fig. 2). When the Hill index was determined using species richness ($a = 0$), the quadratic model had moderate support compared to the linear model ($\Delta\text{AIC}_c = 4.3$); with maximum richness (D_0) at 59.5% lichen cover. When the Hill index was set to the antilog of the Shannon-Weiner measure ($a = 1$), and the reciprocal of the Simpson measure ($a = 2$), the quadratic model had strong support compared to the linear model ($\Delta\text{AIC}_c = 13.7$, and $\Delta\text{AIC}_c = 8.7$, respectively); maximum diversity (D_1) was at 48.2% and (D_2) was at 47.9% lichen cover, respectively (Fig. 2).

Xanthoparmelia ($R = 0.219$, $P = 0.034$) and *S. frustulenta* ($R = 0.292$, $P = 0.004$) contributed proportionally more to the lichen communities as total lichen cover increased (Fig. 3). *Candelariella rosulans* made up a higher proportion of the lichen community as total lichen cover decreased ($R = -0.228$, $P = 0.027$), while *L. tessellata* made up a marginally significantly smaller proportion as cover increased ($R = -0.1932$, $P = 0.062$). The abundances of the other two species, *A. rosulata*, and the most abundant, *C. contorta*, were not significantly related to total lichen cover (Fig. 3).

Long-term experiments of colonization and competition traits

Total colonization rate differed significantly among species, but per-abundance colonization rate did not (Kruskal-Wallis nonparametric analysis of variance $X^2_6 = 20.08$, $P = 0.003$ and $X^2_6 = 10.60$, $P = 0.101$ respectively); *Circinaria contorta* and the *Xanthoparmelia* complex showed the highest total colonization rate. However, these two species are also the most abundant; standardizing colonization by abundance resulted in no significant difference amongst species.

Individual thalli of a species differed greatly in growth rates, and the largest variance was observed for the only foliose lichen, *Xanthoparmelia*, which also had the highest average growth rate (Fig. 4d). Overall, species did not differ significantly in maximum growth rate ($F_{6,10} = 1.953$, $P = 0.167$).

Circinaria contorta and *Xanthoparmelia* each "won" ~50% of their encounters with other species; the

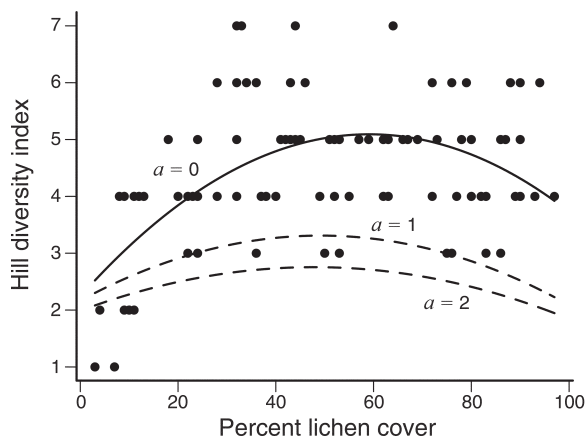


FIG. 2. The relationship between percent lichen cover and Hill diversity indices for different values of a on 98 1-m² plots in 1978. The value of a determines the contribution of species abundances for each measure of diversity (e.g., larger values of a mean that more weight is given to abundant species). Points are displayed only for $a = 0$ (solid line) to show typical variation. When $a = 0$, D_0 is species richness. When $a = 1$, D_1 is the antilog of the Shannon-Weiner index. When $a = 2$, D_2 is the reciprocal of Simpson's index.

remaining species won fewer than 40% (Fig. 4c). Overall, species differed significantly in their competitive abilities ($F_{6,21} = 4.699$, $P = 0.004$). A Tukey's test showed significant pairwise differences between *C. contorta* and *S. frustulenta* ($P = 0.006$), *C. contorta* and *A. fuscata* ($P = 0.032$), and *Xanthoparmelia* and *A. fuscata* ($P = 0.028$), but no differences between the other species. A Kruskal-Wallis test indicated a significant difference in persistence between species ($X^2_5 = 28.66$, $P < 0.001$), where *C. contorta* was the most persistent and the two *Acarospora* species the least (Fig. 4e, Table 1). Spearman's rank correlation tests (Table 1) of all pairs of species complex traits identified no significant pairwise correlations.

Effects of climate change

There was no significant change in the growth rates of *Xanthoparmelia* from 1979 to 2009 ($R^2 = 0.01$, $P = 0.41$). There was also no significant relationship between either annual precipitation rate or mean annual temperature and the growth rate of individual thalli in the *Xanthoparmelia* complex ($P = 0.41$, $R^2 = 0.04$ and $P = 0.65$, $R^2 = 0.01$ respectively, $n = 18$ in both cases).

DISCUSSION

Though rock-dwelling lichens appear to coexist in a spatiotemporally structured community, we found no significant evidence for a trade-off between competitive ability and either total or per-abundance colonization rate among the seven observed lichen species from the long-term experimental plots. In fact, no trade-offs were found between any life history traits measured. The 1978 census data served as an independent test of the competition-colonization trade-off; we did find that individual species exhibited different correlations with disturbance (Fig. 3),

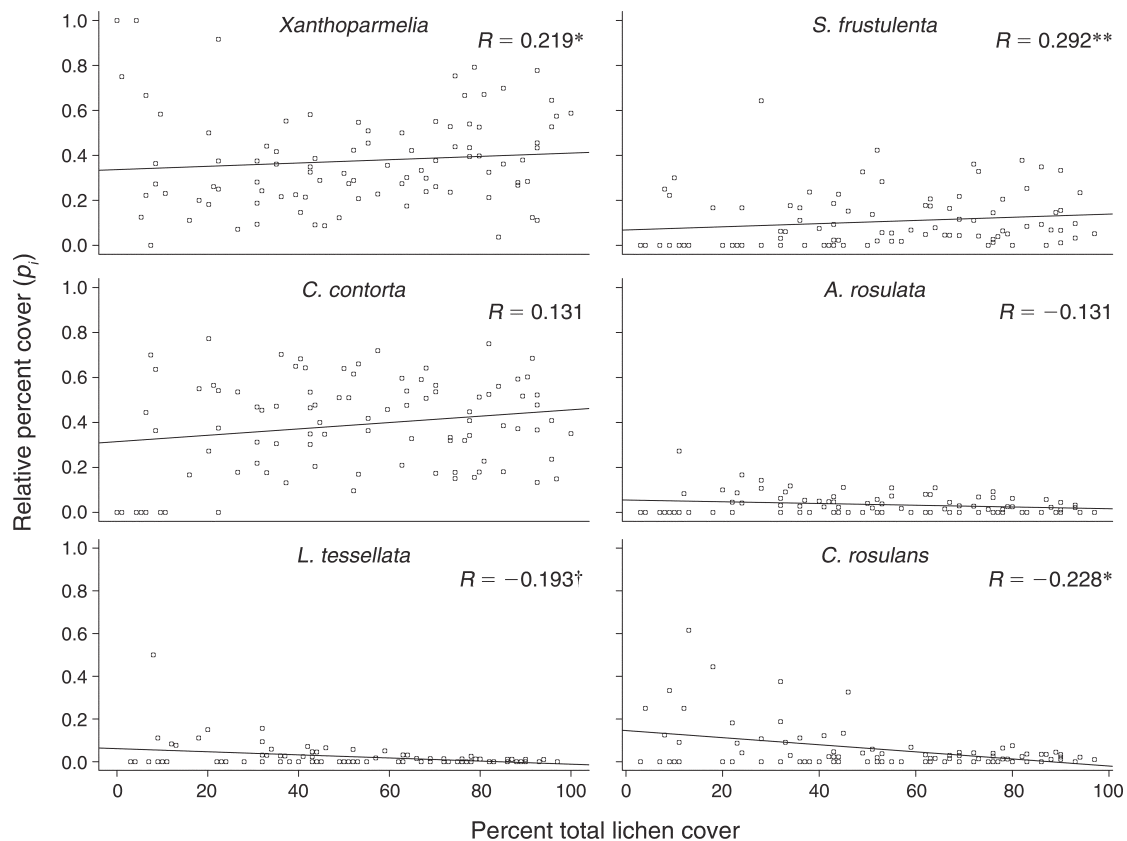


FIG. 3. The abundance of each species, i , as a proportion of the total lichen cover, p_i , plotted against total lichen cover on 98 1-m² plots in 1978. Correlations and significance from linear regressions are indicated for each species. *A. fuscata* and *L. muralis* were not sufficiently abundant for this analysis.

* $P < 0.05$; ** $P < 0.01$; † $P < 0.01$.

but not necessarily in the expected manner. The expected trade-off would predict that good colonizers would be more abundant in high disturbance regimes (low lichen cover), and good competitors would be more abundant in low disturbance regimes (high lichen cover). The relative abundance of *C. rosulans* and, marginally, *L. tessellata* were negatively correlated with total lichen cover, so according to the competition–colonization trade-off, these species should be strong colonizers. However, this prediction was not supported by the experimental results, as both species proved to be poor colonizers (Table 1); in fact, no *C. rosulans* thalli were observed to colonize over the entire 32 years of the long-term study. Two species, *Xanthoparmelia* and *S. frustulenta*, had positive correlations of relative abundance with total lichen cover; therefore, these species should be strong competitors. *Xanthoparmelia* was, in fact, the second best competitor; however, *S. frustulenta* was the worst (Table 1). Based on the abundances in the 1978 census data, the predictions of a simple competition–colonization trade-off for species traits were generally not upheld.

A competition–colonization trade-off has previously been hypothesized to occur in epiphytic lichen communities. However, this trade-off has never been explicitly

tested, perhaps because documenting competitive outcomes in lichen communities requires long-term data. Indirect evidence for such a trade-off exists in the form of observations of young forests being dominated by species with good dispersal abilities (e.g., Gjerde et al. 2012) and a unimodal diversity patterns over a chronosequence of epiphytic lichens on aspens (Ellis and Ellis 2012). Interestingly, other studies of lichen colonization found a relationship between mode of reproduction and colonization ability (Löbel et al. 2009, Johansson et al. 2012). However, we found no obvious relationships between colonization rate and mode of reproduction at the spatial scale studied; of the best colonizers (Table 1), *A. rosulata* mainly reproduced sexually, while *S. frustulenta* reproduced both sexually and asexually.

More broadly, our results are consistent with previous studies that have found little direct evidence for competition–colonization trade-offs contributing to the maintenance of diversity (but see Cadotte et al. 2006, Rodríguez et al. 2007). For example, the competition–colonization trade-off was not found among protozoa in ponds (Limberger and Wickham 2011) or pitcher plants (Kneitel 2012), despite evidence for a genetic constraint among these traits (Cadotte et al. 2006). Additionally,

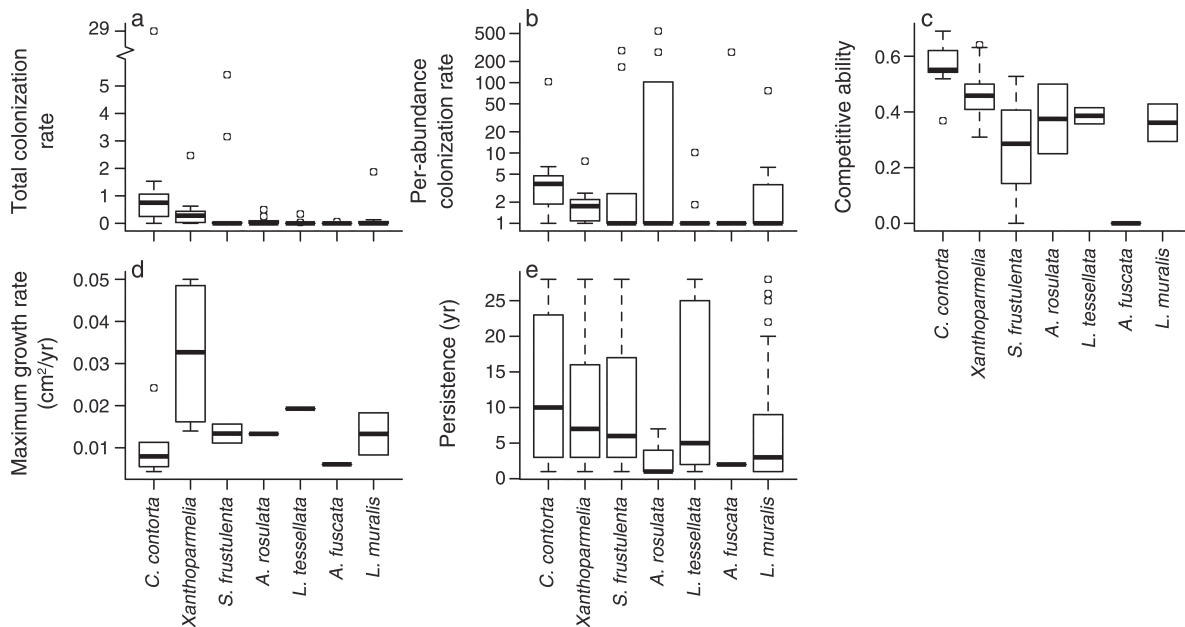


FIG. 4. Distributions of trait values for each of the seven lichen species on the experimental plots. (a) Total colonization rate (number of new colonies established per year per plot). (b) Per-abundance colonization rate (total colonization rate per average species abundance). (c) Competitive ability measured as the percentage of interactions “won” by a species. (d) Growth rate for isolated thalli, based on back-transformed log-transformed values of mean thallus area per year. (e) Persistence measured as the average number of years a species occupied a point.

Yu et al. (2004) failed to find a trade-off among tree-colonizing ants.

Because we did not find a competition–colonization trade-off, it is surprising that we observed diversity patterns consistent with the intermediate disturbance hypothesis (Fig. 2; Grime 1973, Connell 1978). Though the IDH has recently been criticized due to mixed empirical support, mechanisms that can theoretically generate the classic IDH pattern include the competition–colonization trade-off, relative nonlinearity of growth rates, and the storage effect (Shea et al. 2004, Fox 2012). We have concluded that there is no competition–colonization trade-off in this community; thus, it is possible that these other mechanisms are

operating to maintain diversity (Chesson 2000, Amarasakare 2003).

Shea and colleagues (Shea et al. 2004) maintain that understanding mechanisms driving the IDH requires understanding the underlying species life histories. Our long-term experiment suggests that the two dominant species may coexist by using different strategies to maintain high abundances, possibly resulting in relative nonlinearity in their growth rates. Thalli of the crustose lichen, *C. contorta*, persist for long periods while growing very slowly, as seen from the rankings in Table 1. *Xanthoparmelia*, however, takes the opposite strategy: Thalli grow rapidly, but its foliose form leads to the frequent loss of thallus fragments, resulting in a lower

TABLE 1. Ranks of eight lichen species for abundance, total colonization rate, per-abundance colonization rate, maximum growth rate, and competitive and persistence abilities in a 32-year study, and correlations between relative abundance of each species with total lichen cover.

Species	Abundance in 1978	Total colonization rate	Per-abundance colonization rate	Maximum thallus growth rate	Competitive ability	Persistence ability	Relative abundance correlation with total lichen cover
<i>Circinaria contorta</i>	1	1	4	6	1	1	NS
<i>Xanthoparmelia</i>	2	2	6	1	2	4	positive
<i>Staurothele frustulenta</i>	3	3	2	4	6	2	positive
<i>Candelariella rosulans</i>	4	8	8	negative
<i>Acarospora rosulata</i>	5	5	1	3	4	6	NS
<i>Lecidea tessellata</i>	6	6	7	2	3	3	negative
<i>Acarospora fuscata</i>	7	7	3	7	7	7	NS
<i>Lecanora muralis</i>	8	4	5	5	5	5	NS

Notes: The highest value is 1. “Positive” and “negative” indicate the sign of the correlation between relative abundance of a species and total lichen cover, and “NS” indicates a nonsignificant correlation. See Fig. 4 legend for descriptions of terms. Some ranks could not be determined for *C. rosulans*, because it was not found on the long-term experimental plots (ellipses).

probability of persisting at a given point. Interestingly, because of their high relative abundances, *Xanthoparmelia* and *C. contorta* are predominantly in competition with each other, but seem to be equally matched. Although the foliose *Xanthoparmelia* often overgrows the crustose, *C. contorta*, *C. contorta* can persist without light underneath *Xanthoparmelia* for many years until *Xanthoparmelia* inevitably flakes off. Though we could not directly observe the mechanisms of competitive replacement with this study, previous studies have suggested that a number of different traits affect competitive outcomes in lichens (reviewed in Armstrong and Welch 2007), including overgrowth ability (Pentecost 1980), high growth rates (Armstrong 1984), high lobe density or thickness (Lawrey 1984), rate of thallus fragmentation (Pentecost 1980, Woolhouse et al. 1985), and allelopathy (Beschel and Weidick 1973).

The competition–colonization trade-off has a long history as a theoretical mechanism of coexistence, and is still being developed as such. Yet there has been little experimental verification of the presence of a competition–colonization trade-off in nature. This lack of verification may be due to the fact that such studies must be performed using multiple species in spatiotemporally structured habitats over long time periods, which is experimentally challenging. Although our study met these criteria, we did not find evidence for a competition–colonization trade-off. We did, however, find that lichen diversity peaked at intermediate levels of disturbance, which is consistent with the IDH pattern. While a trade-off between competition and colonization may be *one* mechanism that can produce an IDH community pattern, our study demonstrated through experimental evidence that it is not the *only* mechanism that can generate this common pattern (see also Roxburgh et al. 2004). Focusing on mechanisms of coexistence that depend on environmental fluctuations will likely be a fruitful path to explaining diversity patterns in future studies. Understanding the broader role of trade-offs, especially with regard to the effects of fluctuating environments caused by disturbances, will require more trait-based, long-term, experimental studies across a variety of natural communities.

ACKNOWLEDGMENTS

T. E. Miller thanks Jim Brown and Diane Davidson for encouraging him to start this experiment as an undergraduate way back in 1978. Thanks to T. H. Nash for helping with identifications in 1978. The authors thank Patricia, Rick, and Bill Miller for help in the field and Brian Bielfelt for help in organizing the photos. We also thank Scott J. Stepan and John J. Schenk for use of equipment and advice in DNA amplification. Insightful comments from two anonymous reviewers improved the manuscript.

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SUPPLEMENTAL MATERIAL

Appendix A

Photographs from 1979 to 2009 of a plot cleared by chipping in 1978 ([Ecological Archives E095-027-A1](#)).

Appendix B

Photographs from 1978 to 2009 of a control plot that was not chipped ([Ecological Archives E095-027-A1](#)).