



Short communication

Biological soil crust community types differ in key ecological functions



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ABSTRACT

Soil stability, nitrogen and carbon fixation were assessed for eight biological soil crust community types within a Mojave Desert wilderness site. Cyanolichen crust outperformed all other crusts in multi-functionality whereas incipient crust had the poorest performance. A finely divided classification of biological soil crust communities improves estimation of ecosystem function and strengthens the accuracy of landscape-scale assessments.

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Biological soil crusts carry out essential ecological roles in desert ecosystems (Evans and Johansen, 1999; Belnap et al., 2003). However, soil crust community types differ in the degree to which they contribute to ecosystem functions (Belnap, 2002; Housman et al., 2006; Strauss et al., 2012). In past studies, crust community types were often simplistically characterized (e.g. light vs. dark, moss vs. lichen). This resulted in difficulties for cross-investigator or cross-regional comparisons. More importantly, simplistic categories mask functional differences in crust types contributing to errors in estimates of ecosystem function. Consequently, ecologists need to refine classifications for crust communities and determine ecosystem function.

The Mojave Desert is rich in crust communities (Pietrasiak et al., 2011a, 2011b; Pietrasiak, 2012) compared to community types reported from other deserts (Pietrasiak, 2012). This study classifies ten biological soil crust community types in the Mojave Desert

(Table 1) and evaluates three ecosystem functions: carbon fixation, nitrogen fixation, and soil aggregate stability for eight of these community types.

Our study area is within the Mojave Desert physiographic province (ca. 35.50° N, 115.68° W). The climate is arid, with a mean annual precipitation of 145 mm and a mean annual temperature of 17 °C (Turk, 2012). Annual rain events are variable and bimodal (Osborn, 1983). Soil parent material is Mesozoic dolomite alluvium. The vegetation is dominated by *Larrea tridentata* and *Ambrosia dumosa*. Within a 2 km² area, ten crust community types were identified (Table 1), with eight prevalent enough for study. Five replicates per crust type were sampled in the field to conduct the field stability test following Herrick et al. (2001). Ten replicates per crust type were collected for laboratory studies of nitrogen and carbon fixation (Fig. 1).

Nitrogen fixation varied significantly ($p < 0.0001$) among crust types (Fig. 1A). Incorporation of ¹⁵N into crust ranged from below detection to over 100 μmol N₂ m⁻² h⁻¹. Cyanolichen crusts had significantly higher nitrogen fixation rates than all other crust types. Hairy moss, darkened moss, and green algal lichen crusts also showed relatively high fixation rates. Two trends were also notable. First, fixation rates were very consistent within crust community type (Fig. 1A). Second, untransformed data varied by

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Table 1

Descriptions of the ten biological soil crust communities identified in the Mojave Desert based upon morphology and dominant taxonomic group as visible in the field with the naked eye, or in some cases, a hand lens. These crust community types are found throughout the arid west and include all types we have observed except the liverwort-dominated crusts found in the coastal sage-scrub.

Crust type code	Crust type identification	Description
IC	Incipient algal/fungal crust	Weakly consolidated, soft crust that breaks apart easily but displays fungal hyphae or cyanobacterial filaments, dominant components are fungi and/or non-heterocytous cyanobacteria (<i>Microcoleus</i> spp., <i>Leptolyngbya</i> spp.); ubiquitous
FC	Fungal crust	Embedded underneath shrub litter or a sand layer in the open, fungal hyphae clearly visible, dominant components are fungi
LAC	Light algal crust	Inconspicuous colored crust dominantly composed of cyanobacteria (mostly <i>Microcoleus</i> spp. and <i>Pseudanabaenaceae</i> spp.) and eukaryotic algae (e.g. <i>Bracteacoccus</i> , <i>Chlorosarcinopsis</i> , <i>Scenedesmus</i> , <i>Chlorella</i>); ubiquitous
DAC	Dark algal crust	Dark-colored crust dominantly composed of cyanobacteria (colored by surface-growing heterocytous taxa in <i>Nostoc</i> , <i>Scytonema</i> , and <i>Hassallia</i>); present but too rare for study in our site, commonly found on granitic soils elsewhere in the Mojave Desert
CLC	Cyanolichen crust	Lichens that have cyanobacterial photobionts, e.g. <i>Collema</i> ; broadly distributed in intershrub spaces
GLC	Green algal lichen crust	Lichens that have green algal photobionts, e.g. <i>Placidium</i> ; broadly distributed in intershrub spaces
SMC	Smooth moss crust	Moss crust with small phyllids on short thalli, e.g. <i>Bryum</i> ; present but too rare for study in our site, commonly found on granitic soils elsewhere in the Mojave Desert
RMC	Rough moss crust	Moss crust with minor hair-like extensions on phyllids, brownish when dry, green to brown-green when moist, e.g. <i>Syntrichia</i> ; broadly distributed in intershrub spaces
HMC	Hairy moss crust	Moss crust with extensive hair-like extensions on phyllids that appear like whitish-gray carpets, e.g. <i>Crossidium</i> , <i>Pterygoneurum</i> ; requiring shady environments
DMC	Dark moss crust	Clearly blackened, moss-dominated crust (mostly <i>Syntrichia</i>), associated with heterocytous cyanobacteria (<i>Nostoc</i> spp.); broadly distributed in intershrub spaces

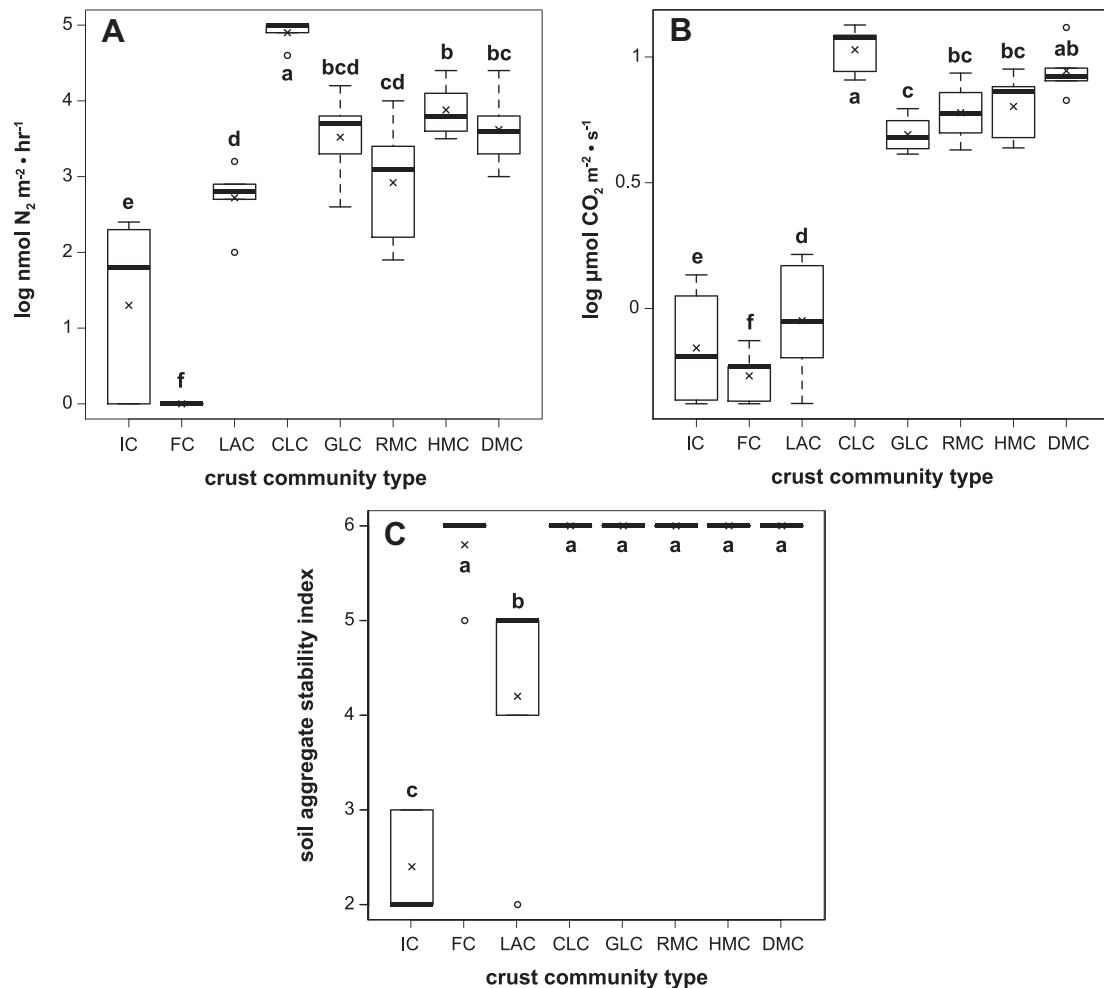


Fig. 1. Boxplots calculated in R (R Core Team, 2012) showing the three ecosystem functions investigated among eight biological soil crust community types. Dark bars represent median values, with boxes enclosing the upper and lower inner quartiles, with extremes indicated by whiskers or circles when the extreme is an outlier (Crawley, 2007), black "x" represent means of log-transformed data. Lowercase letters represent significant differences in means (stability) or means of log-transformed data (N-fixation, C-fixation) detected with ANOVA and the LSD test. For key to crust community types see Table 1. Field collection of dry soil crusts from randomly selected sites occurred over one weekend in April 2011; samples were refrigerated until analysis, which occurred within 30 days. (A) Nitrogen fixation as determined using fixation of ^{15}N enriched gas following methods of Pietrasiak (2012). Briefly, rates were determined following a 24-h rehydration period at field capacity, and a 48-h incubation period, with rates calculated according to Warembourg (1992); (B) carbon fixation as determined following hydration at field capacity from a 2-h incubation period at a photosynthetic photon flux density of $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ at ambient relative humidity and temperature; (C) Herrick's stability index values.

five orders of magnitude between fungal crust (lowest) and the cyanolichen crust (highest). If cyanolichen crusts are abundant, they can potentially be the dominant crust-associated nitrogen fixers in desert ecosystems.

Carbon fixation also varied significantly ($p < 0.0001$) among crust types (Fig. 1B). Cyanolichen crust had the highest fixation rates, but did not differ significantly from darkened moss crust. Light algal crust, incipient algal-fungal crust, and fungal crust showed substantially lower fixation rates than crusts containing moss and/or lichen species (Fig. 1B).

The stability test demonstrated that most crust types had the maximal stability possible with this metric (Fig. 1C). Light algal crust was significantly less stable, but incipient algal-fungal crust was significantly the least stable among all crust types.

This study showed that careful categorization of crust community types can lead to more accurate assessments of their ecological significance. If we had used a more simplistic measure, such as light and dark crust, or moss and lichen crusts, we would have missed the pattern of variation that became clear with the more finely divided classification. The different moss crusts showed minimal variation in ecosystem function. It would be practical to combine these community types. Given the ease with which they can be recognized in the field, the finer classification seems justified. The green algal lichen and cyanolichen crusts were significantly different in both nitrogen and carbon fixation, and future studies should distinguish between these communities. Dark algal crust and smooth moss crusts were present in the study site, but so rare that it was not feasible to include them in this study (Table 1).

Overall, lichen and moss crusts performed best in all ecological functions. The cyanolichen crust, dominated by *Collema tenax* and *Collema coccophorum*, clearly had the highest fixation rates for both carbon and nitrogen. This finding is in agreement with the results of others (Lange et al., 1998; Belnap, 2002; Lange, 2003). High fixation rates may be supported by the carbon concentrating mechanism (Badger et al., 1993), the high nitrogen fixation capacity of the cyanobacterial symbiont (Lange et al., 1998), and prolonged water holding capacity (Lange et al., 1998). Thus, landscapes that support a substantial ground cover of these cyanolichens may have enhanced fertility in terms of nitrogen and carbon. Green algal lichen crusts had observable cyanobacterial colonies growing among lichen squamules, but did not show comparably high nitrogen fixation rates.

Mosses do not fix nitrogen, but are often associated with nitrogen-fixing cyanobacteria (Wu et al., 2009; Zhao et al., 2010). Examination of Clark Mountain hairy moss crusts revealed small colonies of lichenized and free-living cyanobacteria (i.e. *Nostoc*) growing on the soil as well as on the phyllids, and these cyanobacteria are likely responsible for the elevated nitrogen fixation of these crusts.

Light algal crusts were low in both nitrogen and carbon fixation. These crusts are devoid of heterocytous cyanobacteria (Garcia-Pichel and Belnap, 1996; Belnap, 2002; Garcia-Pichel et al., 2003). Typically, the dominant community components in these crusts are filamentous non-heterocytous cyanobacteria such as *Microcoleus* and *Leptolyngbya* species. Minor nitrogen fixation may occur through heterotrophic fixation of symbiotic bacteria living in the sheath material of these filamentous cyanobacteria (Steppe et al., 1996) or due to sparse free-living heterocytous cyanobacteria (Garcia-Pichel and Belnap, 1996).

Fungal crusts at the Clark Mountains mostly formed underneath the litter layer adjacent to shrubs (especially with *L. tridentata*). These crusts generally lack cyanobacteria and are associated with a rich heterotrophic microbial community as well as an evident coccoid green algal assemblage. In contrast to the study by Zaady et al. (1998), heterotrophic nitrogen fixation was minimal in fungal crusts from our study site.

This is the first instance in which different crust community types have been compared based on their stability index values. Previous studies using Herrick's stability test focused instead on the relationships between soil aggregate stability and total crust cover, or reported mean values of mixed community crusts (Bowker et al., 2008; Chaudhary et al., 2009; Carpenter and Chong, 2010; Herrick et al., 2010). In our study, only incipient crusts showed depressed stability values. These findings indicate that all crusts contribute to stability even if they do not play significant roles in nitrogen and carbon fixation. Thus, prevention of erosion due to water and wind represents the major ecosystem function that is common to all crust types.

In conclusion, if a finely divided classification system were used, much greater precision and accuracy would be possible when estimating fixation rates and importance of crust community types at the landscape scale.

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References

- Badger, M.R., Pfanz, H., Büdel, B., Heber, U., Lange, O., 1993. Evidence for the functioning of photosynthetic CO_2 -concentrating mechanisms in lichens containing green algal and cyanobacterial photobionts. *Planta* 191, 57–70.
- Belnap, J., 2002. Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils* 35, 128–135.
- Belnap, J., Büdel, B., Lange, O.L., 2003. Biological soil crust: characteristics and distribution. In: Belnap, J., Lange, O.L. (Eds.), *Biological Soil Crusts: Structure, Function, and Management*, pp. 3–30. Rev. 2nd Print. Berlin.
- Bowker, M.A., Belnap, J., Bala Chaudhary, V., Johnson, N.C., 2008. Revisiting classic water erosion models in dryland: the strong impact of biological soil crusts. *Soil Biology and Biochemistry* 40, 2309–2316.
- Carpenter, D.R., Chong, G.W., 2010. Patterns in the aggregate stability of Mancos Shale derived soils. *Catena* 80, 65–73.
- Chaudhary, V.B., Bowker, M.A., O'Dell, T.E., Grace, J.B., Redman, A.E., Rillig, M.C., Johnson, N.C., 2009. Untangling the biological contributions to soil stability in semiarid shrublands. *Ecological Applications* 19, 110–122.
- Crawley, M.J., 2007. *The R Book*. John Wiley & Sons, Ltd, West Sussex, UK.
- Garcia-Pichel, F., Belnap, J., 1996. Microenvironments and microscale productivity of cyanobacterial desert crusts. *Journal of Phycology* 32, 774–782.
- Garcia-Pichel, F., Johnson, S.L., Youngkin, D., Belnap, J., 2003. Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microbial Ecology* 46, 312–321.
- Herrick, J.E., Whitford, W.G., de Souza, A.G., Van Zee, J.W., Havstad, K.M., Seybold, C.A., Walton, M., 2001. Field soil aggregate stability kit for soil quality and rangeland health evaluations. *Catena* 44, 27–35.
- Herrick, J.E., Van Zee, J.W., Belnap, J., Johansen, J.R., Remmenga, M., 2010. Fine gravel controls hydrologic and erodibility responses to trampling disturbance for coarse-textured soils with weak cyanobacterial crusts. *Catena* 83, 119–126.
- Housman, D.C., Powers, H.H., Collins, A.D., Belnap, J., 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. *Journal of Arid Environments* 66, 620–634.
- Evans, R.D., Johansen, J.R., 1999. Microbiotic crusts and ecosystem processes. *Critical Reviews in Plant Sciences* 18, 183–225.
- Lange, O.L., 2003. Photosynthesis of soil-crust biota as dependent on environmental factor. In: Belnap, J., Lange, O.L. (Eds.), *Biological Soil Crusts: Structure, Function, and Management*, pp. 217–240. Rev. 2nd Print. Berlin.
- Lange, O.L., Belnap, J., Reichenberger, H., 1998. Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO_2 exchange. *Functional Ecology* 12, 195–202.
- Osborn, H.B., 1983. Timing and duration of high rainfall rates in southwestern United States. *Water Resources Research* 19, 1036–1042.
- Pietrasiak, N., 2012. Effects of Land Surface Characteristics on Pedogenesis, Biological Soil Crust Community Diversity, and Ecosystem Functions in a Mojave Desert Piedmont Landscape. University of California, Riverside. Ph.D. dissertation.
- Pietrasiak, N., Johansen, J.R., Drenovsky, R.E., 2011a. Geologic composition influences distribution of microbiotic crusts in the Mojave and Colorado Deserts at the regional scale. *Soil Biology and Biochemistry* 43, 967–974.
- Pietrasiak, N., Johansen, J.R., LaDoux, T., Graham, R.C., 2011b. Spatial distribution and comparison of disturbance impacts to microbiotic soil crust in the Little San Bernardino Mountains of Joshua Tree National Park, California. *Western North American Naturalist* 71, 539–552.

- R Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org/>.
- Steppe, T.F., Olson, J.B., Paerl, H.W., Litaker, R.W., Belnap, J., 1996. Consortial N₂ fixation: a strategy for meeting nitrogen requirements of marine and terrestrial cyanobacterial mats. *FEMS Microbiological Ecology* 21, 149–156.
- Strauss, S.L., Day, T.A., Garcia-Pichel, F., 2012. Nitrogen cycling in desert biological soil crusts across biogeographic regions in the Southwestern United States. *Biogeochemistry* 108, 171–182.
- Turk, J.K., 2012. Vesicular Horizon Distribution, Properties, and Pedogenic Processes in Deserts of the Western United States. University of California, Riverside. Ph.D. dissertation.
- Warembourg, F.R., 1992. Nitrogen fixation in soil and plant systems. In: Knowles, R., Blackburn, T.H. (Eds.), *Nitrogen Isotope Techniques*. Academic Press, San Diego, pp. 127–156.
- Wu, N., Zhang, Y.M., Downing, A., 2009. Comparative study of nitrogenase activity in different types of biological soil crusts in the Gurbantunggut Desert, Northwestern China. *Journal of Arid Environments* 73, 828–833.
- Zaady, E., Groffman, P., Shachak, M., 1998. Nitrogen fixation in macro- and microphytic patches in the Negev Desert. *Soil Biology and Biochemistry* 30, 449–454.
- Zhao, Y., Xu, M., Belnap, J., 2010. Potential nitrogen fixation activity of different aged biological soil crusts from rehabilitated grasslands of the hilly Loess Plateau, China. *Journal of Arid Environments* 74, 1186–1191.