

Testing for consistency in ecosystem engineering: do cushion plants always turn up the heat?

Mia Momberg, Peter C. le Roux

Department of Plant and Soil Sciences, University of Pretoria, South Africa, 0002

Corresponding author: M. Momberg (miamomberg@gmail.com)

Declarations of interest: none

Abstract

Ecosystem engineers influence community structure and functioning by altering habitat and resource availability. However, few studies have assessed how consistent ecosystem engineers' impacts are on abiotic habitat conditions and/or community characteristics, either across species or between habitats. Here we test for the consistency of ecosystem engineering across, and within, cushion-forming plant species, a group of ecosystem engineers that are dominant in polar and alpine environments, by reviewing studies that document their effects on temperature. We find inconsistent effects, with cushion plants having contrasting impacts on temperatures in different studies. Even after limiting analyses to a single cushion plant morphology type or to just a single species, impacts on temperature were still inconsistent between studies. Therefore, while cushion plants have relatively consistent impacts on plant communities (e.g. increasing local species richness), their impact on temperature may not be the overarching abiotic mechanism driving this ecological effect. These results, therefore, highlight the need to explicitly test if ecosystem engineers' biotic and abiotic impacts are consistent through space and time, and emphasize the importance of understanding context-dependence in the outcome of biotic interactions.

Keywords: abiotic effects, cushion plant, ecosystem engineering, temperature.

Introduction

Ecosystem engineers influence community structure and functioning through changing the availability of resources and, thereby, modifying the occurrence of different types of microhabitats (Jones et al., 1994; Alper, 1998; Romero et al., 2015). Ecosystem engineering takes place across all habitats and is known to significantly influence biodiversity patterns in many parts of the world (Jones et al., 1994). These impacts chiefly occur through ecosystem engineers' impacts on abiotic conditions (although not exclusively; e.g. Estes and Palmisano, 1974), with species

altering, for example, stream flow properties (Wright et al., 2002), water infiltration rates (Dangerfield et al., 1998), and soil characteristics (Erpenbach et al., 2017).

It is less well understood, however, whether ecosystem engineers have the same effect in different ecosystems (Baker et al., 2013). For example, the activity of a single ecosystem engineer species (e.g. burrowing by aardvark) can have different effects on both abiotic (e.g. soil moisture and compaction) and biotic characteristics (e.g. species richness) in different biomes (Louw 2017). Similarly, the impact of burrowing prairie dog species on vegetation is context-dependent, varying with prairie dog foraging behaviour and the dominant grasses' grazing tolerance (Baker et al., 2013). Even within a small area there may be differences in the impacts of ecosystem engineers, with, for example, the Japanese seaweed *Sargassum muticum* having contrasting effects on biodiversity depending on whether its ecosystem engineering creates a novel environment within a community or just increases the availability of an existing type of microhabitat (Buschbaum et al., 2006). In contrast, however, different species which share common characters may perform the same ecosystem engineering function, with several different plant species of the same growth form having consistent positive impacts on local plant diversity (Badano & Cavieres 2006). It is therefore important to understand the potential for intra- and inter-specific variation in ecosystem engineers' impacts, as shifts in the nature of engineering effects through space and time will constrain our ability to predict their impacts on communities (e.g. under climate change or during ecosystem restoration).

Cushion plants, a key polar and alpine growth form, are frequently identified as ecosystem engineers (e.g. Badano et al., 2006, Antonsson et al., 2009, Molenda et al., 2012) because they are often nurse species, and consistently increase local species richness in abiotically stressful environments (Arroyo et al., 2003, Brancaleoni et al., 2003, Antonsson et al., 2009, Arredondo-Nuñez et al., 2009, although see Dvorský et al., 2013). Further, cushion plants may increase plant and invertebrate community diversity and phylogenetic uniqueness of communities (Cavieres et al., 2002, Badano et al., 2006, Sklenář, 2009, Molenda et al., 2012, Butterfield et al., 2013). These biotic impacts of cushion plants are thought to be due to the species increasing the availability of some resources and having an ameliorative effect on microclimatic conditions (e.g. Badano et al., 2006). Due to their hemispherical shape, cushion plants have a low surface area to volume ratio, reducing the rates of heat and moisture loss in the cold and windy environments where they are dominant (Moseley, 1879, Körner, 2003, Aubert et al., 2014). Furthermore, as a result of their compact surface and tightly-packed leaves, cushion plants accumulate organic matter (including their own senesced leaves) and wind-blown fine soil particles between their stems, increasing nutrient availability (Ralph, 1978, Ramsay, 1992, Kleier and Rundel, 2004, Sklenář, 2007). As a result, cushion plant species typically strongly modify their microhabitat conditions, with these abiotic impacts being considered the mechanism for their influence on biotic communities (Badano et al., 2006).

This study, therefore, reviews the influence of cushion-forming plant species on temperature, a key abiotic microhabitat characteristic in alpine and polar habitats,

testing whether the effects of ecosystem engineering are consistent across and within cushion plant species. We expected that cushion plants would consistently increase temperatures due to the cushion growth form being a morphological feature associated with heat-trapping and retention (Körner, 2003).

Methods

We followed a systematic keyword-based search on Web of Science, using “cushion plant” and “temperature” as keywords and then eliminated papers whose methodology did not compare temperature measurements between a cushion plant and adjacent substrate at comparable depths. We then searched several databases and hard-copies of journals to add any additional papers that may have been missed by the systematic search. This resulted in twenty-five publications, covering 20 cushion plant species that compared temperatures within or underneath a cushion plant with temperatures outside of the cushion plant were found (see details of all studies in Appendix 1). Due to some studies investigating multiple cushion plant species, 30 unique sets of results were available. The duration of temperature measurements ranged from two days to four months (see e.g. Hupp et al., 2017, which was not included due to insufficient sample size).

The impact of a cushion plant species on temperature was categorized as “warming” (or “cooling”) when temperatures within the cushion plant were significantly warmer (cooler) than adjacent substrate temperatures or air temperatures or, if statistical analyses had not been run, when all temperature measurements were higher (lower) within the plant than in the adjacent substrate. All other results were categorized as “other”, which included datasets where the effects of cushions on temperature were inconsistent (e.g. at certain times of the day warming was evident, but at other times cooling occurred) and datasets where temperature differences were compared statistically and found to be not significant. The impact of a cushion plant on temperature was categorized as buffering when the temperature range within the plants was significantly lower than the range of temperature in the adjacent substrate. An important caveat here is that the majority of the studies measured temperatures over relatively short periods.

Chi² tests, with Yate’s continuity correction for small sample sizes, were performed to determine whether the results reported were significantly different from expectations (i.e. that all studies would report cushion plants to be warmer than the adjacent substrate; limited to comparisons where $n > 5$). All of the tests showed observed counts of studies deviated significantly from expectations ($p < 0.05$), but, due to the small sample size for these tests, a simpler vote-counting approach was also considered here. While the focus of this review was on temperature, when papers reported moisture and soil characteristics in addition to temperature, these results were also extracted.

Cushion-forming species were categorised by morphological type following Aubert et al. (2014), based on their height, shape and compactness. The majority of the species were classed as “Intermediate between hemispherical and flat”, with five

other categories represented. There were only two cushion morphology types represented in more than one study, and those which were only represented in one study were grouped with the six species not listed by Aubert et al. (2014) into the category “other”. We expected that there might be differences in thermal effects between cushion types due to differences in shape and compactness (which affect heat and moisture retention).

Results

Temperatures within cushion plants were significantly and/or consistently warmer than the adjacent substrate in 34% of datasets, with 28% of datasets indicating the opposite pattern (Table 1).

The impacts of cushion plant species remained inconsistent when datasets were split by cushion plant morphology type (Table 1). Moreover, even individual species that were examined in multiple studies did not have consistent effects on temperatures for four out of five species (Table 1). For example, *Azorella monantha*'s impact on thermal conditions was examined in five different studies (all of which were conducted during the growing season in the Andes), with the cushion plant being warmer than the surrounding soil in two studies (Arroyo et al., 2003, Cavieres et al., 2007), but cooler in the third (Badano et al. 2006). The other two studies report more complex effects, with the difference in temperature between the cushion plant and the adjacent substrate being dependent on ambient temperature (Cavieres et al., 2008) or time of the day (Molina-Montenegro et al., 2006).

The impacts of cushion-forming species on soil properties were also largely inconsistent, although there was a trend for higher soil moisture, nitrogen and potassium associated with cushion plant species (Table 2).

Discussion

Cushion plants did not have consistent impacts on thermal conditions, either within or across species and morphological types. The inconsistent impact of cushion plants on thermal conditions was not due to variation between different cushion plant morphology types or between species, as varying effects on temperature were observed within morphological groups, and even within species. Variation in the impact of different cushion plant species on microhabitat temperature has previously been documented, with more compact species observed to show slower rates of temperature change than less compact species (Ruthsatz 1978). Moreover, our results align well with recent findings that altitudinal variation in the morphology of the cushion plant *Silene acaulis* is associated with the magnitude of the species' microclimatic modifications (e.g. at higher altitudes plants were more compact and had larger impacts on thermal conditions; Bonanomi et al. 2015). This group of ecosystem engineers therefore does not have a uniform impact on this abiotic microhabitat characteristic, suggesting that their impact on temperature is not the general mechanism driving the local increase in species richness associated with

Table 1 Impacts of cushion plant species on temperature relative to the adjacent substrate, split by cushion type and species (where multiple studies independently examined the same cushion types or species). Studies that compared cushion plant temperature to air temperature (and not substrate temperature) are included in totals, and indicated in parentheses. See Appendix for details.

Cushion plant species	Warming	Cooling	Buffered	Other	Total
All species	11 (4)	10	4 (2)	9 (2)	34
C & F types*	3	6	2	5 (1)	16
C type	1	2	1 (1)	2	6
Low cushion	1	1	.	1	3
Other types	6 (4)	1	1 (1)	1 (1)	7
<i>Arenaria polytrichoides</i>	.	2	.	1	3
<i>Azorella compacta</i>	.	1	.	1	2
<i>Azorella monantha</i>	2	1	.	2	5
<i>Laretia acaulis</i>	1	3	1	1	6
<i>Silene acaulis</i>	1	1	.	.	2

*Cushion types: C & F types = intermediate between hemispherical and flat, C type = hemispherical. From Aubert *et al.* (2014).

Table 2 Effects of cushion plant species on soil properties, relative to the adjacent substrate.

Parameter	Increase	Decrease	Other
Soil moisture	9	.	4
Soil organic matter	3	1	2
Macronutrients	.	.	1
Nitrogen (N, NH ₄ or NO ₃) or available nitrogen	6	2	3
Phosphorous (P) or available phosphorous (PO ₄)	1	2	4
Potassium (K) or available potassium	6	.	2
Calcium (Ca)	1	.	1
Magnesium (Mg)	1	.	1
Copper (Cu)	.	1	.
Iron (Fe)	.	1	.
Sodium (Na)	1	.	1
pH	.	2	1

cushion plants in cold and windy environments. Since soil moisture was more consistently affected by cushion plants than temperature, increased moisture availability should be investigated as a potentially broadly important driver of the ecological impacts of cushion plant ecosystem engineering (see also Mihoč et al., 2016). More broadly, these results suggest the potential for considerable intra-specific variation in ecosystem engineering (see Chen et al. 2019), highlighting how a species' impact can differ strongly across sites, and raising the question of whether ecologically-meaningful within site variation may generally exist in engineering impacts.

A limitation of this study is that short-term microhabitat data are typically collected, and measurements conducted across longer periods may potentially show different patterns. Future studies should therefore focus on collecting data which can compare across different weather conditions (e.g. allowing contrasts between windy and windstill conditions) and seasons. The inconsistent effects of cushion plants on temperature found across the different studies could be due to data being collected under differing weather conditions and at different depths in the soil. For example, seasonal differences in the effects of cushion plants on temperatures have been observed, and soil temperature fluctuations are influenced by depth below soil surface (Ruthsatz, 1978). Wind conditions may also be a contributor to the thermal buffering effects of cushion plants and future studies should investigate whether wind exposure affects the magnitude of thermal buffering. Cushion plants growing in wind exposed sites, for example, may lose heat faster and show no heating or buffering effect. In contrast, in windstill areas cushion plants may be more likely to maintain warmer temperatures than the surrounding soil. Other environmental drivers such as soil type, disturbance regime (including both biotic and abiotic processes), vegetation cover and vegetation structure could also affect patterns of ecosystem engineering and in order to accurately predict the engineering effects of a group of species a thorough understanding of all of these factors may be required.

More broadly, these results suggest that ecosystem engineers may have context-dependent biotic and abiotic impacts across environments (following, e.g., Baker et al., 2013). This is in agreement with other studies of ecosystem engineers, where, for example, the impact of epigeic earthworms on soil microarthropods varies with earthworm density, shifting towards more negative impacts with increasing earthworm density (Eisenhauer, 2010). Similarly, while some ecosystem engineers, like Pacific salmon, have consistent effects on both biotic (e.g. increasing macroinvertebrate biomass and fish growth rate) and abiotic (e.g. increasing dissolved nutrient content) characteristics, the magnitude of their impacts vary depending on environmental and biotic parameters (Janetski et al., 2009). Therefore, spatial (and, potentially, temporal) variation in the impacts of ecosystem engineers should be explicitly examined if aiming to predict the impact of these species beyond a single species or a single site. For example, Cavieres et al. (2002) suggested that ecosystem engineers, and cushion plants specifically, may act as micro-refugia during climate change, although it is unclear if their abiotic impacts will remain the same under changing environmental conditions. Consequently, there is not sufficient evidence to a priori assume consistency in the influence of ecosystem engineers,

and spatial and temporal replication should be incorporated into studies of ecosystem engineering whenever possible.

Acknowledgements

We thank Stephni van der Merwe, Natalie Haussmann and two reviewers for helpful suggestions on earlier versions of this manuscript.

References

- Alper, J., 1998: Ecosystem 'engineers' shape habitat for other species. *Science*, 280: 1195-1196.
- Antonsson, H., Björk, R. G. & Molau, U., 2009: Nurse plant effect of the cushion plant *Silene acaulis* (L.) Jacq. in an alpine environment in the subarctic scandes, Sweden. *Plant Ecology & Diversity*, 2: 17-25.
- Arredondo-Nuñez, A., Badano, E. I. & Bustamante, R. O., 2009: How beneficial are nurse plants? A meta-analysis of the effects of cushion plants on high-andean plant communities. *Community Ecology*, 10: 1-6.
- Arroyo, M. T. K., Cavieres, L. A., Peñaloza, A. & Arroyo-Kalin, M. A., 2003: Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, 169: 121-129.
- Aubert, S., Boucher, F., Lavergne, S., Renaud, J. & Choler, P., 2014: 1914-2014: A revised worldwide catalogue of cushion plants 100 years after Hauri and Schroter. *Alpine Botany*, 124: 59-70.
- Badano, E. I., Jones, C. G., Cavieres, L. A. & Wright, J. P., 2006: Assessing impacts of ecosystem engineers on community organization: A general approach illustrated by effects of a high-andean cushion plant. *Oikos*, 115: 369-385.
- Badano, E. I. & Cavieres, L. A., 2006: Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography*, 33: 304-313.
- Baker, B. W., Augustine, D. J., Sedgwick, J. A. & Lubow, B. C., 2013: Ecosystem engineering varies spatially: A test of the vegetation modification paradigm for prairie dogs. *Ecography*, 36: 230-239.
- Bonanomi, G., Stinca, A., Chirico, G. B., Ciaschetti, G., Saracino, A. & Incerti, G., 2015: Cushion plant morphology controls biogenic capability and facilitation effects of *Silene acaulis* along an elevation gradient. *Functional Ecology*, 30: 1216-1226.
- Brancaleoni, L., Strelin, J. & Gerdol, R., 2003: Relationships between geomorphology and vegetation patterns in subantarctic andean tundra of Tierra del Fuego. *Polar Biology*, 26: 404-410.

- Buschbaum, C., Chapman, A. S. & Saier, B., 2006: How an introduced seaweed can affect epibiota diversity in different coastal systems. *Marine Biology*, 148: 743-754.
- Butterfield, B. J., Cavieres, L. A., Callaway, R. M., Cook, B. J., Kikvidze, Z., Lortie, C. J., Michalet, R., Pugnaire, F. I., Schöb, C., Xiao, S., Zaitchek, B., Anthelme, F., Björk, R. G., Dickinson, K., Gavilán, R., Kanka, R., Maalouf, J. P., Noroozi, J., Parajuli, R., Phoenix, G. K., Reid, A., Ridenour, W., Rixen, C., Wipf, S., Zhao, L. & Brooker, R. W., 2013: Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*, 16: 478-486.
- Cavieres, L., Quiroz, C. & Molina-Montenegro, M., 2008: Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: Are there differences between nurses? *Functional Ecology*, 22: 148-156.
- Cavieres, L. A., Arroyo, M. T. K., Peñaloza, A., Molina-Montenegro, M. & Torres, C., 2002: Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science*, 13: 547-554.
- Cavieres, L. A., Badano, E. I., Sierra-Almeida, A. & Molina-Montenegro, M., 2007: Microclimatic modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in the high Andes of central Chile. *Arctic, Antarctic, and Alpine Research*, 39: 229-236.
- Chen, J., He, X.-F., Wang, S.-W., Yang, Y. & Sun, H., 2019: Cushion and shrub ecosystem engineers contribute differently to diversity and functions in alpine ecosystems. *Journal of Vegetation Science*, 30: 362-374.
- Dangerfield, J., McCarthy, T. & Ellery, W., 1998: The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *Journal of tropical Ecology*, 14: 507-520.
- Dvorský, M., Doležal, J., Kopecký, M., Chlumská, Z., Janatková, K., Altman, J., de Bello, F. & Řeháková, K., 2013: Testing the stress-gradient hypothesis at the roof of the world: Effects of the cushion plant *Thylacospermum caespitosum* on species assemblages. *PLoS One*, 8: e53514.
- Eisenhauer, N., 2010: The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. *Pedobiologia*, 53: 343-352.
- Erpenbach, A., Bernhardt-Römermann, M., Wittig, R. & Hahn, K. (2017). The contribution of termite mounds to landscape-scale variation in vegetation in a West African national park. *Journal of Vegetation Science* 28: 105-116.
- Estes, J. A. & Palmisano, J. F., 1974: Sea otters: Their role in structuring nearshore communities. *Science*, 185: 1058-1060.
- Hupp, N., Llambí, L. D., Ramírez, L. & Callaway, R. M., 2017: Alpine cushion plants have species-specific effects on microhabitat and community structure in the tropical Andes. *Journal of Vegetation Science*, 28: 928-938.

- Janetski, D. J., Chaloner, D. T., Tiegs, S. D. & Lamberti, G. A., 2009: Pacific salmon effects on stream ecosystems: A quantitative synthesis. *Oecologia*, 159: 583-595.
- Jones, C. G., Lawton, J. H. & Shachak, M., 1994: Organisms as ecosystem engineers. *Ecosystem management*, pp. 130-147. Springer.
- Louw, M. A., 2017: Testing of consistency in the impacts of burrowing on soil and vegetation across biomes. M.Sc. dissertation. Department of Plant and Soil Sciences, University of Pretoria, South Africa.
- Kleier, C. & Rundel, P. W., 2004: Microsite requirements, population structure and growth of the cushion plant *Azorella compacta* in the tropical Chilean Andes. *Austral Ecology*, 29: 461-470.
- Körner, C., 2003: *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Springer Berlin, Heidelberg.
- Mihoč, M., Giménez-Benavides, L., Pescador, D., Sánchez, A., Cavieres, L. & Escudero, A., 2016: Soil under nurse plants is always better than outside: A survey on soil amelioration by a complete guild of nurse plants across a long environmental gradient. *Plant and soil*, 408: 31-41.
- Molenda, O., Reid, A. & Lortie, C. J., 2012: The alpine cushion plant *Silene acaulis* as foundation species: A bug's-eye view to facilitation and microclimate. *PLoS ONE*, 7: e37223.
- Molina-Montenegro, M. A., Badano, E. I. & Cavieres, L. A., 2006: Cushion plants as microclimatic shelters for two ladybird beetles species in alpine zone of central Chile. *Arctic, Antarctic, and Alpine Research*, 38: 224-227.
- Moseley, H. N. (1879) *Prince edward islands. The Crozet Islands. Notes by a naturalist on the challenger*. London, Macmillan and co., London.
- Ralph, C. P., 1978: Observations on *Azorella compacta* (Umbelliferae), a tropical Andean cushion plant. *Biotropica*, 10: 62-67.
- Ramsay, P. M., 1992: *The páramo vegetation of Ecuador: The community ecology, dynamics and productivity of tropical grasslands in the Andes*. School of Biological Sciences, University of Wales, Bangor, Gwynedd.
- Romero, G. Q., Gonçalves-Souza, T., Vieira, C., Koricheva, J., 2015: Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, 90: 877-890.
- Ruthsatz, B., 1978: Las plantas en cojín de los semi-desiertos andinos del noroeste Argentino. *Darwiniana*, 21: 491-539.
- Sklenář, P., 2007: Temperature environment of *Xenophyllum humile* (Kunth) v.A. Funk, a high Andean cushion plant. *Arnaldoa*, 14: 97-104.
- Sklenář, P., 2009: Presence of cushion plants increases community diversity in the high equatorial Andes. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 204: 270-277.

Wright, J. P., Jones, C. G. & Flecker, A. S., 2002: An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, 132: 96-101.