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Original

Availability:

This version is available <http://hdl.handle.net/11390/1104436> since 2020-03-05T19:05:12Z

Publisher:

Published

DOI:10.1111/1365-2435.12596

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Journal:	<i>Functional Ecology</i>
Manuscript ID	FE-2015-00563.R1
Manuscript Type:	Standard Paper
Date Submitted by the Author:	21-Sep-2015
Complete List of Authors:	Bonanomi, Giuliano; University of Naples Federico II, Department of Agriculture Stinca, Adriano; University of Naples Federico II, Department of Agriculture Chirico, Giovanni; University of Naples Federico II, Department of Agriculture Ciaschetti, Giampiero; Majella National Park, Saracino, Antonio; University of Naples Federico II, Department of Agriculture Incerti, Guido; University of Naples Federico II, Department of Agriculture
Key-words:	plant community, plant-plant interaction, competition, microclimate, soil fertility, species richness, stress-gradient hypothesis, severity-interaction relationships

**Cushion plant morphology controls biogenic capability and
facilitation effects of *Silene acaulis* along an elevation gradient**

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Running headline: Cushion morphology modulates *Silene* facilitation

Summary

1. The stress-gradient hypothesis (SGH) predicts that the balance of plant-plant interactions shifts along abiotic environmental gradients, with facilitation becoming more frequent under stressful conditions. However, recent studies have challenged this perspective, reporting that positive interactions are, in some cases, more common at the intermediate level of environmental severity gradients. Here we test whether and how neighbour effects by *Silene acaulis* cushions vary along a 700 m wide altitudinal transect, in relation to cushion morphological traits and environmental severity.

2. Field measurements along the gradient, within and outside cushions, included (i) species richness and cover of coexisting vascular plants, (ii) cushion morphology, (iii) above- and below-ground microclimate, and (iv) soil quality. We used the relative interaction index (RII) to decouple neighbour trait effects and environmental severity effects on plant diversity at different elevations.

3. The ability of the cushion plant to facilitate heterospecifics shifts considerably along the elevation gradient, being greatest at the intermediate level. On the other hand, *Silene* morphological traits steadily change along the gradient, from lax, soft and flat-shaped cushion habits at low elevation to tightly knit and dome-shaped habits at high elevation.

4. Cushion morphological changes are associated with mitigating effects on microclimate, indicating that cushions effectively act as a heat-trap at medium and high elevations, while at low elevations the soft and flat cushions avoid excessive heat accumulation by tight coupling with the surrounding atmosphere. At the upper end of the gradient, cushion cespitose-pulvinate compactness and high stem density appear to be critical traits in modulating the net effect of plant-plant interaction, since the space available for hosting other vascular species is considerably reduced.

44 **5.** In conclusion, this work provides a mechanistic link between plant morphological traits,
45 associated biogenic microclimate changes and variation in net plant-plant interactions along
46 the explored severity gradient. Our findings support an alternative conceptual model to SGH,
47 with plant facilitation collapsing at the upper extreme of the abiotic stress gradient.

48

49 **Key words:** plant community, plant-plant interaction, competition, microclimate, soil
50 fertility, species richness, stress-gradient hypothesis, severity-interaction relationships, relative
51 interaction index, stem density.

52

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Introduction

Although competition has been considered the major interaction process in regulating natural plant community dynamics (Tilman 1988), environmentally mediated positive non-trophic species interactions (i.e. facilitation, reviews in Brooker *et al.* 2008) have been reported in a variety of ecosystems, including alpine habitats (Callaway *et al.* 2002). Facilitation may be crucial for understanding plant community structure (Bruno, Stachowicz & Bertness 2003), productivity (Badano & Marquet 2009) and diversity (Hacker & Gaines 1997; McIntire & Fajardo 2014).

A growing body of empirical evidence indicates that facilitation and competition operate simultaneously, thus affecting the final outcome of plant-plant interactions (Holmgren, Scheffer & Huston 1997; Callaway 2007). Net positive interactions occur in a wide range of ecosystems (Bonanomi, Incerti & Mazzoleni 2011), but are more common under stressful ecological conditions (He, Bertness & Altieri 2013). The stress-gradient hypothesis (SGH; Bertness & Callaway 1994) posits that positive interactions will be more common in abiotically stressful than benign habitats, and that the net beneficial effect of a potential nurse plant increases with increasing environmental stress gradient. This occurs because the positive components of the interaction progressively outweigh the negative aspects due to resource consumption. However, recent studies have challenged this perspective, reporting that positive interactions are, in some cases, more common at the intermediate level of environmental severity gradients (Michalet *et al.* 2006; Holmgren & Scheffe 2010). The shape of the severity interaction relationship (SIR; Brooker *et al.* 2006) can vary along environmental gradients, being linear, showing a plateau, or being hump-shaped (e.g. Kawai & Tokeshi 2007; le Roux & McGeoch 2010). The hump-shaped SIR occurs when the net interaction between species is more positive at the intermediate level of environmental severity than at lower or higher stress conditions. Hump-shaped SIR may arise

79 when the competitive component of the interaction does not decrease with increasing habitat
80 severity. Thus the potential plant beneficiary will suffer intense competition at the lower end
81 of the gradient, and both competition and intense abiotic stress at the upper end (Brooker *et*
82 *al.* 2006). Depending on the climate and the limiting stress factor for the neighbour species
83 involved in the interaction, a variation in net plant interaction along an altitudinal gradient can
84 be ascribed to two non-mutually exclusive mechanisms, either "environmental-severity" or
85 "neighbour trait" effects (Michalet *et al.* 2014). In the case of facilitative interaction, the first
86 effect will correspond to a decrease with altitude in the beneficiary performance in the
87 absence of the nurse species, merely as a result of increasingly harsh environmental
88 conditions. On the other hand, changes in beneficiary performance in the presence of the
89 nurse plant along the environmental gradient can be due to a shift in key morphological or
90 functional traits affecting the nurse facilitation capability.

91 Although the hump-shaped SIR model could be related to the changing ability of
92 plants to act effectively as nurse species, this explanation has not yet been fully explored (but
93 see Schöb *et al.* 2013). Examples of nurse-traits changing with time, space and environmental
94 gradients are well known. For example, the build-up of soil fertility islands under nurse
95 canopies can require decades or even centuries to accumulate nutrients and carbon stock in
96 the underlying soil (Facelli & Brock 2000). Local habitats can affect the efficacy of
97 facilitation as well. Oak trees (*Quercus douglasii*) in the Californian savannah exhibit either a
98 deep root system oriented to explore the water table, or an extensive network of shallow roots
99 exploiting water infiltrating in the topsoil. Interestingly, trees with shallow roots do not act as
100 nurses for herbaceous plants, because below-ground competition overrides the facilitating
101 effect of canopy shading and litter, as occurs for deep-rooted trees (Callaway 1990). In
102 Israel's semi-arid shrubland, the facilitative effect of dwarf shrubs (*Sarcopoterium spinosum*)
103 has a unimodal pattern in relation to canopy density and shrub age (Reisman-Berman 2007).

104 Recently, [Incerti *et al.* \(2013\)](#) reported that the facilitation capability of tussock grass
105 *Ampelodesmos mauritanicus* has a clear ontogenetic shift modulated by fire occurrence, with
106 only large and recently burnt tussocks operating as nurse plants for the recruitment of
107 coexisting species.

108 These examples demonstrate that the ability of a plant to modify the surrounding
109 biotic and abiotic environment, and thus act as a nurse, is affected by its structure and
110 morphology ([Crutsinger, Strauss & Rudgers 2010](#); [Michalet *et al.* 2011](#); [Schöb *et al.* 2013](#)).
111 Plant morphology can change along environmental gradients as a result of intraspecific
112 genetic differences or phenotypic plasticity ([Nicotra *et al.* 2010](#)). Thus a plant's biogenic
113 ability to modify the surrounding environment and hence its facilitation capability may also
114 change ([Schöb *et al.* 2013](#)).

115 Here, we test whether and how the SIR changes in relation to nurse plant morphology
116 and corresponding biogenic capability. Our model system to test this hypothesis is *Silene*
117 *acaulis* (L.) Jacq. subsp. *bryoides* (Jord.) Nyman (hereinafter *Silene*), an alpine cushion plant
118 widespread in the Northern Hemisphere ([Körner 2003](#)). *Silene* is well known as a nurse plant,
119 because it ameliorates microclimatic conditions by yielding warmer temperatures, creating
120 more stable moisture conditions and improving soil quality within its compact canopy
121 ([Molenda, Reid & Lortie 2012](#); [Körner 2003](#)). At the study site *Silene* occurs along a wide
122 elevation gradient, sampled with high density to assess the SIR shape with higher detail,
123 compared with previous studies ([Brooker *et al.* 2008](#)). To explore the mechanisms underlying
124 changes in *Silene* facilitation along the altitudinal gradient, we decoupled the role of
125 environmental severity effects and neighbour trait effects. Field measurements were carried
126 out to (1) evaluate the effects of *Silene* cushions on the spatial distribution of coexisting
127 vascular plant species, (2) quantify the effects of the elevation gradient on cushion

128 morphology, (3) assess the effect of the *Silene* canopy on the above- and below-ground
129 microclimate, as well as on soil quality. Specifically, we asked:
130 (1) what is the SIR shape in the *Silene* plant communities along the severity gradient?
131 (2) are environmental severity effects and neighbour trait effects mutually exclusive or co-
132 occurring along the altitudinal gradient?
133 (3) do *Silene* cushion morphology and related biogenic effects change along the severity
134 gradient?
135 (4) what are the relationships between nurse-trait changes and plant-plant interactions along
136 the environmental severity gradient?

137

Materials and Methods

Study system

Our study sites are located on the north-east facing slope of the Majella massif (Central Italy; [Fig. S1, Supporting Information](#)). Details on local soil can be found in [Whitehead \(1951\)](#). Mean annual rainfall is 1613 mm and the mean annual temperatures are 3.6 °C, 3.1 °C and 0.0 °C at 2,125, 2,405 and 2,730 m a.s.l., respectively ([Stanisci et al. 2005](#)). *Silene* is a long-lived evergreen cushion-forming plant with a woody taproot and highly branched stem ([Daubenmire 1941](#)). At the study site *Silene* forms cushions of different compactness, with a diameter up to 200 cm and a maximum height of 25 cm, at elevations ranging from ~2,000 to ~2,750 m. Such an altitudinal gradient, with a mean annual temperature of 3.6 °C at 2125 m, and a lapse rate of 0.6 °C per 100 m of elevation, corresponds to a sharp reduction in species richness ([Stanisci et al. 2005](#)) and thus was used as a surrogate for environmental severity ([Austin 2002](#); [Körner 2003](#); [Körner 2007](#)).

Sampling design

Field sampling was designed to assess differences in environmental conditions occurring within and outside *Silene* cushions along the altitudinal gradient. Sixty cushions (hereinafter IN) and paired adjacent open areas (OUT) were sampled in July 2012 along a 664 m altitudinal transect up to 2736 m, at approximately 15-m intervals ([Figs S1 and S2, Supporting Information](#)), where medium to large size cushions (diameter 40-120 cm) were randomly selected. Sampling areas were delimited by a malleable wire belt, first shaped around the plant perimeter and then placed at a distance < 1 m, in a randomly selected direction. The percent cover of plant species occurring in each sampling area was visually

estimated. Plants were directly identified in the field. Specimens of critical taxa were collected and identified in the laboratory following [Pignatti \(1982\)](#).

Cushion morphology

In the field, we measured maximum height and diameter at four orientations of all 60 *Silene* cushions. We also collected plant material by inserting a metallic cutting ring (7 cm in diameter, 10 cm high) into each cushion at its maximum height, to assess cushion compactness. Such destructive sampling was limited to a subset of 20 plants to reduce the impact on the local *Silene* population. In the laboratory, we measured stem density (i.e. stem number per cm²) and bulk density (i.e. the ratio of oven-dried weight to volume, mg/cm³) of collected ring samples.

Microclimatic data

We measured soil and cushion temperature along the vertical profile at 40 out of the 60 locations with a stainless steel temperature probe (20 kW NTC Thermistor, accuracy ± 0.2 °C at 0 °C, Salmoiraghi, Italy), in both sampling areas: IN, at 2 and 4 cm depth within the canopy, and at 10 and 20 cm depths in the underlying soil; OUT, at 2, 4, 10 and 20 cm soil depths. All measurements were taken in July 2012 at midday with sunny weather.

We monitored microclimate every ten minutes during a 52-day period, from 28 July to 17 September 2012, in two sites at medium altitude (2,336 m a.s.l.) and at the upper limit (2,697 m a.s.l.) of the altitudinal range. At each site monitoring was replicated in three randomly selected cushions (IN) and paired open areas (OUT). We used a data logger (Em50 Decagon, Pullman, WA, USA) equipped with sensors for soil water content (SWC) and temperature (5TM Decagon, Pullman, WA, USA), positioned at 4 cm depth, and for air temperature/humidity (VP-3, Decagon, Pullman, WA, USA), positioned 10 cm above the

canopy. To gain further insights about the surface temperature of IN and OUT areas, we acquired IR images with a thermal camera (Fluke Yi25 FLIR Systems, West Malling, UK), positioned at nadir 1 m above the plant canopy on several sunny days during summer 2012.

Soil data

We collected ~500 g of soil under each of the 20 plants surveyed to assess cushion compactness, and in the adjacent OUT areas. All samples were collected from the topsoil layer (0-20 cm), where *Silene* (Daubenmire 1941) and most of the coexisting herbaceous plants [Bonanomi, personal observation] are rooted. Samples were packed in polyethylene bags, transferred to the laboratory and sieved through a 2 mm mesh to separate coarse and fine fractions. The fine fraction was characterised by standard methods (Sparks *et al.* 1996) measuring electrical conductivity in 1:5 soil:water extracts, pH in 1:2.5 soil:water suspensions, organic C content by chromic acid titration method, and total N by flash combustion with a CNS Elemental Analyser (Thermo FlashEA 1112).

Shape of the SIR and underlying effects

The effect of *Silene* cushions on coexisting plants was first assessed by calculating the differences in plant cover and species richness between IN and OUT areas at each location along the altitudinal transect. We then employed the method by Michalet *et al.* (2014) to disentangle altitude and trait-level effects on net plant interactions. Effect size was measured using the relative interaction index (RII), a symmetrical estimate widely used in plant ecology (Armas, Ordiales & Pugnaire 2004). We calculated RII to quantify the effect of neighbours (i.e. *Silene* cushions) according to the following equation:

$$RII_{\text{neighbours}} = (r_N - r_C) / (r_N + r_C)$$

where r_N and r_C are the response (either plant cover or species richness) with and without neighbours (i.e. IN and OUT area, respectively). $RII_{\text{neighbours}}$ indicates the size of neighbour effect, where negative and positive mean values, when significantly different from zero, indicate prevailing competition and facilitation, respectively, while mean values not significantly different from zero correspond to a neutral net interaction. Considering the amplitude of the altitudinal transect and its morphological discontinuity in the sampled slope profile (Figs S1 and S2, Supporting Information), $RII_{\text{neighbours}}$ was separately calculated for all paired IN-OUT areas within three altitudinal belts, corresponding to low (2080-2250 m), medium (2330-2550 m) and high (2600-2800 m) elevations. Hence, $RII_{\text{neighbours}}$ was used to assess changes in magnitude and direction of the interactions of *Silene* with coexisting plants along the altitudinal gradient. Further, in order to separate the net effect of *Silene* from that of environmental factors, we calculated RII to quantify the effect of altitude, as follows:

$$RII_{\text{altitude}} = (r_H - r_L) / (r_H + r_L)$$

where r_H and r_L are the responses (either plant cover or species richness) at higher and lower altitude, respectively. RII_{altitude} was calculated separately for plant response with and without neighbours (i.e. IN and OUT areas, respectively), comparing low vs medium and medium vs high altitude belts. According to Michalet *et al.* (2014), RII_{altitude} indicates the size of the altitude effect on target plant performance, where negative and positive values, when significantly different from zero, indicate better performance at lower and higher altitude, respectively. Therefore, if there is a significant shift in $RII_{\text{neighbours}}$ along the altitudinal transect, then RII_{altitude} can be used to attribute changes to an environmental severity effect, a neighbour trait effect, or both, if RII_{altitude} without neighbours, RII_{altitude} with neighbours, or both are significantly different from zero.

Data analysis

We used generalized linear models (GLM) to assess first and second order effects of sampling area (either IN or OUT) and elevation on plant cover and species richness. Sampling area was treated as a fixed factor, whereas elevation was treated as a continuous covariate.

Means with 95% confidence limits of RII were tested for difference from zero by one-sample mean t-tests, while one-way ANOVA and post-hoc Duncan tests were used to assess significant differences between $RII_{\text{neighbours}}$ means at different altitude, as well as significant differences between RII_{altitude} means.

The relationships between cushion morphological traits, temperature and elevation were analysed by 3D scatterplots and assessed by pair-wise linear and exponential correlation.

Soil quality differences between IN and OUT areas were assessed by t-test for paired samples. After removing temporal autocorrelation from the temperature time series using a first order auto regressive integrated moving average model [ARIMA (1,1,1)], differences between IN and OUT areas at the two sampled elevations were assessed by the non-parametric Wilcoxon test for paired samples since normality assumptions were not met (Shapiro-Wilk W test, $N=7,488$ and $P < 0.001$ for all tested cases). Occurrence of higher temperatures inside *Silene* cushion compared with paired OUT areas was tested for statistical significance against two null models: an expected percent frequency of 50% (i.e. no cushion effect) using the Yeates corrected chi-squared test, and a random cushion effect obtained by random permutations ($N=10000$) of observed temperatures. In the latter case, P values were calculated as the fraction of permutations that yielded equal or higher response compared with the observed value, following [Slade & Hall \(1999\)](#). All statistical analyses were performed using the software package STATISTICA 6 (StatSoft, Tulsa, Oklahoma). Statistical significance was evaluated in all cases at $P < 0.05$ and $P < 0.01$.

Results

Plant interaction response along the elevation gradient

A total of 73 and 65 plant species were recorded inside *Silene* cushions and in the open areas, respectively (Table S1, Supporting Information). Raw data of plant cover and species richness were negatively correlated with elevation ($r = -0.49$ and -0.38 , respectively, $P < 0.01$ in both cases), while differences between paired IN and OUT areas showed hump-shaped relationships (Fig. 1). GLM models for plant cover and species richness showed significant effects due to *Silene* presence-absence, altitude and their interaction (Table S2, Supporting Information).

Analysis of RII confirmed a hump-shaped relationship with elevation both for plant cover and species richness (Fig. 2), showing changes in net plant-plant interactions along the altitudinal transect. For plant cover, $RII_{\text{neighbours}}$ indicated a significant shift from net competition ($RII_{\text{neighbours}} < 0$) at low elevation, to facilitation ($RII_{\text{neighbours}} > 0$) at medium altitude, with net positive interaction still holding but decreasing at high altitude. Changes from low to medium altitude were due to a combined environmental severity and neighbour trait effect. In particular, plant cover outside *Silene* cushions decreased with altitude due to environmental constraints ($RII_{\text{altitude}} < 0$ without neighbour), while plant cover within cushions increased with altitude due to neighbour trait effect ($RII_{\text{altitude}} > 0$ with neighbour). From medium to high altitude, plant cover within *Silene* cushions decreased due to neighbour trait effect ($RII_{\text{altitude}} \text{ with neighbour} < 0$), while it did not change significantly outside cushions ($RII_{\text{altitude}} \text{ without neighbour}$ not significantly different from 0).

Considering species richness (Fig. 2), a neutral net interaction was observed at low altitude ($RII_{\text{neighbours}}$ not significantly different from 0), which shifted to facilitative at medium elevation ($RII_{\text{neighbours}} > 0$), and reverted to neutral at high altitude (Fig. 2). Such changes were due to a combined effect of environmental severity and nurse trait. From low to medium

altitude, a decrease in species richness, more pronounced outside than within the cushions (RII_{altitude} was higher with than without neighbour, both values < 0), indicated that a change in nurse trait limited the negative effect of environmental severity on plants coexisting with *Silene*. At higher altitude, an increase in species richness in the OUT area (RII_{altitude} without neighbour > 0) and a decrease inside the cushions (RII_{altitude} with neighbour < 0), indicated a release of the facilitative nurse-trait effect observed at medium altitude.

Cushion biogenic effects on soil and microclimate

Nurse trait effects were unrelated to cushion effects on soil quality. Indeed, soil parameters inside *Silene* cushions were significantly different compared to open areas, with higher organic C content, salinity, total N, and C/N ratio, and lower pH (Table 1). However, for such variables, neither raw data nor differences between IN and OUT areas were associated to altitude, with the exception of soil pH in the OUT area, showing positive correlation ($r = 0.34$ and $P < 0.05$).

Conversely, microclimatic data provided an interesting frame of reference to interpret nurse trait effects. As expected, temperature decreased along soil vertical profiles at all locations. Temperature inside the cushion was consistently higher than outside, both considering surface temperature at noon, during sunny days, and values along the vertical profile at -2 and -4 cm, but not at greater depths (Fig. S5, Supporting Information). This pattern was consistent along the altitudinal transect at -4 and -10 cm soil depths, though the difference between paired IN and OUT values was not associated with elevation (Fig. S6, Supporting Information). Conversely, temperature differences between the cushion and surrounding air showed a significant linear increase with altitude (Fig. S6, Supporting Information), consistent with an increasing mitigating effect of the *Silene* cushion along the transect. On the other hand, temperature differences between the cushion and the surrounding

310 air and soil were positively associated with cushion compactness metrics (Table 2). Stem
311 density and bulk density, as well as cushion maximum height, in turn increased with altitude
312 (Table 2), showing extreme cushion compactness and convexity at high elevation (Fig. 3, Fig.
313 S4, Supporting Information).

314 Microclimatic monitoring during the growing season showed significantly lower air
315 temperature at high compared to medium elevation (Wilcoxon U test on de-autocorrelated
316 time series, $P < 0.001$). Contrasting results related to the beneficial effect of *Silene* cushions
317 were observed at different altitudes. At high elevation, temperature within cushions was
318 significantly higher than in open areas (Fig. S7, Supporting Information), both considering
319 paired data (Wilcoxon U test on de-autocorrelated time series, $P < 0.001$), and the occurrence
320 of positive differences under both null models of random cushion effect (random permutation
321 test, $P < 0.01$) and no cushion effect (Yates corrected Chi-squared test, $P < 0.001$). However,
322 at such elevations, temperature inside *Silene* cushions showed extreme daily ranges, not
323 detected outside or at the lower altitude (Fig. 4).

324 Time series of soil moisture inside and outside the cushions were different, exhibiting
325 rapid and nearly insensitive responses to rainfall bursts, respectively (Fig. S8, Supporting
326 Information). However, data were similar at the two elevations, hence difficult to relate to
327 plant interaction changes along the altitudinal transect.

328

Discussion

The ability of *Silene* to facilitate heterospecific plants shifts along the elevation gradient, being highest at the intermediate level of environmental severity. Our data provide a possible mechanistic link between *Silene* morphological traits and their ability to modify the microclimate within the cushion. These results suggest that shifts in nurse traits, and the associated changes in microclimatic conditions once disentangled from environmental constraints, can control net plant-plant interactions along the severity gradient. Interestingly, *Silene* showed a substantial plastic morphological response with increasing altitude that resulted in a hump-shaped facilitative impact on coexisting plants along the altitudinal gradient. In this regard, cushion stem density appears to be a critical trait in modulating the net effect of *Silene* on plant-plant interaction.

Plant interaction balance along the severity gradient

Consistent with previous studies (Antonsson *et al.* 2009; Cranston *et al.* 2012), we showed that the *Silene* cushion facilitates many heterospecifics, including annual and perennial forbs, grasses and sedges. At the community level, we found that *Silene* plant-plant interactions, passing from low to medium up to high altitude, shift from negative to positive and to neutral, with differences in magnitude depending on the metric of plant performance (either cover or species richness). Effect size, as expressed by RII, was higher at intermediate elevations and inside the cushion, resulting in a hump-shaped SIR with its maximum indicating a facilitation peak and not a competition release. This result contrasts with previous reports of monotonic increases with elevation, both on *Silene* (Antonsson *et al.* 2009; Cranston *et al.* 2012) and other alpine cushion plants (Cavieres *et al.* 2002; 2005). However, in the above studies no information was provided about the full altitudinal range of the nurse, and the explored ranges were much shorter (300 m for Antonsson *et al.* 2009, 243 m for Cranston *et al.* 2012, 200 m

for [Cavieres *et al.* 2002](#) and [2005](#)) and based on fewer sites than in our system. Our finding highlights the importance of using the full length of the severity gradient to properly identify the SIR shape ([le Roux & McGeoch 2010](#)).

Hump-shaped SIR has been explained by dominance of the competition component at low severity levels, a positive balance of competitive and facilitative effect at intermediate levels of the gradient, and a combined role of competition and extreme stress at the upper end of the severity gradient ([Maestre *et al.* 2009](#)). In our study, this model holds true at low and medium altitudes, while at higher elevation the community performance diminished only within the nurse, where facilitative effects were released due to extreme cushion compactness. Hence, the SIR shape decline at high altitude was related to nurse trait changes in response to extreme stress, and not to increasing competition and/or extreme stress of coexisting plants. In a recent meta-analysis, [Michalet *et al.* \(2014\)](#) reported an increase in facilitation from high to low altitude for the Mediterranean climatic region, related to the opposing stress gradients of cold and aridity. However, the meta-analysis by [Michalet *et al.* \(2014\)](#) was based on the classification of previous evidence into two general altitudinal levels, not directly comparable to our transect. Their findings would be consistent with our results limited to a facilitation shift from high to medium altitude belts, but not at lower elevation, indicating that species interaction responses are strictly dependent on the specific altitudinal range and resolution investigated in single studies. Furthermore, while our study system is located in the Mediterranean region, the local climate, according to a finer classification ([Stanisci, Pelino & Blasi 2005](#)), is "subalpine-alpine humid", and *Silene* plant communities are classified as "alpine" ([Körner 2003](#); [Antonsson *et al.* 2009](#); [Cranston *et al.* 2012](#)), hence not directly fitting with the classification used in the cited meta-analysis.

The conceptual integration of hump-shaped SIR in plant community models, as in the case of species richness-biomass relationships, has been discussed and resolved ([Michalet *et*](#)

al. 2006). On the other hand, the integration of hump-shaped SIR into the stress-gradient hypothesis (SGH; Bertness & Callaway 1994) is more problematic (e.g. Kawai & Tokeshi 2007). Indeed, the SGH theoretical model predicts a linear increase in the intensity of facilitation as environmental conditions become harsher (Bertness and Callaway 1994), which was supported by empirical tests in plant communities (Callaway *et al.* 2002, Cavieres *et al.* 2006). Evidence of hump-shaped SIR is often reported for biotic stress gradients, mostly by grazing pressure (e.g. Brooker *et al.* 2006, Smit *et al.* 2007, Le Bagousse-Pinguet *et al.* 2012, Bakker *et al.* 2013), while reports under abiotic severity are more rare (e.g. Maestre & Cortina 2004). Previous attempts to summarise this topic indicated weak evidence for the linear model (Maestre *et al.* 2005), showing non-linear patterns consistent with facilitation peak at intermediate stress conditions (Holmgren *et al.* 2012). Hump-shaped responses cannot be explained by the SGH hypothesis, and require an alternative theoretical model in which net interaction collapses at the upper extreme of the abiotic stress gradient (Michalet *et al.* 2006, Maestre *et al.* 2009, Holmgren & Scheffer 2010). Our results clearly support such an alternative model, adding a specific, mechanistic explanation for facilitation collapsing, based on morphological trait shift in the nurse population. Indeed, *Silene* survives at the upper limit of its distributional range, showing an extreme increase in cushion compactness, which in turn limits its nurse capability at the expense of coexisting plants. Such findings provide a novel contribution to the study of shifts in functional traits along environmental gradients, as related to plant interactions (Schöb *et al.* 2013).

Cushion traits, biogenic capability and facilitation mechanisms

Cushion plants are specifically adapted to the alpine climate because their low stature and compact form make them heat traps that decouple their internal climate from the outside (Körner 2003). Cushion structure can differ, ranging from relatively “soft” such as in *Silene*,

404 to extremely compact such as in *Azorella* spp. (Körner 2003). Here we found that *Silene* stem
 405 density and compactness progressively increased along the elevation gradient, associated with
 406 microclimate amelioration, particularly warming, inside the cushion. Changes in plant
 407 functional traits have been reported along elevation gradients (e.g. Cordell et al 1998; Hultine
 408 & Marshall 2000). Recently, Schöb et al. (2013) reported similar changes in cushion traits
 409 (i.e. increase in cushion compactness) for *Arenaria tetraquetra*. At this stage we do not know
 410 whether the observed variability in cushion compactness is genetically determined, whether it
 411 is a phenotypic plastic response to the environment, and whether the change in this trait
 412 benefits the species itself. In a long-term experiment manipulating temperatures and nutrients,
 413 *Silene* exhibited a prompt plastic phenotypic response by increasing its photosynthetic area,
 414 but survival was negatively affected (Alatalo & Little 2014). While it can be hypothesised that
 415 cushion morphology changes with altitude to effectively adapt to local thermal conditions
 416 (Gauslaa 1984; Körner 2003), further studies are required to assess the role of cushion stem
 417 density on *Silene* fitness and the underlying controlling factors.

418 Our results provide mechanistic links between cushion traits and changes in
 419 facilitation intensity. Differently from lower elevation, at the upper end of the altitudinal
 420 gradient, the plants rooted inside *Silene* cushions can experience beneficial higher
 421 temperatures, compared with open areas. In such conditions, the temperature mitigation effect
 422 inside the cushion is maximised, but facilitation by *Silene* is reduced, which appears
 423 paradoxical. A possible explanation comes from the observation of large daily temperature
 424 ranges within the cushion, with the beneficiary potentially stressed by extreme values
 425 (compare high elevation data in Figs 3 and 4). Although not previously reported for cushion
 426 plants (review in Anthelme et al. 2014), this pattern could be related to a progressive change
 427 in cushion shape, from almost flat at low elevation, to dome-shaped and hemispherical at
 428 higher altitude, consistent with our observations on cushion height. Indeed, a highly convex

429 habit, while minimising surface-to-volume ratio and heat loss, maximises radiation
430 absorbance by perpendicularly exposing different portions of the cushion to solar radiation
431 during daytime (Gauslaa 1984).

432 Another mechanism of facilitation release at high elevation is merely the limited
433 empty space available within the cushion for seed trapping and/or root development by the
434 beneficiary, due to the extremely compact and dense canopy of the nurse. Limitation for plant
435 establishment and growth has been proposed for tight cushion species such as *Azorella*
436 *madreporica* (Fajardo, Quiroz & Cavieres 2008) and *A. monantha* (Arroyo *et al.* 2003). We
437 have no experimental data directly supporting this hypothesis. However, at high elevation
438 plant texture was so compact that it almost prevented the temperature probe being inserted
439 into the cushion [Bonanomi G., personal observation]. Although the negative effects of high
440 cushion compactness and surface convexity may well outweigh the beneficial, mitigating
441 effects on mean temperatures inside the cushion, future investigation of the relationships
442 between cushion traits and beneficiary response will clarify the possible mechanisms of
443 facilitation release under intense environmental severity.

444 Among the possible causal mechanisms of *Silene* facilitation, amelioration of
445 microclimatic conditions inside the plant canopy was previously invoked (Molenda *et al.*
446 2012). Findings about the ability of *Silene* to modulate internal microclimate are
447 contradictory, including reports of temperature inside cushions higher than the surrounding air
448 (Arroyo *et al.* 2003), but contrasting evidence of both higher (Arroyo *et al.* 2003) and lower
449 (Hacker & Gaines 1997; Cavieres, Quiroz & Molina-Montenegro 2008; Yang *et al.* 2010)
450 cushion temperature compared with the adjacent bare soil. Such inconsistency could be
451 explained with the occurrence of steep thermal gradients within the cushion body, warmer on
452 the surface but colder at depth > 10 cm compared with the surrounding air (Fig. S5,
453 Supporting Information, see also Körner 2003). Unfortunately, most studies fail to report the

exact depths of sensor placement, making it difficult to compare studies concerning *Silene* (e.g. Molenda *et al.* 2012) and other cushion plants (e.g. Cavieres *et al.* 2008).

Silene improves soil fertility, with higher N and organic C content found under the cushions, compared with the open areas. This is consistent with a recent report (Massaccesi *et al.* 2015) and previous studies on other cushion plants (Nuñez, Aizen & Ezcurra 1999; Cavieres *et al.* 2008; Yang *et al.* 2010; Schöb *et al.* 2013). Although the nurse capability of *Silene* is likely to be due, at least in part, to its effect on soil quality, such an ameliorative impact does not change along the elevation gradient. It cannot therefore be related to the observed hump-shaped SIR.

Conclusions

This is one of the first studies (but see Schöb *et al.* 2013) that demonstrates a mechanistic link between changes in nurse morphological traits, associated with microclimate, and a shift in facilitative effects along a severity gradient. This bears importance for the general understanding of plant-plant interactions in relation to stress gradients. However, in this study only indirect evidence of facilitation is reported (i.e. altitudinal associations between plant species inside *Silene* cushions with different morphological traits), while we acknowledge that such spatial patterns can be partially due to the specific distribution of external abiotic factors (Callaway 2007). Further field experiments, including manipulation of the cushion structure, are needed to prove the occurrence of *Silene* facilitative effects and to clarify the relative importance of different facilitative mechanisms.

Acknowledgements

477 The Majella National Park authority allowed the field surveying and sampling in the study
478 site. This work was partially funded by the NURSE project granted to AS at the University of
479 Naples Federico II.

480

481 **Data Accessibility**

482 All data used in this manuscript are present in the manuscript and its Supporting Information.

483

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649

TABLES

Table 1. Effects of *Silene* cushion on soil fertility. Properties of soil sampled in the top 20 cm under *S. acaulis* cushions (IN) and in external adjacent plots (OUT). For each soil parameter, results of testing for significant difference between the IN and OUT areas are shown ($N = 40$).

Soil parameter	OUT	IN	t-test		
	Mean \pm SE	Mean \pm SE	t	df	P
Texture, fraction > 2 mm (%)	1.15 \pm 0.1	1.14 \pm 0.2	5.044	38	< 0.0001
pH	8.03 \pm 0.15	7.85 \pm 0.12	-2.072	38	0.0451
Salinity ($\mu\text{S cm}^{-1}$)	1199 \pm 67	1319 \pm 87	2.587	38	0.0136
Organic matter (g kg^{-1})	121.9 \pm 54	389.5 \pm 99	4.185	38	0.0002
Total N (g kg^{-1})	6.1 \pm 2.3	9.7 \pm 3.1	1.406	38	0.1678
C-to-N ratio	11.6 \pm 2.2	23.2 \pm 2.9	3.292	38	0.0022

Table 2. Association between *Silene* cushion morphology and microclimate. Matrix of pairwise linear and exponential correlations (Pearson's *r* with associated *P*-value in brackets, N=20 in all cases) for cushion stem and bulk densities; differences of temperature between inside and outside the cushion at 4 cm depth (IN–OUT) and between inside the cushion and surrounding air (IN–Air), and altitude. Correlation between cushion maximum height and altitude is also reported.

664

	IN–OUT	IN–Air	Altitude
Stem density (n cm ⁻²)	0.4883 (0.029)	0.6275 (0.003)	0.9020 (< 0.001)
log(stem density)	0.4988 (0.025)	0.7101 (<0.001)	0.9362 (< 0.001)
Bulk density (mg cm ⁻³)	0.4560 (0.043)	0.4818 (0.031)	0.9066 (< 0.001)
log(bulk density)	0.4692 (0.037)	0.5537 (0.011)	0.9401 (< 0.001)
Cushion maximum height			0.6312 (< 0.001)

665

666

FIGURE LEGENDS

Fig. 1. Plant-plant interaction along the elevation gradient. Differences in plant cover and species richness between the areas within the perimeter of *Silene* cushions (IN) and equal-sized paired open areas (OUT), along the elevation gradient. Fitting curves are 2nd-degree polynomial functions. Pairwise differences between IN and OUT for all data pooled, and for different altitudinal belts, are shown in the insets (means \pm 95% confidence interval; asterisks indicate significantly highest values in independent sample t-test: ***, $P < 0.001$; *, $P < 0.05$) and in [Fig. S3, Supporting Information](#), respectively.

Fig. 2. Environmental severity and neighbour trait effects on plant-plant interactions. Relative Interaction Index (RII) for plant cover (top) and species richness (bottom). Mean with 95% confidence limits of RII_{neighbours} at low, medium, and high altitudes (left) and of RII_{altitudes} without and with *Silene* neighbours at low-to-medium and medium-to-high altitudes (right). Stars below or above dots indicate significant RII values obtained from one sample t-tests (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: not significant). P -values on each graph indicate the result of the one-way ANOVAs for the altitude (left) and neighbour (right) effects; letters above dots indicate significantly different groups according to post-hoc Duncan tests (detailed statistical results are in [Tables S3 and S4, Supporting Information](#)).

Fig. 3. *Silene* cushion morphology and effects on microclimate along the elevation gradient. Rings collected from cushions at three altitudinal levels showing different plant compactness (top). Differences in temperatures (ΔT) recorded in soil at 4 cm depth inside (IN) and outside (OUT) *Silene* cushions, as a function of altitude and either cushion stem density (left) or bulk density (right). Colour range for data points indicates differences between soil (IN) and air

692 temperature. Pairwise correlations among all variables were statistically significant (Table 2,
693 [Fig. S3, Supporting Information](#)).

694

695 **Fig. 4.** Time series of temperature inside and outside *Silene* cushions at different elevation.
696 Temperature at 4 cm depth inside the *S. acaulis* canopy (IN) and paired open bare soil (OUT)
697 in two sites at different elevation (2,336 and 2,697 m a.s.l., respectively). Data were recorded
698 every ten minutes for 52 consecutive days during the 2012 growing season.

699

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700 **Supporting Information Captions**

701 **Figure S1.** Overview of the study site.

702 **Figure S2.** *Silene* cushion morphology and sampling points along the elevation transect.

703 **Figure S3.** Changes in plant diversity along the elevation gradient.

704 **Figure S4.** *Silene* cushion morphology along the elevation gradient.

705 **Figure S5.** Temperature profiles inside and outside *Silene* cushions.

706 **Figure S6.** *Silene* cushion effects on microclimate along the elevation gradient.

707 **Figure S7.** Relationship between temperatures inside and outside *Silene* cushions.

708 **Figure S8.** Time series of soil water content inside and outside *Silene* cushions.

709 **Table S1.** List of plant species recorded along the sampled altitudinal transect.

710 **Table S2.** Generalized linear models (GLM) of plant cover and species richness.

711 **Table S3.** Result of statistics on relative interaction index (RII) for plant cover and species
712 richness.

713 **Table S4.** Result of one-way ANOVA tests on relative interaction index (RII) for plant cover
714 and species richness.

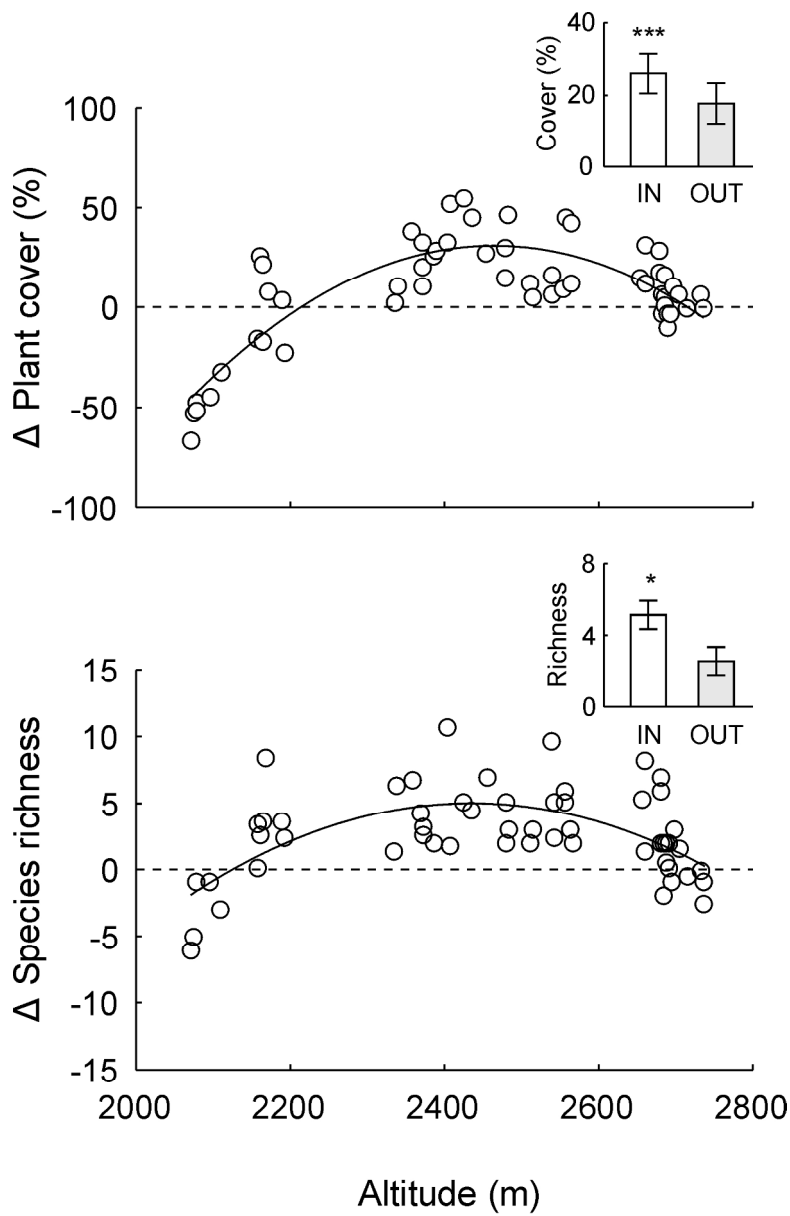
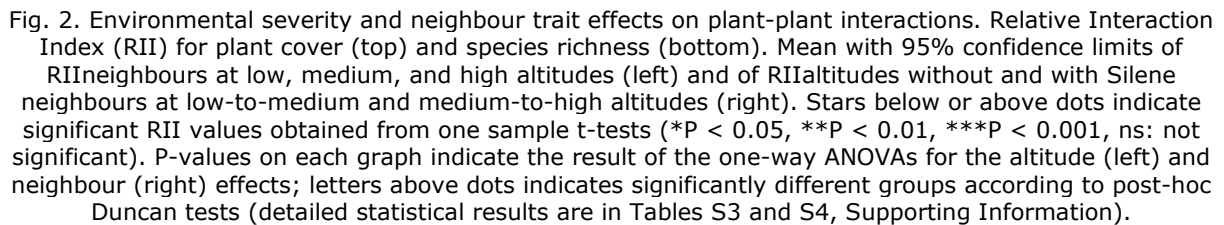


Fig. 1. Plant-plant interaction along the elevation gradient. Differences of plant cover and species richness between the areas within the perimeter of *Silene* cushions (IN) and equal-sized paired open areas (OUT), along the elevation gradient. Fitting curves are 2nd-degree polynomial functions. Pairwise differences between IN and OUT for all data pooled, and for different altitudinal belts, are shown in the insets (means \pm 95% confidence interval; asterisks indicate significantly highest values in independent sample t-test: ***, $P < 0.001$; *, $P < 0.05$) and in Fig. S3, Supporting Information, respectively.



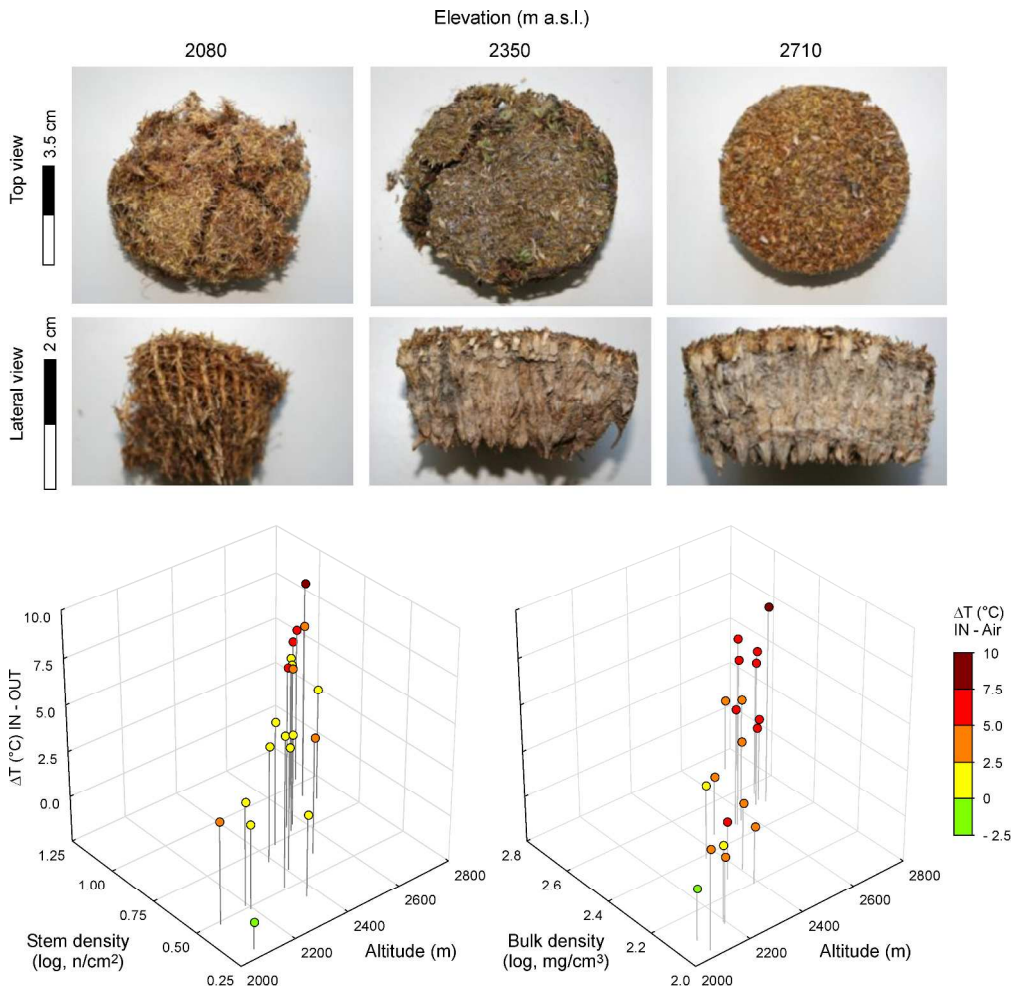


Fig. 3. *Silene* cushion morphology and effects on microclimate along the elevation gradient. Rings collected from cushions at three altitudinal levels showing different plant compactness (top). Differences in temperatures (ΔT) recorded in soil at 4 cm depth inside (IN) and outside (OUT) *Silene* cushions, as a function of altitude and either cushion stem density (left) or bulk density (right). Colour range for data points indicates differences between soil (IN) and air temperature. Pairwise correlations among all variables were statistically significant (Table 2, Fig. S3, Supporting Information).

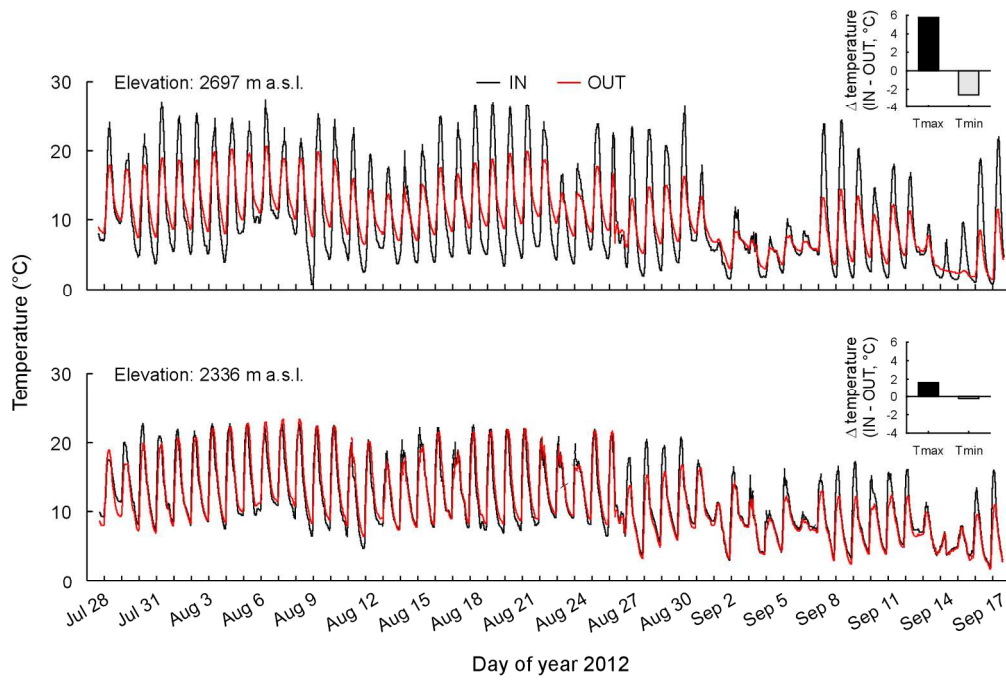


Figure 4. Time series of temperature inside and outside *Silene* cushions at different elevation. Temperature at 4 cm depth inside *S. acaulis* canopy (IN) and paired open bare soil (OUT) in two sites at different elevation (2,336 and 2,697 m a.s.l., respectively). Data were recorded every ten minutes for 52 consecutive days during the 2012 growing season.