

Outcomes of biotic interactions are dependent on multiple environmental variables

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Abstract

Question: Can variation in the outcome of biotic interactions in relation to environmental severity be more accurately predicted when considering multiple stress and/or disturbance variables?

Location: Arctic-alpine tundra in Kilpisjärvi, North-Finland.

Methods: To test the impact of including multiple environmental variables in analyses of the outcomes of biotic interactions, we modelled reproductive effort and cover of 17 arctic-alpine species as a function of *Empetrum nigrum* ssp. *hermaphroditum* cover, geomorphological disturbance and soil moisture with statistical interactions of the explanatory variables included. We implemented a best-subset approach using generalised linear models (GLM) and selected the best model for each species based on Akaike's information criteria (AIC).

Results: For the majority of species, models including multiple environmental variables were selected as best. Reproductive effort depended on one or both environmental variables for all species and 14 species were additionally influenced by *Empetrum*, with the impact of *Empetrum* varying with abiotic conditions in all but one of those species. Moreover, the 3-way interaction of three explanatory variables was included in the best-fit models for six species. The impact of *Empetrum* on species cover showed a similar pattern, with 11 species affected by *Empetrum* and its statistical interactions with one or both abiotic variables.

Conclusions: Biotic interactions have an important role in arctic-alpine vegetation, but to fully understand variation in their effects multiple environmental factors should be explicitly considered. In this study the outcome of biotic interactions was frequently dependent on two abiotic variables (and occasionally additionally on their statistical interaction). Therefore, we demonstrate that studies based on only one environmental factor may cause misleading interpretations of the nature of biotic interactions in plant communities where there are multiple independent variables underlying the habitat severity gradient.

Keywords competition; *Empetrum nigrum* ssp. *hermaphroditum*; facilitation; plant-plant interactions; reproductive effort; stress-gradient hypothesis

Nomenclature: Hämet-Ahti et al. (1998)

Abbreviations: GLM = generalized linear model, AIC = Akaike's information criteria, SGH = Stress-gradient hypothesis, GEE = generalized estimate equation,

Running head: Biotic interactions and multiple abiotic variables

Introduction

Biotic interactions, both positive and negative, are recognized as important factors in shaping vegetation distribution, composition and succession (Lortie et al. 2004, Michalet et al. 2006, Brooker et al. 2008). Positive interactions can enhance growth, reproduction and survival (Callaway 1995, Schöb et al. 2012) and may expand species distributions (Bruno et al. 2003, le Roux et al. 2012), while negative interactions may reduce the performance of individual plants and can exclude species from otherwise favourable habitats (Sexton et al. 2009). While positive and negative interactions can occur simultaneously, net positive interactions are predicted to be more common than net negative interactions in abiotically extreme environments (Bertness and Callaway 1994, Brooker and Callaghan 1998, Brooker et al. 2008). This idea has been formalized as the “stress-gradient hypothesis” (SGH), with many studies showing support for its predictions (e.g. Choler et al. 2001, Callaway et al. 2002, Olofsson 2004, He et al. 2013). However, support for the SGH is not unequivocal as some studies have demonstrated more complex responses, suggesting that further refinements of this model are required to improve its generality (Maestre et al. 2009a, Malkinson and Tielbörger 2010, although see also He et al. 2013).

One possible reason for discrepancies between the predictions of the SGH and observed patterns is that most studies attempting to test the predictions of the SGH only examine variation in the outcome of biotic interactions in response to one environmental factor, while in natural systems the overall “severity” gradient (sensu Brooker and Callaghan 1998) comprises multiple co-occurring environmental variables that often vary independently of each other (Kawai and Tokeshi 2007, Brooker et al. 2008, Maestre et al. 2009a, Maalouf et al. 2012). Some studies have tried to minimize the problem of multiple independent environmental variables by focusing on systems where the dominant environmental gradients run approximately parallel (e.g. altitudinal; Callaway et al. 2002 or salinity gradients; Crain et al. 2004). However, as suggested by Kawai and Tokeshi (2007; see also Riginos et al. 2005, Elmendorf and Moore 2007, Maestre et al. 2009b, Armas et al. 2011, Soliveres et al. 2011, Maalouf et al. 2012, Schöb et al. 2013), explicit consideration of several abiotic variables may offer improved understanding of the factors determining spatio-temporal variation in the outcome of species interactions, particularly in habitats characterized by multiple key environmental variables. Indeed, one problem with lumping multiple environmental stresses and disturbances into a single composite severity gradient is that the impact of species interactions may differ depending on the nature of the environmental variables (Dullinger et al. 2007, Kawai and Tokeshi 2007). Thus, careful and explicit consideration of the dominant environmental variables in a habitat may be required, especially when the variables differ in their nature (e.g. stress versus disturbance, or resource versus non-resource: Grime 1977, Maestre et al. 2009a, but see also He et al. 2013).

The SGH has proven useful for predicting spatial and temporal variation in the effects of biotic interactions, particularly in arctic and alpine environments (Choler et al. 2001, Olofsson 2004, Dullinger et al. 2007, He et al. 2013, Schöb et al. 2013). These high latitude and/or altitude systems are usually characterized by pronounced variability in

environmental conditions over small spatial scales and relatively few interacting species, consequently providing a powerful study system to test the impacts of biotic interactions and environmental variables on plant performance (Brooker and Callaghan 1998, Dormann and Brooker 2002, Wisz et al. 2013). In these systems, the most important abiotic environmental variables are generally represented by temperature, soil moisture and nutrients, and geomorphological disturbances (Billings 1973, Gough et al. 2000, Virtanen et al. 2006, Virtanen et al. 2010). Thus, particularly given the substantial fine-scale spatial variation in abiotic conditions in arctic-alpine habitats (e.g. Isard 1986), a better understanding of the outcome of plant-plant interactions may be gained by moving beyond the consideration of individual variables in isolation.

The aim of this work is thus to examine whether the consideration of multiple environmental variables improves predictions of the outcomes of biotic interactions as suggested, but not explicitly tested, by earlier studies. This question is addressed by the statistical analysis of a detailed and field-quantified dataset from arctic-alpine tundra in northern Europe. The impact of a dominant dwarf shrub (*Empetrum nigrum* ssp. *hermaphroditum*) on the reproductive effort of 17 co-occurring vascular plant species was examined under varying soil moisture and geomorphological disturbance conditions (i.e. in response to variation in two key environmental variables) using spatial modelling. We used the number of flowers and fruits per species as a measure of reproductive effort. Reproductive effort was chosen for analysis as it is an important indicator of a plant's response to interactions with co-occurring individuals due to its contribution to an individual's fitness (Tielbörger and Kadmon 2000, Brooker et al. 2008, Malkinson and Tielbörger 2010). Further, we confirm the generality of our results by repeating analyses for each species' cover, a metric more commonly examined in previous studies (e.g. Maestre et al. 2009b).

Material and Methods

Study site

Fieldwork was conducted in July 2011 in north-west Finland (69° 3' N, 20° 48' E), in arctic-alpine tundra dominated by dwarf-shrubs (*Ericaceae* and *Empetraceae* species) and graminoids. The study site was situated at c. 700 m a.s.l. on the northern slope of the Saana massif, roughly 100 m above the treeline (see le Roux et al. 2013b, le Roux et al. 2013c for further site details). At the nearby Kilpisjärvi meteorological station (< 2 km distance; 480 m a.s.l.), mean July temperature is 11.2 °C and mean annual precipitation 487 mm (1981 – 2010; Finnish Meteorological Institute; www.fmi.fi). Spring 2011 was warmer than usual, resulting in the growing season starting 1 - 2 weeks earlier than average and providing good conditions for the growth and flowering of species.

The dominant vascular plant species at the site was *Empetrum nigrum* ssp. *hermaphroditum* (referred to as *Empetrum* from hereon). It is an evergreen dwarf shrub which dominates in low-nutrient, acidic arctic-alpine ecosystems (Tybirk et al. 2000). This species has a broad geographical distribution and has been widely investigated (Bell and Tallis 1973, Nilsson et al. 1993, Bråthen et al. 2010), including studies of its interaction with other species (e.g. Carlsson and Callaghan 1991, Bråthen et al. 2010, Pellissier et al. 2010, le Roux et al. 2012). *Empetrum* impacts other species both through competitive and allelopathic mechanisms, by forming dense mats (Tybirk et al. 2000, Aerts 2010) and producing allelopathic compounds (Nilsson 1994). As a result, *Empetrum* reduces seedling germination and survival in many co-occurring species (Nilsson and Zackrisson 1992), and is associated with lowered vascular species richness (Aerts 2010). A thick layer of *Empetrum*-derived peat may accumulate where there are dense mats of this species, improving the soil moisture-holding capacity (Edwardsen et al. 1988, Williams 1988), but also contributing to the

accumulation of allelochemicals and reducing the availability of nitrogen and phosphorus (Eskelinen 2010). *Empetrum* may also have positive effects on some co-occurring species, ameliorating microclimate conditions (by, e.g. increasing wind shelter and snow accumulation), maintaining ericoid mycorrhiza, providing associational refuges, inhibiting soil movement and reducing soil moisture loss (Burgess 1951, Williams 1988, Shevtsova et al. 1997, Tybirk et al. 2000, Grau et al. 2010).

Two of the key environmental factors influencing vegetation patterns in this habitat type are geomorphological disturbance and soil moisture (Billings 1973, Hjort and Luoto 2009, le Roux et al. 2013a, le Roux et al. 2013c). Geomorphological disturbances primarily cause soil movement, destroying vegetation and inhibiting growth and reproduction (Virtanen et al. 2010). However, geomorphological disturbances may also create space for the establishment for new individuals and bring soil nutrients closer to the surface, increasing their accessibility to vegetation (Jonasson and Sköld 1983). Soil moisture is a limiting factor for vegetation in arctic environments, particularly in mid- and late-growing season (Billings 1973, Williams 1988, le Roux et al. 2013a), and may have high spatial variability at fine scales due to soil conditions and mesotopography (Isard 1986, Aalto et al. in press).

Data collection

The study area comprised 960 x 1 m² cells arranged in six 8 x 20 m grids. The maximum distance between grids was 110 meters, minimizing variation in altitude, macroclimate, bedrock and species source pool. In each cell, vascular plant species were identified, their cover visually estimated and their reproductive effort (i.e. flowers and/or fruits) counted. Species' reproductive effort was not quantified for species where all individual were flowering (e.g. *Juncus* sp.) or where flowers or fruits were too abundant to count (*Betula nana*, *Vaccinium myrtillus*, *Juniperus communis*, *Phyllodoce caerulea*). Seventeen species

produced fruits or flowers in ≥ 20 cells and were analysed in this study (see Table S1 in Appendix S1 in Supporting Information).

Five geomorphological disturbances were quantified in all 1 m² cells: temperature-driven solifluction and cryoturbation, wind-driven deflation, and fluvial erosion and accumulation following Hjort and Luoto (2009). The percentage of each cell covered by active disturbances was visually estimated, with the activity of features defined by observations of topsoil material (e.g. frost heaving and cracking, mass wasting, soil displacement), as well as fluvial erosion and sedimentation (Hjort and Luoto 2009). These five variables were summed to form one integrated measure of disturbance, representing the cover of disturbed top soil in the cell.

Soil moisture was measured as volumetric water content on three occasions (> 24 hours after rainfall) using a hand-held TDR sensor (FieldScout TDR 300, Spectrum Technologies, Plainfield, IL, USA; using 12 cm sensor rods), recording the average value measured across at least three points per quadrat. As the correlation of the soil moisture values between the different sampling events was high ($r > 0.88$), the mean soil moisture across all sampling events was used in analyses. Subsequent soil moisture measurements (during the 2012 growing season) were also strongly correlated with these values, demonstrating a strong temporal consistency in the spatial variation of this resource.

Statistical methods

To analyse variation in *Empetrum*'s impact on neighbouring species under different soil moisture and disturbance conditions, multivariate modelling techniques were used. Species' reproductive effort and cover in each cell were modelled as a function of *Empetrum* cover, soil moisture and geomorphological disturbance, limiting analyses to cells where a response species was present (min. $n = 55$; see Table S1 in Appendix S1). Four statistical interactions

were included as model terms to allow the impact of *Empetrum* to vary with soil moisture and disturbance level (*Empetrum* x disturbance; *Empetrum* x soil moisture; *Empetrum* x disturbance x soil moisture), and to allow the impact of soil moisture to vary with disturbance level (disturbance x soil moisture). All models of reproductive effort also included the response species' own cover in each cell as a covariate to account for size-related variation in fruit and/or flower production. Disturbance and *Empetrum* cover were log-transformed prior to analysis to reflect the non-linear relationship between their cover and potential impacts (le Roux et al. 2013c). Due to a weak correlation between predictors (maximum $r = 0.4$), collinearity was not considered a problem for these analyses.

Analyses were implemented using generalized linear models (GLM) assuming a Poisson-distribution of errors for the models of reproductive effort and a binomial distribution of errors for species cover. All possible combinations of the predictor variables were examined, following a best subsets regression approach resulting in 18 different models. For each species all the possible models were analysed and then ranked by Akaike's Information Criterion (AIC) to identify the best-fit model (Burnham and Anderson 2002). Additionally, to account for potential spatial structure in the data (Legendre and Fortin 1989), analyses were repeated using spatially-explicit generalized estimating equation models (GEE) with a fixed correlation structure to model spatial dependency in the data (following Carl and Kühn 2007). Prior to GEE analyses two outlying flower abundance values and one outlying cover value for *Festuca ovina* were adjusted to ensure model convergence in reproductive effort modelling (values reduced to next highest observed value). GLM and GEE results were compared and since the sign of the responses were almost identical (Tables S2 and S3 in Appendix S1), we assume that spatially-non-explicit models (GLM) were able to adequately account for any spatial non-independence in the dataset. Analyses were conducted in R (R Development Core Team 2011, 2013).

This study design enables examination of variation in the impacts of biotic interactions under a broad range of environmental conditions and allows the impact of *Empetrum* on co-occurring species to vary with abiotic severity (as predicted by the SGH; following Meier et al. 2011, le Roux et al. 2012), although it does limit species responses to linear relationships. By using an observational approach we avoided unintended impacts on environmental conditions associated with manipulative treatments, particularly in stressful environments (Callaway 1995, Brooker et al. 2008, Aerts 2010). A potential concern about the observational approach implemented, is that the documented patterns may reflect some unmeasured underlying process, making it difficult to separate correlation from causation (Araújo and Luoto 2007). However, since there are many manipulative studies examining the mechanisms through which *Empetrum* interacts with other species (e.g. Carlsson and Callaghan 1991, Nilsson et al. 1993, Grau et al. 2010) it is reasonable to infer ecological process from spatial pattern (see also McIntire and Fajardo 2009, Bertolo et al. 2012).

Results

In analyses of reproductive effort, geomorphological disturbance was included as a predictor variable in all best-fit models, with soil moisture included in 14 out of 17 species' best-fit models (Table 1, and Tables S2 and S3 in Appendix S1, for detailed results). *Empetrum* was included in the best-fit models for 14 species, and with related interaction terms (*Empetrum* x geomorphological disturbance/soil moisture and *Empetrum* x geomorphological disturbance x soil moisture) retained in the models for 13 species (Table 1). The interaction term reflecting variation in the effect of geomorphological disturbance with soil moisture was also included to the majority of species best-fit models (Table 1). Thus when modelling the reproductive

effort of 17 species, all species showed a dependence on abiotic conditions, while 14 species were additionally influenced by *Empetrum*, with the effect of *Empetrum* varying based on abiotic conditions in all but one of those species.

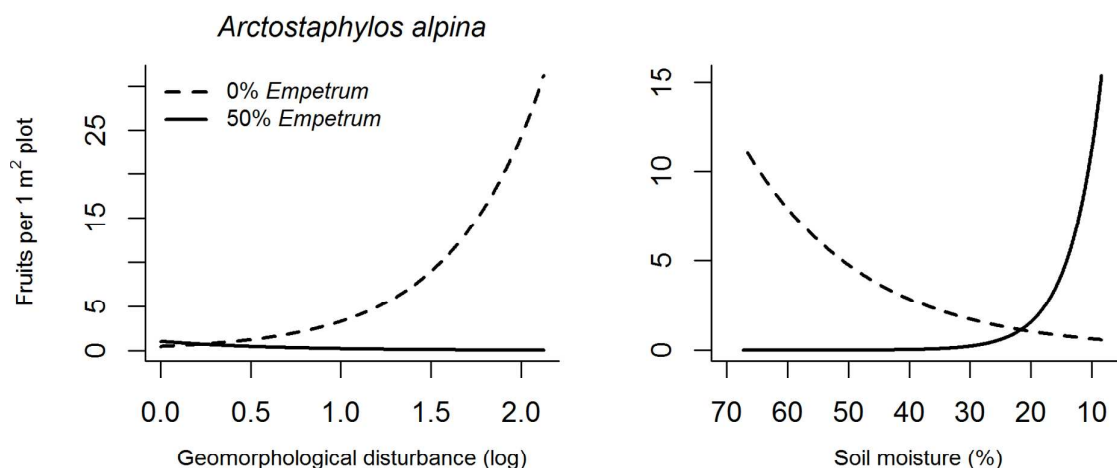


Figure 1. Predictions of the impacts of *Empetrum nigrum* ssp. *hermaphroditum* on the reproductive effort *Arctostaphylos alpina* in response to variation in two environmental variables. Increased geomorphological disturbance impacts positively on *A. alpina* reproductive effort in the absence of *Empetrum*, with the inverse occurring when *Empetrum* is present (left panel). Decreasing soil moisture was negatively correlated with *A. alpina* reproductive effort in the absence of *Empetrum*, but the presence of *Empetrum* reverses the direction of this relationship (right panel). Note that in right panel the x-axis is reversed to represent increasing stress related to drier conditions. Predictions were made from the best-fit GLM models, assuming either the absence of *Empetrum* or 50 % *Empetrum* cover (i.e. corresponding to the 10th and 90th percentiles of the observed *Empetrum* cover).

Examining all of the best-fit reproductive effort models where *Empetrum* was retained as a predictor, the effect of *Empetrum* on neighbouring species reproductive effort

became more positive with increasing disturbance for eight out of twelve species and with decreasing soil moisture for four out of ten species (Table 2 and see examples in Fig. 1 and Figs S1-S3 in Appendix S2). Only for one species (*Bistorta vivipara*) did the impact of *Empetrum* not clearly vary with soil moisture or disturbance levels.

Repeating analyses for species cover supports the significance of *Empetrum*'s impact on other species and the observation that *Empetrum*'s effect varies with abiotic conditions. In cover analyses, *Empetrum* was included in best-fit models for twelve species, with its impact varying along one or both environmental gradients for eleven of these species (i.e. biotic-abiotic or 3-way interaction terms were included in best-fit models; Table S3 in Appendix S1).

Discussion

The effect of *Empetrum* on the reproductive effort and cover of vascular plants in arctic-alpine tundra was clearly related to abiotic stress and disturbance variables, highlighting how the outcome of biotic interactions can be dependent on multiple environmental variables. Indeed, while the abundance of *Empetrum* strongly impacted co-occurring species (supporting the idea that vegetation properties cannot be explained by abiotic conditions only; Wisz et al. 2013, also e.g. Pellissier et al. 2010, le Roux et al. 2012) the influence of *Empetrum* on most sub-ordinate species appeared to be mediated by soil moisture and/or geomorphological disturbance levels. This finding strongly supports recent studies suggesting that the nature of biotic interactions depends on multiple environmental factors (Bertness and Callaway 1994, Brooker and Callaghan 1998, Dullinger et al. 2007, Kawai and Tokeshi 2007, Maestre et al. 2009b, Schöb et al. 2013). Therefore, in addition to the direct impacts of soil moisture and

disturbance, both of these abiotic variables also are likely to have an indirect effect on subordinate species by changing the balance of their positive and negative interactions with *Empetrum*. Further on, for many species the outcome of biotic interactions varied between environmental gradients. Thus, by showing that most species best-fit models included multiple abiotic variables and biotic-abiotic interaction terms, we demonstrate that the explicit consideration of multiple environmental variables improves predictions of reproductive effort and cover, highlighting a potential limitation of studies that only examine variation in the outcome of biotic interactions in response to one environmental factor.

Our results agree broadly with a developing body of theory that the impacts of biotic interactions are contingent on abiotic conditions (Bruno et al. 2003, Dullinger et al. 2007, Brooker et al. 2008), yet they do not provide perfect support for the SGH. For reproductive effort, geomorphological disturbance was retained as a predictor in all models, with higher levels of geomorphological disturbance tending to be associated with more positive impacts of *Empetrum*. This mediating effect of geomorphological activity on the impact of *Empetrum* was more consistent than the effect of soil moisture. Facilitation might, actually, be most common in environments where stress is caused by non-resource related environmental factors, since the presence of a plant can often potentially ameliorate non-resource related stresses for other species (e.g. through shading or sheltering), whereas in the environments where environmental stress is driven by resource limitation, negative competitive interactions between species may be equally possible (following the idea of Maestre et al. 2009a). Given the low growth form and the dense peat and root layer formed by *Empetrum* (Shevtsova et al. 1997, Tybirk et al. 2000), it is likely that this species may ameliorate the negative impacts of substrate instability and wind-driven evaporation and deflation on some co-occurring species. An alternative explanation of this pattern, however, may be that more intense geomorphological disturbances weaken *Empetrum*'s allelopathic

effects by, for example, transporting allelochemicals deeper into the soil (see e.g. Bråthen et al. 2010). Nonetheless, it appears that geomorphological disturbance affects all species reproductive effort, specifically with higher disturbance levels generally associated with an increasingly positive effect of *Empetrum* on neighbouring individuals.

In contrast to geomorphological disturbance, soil moisture was less commonly retained in best-fit models for species reproductive effort. Moreover, while soil moisture level seems to mediate *Empetrum*'s biotic impact in ten species, the nature of this statistical interaction was not consistent across species. While there are only few comparable studies from alpine and/or tundra habitats (e.g. Schöb et al. 2013), soil moisture has been used as a severity gradient in many SGH studies conducted in arid regions, where it has also often given inconsistent results when examining the outcome of plant-plant interactions under different soil moisture conditions (Maestre et al. 2005, Lortie and Callaway 2006). Our results may reflect that arctic and alpine species are relatively well adapted to fluctuations in soil moisture (Körner 2003) or that due to *Empetrum*'s dense growth form the negative impacts of competitive interactions (e.g. for light and/or soil nutrients) overwhelm any possible positive effects of *Empetrum* maintaining higher soil moisture levels. Irrespective of the mechanism driving these results, it appears that overall the outcomes of biotic interactions along multiple gradients may be quite strongly species-specific (in agreement with, e.g. Wang et al. 2008, Maalouf et al. 2012) rather than severity gradient-specific (He et al. 2013). Species-specific results, by highlighting differences in responses between species, support the suggestion that multiple species should be examined in studies of biotic interactions when wanting to generalize results, as recognized in both theoretical (Brooker et al. 2008) and experimental approaches (Choler et al. 2001, Callaway et al. 2002, Dullinger et al. 2007, Maestre et al. 2009b, Butterfield et al. 2013).

Analyses of species cover supported the results for reproductive effort. While there are differences between species' best-fit models and coefficients from reproductive effort and species cover analyses, crucially, both sets of results demonstrate the importance of biotic interactions and the dependence of their outcomes on environmental conditions.

One approach to tackle the problem of accurately describing severity gradients that comprise multiple independently varying abiotic factors has been the use of productivity (or a surrogate of productivity, including biomass) as an integrated measure of abiotic severity (Dullinger et al. 2007, Maestre et al. 2009b, Armas et al. 2011). The main advantage of examining the outcome of species interactions along a productivity gradient is that productivity represents a simple integrated measure of the impact of environmental severity on vegetation (Elmendorf and Moore 2007). As a result, using a productivity gradient as a proxy for multiple abiotic variables also avoids complications associated with statistical interactions between abiotic predictors (Olofsson and Shams 2007, Maalouf et al. 2012). However, the problem with the use of productivity as a surrogate for multiple abiotic gradients is that it may hide variation in the underlying individual abiotic variables. Thus it appears that the best approach for understanding spatio-temporal variation in the outcome of plant-plant interactions is to measure and incorporate all relevant environmental variables.

Conclusions

Simultaneous consideration of multiple abiotic variables revealed that studies based on only one environmental factor may cause misleading interpretations of the nature of biotic interactions. Both the level and the type of environmental severity affected the outcomes of biotic interactions, highlighting the context-dependence of plant-plant interactions.

Additionally, due to strong variation between species, results based on one pair of species cannot simply be generalized across an entire community. Incorporating species traits into analyses of biotic interactions may account for some of this variation between species, and therefore deserves further attention. The SGH is a useful heuristic model, but care must be taken when applying it to natural systems where many underlying abiotic factors combine to determine the environmental severity gradient. Thus, more multivariate analyses are likely to boost our understanding how the outcomes of plant-plant interactions are dependent on abiotic conditions.

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Supporting Information

Appendix S1. Prevalence of study species and detailed results (Tables S1, S2, S3 in .pdf format).

Appendix S2. Additional figures for example study species.

Table S1. Prevalence of study species.

Table S2. Best-fit generalized linear models (GLM) for each species, and the corresponding generalized estimating equation models (GEE) for analyses of reproductive effort.

Table S3. Best-fit generalized linear models (GLM) for each species, and the corresponding generalized estimating equation models (GEE) for analyses of species cover.

Table 1. Best-fit generalized linear models for species reproductive effort, with the +/- sign presented for all terms retained in the final models. For *Empetrum* x Geomorphological disturbance/Soil moisture interaction terms, outcomes of biotic interactions are presented by arrows: Upward arrows indicate shifts to more positive outcome with increasing stress (i.e. increasing disturbance and decreasing soil moisture), and thus support for the stress-gradient hypothesis (SGH). Downward arrows indicate more negative outcomes of biotic interaction with increasing stress and thus contrast with predictions from the SGH. Directions of arrows are based on visual interpretations (see an example in Fig 1).

Species	Species cover ^a	Disturbance	Soil moisture	<i>Empetrum</i> cover	<i>Empetrum</i> : Disturbance	<i>Empetrum</i> : Soil moisture	Disturbance : Soil moisture	<i>Empetrum</i> : Disturbance : Soil moisture
<i>Anthoxanthum alpinum</i>	+	+		-	+ (↗)			
<i>Arctostaphylos alpina</i>	+	+	+	+	- (↘)	- (↗)	-	+
<i>Bistorta vivipara</i>	+	+	+	-				
<i>Carex bigelowii</i>	+	-	-	+	- (↗)	- (↘)	+	+
<i>Cassiope tetragona</i>	+	+	+	+	- (↘)	- (↘)	-	
<i>Deschampsia flexuosa</i>	+	+						
<i>Festuca ovina</i>	+	-	-	-	- (↘)	+ (↘)	+	
<i>Hierochloe alpina</i>	+	-	-	+	+ (↗)	- (↗)	+	-
<i>Linnea borealis</i>	+	+	-	-	- (↘)	- (↘)	-	+
<i>Pedicularis lapponica</i>	+	-	-	-		+ (↘)	+	
<i>Salix herbacea</i>	+	+	-	-	+ (↗)	+ (↘)	-	-
<i>Sibbaldia procumbens</i>	+	+	-					
<i>Trientalis europaea</i>	+	+	+	+	- (↗)	- (↘)	+	+
<i>Vaccinium uliginosum</i>	+	-	+					
<i>Vaccinium vitis-idaea</i>	+	-	-	+	+ (↗)	- (↗)		
<i>Veronica alpina</i>	-	+	+	-	+ (↗)		-	
<i>Viola biflora</i>	+	-	-	-	+ (↗)		+	

^a Cover of the species being modelled (automatically included as a covariate in all models).

Supporting Information to the paper Mod, H.K., le Roux, P.C. & Luoto M. Outcomes of biotic interactions are dependent on multiple environmental variables. *Journal of Vegetation Science*.

Appendix S1. Prevalence of the study species and detailed results.

Table S1. The prevalence of the study species. Values in parentheses represent two outlying flower abundance values and one outlying cover value for *Festuca ovina* that were adjusted prior to analysis of reproductive effort by GEE models to ensure model convergence (values reduced to next highest observed value). Full species names in Table 1.

Species	Cells where species produced flowers and/or fruits ^a	Cells where species present ^a	Maximum number of flowers or fruits per cell	Maximum cover (%)
<i>A. alpinum</i>	72	123	16	1
<i>A. alpina</i>	22	55	18	10
<i>B. vivipara</i>	95	247	9	2
<i>C. bigelowii</i>	157	537	12	2
<i>C. tetragona</i>	52	100	75	12
<i>D. flexuosa</i>	46	238	9	3
<i>F. ovina</i>	130	461	13 (25)	5 (10)
<i>H. alpina</i>	34	140	5	0.5
<i>L. borealis</i>	157	321	20	10
<i>P. lapponica</i>	47	328	5	3
<i>S. herbacea</i>	120	412	40	15
<i>S. procumbens</i>	54	122	12	2
<i>T. europaea</i>	24	77	12	5
<i>V. uliginosum</i>	25	187	5	20
<i>V. vitis-idaea</i>	311	845	25	8
<i>V. alpina</i>	34	85	5	1
<i>V. biflora</i>	22	258	5	5

^a Out of 960 cells.

Table S2. Best-fit generalized linear models (GLM) for each species (selected by AIC), and the corresponding generalized estimating equation models (GEE) for analyses of reproductive effort. * $p = 0.01 - 0.05$, ** $p = 0.001 - 0.01$, *** $p < 0.001$. Full species names in Table 1. Adjusted R^2 and D^2 (R^2 equivalent for GEE models) values are provided for the GLM and GEE models respectively, AIC weights only for GLM models.

Species	Model	Adjusted R^2 and D^2	AIC weight	Species cover	Disturbance	Soil moisture	<i>Empetrum</i>	<i>Empetrum</i> : Disturbance	<i>Empetrum</i> : Soil moisture	Disturbance : Soil moisture	Disturbance : Soil moisture
<i>A. alpinum</i>	GLM	12 %	0.3431	0.7884*	0.2894		-2.1525**	1.3349*			
	GEE	9 %		0.4800	0.3827		-2.1328	1.4218			
<i>A. alpina</i>	GLM	19 %	0.3750	0.1823***	5.3999	0.1265	7.4907**	-7.2090**	-0.2569*	-0.1255	0.1859
	GEE	23 %		0.1823	5.3999	0.1265	7.4907	-7.2090	0.2569	-0.1255	0.1859
<i>B. vivipara</i>	GLM	33 %	0.2117	1.0434***	0.5898**	0.0225**	-1.0266***				
	GEE	33 %		1.0492***	0.4528	0.0233*	-0.9817**				
<i>C. bigelowii</i>	GLM	31 %	0.9770	2.9645***	-1.2439***	-0.0439**	0.4432	-1.0542	-0.0956**	0.0258**	0.0908**
	GEE	14 %		2.5647***	-0.2760	-0.0185	1.1908	-1.6113	-0.1052	0.0099	0.0915
<i>C. tetragona</i>	GLM	25 %	0.3648	0.1697***	2.4090***	0.1010***	2.2134***	-0.2800	-0.0414**	-0.0733***	
	GEE	21 %		0.1560**	2.3558	0.0910	1.6160	-0.0767	-0.0307	-0.0761*	
<i>D. flexuosa</i>	GLM	20 %	0.2017	0.8033***	0.4776*						
	GEE	15 %		0.6574***	0.6038'						
<i>F. ovina</i>	GLM	44 %	0.7148	0.6252***	-0.7320*	-0.1683***	-2.7421***	-0.4801*	0.0846***	0.0580***	
	GEE	44 %		0.5654***	-0.7399	-0.1651***	-2.6932***	-0.3951	0.0825**	0.0582**	

<i>H. alpina</i>	GLM	17 %	0.4866	8.8782***	-8.5630**	-0.0172	0.3654	6.4714*	-0.0710	0.2446**	-0.1800
	GEE	13 %		8.2291**	-6.4996*	-0.0018	0.8355	4.6283	-0.0923	0.1853	-0.1166
<i>L. borealis</i>	GLM	11 %	0.9059	0.2440***	6.8983***	-0.0062	-0.2357**	-3.9076**	-0.0064	-0.1957***	0.1101**
	GEE	9 %		0.2244**	5.7804	-0.0073	-0.5589	-2.8222	0.0067	-0.1650	0.0835
<i>P. lapponica</i>	GLM	39 %	0.2218	1.4192***	-2.1320**	-0.0146	-4.5801***		0.0793**	0.0390*	
	GEE	26 %		1.2931***	-3.0822*	-0.0367	-4.3149*		0.0774	0.0605*	
<i>S. herbacea</i>	GLM	42 %	0.5739	0.1483***	0.8386**	-0.0338**	-3.8975***	1.6937*	0.0978***	-0.0246**	-0.0426
	GEE	38 %		0.1616***	0.9048	-0.0281	-2.9183	0.6924	0.0631	-0.0310	0.0039
<i>S. procumbens</i>	GLM	37 %	0.1575	1.4283***	1.2450***	-0.0131					
	GEE	39 %		1.4138***	1.2819**	-0.0150					
<i>T. europaea</i>	GLM	27 %	0.4915	0.4146***	3.6059	0.0455	2.3275	-9.4620*	-0.1367*	0.1708*	0.4156**
	GEE	37 %		0.4138**	2.6512	0.0593	2.8097	-7.7875	-0.1481	-0.1374	0.3528
<i>V. uliginosum</i>	GLM	2 %	0.1763	0.0431	-0.5104	0.0213					
	GEE	1 %		0.0695	-0.5262***	0.0142					
<i>V. vitis-idaea</i>	GLM	27 %	0.1573	0.4546***	-0.3330**	-0.0453***	0.4657*	0.1797	-0.0124		
	GEE	14 %		0.4271***	-0.2552	-0.0400*	0.1478	0.1693	-0.0023		
<i>V. alpina</i>	GLM	9 %	0.3060	-17.5497	5.2936*	0.0773*	-2.9683*	2.2190*		-0.1153*	
	GEE	15 %		-39.0120	5.9435	0.1924`	-2.8634	2.0985		-0.1267	
<i>V. biflora</i>	GLM	14 %	0.2322	0.3173	-1.6433	-0.1038*	-3.7038*	2.7043*		0.0492	
	GEE	6 %		0.2835	-1.6536	-0.1002*	-3.8005*	2.8121		0.0489	

<i>L. borealis</i>	GLM	15 %	0.2663	0.7959***	-0.0127	0.0286	-0.4830**			
	GEE	5 %		0.8318***	-0.0120	0.0024	-0.4800			
<i>P. lapponica</i>	GLM	11 %	0.1655	-0.1780	0.0183**	-0.2023*				
	GEE	2 %		-0.0809	0.0067	-0.0526				
<i>S. herbacea</i>	GLM	54 %	0.9970	2.9997***	0.0298***	1.1021**	-2.6518***	-0.037**	-0.0661***	0.0525***
	GEE	< 1 %		1.9561**	0.0228	0.9116	-1.4407	-0.0284	-0.0418	0.0383
<i>S. procumbens</i>	GLM	9 %	0.2890	0.3574**						
	GEE	7 %		0.2986*						
<i>T. europaea</i>	GLM	9 %	0.4440	-1.6583	-0.0351	-0.1312	-3.3471	-0.0091	0.029	0.1451*
	GEE	< 1 %		-1.6583	-0.0351	-0.1312	-3.3471	-0.0091	0.0290	0.1451
<i>V. uliginosum</i>	GLM	5 %	0.6630	-0.5626**	-0.0232**	-1.5980***	0.9144***	0.0412***	-0.0147**	
	GEE	3 %		-0.5785	-0.0122	-1.1985	0.8329	0.0316	-0.0131	
<i>V. vitis-idaea</i>	GLM	11 %	1.000	1.2685***	0.0096	0.7502***	-1.3092***	-0.0104*	-0.0332***	0.0415***
	GEE	< 1 %		0.3887	0.0029	0.5326	-0.6890	-0.0038	-0.0108	0.0212
<i>V. alpina</i>	GLM	0 %								
<i>V. biflora</i>	GLM	28 %	0.8318	1.8968***	0.0588***	1.4216*	-2.2838**	-0.0515**	-0.039***	0.0548**
	GEE	< 1 %		1.7130*	0.0620**	1.1670	-1.2734	-0.0466	-0.0361*	0.0347

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Appendix 2. Additional figures for the results section.

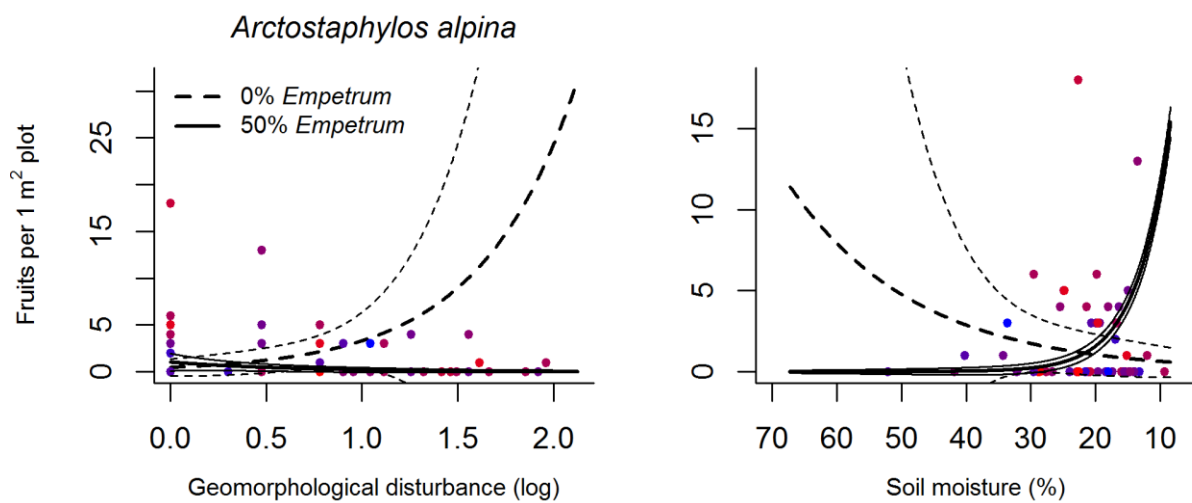


Figure S1. Predictions of the impacts of *Empetrum nigrum* ssp. *hermaphroditum* on the reproductive effort of *Arctostaphylos alpina* (mean \pm 2 S.E.) in varying geomorphological disturbance and soil moisture conditions. Symbol colour indicates *Empetrum* cover, with red representing high cover and blue representing low cover. Note that in right hand side panel the x-axis is reversed to represent increasing stress related to drier conditions. Predictions were made from the best-fit GLM models, assuming either the absence of *Empetrum* or 50 % *Empetrum* cover (i.e. corresponding to the 10th and 90th percentiles of the observed *Empetrum* cover).

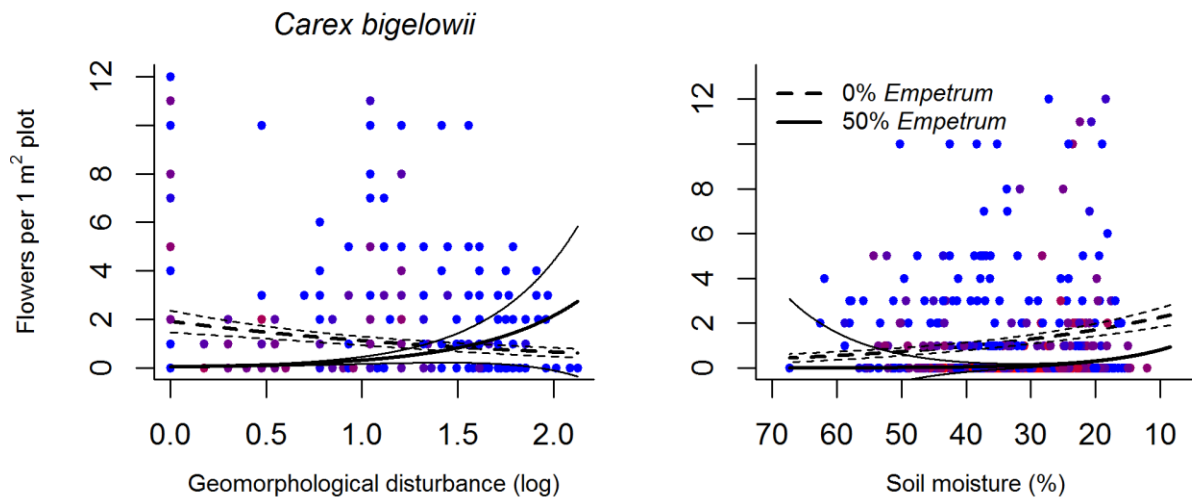


Figure S2. Predictions of the impacts of *Empetrum nigrum* ssp. *hermaphroditum* on the reproductive effort of *Carex bigelowii* in varying geomorphological disturbance and soil moisture conditions. For detailed figure legend, see figure S1.

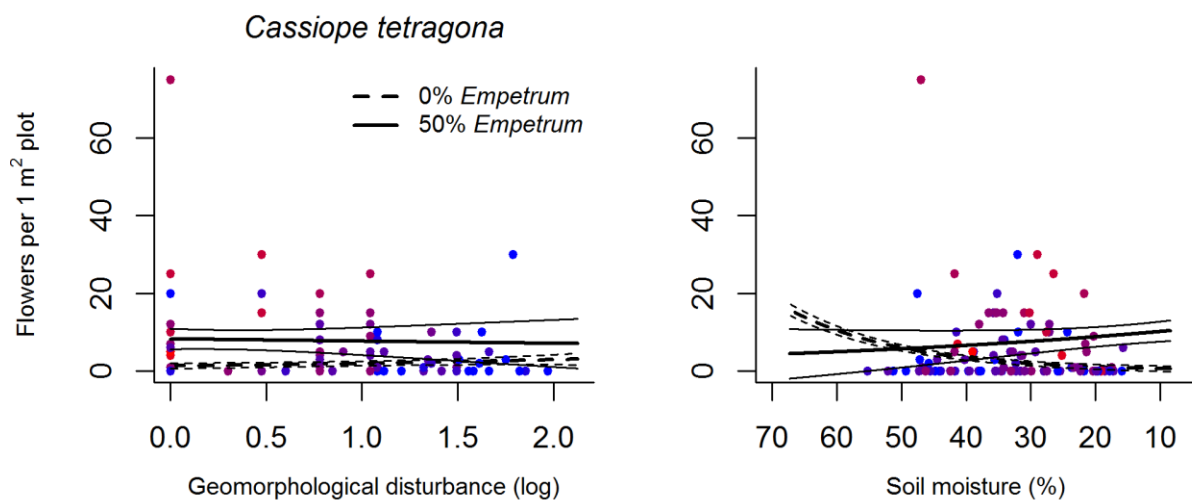
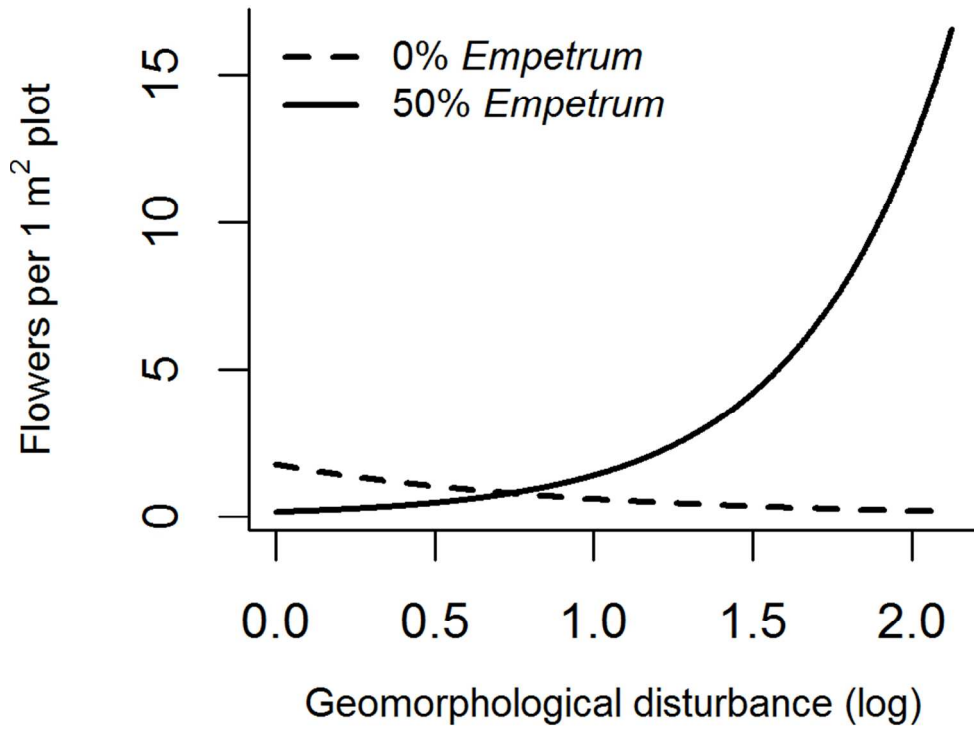


Figure S3. Predictions of the impacts of *Empetrum nigrum* ssp. *hermaphroditum* on the reproductive effort of *Cassiope tetragona* in varying geomorphological disturbance and soil moisture conditions. For detailed figure legend, see figure S1.

The outcomes of biotic interactions are predicted to vary along environmental severity gradients. Using an observational approach, we demonstrate that explicitly considering multiple environmental factors provides better estimates of the impacts of biotic interactions. Therefore, studies based on a single abiotic variable may reach incorrect conclusions about the nature of biotic interactions where multiple independent variables underlie the severity gradient.

Trientalis europaea



85x79mm (300 x 300 DPI)



Empetrum nigrum ssp. *hermaphroditum*. Photo by P. O. Niittynen.
251x170mm (300 x 300 DPI)

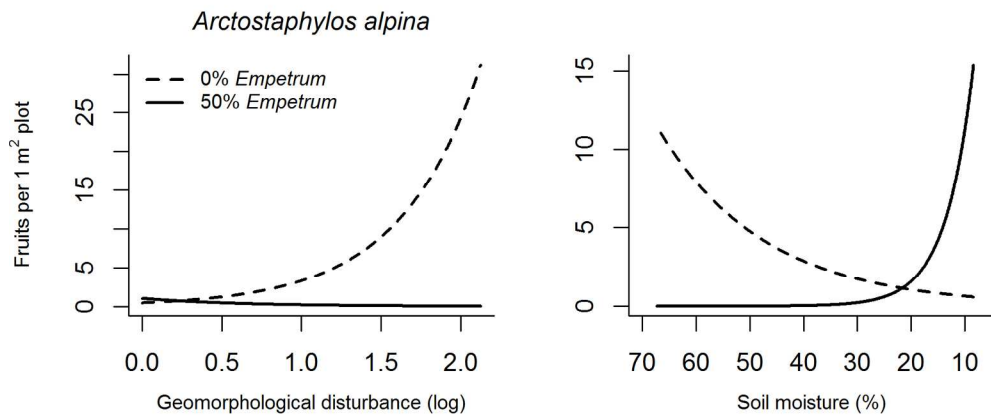


Figure 1. Predictions of the impacts of *Empetrum nigrum* ssp. *hermaphroditum* on the reproductive effort *Arctostaphylos alpina* in response to variation in two environmental variables. Increased geomorphological disturbance impacts positively on *A. alpina* reproductive effort in the absence of *Empetrum*, with the inverse occurring when *Empetrum* is present (left panel). Decreasing soil moisture was negatively correlated with *A. alpina* reproductive effort in the absence of *Empetrum*, but the presence of *Empetrum* reverses the direction of this relationship (right panel). Note that in right panel the x-axis is reversed to represent increasing stress related to drier conditions. Predictions were made from the best-fit GLM models, assuming either the absence of *Empetrum* or 50 % *Empetrum* cover (i.e. corresponding to the 10th and 90th percentiles of the observed *Empetrum* cover).
169x79mm (300 x 300 DPI)