

Climatic niche groups: A novel application of a common assumption predicting plant community response to climate change



Mark C. Bilton^{a,*}, Johannes Metz^b, Katja Tielbörger^a

^a University of Tübingen, Plant Ecology Group, Institute of Evolution and Ecology, Auf der Morgenstelle 5, D-72076 Tübingen, Germany

^b University of Potsdam, Plant Ecology & Nature Conservation Group, Institute of Biochemistry and Biology, Maulbeerallee 3, 14469 Potsdam, Germany

ARTICLE INFO

Article history:

Received 3 July 2015

Received in revised form 12 February 2016

Accepted 22 February 2016

Available online 23 February 2016

Keywords:

Annual plant communities
Bioclimatic envelope modelling
Climate change manipulations
Experimental evidence
Plant functional groups
Rainfall niche

ABSTRACT

Defining species by their climatic niche is the simple and intuitive principle underlying Bioclimatic Envelope Model (BEM) predictions for climate change effects. However, these correlative models are often criticised for neglecting many ecological processes. Here, we apply the same niche principle to entire communities within a medium/long-term climate manipulation study, where ecological processes are inherently included.

In a nine generation study in Israel, we manipulated rainfall (Drought –30%; Irrigation +30%; Control natural rainfall) at two sites which differ chiefly in rainfall quantity and variability. We analysed community responses to the manipulations by grouping species based on their climatic rainfall niche. These responses were compared to analyses based on single species, total densities, and commonly used taxonomic groupings.

Climate Niche Groups yielded clear and consistent results: within communities, those species distributed in drier regions performed relatively better in the drought treatment, and those from wetter climates performed better when irrigated. In contrast, analyses based on other principles revealed little insight into community dynamics. Notably, most relationships were weaker at the drier, more variable site, suggesting that enhanced adaptation to variability may buffer climate change impacts.

We provide robust experimental evidence that using climatic niches – commonly applied in BEMs – is a valid approach for eliciting community changes in response to climate change. However, we also argue that additional empirical information needs to be gathered using experiments in situ to correctly assess community vulnerability. Climatic Niche Groups used in this way, may therefore provide a powerful tool and directional testing framework to generalise and compare climate change impacts across habitats.

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1. Introduction

There is a distinct lack of understanding as to how plant communities across the globe will respond to climate change. Two often heralded approaches of investigation have been Bioclimatic Envelope Models (BEMs) (Bakkenes et al., 2002; Pearson and Dawson, 2003; Thomas et al., 2004; Thuiller et al., 2005; Randin et al., 2009; Bellard et al., 2012; IPCC, 2014) and medium/long-term experimental manipulations (Harte and Shaw, 1995; Grime et al., 2000; Zavaleta et al., 2003; Peñuelas et al., 2007; Lloret et al., 2009; Tielbörger et al., 2014). However, despite the accumulating evidence in both approaches, we still lack an ecologically sound and

general framework that would enable us to predict the response of organisms to climate change.

BEMs commonly define species using the climatic niche they currently occupy and project their shift in range/abundance as the climate changes (Thuiller et al., 2008; Ehrlén and Morris, 2015). However, while species distributions provide an intuitive logic to relate and combine specific plant adaptations to climate – reflecting their abiotic requirements and outcomes of biotic interactions – there is a growing consensus that some of the simpler models neglect too many ecologically meaningful processes, e.g. dispersal, changing interactions, evolutionary history, other abiotic adaptations (Davis et al., 1998; Botkin et al., 2007; Dormann, 2007). Consequently, BEMs often give varied or inaccurate predictions for the rate and magnitude of species/community change along gradients (Thuiller, 2004; Diamond et al., 2012; Pottier et al., 2013). In contrast, in situ climate manipulation experiments inherently incorporate many ecological/community processes, and therefore provide a solid basis for parameterising and validating predictions.

* Corresponding author. Tel.: +49 7071 2974246.

E-mail addresses: mark.bilton@uni-tuebingen.de (M.C. Bilton), johmetz@uni-potsdam.de (J. Metz), katja.tielboerger@uni-tuebingen.de (K. Tielbörger).

However, these experiments need clearer directional hypotheses about their expected responses to climate manipulations to be extrapolated beyond isolated case-studies and applied to wider areas (McMahon et al., 2011; White et al., 2012), and typically lack the power or the means to allow for direct comparison between communities (Tielbörger et al., 2014).

One potential solution to improve and compare different predictions would be to combine the advantages of both approaches utilising the intuitive logic set out by BEMs and classify species along a climatic niche axis into Climatic Niche Groups (CNGs) (e.g. species more commonly found in drier/warmer or wetter/cooler environments) (McMahon et al., 2011), then follow the CNG responses within climate manipulation studies.

Functional groups have proved popular and successful in ecology by using traits, which covary with environmental gradients, to generalise predictions of community structure and response (Grime et al., 1997; Smith et al., 1997). Similarly, as a functional grouping, the CNG approach may prove more specific than whole community analyses, and more powerful than single species analyses, by breaking down the community into common directional responses and overcoming many sources of variation. The CNG approach would base its predictions upon one simple overriding trait parameter ('realised niche distribution'—created from commonly collected biological records and climate data), which in principle embraces the wide range of different trait strategies that allow plants to persist in particular climates. In theory, similar predictive accuracy could be gained by using other functional ecology techniques that rely on single trait or multiple trait (strategy) classifications. However, these are complex, require large-scale screening experiments (Grime et al., 1997; Lavorel and Garnier, 2002), and have so far had limited success in climate change studies (Diaz and Cabido, 1997; Laurent et al., 2004; Evans et al., 2011; Bartlett et al., 2012; Diamond et al., 2012). Likewise, simple taxonomic and life-form groups (such as legumes, grasses, shrubs), have often proved popular in experiments (Suttle et al., 2007; Yang et al., 2011) and climate models (IPCC, 2007). Generalisations can be drawn from taxonomic/life-form groups, as they contain some trait similarities in phylogeny. However, species within these groups often inhabit very different climatic conditions (Lavin et al., 2004), and are therefore likely to respond differently to a changing climate.

While the climatic niche principle is commonly applied in BEMs, so far strong ecologically based evidence in support of this is still lacking, reflecting the many criticisms BEMs have met in several studies (Botkin et al., 2007; Dormann, 2007). Currently, most empirical support has come from observational studies, which are limited in their ability to isolate causal factors. Recently, a number of articles have reported observed compositional shifts in a process referred to as "Thermophilization"—an increase in warmer distributed species across mountains (Gottfried et al., 2012), tundra (Elmendorf et al., 2015) and forest ecosystems (De Frenne et al., 2013; Feeley et al., 2013; Duque et al., 2015). Community based evidence for climate induced change is less prominent for rainfall distributions, even though drought tolerance is often correlated with species distribution (e.g. Engelbrecht et al., 2007). However, evidence for directional short-term community shifts in response to extreme climatic events such as drought (Milton and Dean, 2000; Bowers, 2005; Barbeta et al., 2015) and ENSO events (Holmgren et al., 2006; Comita and Engelbrecht, 2009) are commonplace, suggesting that the principle may be applicable. Indeed, "dry affiliate" species were noted to increase in abundance and growth in tropical forests (Feeley et al., 2011; Butt et al., 2014), which may have been a legacy of an El Niño drought, or potentially reflect increased aridity due to long-term climate change.

Few studies though have actually applied the climatic niche principle to climate experiments, where the effectiveness of species distributions in forming predictions has been mixed: ant responses

were compared to BEMs in a warming experiment in the USA (Diamond et al., 2012); planted seeds of twelve different latitudinal range species were exposed to manipulations (Pfeifer-Meister et al., 2013); and responses of six plant species were explored in a short-term central European experiment (Bütöf et al., 2012). The strongest evidence comes from thermal niches in tundra areas (Elmendorf et al., 2015), where the mean index of community temperature distribution was shown to increase under warming manipulation. Indeed, by combining multiple functional adaptations founded in evolutionary history which are likely to be responsive to climate change, the CNG approach has the potential to find mechanistic, directional and interpretable results when applied to community climate manipulations. In addition, by being simple to implement, any quantitative findings using CNGs in manipulation studies may then provide general patterns suitable for comparison across different habitats.

To test the potential of the CNG approach, we applied it to a 9-year climate manipulation experiment in Israel (Tielbörger et al., 2014), where rainfall and water availability are among the most important abiotic factors. At two sites of contrasting rainfall, climate manipulations were constructed with increased (+30%), decreased (−30%) and ambient (control) rainfall conditions. The plant communities mainly consisted of short-lived annual species, thereby exposing a new generation each year to the experimental selection. The response of the communities were monitored in depth, as the number of individuals per species. This provided a strong test of the CNG approach, allowing for direct comparison to previously reported whole community responses (Tielbörger et al., 2014) – which found very little response to the climate manipulations – as well as a comparison to single species and taxonomic grouping approaches. Using the CNG approach, we aim to elucidate whether species distributions and their climatic niche result in predictable responses to climate change thereby validating the principle used in BEM/species distribution modelling. Specifically, we hypothesised that those species more commonly observed in wetter climates in Israel would increase in the irrigated treatment, whereas the species originating from drier climates would increase when droughted. Moreover, the standardised CNG approach allowed us to evaluate whether the rate and extent of change differed in our two study sites. If the change was more so in the drier, more variable site, this would confirm previous suggestions that communities in drier regions are especially vulnerable to climate change (Sala et al., 2000; Golodets et al., 2015). However, if less so, it would support the notion that species inhabiting drier environments express strong adaptations to environmental variability which will buffer climate change impacts (Tielbörger et al., 2014).

2. Materials and methods

2.1. Site descriptions

In 2002, two climate manipulation sites (see Tielbörger et al., 2014 for full details) were set up centrally along a steep rainfall gradient that runs from the north (800 mm yr^{−1}) to the south (20 mm yr^{−1}) of Israel (Israel Meteorological Service, <http://www.ims.gov.il/IMSeng/CLIMATE>). Although the full experiment comprised of four sites (Tielbörger et al., 2014) only the two central sites contained experimental manipulations, and are thus presented in our study. The sites were set approximately 50 km apart and will continue to be named in relation to their rainfall climatic type, with the higher and more consistent inter- and intra-annual rainfall (given by coefficient of variation C.V.) at the 'Mediterranean' site (N31°42' E35°03'; mean rainfall 550 mm yr^{−1}, C.V. 22); with lower and more variable rainfall at the 'Semi-Arid' site (N31°23'

E34°54'; mean rainfall 260 mm yr⁻¹, C.V. 32). Both sites were similar in the geology of their bedrock (limestone), both on south facing slopes, at similar altitudes (approx. 600 m a.s.l.); had similar mean annual temperatures (18 °C) and possessed the following soil types (Mediterranean: Hard chalk Terra Rossa; Semi-Arid: Brown Rendzina) (Holzapfel et al., 2006).

The plant communities were semi-natural shrublands, with an approximate overall vegetative cover of 50% (Semi-Arid) and 75% (Mediterranean). The focus of our study was on the herbaceous communities living between and under shrubs. These communities consisted mainly of winter annuals, and were the key component of the system as they contributed approx. 85% of all plant species, and accounted for the majority of the ANPP (80–90% Semi-Arid and 50–90% Mediterranean; Tielbörger et al., 2014). With no rain during summer, the main growing season was between November and May, with shorter seasons at the drier site. In 2002, the entire experimental area at both sites was fenced to prevent inconsistencies arising from livestock grazing, and remained fenced for the duration of the data presented (9 years, until 2010).

2.2. Climate manipulations

In both the Mediterranean and Semi-Arid sites, three permanent rainfall manipulation treatments were constructed: 'irrigated' (approx. +30% rainfall); 'drought' (approx. –30% rainfall); and 'control' (natural rainfall conditions). Each treatment plot covered 10 m × 25 m and was replicated five times within each site. Within 'irrigated' plots, sprinkler systems spraying water from 50 cm above ground level added 10 mm of water after each major rain event (>5 mm), until +30% of the long-term average rainfall was reached (Tielbörger et al., 2014).

Within 'drought' plots, two systems were used. Between 2003 and 2006, retractable rainout shelters, built of transparent PVC placed 2 m above the ground, were manually closed over the areas during every second rain event. Due to persistent natural damage by strong winds during rainstorms and the manpower required to operate the system, from 2006/2007 onwards, more robust permanent structures were used. Strips of transparent PVC 20 cm wide and separated by 40 cm gaps covered the entire area, 2 m above the ground. These strips intercepted 30% of the rainfall, and the height allowed an even distribution of rain to reach the plot surface.

Soil measurements confirmed that the applied rainfall manipulations had significant effects on soil moisture, especially in the drought treatment (Tielbörger et al., 2014). Soil moisture was significantly lower in the drought plots (approx. 28% average reduction), intermediate in control plots, and highest (approx. 8% increase) in irrigated plots. Temperatures were also increased in drought plots (average increase 0.6 °C) and decreased in irrigated plots (average decrease 0.9 °C), further adding to the realism of our manipulations with respect to climate change predictions for the region (Smiatek et al., 2011), but potentially adding variation to any selection processes related to rainfall.

2.3. Plant data collection

We placed ten 20 cm × 20 cm permanent quadrats within each plot. Five quadrats were positioned in open patches between shrubs and five under shrub canopies, to provide a good representative sample of a plot community. At peak flowering (March–April) the identity and number of individuals of each species was recorded. Recording was first carried out in March 2002, before any rainfall manipulations, then for eight years of manipulation (2003–2010). This provided us with a dataset for 2 sites (Mediterranean and Semi-Arid), 3 treatments per site (irrigated, drought, control), 5 plots per treatment, 10 quadrats per plot (total 300 quadrats per year), for

a total of 9 years (i.e. plant generations). Mean and max densities and species richness values in the quadrats were: Mediterranean (dens.=44; 550; SpRi=8.4; 23) and Semi-Arid (dens.=38; 360; SpRi=6.0; 24). Over the nine year period, natural rainfall was recorded at each site using rain gauges and local weather station information.

2.4. Plant species groupings

We aimed to assess the power of the CNGs for explaining community responses to climate manipulations and compare it to other commonly reported approaches. Therefore, using only the annual plants from the dataset (>96% of total individuals recorded), the data was amalgamated in four different ways for analysis: (i) 'Climatic Niche Groups' (ii) 'Single species'; (iii) 'Taxonomic groups'; (iv) 'All species'. (i) For the main 'CNG' approach of the study we created four groups: CNG1 (species independently observed occurring in the driest habitats in Israel in terms of rainfall); to CNG4 (species observed in the wettest habitats) (Appendix C). To create these groups, firstly we cross-checked each species with an open-access online GIS database (BioGIS, 2012: <http://www.biogis.huji.ac.il/>), to obtain independent information on their observed species distributions within Israel. To ensure quality of the range data, we confirmed that for each species >50 occurrences were observed (typically >> 100) [N.B. the occurrence data is compiled from numerous quality sources e.g. research botanists/National Park surveys/Herbarium data/some citizen science (BioGIS, 2012)]. We then extracted niche values for each species as given by the website for mean annual rainfall. Niche values were derived from climate data corresponding to each observation/occurrence of the species. These individual species rainfall niche values were then grouped together into the four CNGroups, spanning similar ranges of average annual rainfall (approximately 130 mm), with: CNG1 (100–230 mm); CNG2 (230–360 mm); CNG3 (360–490 mm); and CNG4 (490–620 mm: one outlier at 640 mm). These particular fixed boundaries were arbitrarily chosen to ensure that all four groups were present at both sites and that the same species (or species within the same niche range) could be compared between sites. Therefore, many species in a group were present at both experimental sites (Table 1, Appendix C), and the groups represented different community proportions at each site representative of their climatic type (e.g. group as a proportion of community: CNG2 SA '0.66' Med '0.08'; CNG3 SA '0.26' Med '0.70'; Table 1). While results for these groups are reported, many other group boundaries were tested (e.g. different fixed boundaries, equal number of species per group, equal proportion of the community represented by a group) and a formal group sensitivity analysis was performed (see Section 2.6) to ensure that results were independent of group make-up. For the other approaches: (ii) Abundances of all 117 'single species' were analysed separately (Appendix C); (iii) We summed species abundances per quadrat using the classical taxonomic species categories (3 groups: 'legume'; 'grass'; 'other', Appendix C); (iv) We created a fourth dataset summing together individuals from all annual species.

2.5. Statistical analyses

To all four datasets (CNGs, single species, taxonomic groups, all species) we applied Generalised Linear Mixed Models (GLMM) using the GLIMMIX package within SAS® software version 9.3. In all GLMM analyses, the data being modelled was the mean number of individuals at a quadrat scale (sum of species within groups and mean of the 10 quadrats within plots). In most cases the data had a negative binomial distribution, so this was used throughout with a log link function.

Table 1
The distribution of species at the two sites in Israel within the Climatic Niche Group (CNG) classifications. Mean occupancy calculated per quadrat (20 cm × 20 cm); Proportional occupancy estimated by summing the mean occupancy of each species; Rainfall range given by average rainfall per year (calculated on BioGIS website) from driest to wettest species in a group.

	CNG1	CNG2	CNG3	CNG4
Semi-Arid				
Species No.	11	21	39	25
Mean occupancy (inds.)	2.63	26.84	10.68	0.71
Proportional occupancy	0.06	0.66	0.26	0.02
Rainfall range (mm)	From	243	374	489
	To	361	486	640 (582*)
	Range	118	112	151 (93*)
Mediterranean				
Species No.	5	16	40	42
Mean occupancy (inds.)	0.69	3.49	30.49	9.06
Proportional occupancy	0.02	0.08	0.70	0.21
Rainfall range (mm)	From	243	374	489
	To	361	486	640 (615*)
	Range	118	112	151 (126*)

* Rainfall niche values without single outlying species (see Appendix S1).

We estimated and compared the change of individuals over time (slope) in the different rainfall manipulation treatments (irrigated, drought, control). Rainfall proved to be a major contributor to variance between years, and rainfall in different years prior to the growing season had stronger correlations with different species groups, suggestive of plant strategies (see Appendices B and E), but were not correlated with each other. Therefore, the formula for each GLMM analysis contained rainfall at year T (rainfall in growing season), T-1 (rainfall 1 year prior to growing season) and T-2 (rainfall 2 years prior to growing season) as underlying covariates. However, the fixed effects important for the hypotheses testing were the interaction between the continuous variable 'Year' (2002 to 2010) with the categorical factor 'Treatment'. 'Plots' were nested as a random effect for each intercept.

2.6. Group sensitivity analysis

To ensure our emerging patterns from the CNG analysis were not an artefact of the boundaries chosen, we performed formal robustness tests. We created multiple 'Cumulative Species Groups' for the two sites in two ways ('dry-first' and 'wet-first'). Initially, we ranked the species from the lowest (driest) to the highest (wettest) average rainfall niche values, obtained using the BioGIS website. Then we created separate groups totalling the same number as there were species per site (Semi-Arid: 96 groups; Mediterranean: 103 groups). Each group contained a different number of species, cumulatively added in rainfall niche ranking order. In the 'dry-first' method, the first group contained just the lowest ranking species, the second group contained the two driest species, and groups were made consecutively adding the next ranking species until the final group which contained all species from a site and included the wettest species. For the 'wet-first' method, the first group contained only the species with the highest ranking rainfall average, and the groups were constructed adding each lower ranked species in sequence, with the driest species added to the final group, which again contained all the species from a site. The same GLMM analysis, described above, was applied to all of the different Cumulative Species Groups within each site. When comparing the Year × Treatment interactions, we could determine how the number of species in a group, and the direction of cumulative adding, affected their difference in trend response between the irrigated and drought treatments. Using mean occupancy of each species over the course of the experiment (i.e. mean number of individuals per quadrat per year at each site regardless of treatment), we could also calculate a rough approximation for the group as a proportion of the entire community to determine

how much of the community was responding to the different treatments.

In addition, we performed a 'jackknife' analysis to highlight the influence of each individual species on results within each group (Appendix D).

3. Results

3.1. Treatment effects

For the main approach of CNGs, at the Mediterranean site, the GLMMs for all four groups showed significant slope differences between treatments in directions in accordance with our hypotheses (Fig. 1). For the two driest CNGs, densities increased relatively more over the nine year experiment in the drought treatment than in the irrigated (CNG1: estimated treatment difference $-0.50 p < 0.05$; CNG2: treatment difference $-0.18 p < 0.05$), whereas for the two wettest groups, densities increased more in the irrigated treatment than the drought (CNG3: treatment difference $0.08 p < 0.01$; CNG4: treatment difference $0.09 p < 0.01$) (Fig. 1).

At the Semi-Arid site, the species distributed in the driest regions of Israel (CNG1), increased relatively and significantly more in the drought treatment than in the irrigated ($p < 0.05$, Fig. 1). Although no significant effects were found for the other CNGs (2–4), there was still a clear hierarchical switch in slope differences across the groupings as hypothesised. For CNG1 the differences between slopes in the dry and wet treatments were: -0.21 (CNG1 increased most in the drought treatment), -0.01 (CNG2), 0.03 (CNG3 increased more in the irrigated treatment), 0.22 (CNG4 increased most in the irrigated treatment).

For single species in the Mediterranean site, density slopes for only five species out of 103 were significantly different between irrigated and drought treatment ($p < 0.05$) (2 performed better in drought; 3 better in irrigated) (Table 2). In the Semi-Arid site, four species out of 96 showed a significant difference between treatments over time ($p < 0.05$) (3 better in drought; 1 better in irrigated). With no multi-testing correction applied, these values were approximately equal to those expected by chance.

For the taxonomic groupings 'Grass' and 'Other' species, there were no significant treatment effects at either site. However, 'Legume' densities increased relatively more in the irrigated treatment than the drought at the Mediterranean site (slope dif. = 0.13 ; $t = 2.34$; $p < 0.05$; Appendices A and E). A similar, but non-significant pattern was also present for Legumes at the Semi-Arid site (slope dif. = 0.11 ; $t = 1.19$; $p = 0.23$; Appendix A).

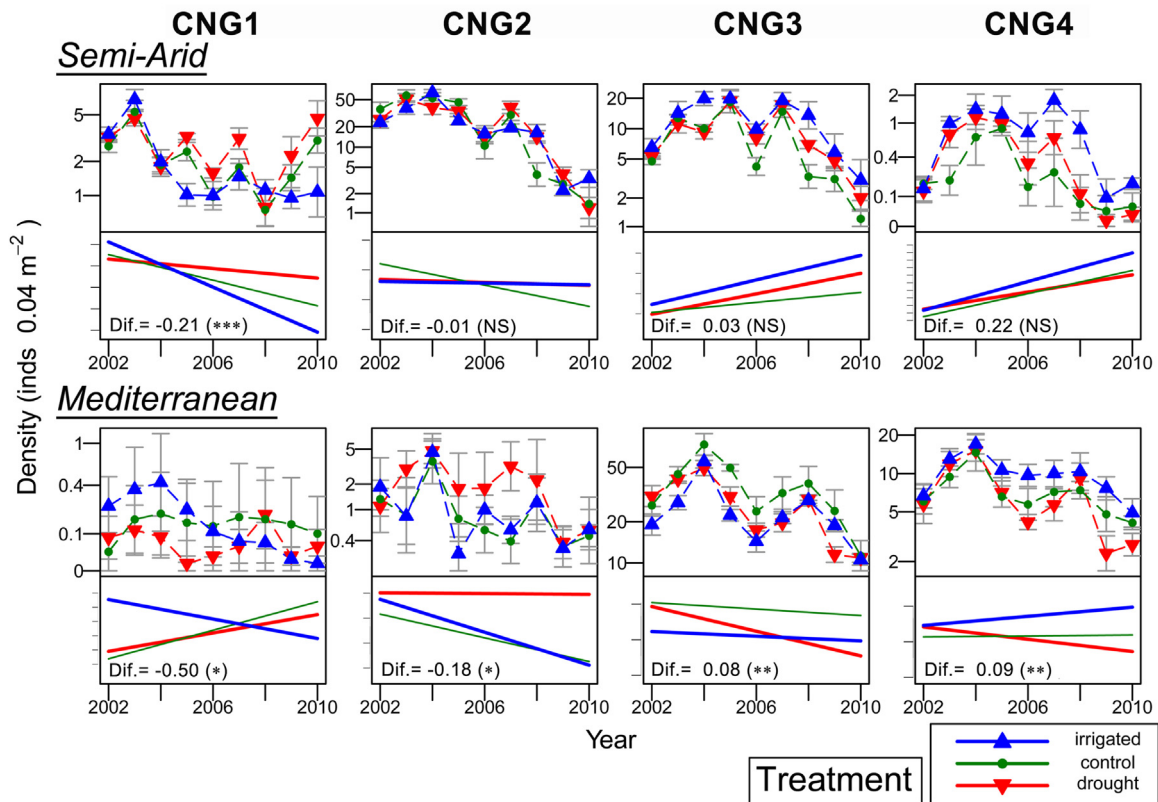


Fig. 1. CNG response to climate manipulations. The density response of grouped annual species exposed for eight years (+1 baseline year) to three climate manipulations: 'irrigated' (+30% water); 'control' (natural rainfall conditions); 'drought' (−30% water). Treatments imposed at two sites ('Semi-Arid' and 'Mediterranean') and species grouped within four Climatic Niche Groups. Points indicate mean densities per quadrat, with associated SE. Lines show the estimated GLMM models with associated tick marks on lower panels indicating a change in 0.5 on the negative binomial scale (see Section 2). 'Dif' indicates the difference between the estimated slope in the irrigated and drought treatment with associated significance (d.f. = 114) (NS = non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 2

All significant single species from GLMM analyses, comparing density response to 8 years (+1 baseline year) of rainfall manipulation (Total species tested: SA 96; Med. 103). Table indicates the treatment in which the species performed relatively better (Drought −30% or Irrigated +30% rainfall) and the significance of the statistic without multi-testing correction for species (d.f. = 114): * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	Improved treatment response	t-Value	CNG
Semi-Arid			
<i>Carrichtera annua</i>	Drought	−3.80***	1
<i>Crithopsis delileana</i>	Drought	−2.01*	2
<i>Galium judaicum</i>	Drought	−2.41*	3
<i>Atractylis cancellata</i>	Irrigated	2.91**	2
Mediterranean			
<i>Stipa capensis</i>	Drought	−2.00*	1
<i>Filago palaestina</i>	Drought	−2.40*	2
<i>Hymenocarpus circinnatus</i>	Irrigated	2.65**	3
<i>Trifolium stellatum</i>	Irrigated	3.40***	4
<i>Picris galilaea</i>	Irrigated	2.50*	4

For the total number of individuals, at the Mediterranean site we found that the estimated slope was relatively steeper in the irrigated treatment than the drought (slope dif. = 0.05; $t = 2.05$; $p < 0.05$). There was no such significant relationship in the Semi-Arid site.

For all GLMM analyses, the Year \times Treatment interaction had d.f. = 2114; and the contrasts compared to the t -distribution had d.f. = 114, with a 3-test Tukey–Kramer adjustment.

3.2. Group sensitivity analysis

For the Cumulative Species Group analysis (Fig. 2), the general patterns for the two sites were the same, and confirmed that

group boundaries were rarely important qualitatively. Groups created from a small number of species (e.g. 1–3 species) tended to be unpredictable, and non-significant. However, clear patterns as hypothesised (a negative difference in treatment slopes starting at driest species; a positive difference in treatment slopes starting at wettest species) were seen from groups containing five or six species (Fig. 2). As seen in the main analysis, patterns remained stronger at the Mediterranean site than the Semi-Arid, however within a site, stronger patterns than those reported in the main analysis could be found using particular and site specific numbers of species and/or group community proportions. For example, in the 'dry-first' groupings (bottom graphs Fig. 2), a larger proportion of the community at the dry end of the scale responded to the manipulations at the Semi-Arid site (peaking in strength (highest F -value) at the 8th species or 5% of the community) compared to a smaller proportion at the Mediterranean site (strongest at 6th species or 1.6% of the community). Conversely, for the 'wet-first' groupings (top graphs Fig. 2) it was the larger proportion at the wet end of the scale which responded strongest to the manipulations at the Mediterranean site (21 species or 10% of the community) compared to at the Semi-Arid site (25 species or 1.7% of the community).

4. Discussion

We have demonstrated a simple way of categorising species into functional groups based on their observed rainfall niche (Climatic Niche Groups, CNGs)—an intuitive principle often proposed by species distribution and BEM models. Manipulation experiments inherently incorporate the majority of ecological processes often neglected by models, and expose communities to a known selection

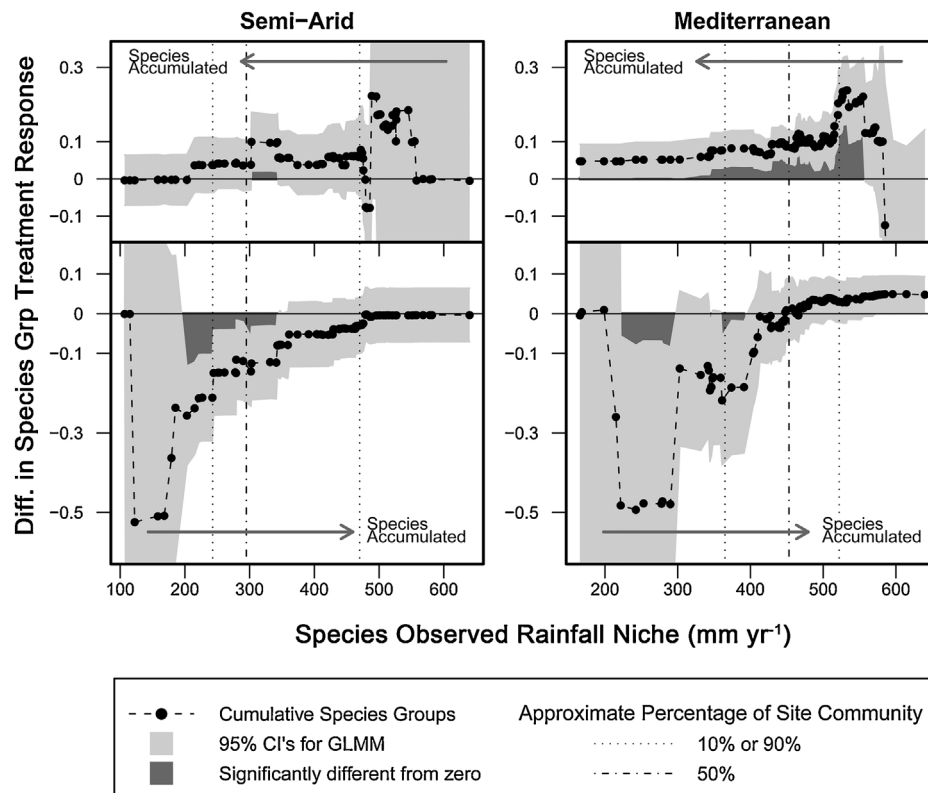


Fig. 2. 'Cumulative Species Group' analyses, for two sites ('Semi-Arid'; 'Mediterranean') subjected to long-term rainfall manipulations. Each data point represents a group containing different numbers of species, cumulatively added in rank order of species' average rainfall niche value (x-axis). Upper graphs show 'wet-first' groups i.e. right-hand side groups contain just wettest species. Lower graphs show 'dry-first' groups i.e. left-hand side groups contain just driest species. Proportion of the plant community attributed to a group is indicated by vertical lines: cumulative groups containing all species equal 100% of the community, groups from 'dry-first' or 'wet-first' method were reciprocal proportions e.g. species group containing 10% in dry-first method when omitted from wet-first method represent 90%. Y-axis is the difference, for each group, between the GLMM estimated slope in the drought and irrigated treatment, positive values indicate greater slopes when irrigated, negative values indicate greater slopes under drought. Statistical significance alpha p -value < 0.05.

driver difficult to elucidate from observational studies. By finding distinct sensitivities of different components of the community to simulated climate change using the CNG approach, we therefore provide ecologically sound evidence to support predictable community shifts using this principle. Here, the CNG technique was applied to an extensive climate change experiment situated along a rainfall gradient where 'very few differences between treatments were observed in the vegetation response variables' via standard whole-community univariate and multivariate statistical approaches (Tielbörger et al., 2014), and little response was found in the current study for single species or traditionally used taxonomic groups. Despite the difficult nature of the dataset – set in a highly variable species-rich system, with multiple minor or fluctuating changes occurring through time and space – the CNG approach successfully overcame this variance and identified consistent and hypothesised shifts in community composition under simulated climate change, finding: increases in those species associated with drier habitats if the rainfall should decrease; and increases in species associated with wetter habitats, should rainfall increase. Notably these relationships were weaker at the drier, more variable site, contradicting one view that communities in more arid environments are more vulnerable (Sala et al., 2000; Cleland et al., 2013; Golodets et al., 2015) and corroborating our earlier notion that naturally variable ecosystems may be less affected by climate change (Tielbörger et al., 2014).

4.1. Climatic niche groups: A predictive classification

CNGs proved to be the strongest and therefore most relevant groupings for eliciting community responses to the climate

manipulations. Intriguingly, these patterns were remarkably consistent across the CNGs within each site, as expressed at both sites by their common switch from a relative increase in drought (CNG1&2) to a relative increase under irrigation (CNG3&4). Our results suggest that the rainfall niche of a species may successfully act as a proxy for the wide range of potential traits and strategies selected for along the rainfall gradient in the Eastern Mediterranean (e.g. phenology, water use efficiency, plasticity, or seed dormancy) thereby responding predictively to the selections imposed by the manipulations. CNG classifications thus succeeded in being a powerful approach for climatic change interpretation and comparison across sites.

In support of our grouping method, the proportional abundance of the different CNGs within the study sites increased (CNG3&4) and decreased (CNG1&2) as expected with increasing mean annual rainfall across the environmental gradient (Appendix C). We are therefore confident that at these experimental sites, climate was a major differentiating selection force, giving the CNGs a greater chance of responding. In addition, our groupings proved to be highly robust, as changing the group boundaries never altered the qualitative patterns, and the Cumulative Species Group approach showed expected continuous trends across the species ranked by rainfall. The cumulative approach also suggested that different species in the particular communities were more likely to change i.e. wetter species at the wetter site; and drier species at the drier site. Such an alteration in community structure, indicates that the dominance hierarchy was indeed changing over time, with the core adapted species shifting in abundance to the greatest extent (Harte and Shaw, 1995; Evans et al., 2011; Yang et al., 2011).

In contrast to CNGs, neither ‘Grasses’ nor ‘Other Species’ showed any differentiated response to the manipulation treatments, indicating that species within these groups counteracted each other, leading to no overall net effect. This was consistent with the fact that these species spread widely across climatic gradients (Appendix C) and hence did not share certain moisture requirements. Indeed, even for ‘Legumes’ where a positive response to irrigation was found, the most parsimonious explanation comes from their climatic distribution. Across Israel, legumes were more frequent in both the wetter habitats and CNGs (Appendix C). CNGs thus appear superior to these repeatedly applied coarse taxonomic and life form groups (Suttle et al., 2007; Yang et al., 2011) to capture and interpret directional responses to precipitation change.

4.2. Functional groups: Offering power and equivalence

Logic might dictate that communities of annual species have the potential to change rapidly under climate change/manipulations, as the altered conditions would select a new generation of genotypes and species progressively each year (Jump and Peñuelas, 2005; Kigel et al., 2011). Even without adaptation, in a system where establishment is mainly limited by rainfall, an increase or decrease in average water supply should support greater or lesser individuals/biomass, respectively. However, a previous study at the same sites (Tielbörger et al., 2014) analysed overall community parameters and found very little alteration due to treatment effects for above-ground biomass, density, species richness, and species composition (using multi-variate RDA). Indeed, even in the present article only a few single species showed significant responses to the rainfall manipulation treatments, the ‘Grass’ and ‘Other species’ taxonomic groups showed no response, and even though the overall total abundances changed in the Mediterranean site, this was slow and only apparent when data from 2010 were included, not for years up until 2009 or before.

In contrast, by analysing groups of species we have found conclusive evidence for community shifts in response to the climatic manipulations (All species; Legumes; and especially CNG groups). It is perhaps surprising that neither single species nor multivariate techniques (Tielbörger et al., 2014) found evidence for change in the dataset with respect to the treatments. However, groupings provide more power to the analyses than multiple single species comparisons by aggregating larger numbers of individuals (assumed to be of similar type), which are likely to offer replacements even if events should prevent other individuals from the same group from establishing. Therefore, groups overcome many problems associated with analysing minor or fluctuating responses in time and space experienced by single species.

Fundamental to functional ecology/grouping approaches is that traits/strategies are linked to provide a test of prediction (Grime et al., 1997; Smith et al., 1997; Bartlett et al., 2012). We show that to provide a good test of prediction and mechanism, groups should be created in a hypothesised way relevant to the test (in this case rainfall change), and preferably with multiple groups across a continuum, to elicit potential and interpretable responses.

The CNG approach may be most beneficial for finding patterns in a system such as ours: a system which is extremely variable in both time and space, where large numbers of species are present in small quantities, with a different set establishing each year. However, CNGs may also be highly suitable in other perennial systems, where temporal and spatial heterogeneity may distort species-level patterns, and whole community patterns may be absorbed by net effects. Indeed, many other manipulation studies have had difficulty in determining clear community responses to the treatments imposed (Fridley et al., 2011; Miranda et al., 2011; White et al., 2014). Possibly, this seemingly more powerful CNG approach could be used in those and other studies, as it seems logical to suggest that

finding patterns of different strengths across habitat types would be more informative than finding no pattern at all. Even in studies where community parameters have been observed to change (e.g. Lloret et al., 2009), CNGs may offer further explanation as to how and which elements of the community are changing. Therefore, by applying the hypothesis driven CNG framework outlined here, maybe consistent changes in community structure can be found and then compared across habitats in a whole variety of ecosystems.

4.3. Comparison of two sites

Since all other environmental variables, except rainfall, were relatively similar at the two sites, we feel that some comparison can be made between them. In all cases, the results were consistently more statistically significant at the Mediterranean site, with generally larger effect sizes for compositional change. The lesser change observed at the Semi-Arid site contradicts the prediction that drier habitats are particularly vulnerable to the expected further aridification in the region (Sala et al., 2000; Smiatek et al., 2011; Golodets et al., 2015).

A possible explanation for this contrast in predictions is that manipulation experiments capture important empirical information about the evolutionary history of the species and therefore are more likely to accurately determine the rate and strength of their response. Clearly, more similar experiments need to be analysed using CNGs to confirm a trend. However, there is growing evidence also from other experiments (Fridley et al., 2011; Miranda et al., 2011) that evolutionary history, possibly related to environmental heterogeneity, may play a key role in determining the resistance of a community to climate change (Bonebrake and Mastrandrea, 2010; Fridley et al., 2011; Miranda et al., 2011; Tielbörger et al., 2014). Key in our system is the fact that natural inter- and intra-annual variability in rainfall is much higher in the Semi-Arid site than at the Mediterranean (Holzapfel et al., 2006). The exposure to greater variability at the Semi-Arid site, may therefore have selected for more/stronger adaptations related to variability which have been observed across the gradient e.g. ‘bet-hedging strategies’ such as seed dormancy (Tielbörger et al., 2012) or ‘large phenotypic plasticity’ (Petrù et al., 2006). Greater expression of adaptations such as these may be able to spread the range of environmental tolerances of the species and make the Semi-Arid community as a whole more resistant to climate change than the Mediterranean—by slowing down the selection of environmental ecotypes. Indeed, a functional trait (FT) approach would provide a more mechanistic interpretation of precisely how and why we see these consistent CNG patterns for community change in relation to climate. In dry annual communities determining precise strategies from traits is not trivial, partly because annuals are often perceived as having a single “ruderal” strategy (*sensu* Grime, 1974). However, a number of studies show that annual plants – particularly along gradients – can be more or less competitive (Holzapfel et al., 2006; Liancourt and Tielbörger, 2009), and even at the dry end of the gradient – where all plants could be considered “drought resistant” – plants may express either strong drought tolerance (Bartlett et al., 2012), or a highly plastic rainfall exploitative strategy (Petrù et al., 2006; Cingolani et al., 2005). Currently, knowledge regarding more complex traits such as stomatal closure, osmotic potential at leaf turgor, seed dormancy, and phenotypic plasticity is unfortunately lacking for the large range of species in our system. Therefore, further examination of these traits may be a valuable next step, to provide a more mechanistic interpretation of the climate responses of species along the climatic niche gradient, and differentiate between different strategies within groups. While the CNG approach is a simple method to determine community responses that negates the need to partake in extensive trait screening – and classifies species as

general drought resistant or more humid/competitive species – an FT approach may ultimately provide even greater predictive power for assessing species/community resistance or vulnerability to climate change.

4.4. Conclusions

We conclude that the use of the climatic niche – commonly used in BEMs – is a valid approach for eliciting community changes in response to climate change. However, to fully interpret community resistance or vulnerability across ecosystems, the contrasting responsiveness of our two study sites indicates that extra empirical information needs to be gathered experimentally in situ—in order to uncover how the results of evolutionary history and ecological processes will interact. Founded on similar principles, the information gained using CNGs within manipulation experiments can facilitate correlative climate change models, to provide ecologically sound and mechanistically relevant predictions for the rate of change in different ecosystems around the globe. Clearly, more long-term experiments, ideally across climatic gradients, need to be conducted or analysed in such a way to provide this information, and to determine the applicability of CNGs in other systems. It seems logical to suggest that CNGs should only be applied in regions where both species distribution and climate data are of reasonable quality, to ensure species niche estimates are as accurate as possible. However, by grouping species we overcome some of the potential problems related to an overreliance on inaccurate single species mapping. The generality of the CNG approach could and should be extended to perennial systems. Potential problems may arise in relation to other environmental heterogeneity (e.g. nutrient availability) that may override the climatic distribution—but our suspicion is, that if good quality distribution maps are recorded over a large area/climate gradient, the main niche axis of climate should remain valid as a predictor. Perennial plants are often recorded as percentage cover, and therefore may prove less precise in any analysis, but again we see no reason why climate selection should not act on these types of systems/datasets. Finally, the climate niche does not have to be limited to rainfall, and could be extended to temperature niche groups when analysing community responses to warming manipulations (Elmendorf et al., 2015). Therefore, relying merely upon commonly collected biological records and climatic data, the ease of application makes CNGs an attractive, powerful and generalisable technique for increasing the predictive accuracy of plant community responses to climate change.

Acknowledgements

We are deeply indebted to Ouria Oren, Hadas Parag, Martina Petrú, Yiftach Talmon, Efrat Elazar and Ifat Granat for their help in the field, the people who collected data for and created the BioGIS database, and to Marcelo Sternberg for managing the sites. This study is part of the GLOWA Jordan River project, funded by the German Federal Ministry of Education and Research (BMBF; 01LW0501 & 01LW0501A1 to KT), and partly funded by the German Research Foundation (DFG; TI338.12-1 to MB and KT).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2016.02.006>.

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