

Habitat connectivity buffers extinction under extreme droughts in experimental metapopulations

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Abstract

Connectivity maintains the spatial dynamics of metapopulations by promoting dispersal between habitat patches, potentially buffering populations and communities against continued global change. However, this function is threatened by habitats becoming increasingly fragmented, and habitat matrices becoming increasingly inhospitable, potentially reducing the resilience and persistence of populations. Yet, we lack a clear understanding of how reduced connectivity interacts with rates of environmental change to destabilise populations. Using laboratory microcosms containing metapopulations of the Collembola *Folsomia candida*, we investigate the impact of habitat connectivity on metapopulation persistence under a range of simulated droughts, a key stressor for this species. We manipulated both drought severity and the number of patches affected by drought across landscapes connected by either good or poor-quality corridors. We measured the time of population extinction, the maximum rate of population decline, and the variability of abundance among patches as criteria to evaluate the persistence ability of metapopulations. We show that whilst drought severity and number of drought-affected patches negatively influenced population persistence, these results were mitigated by increased habitat connectivity, which increased population persistence time and decreased both how fast populations declined and the variability in abundance among patches. Our results suggest that enhancing spatial connectivity can increase the persistence of metapopulations, increasing the time available for conservation actions to take effect, and/or for species to adapt or move in the face of continued stress. Given that fragmentation increases the isolation of habitats, improving habitat connectivity by using good quality corridors may provide a useful strategy to enhance the resistance of spatially structured populations.

Introduction

Whilst droughts are natural phenomenon, their frequency and severity are both increasing due to climate change (Mukherjee et al. 2018), driven by reduced regional precipitation and increased global evaporation (Ault 2020, Dai 2011). Drought has devastating impacts on species and ecosystems, causing increase in species mortality and extinction (Choat et al. 2018, Harrison 2000), loss of biodiversity (Peterson et al. 2021, Tilman and Elhaddi 1992), and declines in ecosystem function and productivity (Atkinson et al. 2014, Ciais et al. 2005).

These pressures are occurring against a backdrop of increasing habitat fragmentation, driven by a range of factors including the extraction of resources, development of settlements, increasing transport links, and proliferation of farming globally. Consequently, many populations are increasingly isolated, impacting their risk of extinction (Crooks et al. 2017, Reed 2004). Corridors have been suggested as positive conservation actions which can be used to reverse the negative effect of fragmentation by promoting dispersal and maintaining gene flow, allowing species to move or adapt in the face of environmental change. Previous studies have shown that enhancing habitat connectivity by corridors can reduce the likelihood of extinction and enhance species diversity in patchy habitats (Chisholm et al. 2011, Damschen et al. 2019), potentially buffering species loss against increasingly inhospitable environments.

Extreme climatic events such as droughts have a devastating impact on the viability of natural populations. Previous studies showed that droughts reduced the survival rate of populations in habitat patches by inducing ecological traps, a phenomenon that occurs when species settle in maladaptive habitats with a poor habitat selection (Hale and Swearer 2016, Robertson and Hutto 2006). For example, Coho salmon (*Oncorhynchus kisutch*) that inhabit intermittent streams used remaining pools as habitats when connectivity was lost, but during drought years a lower survival rate was found in some pools than others (Vander Vorste et al. 2020). Such phenomena have also been reported in other ecosystems (Robertson and Hutto 2006). In this case, dispersal might be key to maintain the dynamics of metapopulations and communities (Hale and Swearer 2016, Hale et al. 2015, Wolfe et al. 2023), as climatic extremes are likely to occur dynamically across time and space, and the quality of habitats can deteriorate or recover when the climate regime changes. Yet, there is relatively few data on the population changes with temporarily and spatially dynamic drought stressors.

Corridor quality is one of the important physical properties determines corridor effectiveness and dispersal success (Bennett et al. 1994, Habel et al. 2020, Li et al. 2021). Specifically, high quality corridors can promote dispersal, leading to greater movement rates to colonised patches compared to poor quality corridors (Li et al. 2021). Hence corridor quality may affect the stability and longevity of corridor-connected metapopulations, by facilitating or impeding movements between habitat patches. However, we currently lack empirical evidence on how corridor quality promotes population persistence, and how it interacts with the increasing severity and frequency of drought stressors.

While historical data has successfully investigated the population consequences of extreme drought events on habitat networks (e.g., Oliver et al. 2013), quantitatively measuring the effect of increasing drought severity and frequency on population declines and – importantly – how this stress might interact with corridors is difficult. However, disentangling the effects of corridor quality on metapopulation persistence in such natural systems (in the absence of high replication and control treatments) is complex. Experimental microcosms provide one alternative method to achieve this, as they allow landscape style manipulations at an observable scale (Altermatt et al. 2015, Benton et al. 2007). Indeed, such systems have previously been used to study the effect of network modularity (e.g., Gilarranz et al. 2017), and the impact of habitat configuration on metacommunities (e.g., Chisholm et al. 2011, Wolfe et al. 2022).

Here we investigate the effect of habitat connectivity on the persistence of metapopulations under drought stressors. We manipulated both drought severity and the number of patches affected by drought in landscapes connected by either good or poor quality corridors. We use 3D printed “four-patch, four-corridor” microcosms containing the soil Collembola *Folsomia candida* as experimental metapopulations and use a fully factorial manipulation where we change the moisture of corridors (good vs poor quality corridors), amount of water added to the patches (severity of drought), and number of patches (from 1 to 4) affected by reduced water availability (number of patches affected by drought). Drought is a known abiotic stressor to *F. candida* populations, as they need a high moisture to survive and reproduce. By monitoring the changes in population abundance in microcosms for a relatively long-period (c.16 weeks, ~ 5 generations), we can measure the effects of corridor quality interacting with drought severity and number of drought patches on the time of extinction, the maximum rate of population decline, and the variability of abundance among patches.

Methods

Model organism

The model organism is the soil arthropod *Folsomia candida* (Collembola, Isotomidae). *F. candida* was reared in petri dishes at room temperature (c. 19), with dry yeast provided as a food resource. Although *F. candida* can survive in drought conditions for short periods by temporarily changing their physiological response (Fountain and Hopkin 2005), humidity is essential to their lifecycle (Waagner et al. 2011). Laboratory studies have shown that both the survival rate and egg production of *F. candida* was decreased when air humidity reduced from 100 to 96% RH (Hilligsoe and Holmstrup 2003, Waagner et al. 2011). *F. candida* eggs are more sensitive to drought and will perish if relative humidity below 98.7% (Holmstrup 2019).

Experimental landscapes

The 3D printed experimental arenas were made from PLA plastic and consisted of four habitats patches (circular: $c \approx 7$ cm in diameter and 1.5cm in height) connected by four corridors ($c \approx 28$ cm in length and 1cm in width) in a square (2x2) configuration, with each habitat patch connected by two corridors. Both habitat patches and corridors were filled with a mixture of plaster of Paris and black dye ($c \approx 0.5$ cm in thickness). Plaster of Paris acts as a substrate for the Collembola to live on which keeps moisture, whilst the black dye makes Collembola more visible for counting (Li et al. 2021). To avoid moisture wicking between the different components of the landscapes (patches and corridors), plastic baffles were printed allowing the moisture of the corridors to be manipulated separately to the moisture of the patches (Fig. 1a).

As Collembola are delicate and not easy to handle, they were inoculated into the four patches of each landscape by tapping individuals (mean \pm SD = 423 ± 317) into each mesocosm. During the experimental set up a potential confounding effect was accidentally introduced whereby microcosms were not randomly assigned to treatment after introducing the Collembola. This may have caused systemic differences in population level responses to treatments (Fig. 2), which we have attempted to account for by including microcosm as a random effect in the statistical models. Thus, food (dry dead yeast) was added to each patch each week (7 ± 2 mg mean \pm SD, $n=30$) throughout the experiment, and thus food was not a limiting factor to growth. Collembola were reared in the microcosms for three weeks prior the start of the treatments to allow populations to stabilise, with 2ml water and 7mg of food added each week to each patch. Clear lids were used to cover the microcosms and stop them drying out too quickly, and all microcosms were placed in dark rearing room to minimise light exposure.

Treatments

We used a fully factorial experiment to investigate the interactive effects of corridor quality with drought severity and the number of drought patches across landscape on the persistence of metapopulations. In the good corridor quality treatment, corridors had 2ml of water added each week to keep them moist (Li et al. 2021), whilst in the poor corridor quality treatment no water was added to the corridors. For each corridor quality treatment (i.e., good or poor), we manipulated drought in two different ways: changing the rate at which the moisture content of patches declined (i.e., drought severity), and the number of patches simultaneously experiencing drought (i.e., number of drought patches). Severe drought was created by reducing the 2ml of water added to each patch by 0.4ml water per week, whilst weak drought was simulated by reducing the 2ml by 0.2ml water per week (Fig. 1b). In addition, a number of patches were also randomly selected to receive no water at all in any given week, and the number impact in this was increased through time (the number of drought patches treatment). The number of patches which did not receive any water was generated by drawing a number (from 0 to 4) from a binomial distribution with the probability increasing from 0 to 1 at either 0.2 per week (i.e., fast increase) or 0.1 per week (i.e., slow increase) (Fig. 1b). This was done for each replicate landscape, and the location of patches impacted by this was randomized for each landscape. We also implemented a constant (control) treatment for each corridor quality group (i.e., good or poor) where 2ml water were constantly added to all the patches each week. This gave us in total two levels of corridor quality (good vs. poor), two levels of drought severity (severe vs. weak), and two levels of increase in number of drought patches (fast vs. slow), and one control group (no change in water through time), with each treatment combination replicated 6 times for a total of 60 replicates.

Population monitoring

Populations in the landscapes were monitored by taking three photos in quick succession of each habitat patch once every week. These pictures were then used to count individuals within each patch using Fiji software (Schindelin et al. 2012), a background subtraction method to determine which individuals are alive by comparing which have moved between the three photos (Mallard et al. 2013). Due to limitation in the quality of the photos taken we were only able to count individuals larger than 0.2mm in length, equal approximately to the size of individuals at eclosion (Johnson and Wellington 1983).

Data analysis

All the statistics were conducted in R (v4.0.2, RCoreTeam 2022). We assessed how corridor quality, drought severity, and number of drought patches influence the persistence ability of metapopulations in three ways. First, we used a generalized linear model (GLM) with a log-link gaussian error to test how those factors influence the time of population extinction. The time of population extinction was defined as the midpoint between the last week which individuals were observed alive in at least one of the four patches of a landscape, and the first time no individuals were observed as being alive. Only three microcosms were alive at the end of experiment (week 16, Fig. 2), but no individuals were observed alive the week after that. Experimental factors (i.e., corridor quality, drought severity, number of drought patches) and all their two-way interactions were included as explanatory variables. As populations were stable and not observed any extinctions until the end of the experiment (Fig. 2), two constant treatments were removed from further analysis.

Second, we used a generalized linear mixed effect model (GLMM) with a zero-inflated negative binomial distribution to investigate how corridor quality, drought severity, and number of drought patches influence the variability of abundance among patches through time. The variability of abundance among patches was defined as the standard deviation of abundances between the four habitat patches. Microcosm identity was included as a random effect to account for the potential differences between microcosms including their starting density. We included time, corridor quality, drought severity, number of drought patches, and their interactions as fixed effects. Of particular interest was how experimental factors (i.e., corridor quality, drought severity, number of drought patches) and time interactively affect the changes in variability, thus we also include their two-way interactions in the fixed effect. Time and experimental factors (i.e., corridor quality, drought severity, number of drought patches) were included as a zero-inflation parameter to account for the overdispersion of zero counts after extinction occurred. Data collected before drought treatment started (i.e., from week 1 to 3) was excluded from model fitting. The model was fitted using ‘glmmTMB’ package (Magnusson et al. 2017).

Finally, we used nonlinear regression curves with a three-parameter logistic function to fit the changes in total population abundance in each habitat network over time. The model was specified as $Y = d / (1 + \exp(-b * (X - e)))$ where Y was total abundance and X was time; d the high asymptote, b the maximum slope and e the time at the maximum slope, were all estimated by models. This is a three-parameter logistic function, and we chose this model due to its simplicity and utility (Kingsland 1982). Models were fitted using ‘drc’ package (Ritz et al. 2015). To explore the effect of treatments on the maximum rate of population change, we extracted the estimated value of b in each model and compared across treatments (Fig. S1). We used a GLM with a gaussian distribution to fit the log-transformed data, where corridor quality, drought severity, number of drought patches, and their two-way interactions was included as predictors.

Results

As expected, drought severity negatively affected the time to population extinction (Table 1, Fig. 3). The number of the patches affected by drought, however, had no effect (Table 1). Corridor quality positively affected the time of population extinction (Table 1), indicating that populations persisted longer in habitats connected by good quality corridors. There was no effect of any of the two-way interactions of treatments on the time of population extinction (Table 1).

Time negatively affected the variability of patch abundance (Table 2), suggesting an overall decrease in variability over time (Fig. 4). The variability of patch abundance was negatively affected by corridor quality, with higher variability found in landscapes connected with poor quality corridors. However, this was not affected by drought severity and number of drought patches (Table 2). There were significant interactions between time and corridor quality, and between time and drought severity (Table 2), suggesting that the effect of corridor quality, as well as drought severity, was largely time dependent. Interestingly, the different changes in variability over time between good and poor corridor quality suggest a contrasting response of populations to stressors due different levels of connectivity. In poor corridor quality, the rate of decrease in variability of patch abundance aggravated as drought continuedly stressed populations, whilst in good corridor quality the rate of decrease in variability eased (Fig. 4). There were no significant interactions between other two-way factors (Table 2).

Corridor quality negatively affected the maximum rate of population decline, with their declining rate being slower in good than poor corridor quality treatment. Surprisingly, increased number of drought patches negatively affected the rate of population decline, but drought severity had no effect (Table 3, Fig. 5). Corridor quality positively interacted with number of drought patches (Table 3). There were no effects of other two-way interactions on the maximum rate of population decline (Table 3).

Discussion

Our results show that, in our experimental microcosms, increased connectivity can buffer a population from extinction caused by drought. Specifically, habitats connected by good quality corridors, not only enabled populations to persist longer when they are threatened by drought severity, but slowed down the rate at which the number of patches across landscapes affected by drought decreased the populations. Surprisingly, connectivity differently affected the survival of populations in each individual patch, as the variability of patch abundance increased or slightly decrease then followed by a sudden decrease in the habitats connected by poor quality corridors, whilst it constantly decreased in the good quality corridors. In what follows, we first discuss the limitations of our approach, and then discuss the results in the context of the literature.

There are two main limitations to our approach. The first is that we did not count individuals in the corridors, as corridors can, potentially at least, provide extra habitats and serve as temporal refugia for species when stressed (Eversham and Telfer 1994). The aim of the work was to investigate how patchy populations response to environmental stressors, thus the individuals dispersing in corridors are largely ignored. The second is the potential confounding effect introduced the set up of the experiment which may explain some of the observed patterns in the abundance dynamics between treatments (Fig 2). This may be due to systematic differences in the body size distributions of the populations in different treatments, however the extinction dynamics largely conform to the expected patterns.

Species are expected to seek new habitats when natal habitats deteriorate. Field studies showed that Collembola have a high dispersal ability for new habitats when experiencing dry conditions (e.g., Ferrin et al. 2022). Consequently, increasing movement between habitats may save populations from local extinction when patches experience inhospitable environmental conditions. Our previous work showed that Collembola were more likely to colonise new habitats connected by good quality corridors, thereby increasing population growth rate in the colonised patches (Li et al. 2021). In this regard, corridor quality corridors may increase their probability of survival by facilitating movements and avoiding dry habitats. Collectively, we demonstrated that good quality corridors reduced the rate of population decline and increased time before extinction caused by drought extremes, highlighting the importance of connectivity in persisting populations in the face of climate change. This not only agrees with previous studies which show that increasing connectivity using corridors can increase the persistence of metapopulations (Gonzalez et al. 1998, Swart and Lawes 1996), but proves their ability to slow down extinction when species are exposed to disastrous environmental conditions. Our results suggest that increasing spatial connectivity across a landscape can to some extent mitigate the negative impact of climatic extremes on populations.

The most striking results were that the variability of patch abundance was negatively related with increased corridor quality, suggesting that connectivity can play an important role in shaping the viability of patchy populations. Thus, when corridor quality was poor, Collembola were constrained in patches as their dispersal ability was limited. Intriguingly, this implies that when connectivity is good the increased migration of individuals around the landscape could put increased pressure on habitats to support large population sizes, increasing the impacts of density dependence if such patterns persist in the long-term. Conversely, individuals being stuck in a patch could cause uneven survival rates among patches when drought extremes occur unpredictably. In such settings, local extinctions were more likely to occur when some patches were turned into ecological traps due to environmental change (Hale and Swearer 2016), thereby increasing the variability of patch abundance in habitats with poor habitat connectance. Similar findings have been previously reported in freshwater systems where drought disrupted the connectivity of habitat pools for some fish species (e.g., Vander Vorste et al. 2020). Furthermore, the changes in variability of patch abundance over time indicates a contrasting pattern of stressed populations towards extinction between habitats with good

and poor connectivity. Specifically, a constant decrease of the variability found in well-connected populations indicates that the density of population in each patch became uniform when experiencing stress, whilst a large variability found in poor connected populations demonstrated an increasing risk of local extinction because of loss of connectivity. Our results suggest that the variability of patch abundance may be a good predictor of population status and monitoring how it changes over time might provide a useful guide to evaluate landscape connectivity for species.

Drought is a climatic extreme which has serious consequences for the persistence of metapopulations, seen here as an increasing drought severity significantly reducing the time that population persisted and increasing the rate of population decline, a phenomenon which is consistent with the prediction that severer drought would cause higher speed of extinction (Cady et al. 2019, Cayuela et al. 2016). Increasing the severity of drought is more likely to cause a strong effect of desiccation, causing a high rate of mortality when reaching species' limits to drought. Collembola are well adapted in humid soil environments and need to absorb water vapor to over their entire life cycles (Bayley and Holmstrup 1999). Some essential life stages such as reproduction cycles and egg incubation in Collembola are highly depended on moisture levels (Holmstrup 2019, Waagner et al. 2011). Meanwhile, young individuals of Collembola are more vulnerable to desiccation than old (Hilligsoe and Holmstrup 2003), increasing drought severity are more likely to reduce the fitness of young adults and cause a further loss of fecundity. This may explain the extinction event occurred at the end of our experiment, and the extinction happens faster with increased severity. Indeed, extreme environmental stressors such as drought has been shown shaping the population dynamics and persistence of many species (e.g., Johansson et al. 2020).

The amount of the favourable habitats within a landscape has been shown to be important for maintaining the persistence of populations (Dytham 1995, Meli et al. 2014). Surprisingly, we found that increasing the number of patches affected by drought at different speeds only negatively affect the maximum rate of population decline, rather than the timing of extinctions, which may suggest a tipping point for environmental conditions as a result of increased drought habitats destabilising populations. The reasons underlying this pattern are largely unexplored though. One possible explanation is that Collembola were able to accumulate sugar and polyols when experiencing dry conditions, temporarily prolonging their survival from dehydration (Fountain and Hopkin 2005, Waagner et al. 2012). Hence, it is possible that individuals living in a habitat patch under drought manipulation (i.e., no water added for a week in our case) might not experience an immediate local extinction due to the accumulation of polyols and sugars, though drought was shown suppressing the viability of populations based on our results (Fig. 2). Adjusting their body conditions may allow them to temporarily survive over a short drought period, however, it may also contribute to a fast decline when the environmental conditions reach to tipping points (Dai et al. 2012). More empirical evidence is needed to examine how increased environmental stress, associated with tipping points, impacts the resilience of spatially structured populations.

In summary, our analyses add to the growing literature describing how increasing connectivity among habitats can buffer metapopulations against population decline and extinction. However, we also show that increased connectivity may increase the variability of populations between patches in a landscape, as individuals can move more easily into patches with more favourable conditions, potentially increasing the effects of density dependence in these highly utilised patches. As habitat fragmentation creates a mosaic of landscapes hosting a variety of spatially structured populations, maintaining good spatial connectivity allows species to move out the dangerous area, and/or allows conservation actions to be taken to avoid mass extinctions when facing extreme climatic events. Ultimately, our work highlights the importance of habitat connectivity in maintaining population viability in the face of climate change. Field evidence is needed to better understand the role of habitat connectivity in persisting populations.

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Author contribution

DL and CC designed the experiment. DL conducted the experiment and analysed data. DL led the writing of the manuscript with suggestion from CC and JM. All co-authors contributed critically to the drafts and gave final approval for publication.

Conflict of interests

The authors declare no conflict of interests.

Data availability

Data is currently available in GitHub repository for peer review (<https://github.com/Dongboli/experimental-data.git>) but will make it available in Dryad once published.

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Table 1 The effect of corridor quality, drought severity, and the number of patches affected by drought on the time of population extinction.

	Estimate	Stand Error	t value	<i>p</i>	
Intercept	2.532	0.038	67.258	<0.001	***
Corridor quality	0.149	0.047	3.163	0.003	**
Drought severity	-0.173	0.053	-3.289	0.002	**
Number of drought patches (NP)	-0.012	0.050	-0.249	0.805	
Corridor quality: drought severity	-0.016	0.058	-0.276	0.784	
Corridor quality: NP	-0.061	0.058	-1.050	0.300	
Drought severity: NP	0.060	0.058	1.026	0.311	

Significant levels: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘’

Table 2 The effect of corridor quality, drought severity, and the number of habitats affected by drought on the variability of patch abundance.

	Estimate	Stand error	z value	<i>p</i>	
(intercept)	4.963	0.242	20.546	<0.001	***
Time	-0.194	0.024	-8.191	<0.001	***
Corridor quality	-0.534	0.272	-1.961	0.050	.
Drought severity	-0.223	0.283	-0.788	0.430	
Number of drought patches (NP)	-0.271	0.273	-0.991	0.321	
Corridor quality: Drought severity	0.049	0.249	0.198	0.843	
Drought severity: NP	0.128	0.248	0.515	0.606	
Drought severity: NP	-0.183	0.249	-0.733	0.463	
Time: Corridor quality	0.166	0.022	7.382	<0.001	***
Time: Drought severity	0.078	0.023	3.384	<0.001	***
Time: NP	0.018	0.022	0.814	0.415	

Significant levels: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1

Table 3 The effect of corridor quality, drought severity, and the number of habitats affected by droughts on the maximum rate of population decline.

	Estimate	Standard Error	z value	<i>p</i>	
Intercept	1.072	0.207	5.187	<0.001	***
Corridor quality	-1.767	0.271	-6.534	<0.001	***
Drought severity	0.314	0.271	1.161	0.252	
Number of drought patches (NP)	-0.620	0.271	-2.291	0.027	*
Corridor quality: Drought severity	-0.297	0.312	-0.951	0.347	
Corridor quality: NP	0.781	0.312	2.501	0.017	*
Drought severity: NP	0.499	0.312	1.596	0.118	.

Significant levels: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1

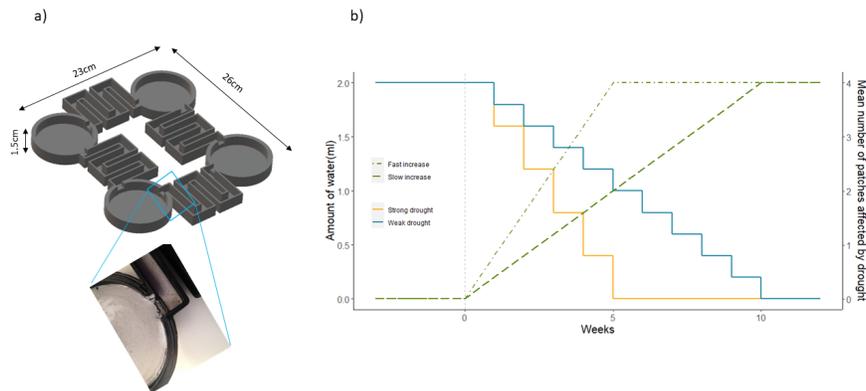


Figure 1 a) The ‘four patch’ microcosm; inset shows a mesocosm complete with a Plaster of Paris fill and the patch-corridor plastic buffer (which prevents moisture moving between the two via the Plaster of Paris); b) The quantity of water added to the microcosms over time and the ensuing number of patches affected by drought. The microcosms experienced drought severity and the number of patches affect by drought at different rates, after treatments start at week 0 (grey dashed line). The number of dry patches in the fast increase in number of drought patches (green dot-dashed line) treatment reaches 4 at week 5, whilst in the slow (green long-dash line) reaches 4 at week 10. Strong drought is created by reducing the amount of water 0.4ml per week (yellow solid line), whilst weak drought is created by reducing water at 0.2ml per week (blue solid line).

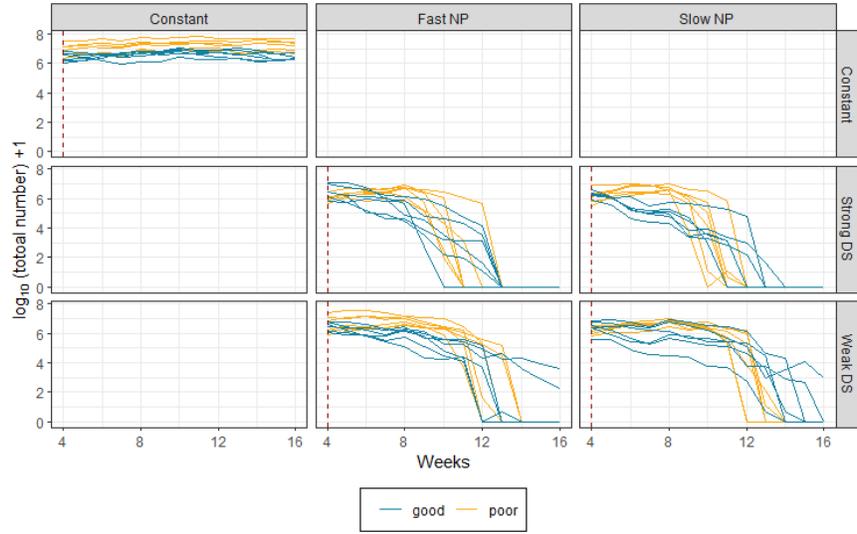


Figure 2 . The total number of individuals in each microcosm changes over time, from the beginning of drought treatment (week 4) to the end of experiment (week 16). Data was log (x+1) transformed; number of replicates for each treatment N=6. Stable lines in two constant treatments indicate that populations were not stressed and increased constantly throughout the experiment. The potential confounding effect mentioned in the methods section can be seen in the differing starting populations across the treatments.

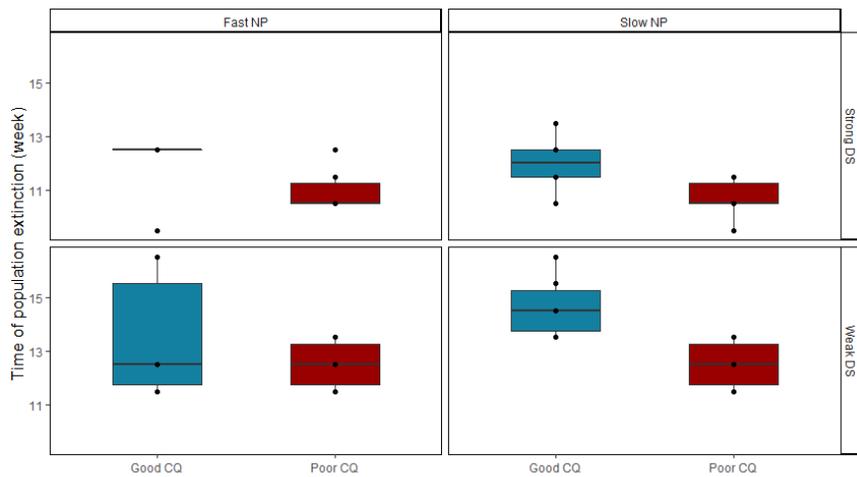


Figure 3 . The effect of corridor quality (CQ), drought severity (DS), and the number of habitats affected by drought (NP) on the time of population extinction. Data is shown as black dots. Blue boxes show good CQ treatment and red boxes show poor CQ treatment. Strong vs. weak DS, fast vs. slow increase in NP are shown in different facets. The maximum and minimum limits are shown by the end of whiskers, and the first and third quartiles of responses are shown by the end of boxplots. The lines inside the boxplots represent the medians. Number of observations $N = 6$.

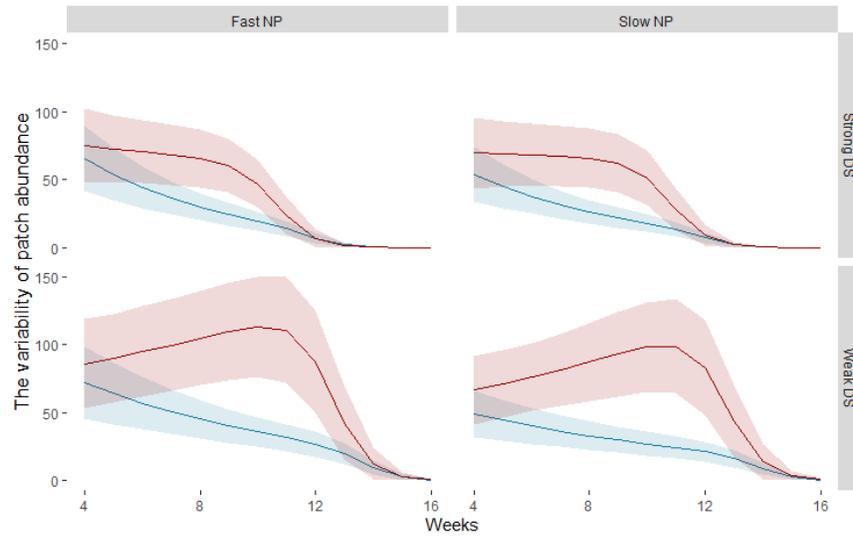


Figure 4 Results from zero-inflated GLMM with a negative binomial distribution show the effect of corridor quality (CQ), interacts with drought severity (DS) and the number of patches affected by drought (NP) on the variability of patch abundance over time. Good CQ is shown in red and poor CQ is shown in blue, with 95% confidence intervals (CI s).

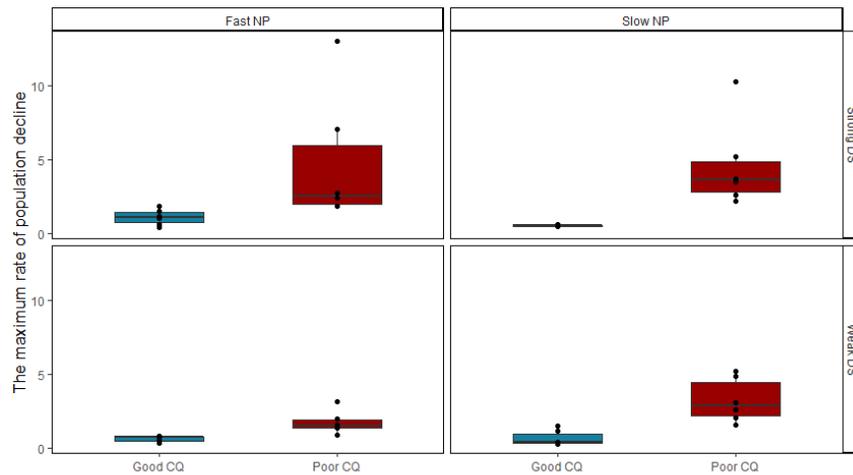


Figure 5 The effect of corridor quality (CQ), drought severity (DS), and the number of patches affected by drought (NP) on the maximum rate of population decline. For annotations, see the legend for Figure 3.