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ORIGINAL ARTICLE

Soil Biota Adversely Affect the Resistance and Recovery of Plant Communities Subjected to Drought

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Abstract

Climate change predictions indicate that summer droughts will become more severe and frequent. Yet, the impact of soil communities on the response of plant communities to drought remains unclear. Here, we report the results of a novel field experiment, in which we manipulated soil communities by adding soil inocula originating from different successional stages of coastal dune ecosystems to a plant community established from seeds on bare dune sand. We tested if and how the added soil biota from later-successional ecosystems influenced the sensitivity (resistance and recovery) of plant communities to drought. In contrast to our expectations, soil biota from later-successional soil inocula did not improve the resistance and recovery of plant communities subjected to drought. Instead, inoculation with soil biota from later successional stages reduced the post-drought recovery of plant communities, suggesting that competition for limited nutrients between plant community and soil biota may exacerbate the post-drought recovery of plant communities. Moreover, soil pathogens present in later-successional soil inocula may have impeded plant growth after drought. Soil inocula had differential impacts on the drought sensitivity of specific plant functional groups and individual species. However, the sensitivity of individual species and functional groups to drought was idiosyncratic and did not explain the overall composition of the plant community. Based on the field experimental evidence, our results highlight the adverse role soil biota can play on plant community responses to environmental stresses. These outcomes indicate that impacts of soil biota on the stability of plant communities subjected to drought are highly context-dependent and suggest that in some cases the soil biota activity can even destabilize plant community biomass responses to drought.

Key words: plant-soil interactions; water availability; succession; sensitivity; resistance; recovery.

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Highlights

- Soil inocula from late-successional stages did not improve the stability of a plant community subjected to drought
- Different soil inocula had differential influences on the drought sensitivity of plant functional groups and individual species
- The impacts of the complexity of soil biota on the stability of plant communities are highly context-dependent

Introduction

Climate change is progressing at an unprecedented pace, causing more frequent and prolonged periods of summer drought in Europe (Stocker 2014). This raises concerns about the capacity of ecosystems to withstand the stress caused by these events. Summer droughts have already led to significant declines in plant survival and growth across Europe (Ciais and others 2005; Schuldt and others 2020). Recent studies suggest that soil communities can play a fundamental role in mediating ecosystem responses to drought, through their impacts on plant communities (van der Putten and others 2016; Jia and others 2021). Yet, empirical field-based evidence of the nature and mechanisms of soil community impacts on the stability of plant communities under drought stress is scarce.

The effects of soil taxa on the drought response of plant communities can be positive, neutral, and negative depending on the structure and composition of the soil communities involved (Kulmatiski and others 2008; Van der Putten and others 2013). For example, the presence of soil mutualists, such as arbuscular mycorrhizal fungi (AMF), can improve plant fitness and the ability to withstand drought through enhancing water and nutrient acquisition (Augé 2001; Mariotte and others 2017; Wu 2017) and therewith maintain and stabilize ecosystem functioning subjected to drought (Jia and others 2021), whereas fungal pathogens may exacerbate plant vulnerability to drought (Kaisermann and others 2017). Hence, the composition of the soil community, especially the presence of soil mutualists and pathogens could play a crucial role in influencing the response of plant communities to drought.

The composition of soil communities is dynamic and changes along succession (Carbajo and others 2011). For example, shifts in the abundance and composition of soil mutualists, such as mycorrhizal fungi, occur from non-mycorrhizal to (mostly arbuscular) mycorrhizal during primary succession (Read 1994; Dickie and others 2013). Additionally, predominant life-history strategies of soil communities have been observed to shift during secondary succession in abandoned land (Hannula and others 2017). For instance, in ex-arable fields, the composition of active fungal communities was reported to shift from fast-growing and pathogenic fungal species to slower-growing fungal species (Hannula and others 2017). In particular, the abundance of saprotrophytic and mycorrhizal fungi tend to increase after land abandonment (Piotrowski and Rillig 2008). Given the important role of some soil microbes, like AM fungi, in mediating plant drought responses (Kaisermann and others 2017; Jia and others 2021), shifts in soil community along with succession are likely to affect plant growth and fitness under stress. Such shifts in soil community composition along with succession are typically not accounted for in studies on plant community stability and recovery. Instead, most studies attributed increases in stability to the dynamics of aboveground plant diversity (Kahmen and others 2005; Van Ruijven and Berendse 2010). The potential role of soil communities in this phenomenon thus remains less understood.

Given that above- and belowground communities are in constant interaction with each other (Van Der Heijden and others 2008; Wubs and others 2019), an explicit test of the direct effects of soil communities on drought responses of plant communities is a challenging task, which requires explicit manipulation of distinct soil communities with the same plant communities. Field experiments demonstrated that soil inoculation from later-successional stages can change the soil community composition (Wubs and others 2016, 2018) and promote succession by suppressing ruderals and promoting the growth of the late-successional species (Kardol and others 2006; Carbajo and others 2011). These successful applications suggest that soil inoculation could be a promising way to examine the role of shifts in soil communities from different successional stages on drought responses of plant communities.

In this study, we experimentally investigated the impact of distinct soil communities on the sensitivity of dune plant community to drought. We manipulated soil communities by adding soil inocula originating from different successional stages of the dune ecosystems to a newly established dune plant community. We hypothesized that plant communities growing in soils inoculated with inocula originating from later-successional

soils will be more resistant to drought and have a faster recovery after drought than those inoculated with earlier successional communities. Half of soil inocula was sterilized to allow separate testing of the effects of abiotic conditions on plant drought sensitivity vs the effects of soil biota per se. We expected that plants grown in plots with living, i.e., non-sterilized soil inocula would show higher stability than those growing with sterile inocula.

Methods

Experimental Design

The experiment was conducted in a bare sandy dune area, surrounded by mixed forest and grassland in Meijendel Nature Reserve, Wassenaar, The Netherlands (52°07′50.4′′N; 4°20′27.6′′E). This site was abandoned after being occupied by a private building, demolished several years before the start of our experiment. The experimental area was thoroughly cleaned from vegetation and associated organic matter, so that only bare sand remained. We opted to conduct the experiment in bare sandy dunes with inherent low soil fertility, because a large stock of soil nutrients would likely support a large native microbial community (Jiang and others 2009; Lozano and others 2014), reducing the effect of soil inoculation. The area was fenced to avoid disturbance by large animals. We collected soil inocula from three types of donor ecosystems in Meijendel Nature Reserve: primary dune vegetation, dune grassland and dune forest. This selection of donor ecosystem types provided us with soil communities developed under highly contrasting conditions, and therefore leading to differences in composition. We employed the ''Independent Soil Sampling'' (ISS) approach (Gundale and others 2017), to enable replication of inocula origin, i.e., for each donor ecosystem type, four distinct donor sites were selected and applied (Figure S1). To manipulate soil community composition, we imposed following treatments: (1) Plots were inoculated with soil inocula originating from different successional stages of dune ecosystems. Twenty-four plots were inoculated with soil inocula originating from primary dune vegetation, 24 plots were inoculated with soil inocula originating from dune grassland and 24 plots were inoculated with soil inocula originating from dune forest (Table S1). (2) Half of the experimental plots where soil inocula was added was treated with sterilized soil inocula where the resident soil community was eliminated through gamma radiation (> 25 KGray gamma radiation, Isotron, Ede, the Netherlands), and the other half was treated with living soil inocula.

The initial design of our experiment included one more treatment: the addition of ectomycorrhizal fungi (EMF) in a full factorial mode with respect to the other two treatments. However, in the year following the establishment of the experiment, a molecular analysis did not detect any of the added EMF species (*Pisolithus arrhizus*; *Cenococcum geophilum*; *Amanita muscaria*; *Hebeloma crustuliniforme*; *Scleroderma sp.*) in the experimental plots. Furthermore, we also found that EMF addition treatment had no impact on aboveground and belowground plant biomass, neither did it affect the soil microbial abundances nor community composition. Therefore, we concluded that the EMF addition treatment failed. Thus, in the current work we opted to ignore this treatment, and used the EMF-treated plots as additional replicates of other treatments. The ultimate replication of our experiment was 12 plots for each combination of soil inocula origin and sterilization treatment.

To speed up the development of a dune plant community, 30 plant species typical for the area were sown in all plots. Twenty-six herbaceous species and two woody perennial shrubs were obtained from Cruydt Hoeck, a company selling seeds of wild plants (www.cruydthoeck.nl). Seeds of two tree species *Betula pubescens* and *Quercus cerris* were purchased at TreeSeeds company (www.treeseeds.com). The complete list of sown plants can be found in Table S2. Each combination of soil inoculum origin and sterilization treatment was replicated 12 times (Table S1). We included two types of control plots. In the control plots of the first type no soil inocula were added, but seeds were added. There were 24 replicates of these control plots. The control plots of the other type entailed no inocula and no seed additions. These plots were used for overall monitoring purposes and not included into the current analysis.

The experiment was established in May 2018. All plots (2 m × 2 m) were surrounded by a plastic sheet dug into the soil to a depth of 40 cm to minimize the interaction between added soil biota and surrounding soil biota. Plots were separated from each other by a bare area of 2 m. Plots were prepared according to the following procedure. First, in each plot, 10 cm of soil was removed. Then, ectomycorrhizal inoculum was added and about 8 cm of the soil previously removed from the same plot was put back into the plot and a seed mixture of 30 plant species was sown in the plot. Subsequently, in the plots subjected to a sterile soil inoculum treatment, 2 cm of sterilized soil was

spread on the surface of each plot. In non-sterile plots, a layer of sterile soil (about 1.5 cm per plot) was added first and an additional layer of live soil (about 0.5 cm per plot) was spread on top. In treatments without any soil inoculum (control), 2 cm of the originally removed soil was put back on the surface.

Drought Event

Generally, the growing season in dune in Netherlands starts at April–May and the vegetation reaches maximum biomass during August (Schaminée and others 1996; Rodríguez-Echeverría and others 2008). In 2020, a severe drought occurred during April–May. The monthly precipitation from April to May of 2020 decreased by 67% and 72% compared to the long-term average (30 years). The precipitation turned back to normal in June. The seasonal precipitation pattern during the experimental period is shown in Figure S2.

Data Collection

At the end of the drought (June 10, 2020), the absolute percentage cover of each species was estimated visually within each plot (2 × 2 m). The newly dead plant cover (that is, cover of plants dead in the current year) was also recorded. On September 10, 2020, we recorded the plant cover again as the cover after drought recovery. To calculate the cover of different functional groups, all plant species found in the plots during the vegetation surveys were divided into three functional groups: grasses, forbs and legumes (Table S3).

Soil samples collected on September 10 from all plots were sieved (2 mm mesh size). A subsample of soil from each plot was weighted to measure total C and N by a Flash EA 1112 elemental analyzer (Thermo Scientific, Rodana, Italy). Mineral N was extracted by shaking 3 g dry soil in 30 mL 0.01 M $CaCl_2$ solution for 2 h at 250 rpm. The suspensions were centrifuged for 10 min at 300 rpm. NO_3^- -N and NH_4^+ -N content were determined in the supernatant using a Skalar Continuous Flow Analyzer. The multi elements of soil were determined on the ICP-OES with 130μL 69% HNO_3. The complete results of soil chemistry can be found in Table S4.

Data Analysis

We quantified the vegetation sensitivity to drought as resistance and recovery (Mariotte and others 2013). Resistance, which is the ability to withstand drought influence, was estimated as the proportion of cover of plants that survived the drought.

Resistance = $\text{Living\_Cover}_{\text{End of drought}}$/ ($\text{Living\_Cover}_{\text{End of drought}}$ + $\text{Dead\_Cover}_{\text{End of drought}}$).

Recovery is the ability of ecosystem to recover after disturbance. The recovery was calculated with two different baselines (Ingrisch and Bahn 2018). Baseline-normalized recovery (BN-recovery) was defined as the ratio of cover after recovery to the living cover at the end of the drought.

BN-recovery = $\text{Living\_Cover}_{\text{End of recovery}}$/ $\text{Living\_Cover}_{\text{End of drought}}$.

Because some plants might be alive even though the aboveground part was dry at the end of drought, and this may contribute to the recovery after drought, we introduced another recovery index, Impact-normalized recovery (IN-Recovery): the ratio of cover after recovery to the sum of dead and living cover at the end of drought.

IN-Recovery = $\text{Living\_Cover}_{\text{End of recovery}}$/ ($\text{Living\_Cover}_{\text{End of drought}}$ + $\text{Dead\_Cover}_{\text{End of drought}}$).

All indices were calculated for the whole plant community as well as for individual plant functional groups.

To enable application of a full factorial analysis, all 24 control plots were a-priori randomly assigned as controls associated with living or sterile soil inocula. A two-way ANOVA was run to test the effects of different types of soil inocula and soil sterilization treatment on the resistance, BN-recovery and IN-recovery of the plant community and functional groups. A one-way ANOVA was conducted across the soil inocula types including the control treatment, followed by a post-hoc test. The post-hoc test was performed using the lsmeans package, with the Turkey method for *p*-value adjustment (Lenth 2016). The effect size of treatment was estimated using the function ''eta_squared()''. Prior to statistical analysis, model assumptions of normality and homoscedasticity were checked on the model residuals (Kozak and Piepho 2018) and variables were transformed when necessary.

To examine whether the effects of the experimental treatments on the cover of individual species were consistent with the response patterns of plant functional groups during different periods, we conducted a Principal Response Curve analysis (PRC) using the ''prc'' function of the vegan 2.5–6 package (Oksanen and others 2013). PRC, also known as Partial Redundancy Analysis, is a multivariate technique for the assessment of experimental treatments on community composition over time (Van Den Brink and Ter Braak 1999) (Moser and others 2007). The principal compo-

nents of the treatments effects on individual species are plotted against time (Van Den Brink and Ter Braak 1999). Differences in plant species composition between soil treatments at the two sampling moments were visualized by a principal-coordinate analysis (PCoA) based on the Bray–Curtis dissimilarity using the vegan 2.5–6 package (Figure S3). All analyses were performed in *R* version 4.0.2 (R Core Team 2020).

Results

Impacts of Different Types of Soil Inocula and Soil Sterilization on the Resistance and Recovery of Plant Community

Soil inocula origin affected the plant community resistance to drought ($F_{3,86} = 3.17$, $p < 0.05$, $\eta^2 = 0.10$; Table 1) where the resistance of the plant community generally declined with the addition of soil inocula compared to non-inoculated control plots (Figure 1a). There was no effect of sterilization on resistance (Table 1).

Plant community BN-recovery (the ratio of cover after recovery to the living cover at the end of the drought) depended on soil inocula origin ($F_{3,86} = 10.44$, $p < 0.01$, $\eta^2 = 0.23$) and was highest in soil with forest inocula. Moreover, BM-recovery was on average higher in plots with sterile inocula than in plots with living inocula ($F_{3,86} = 5.77$, $p = 0.02$, $\eta^2 = 0.04$). The difference between the sterilization treatments, however, depended on the inoculum origin ($F_{3,86} = 3.97$, $p = 0.01$, $\eta^2 = 0.09$; Table 1) and was biggest for forest inocula (Figure 1b).

The IN-recovery of plant community (the ratio of plant cover after recovery to the sum of dead and living cover at the end of drought) was significantly affected by soil inocula origin ($F_{3,86} = 5.72$, $p < 0.01$, $\eta^2 = 0.16$; Table 1). Plant communities grown with forest soil inocula had a higher IN-recovery compared to the control (Figure 1c). Consistent with patterns for plant BN-recovery, community IN-recovery tended to be higher (although not significantly) in plots with sterile soil inocula than in those with living inocula (Figure 1c).

Impacts of Different Types of Soil Inocula and Soil Sterilization on Resistance and Recovery of Plant Functional Groups During Drought and Recovery

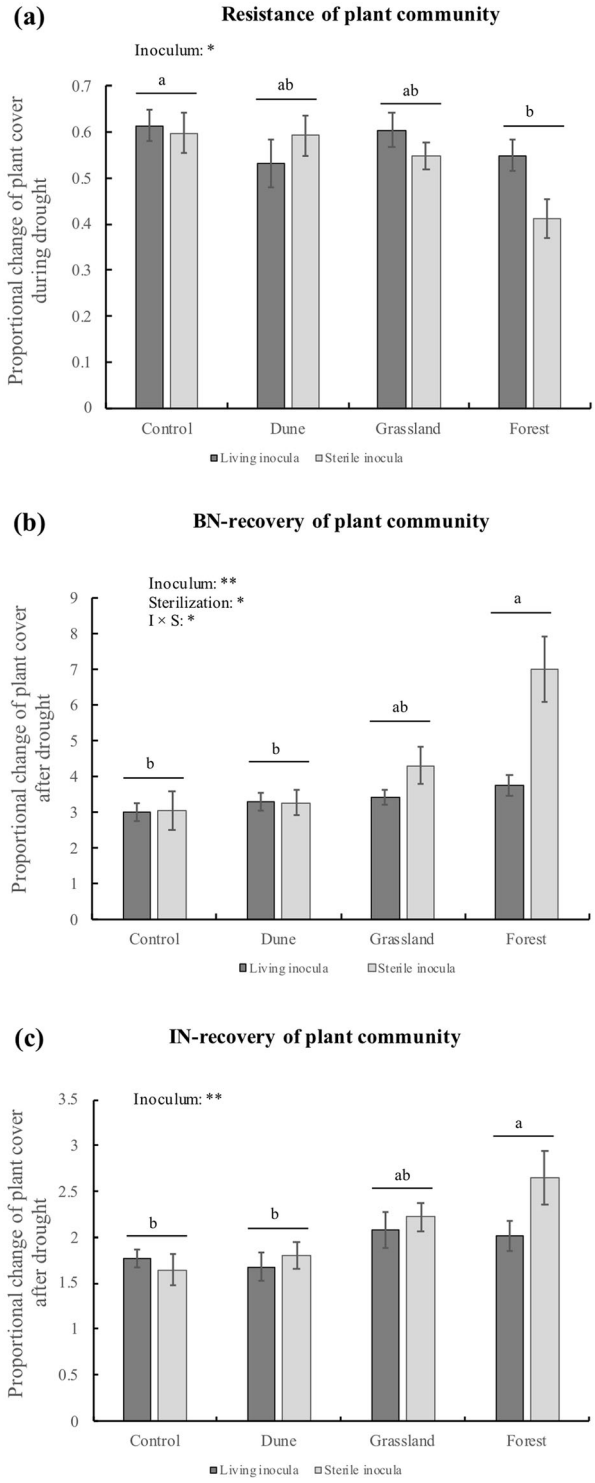
Soil treatments had different effects on the resistance of plant functional groups during drought, but the effect was treatment- and functional group-dependent (Table 2). The resistance of grasses depended on the interaction between soil inocula origin and sterilization treatment ($F_{3,86} = 4.39$, $p < 0.01$, $\eta^2 = 0.12$; Table 2). Resistance of grasses was higher when living inocula from dune forest were added, whereas sterile soil inocula significantly reduced the resistance of grasses (Figure 2a). Soil inoculation treatments had no significant influence on the recovery of grasses. Soil inoculation origin significantly influenced the drought resistance of legume species ($F_{3,83} = 3.65$, $p = 0.02$, $\eta^2 = 0.11$; Table 2). Legumes grown in plots with forest inocula had a lower resistance than with other inocula (Figure 2b). Similar to grasses, soil inoculation treatments did not influence the recovery of legume after drought.

Soil inocula origin and sterilization significantly influenced the resistance of forbs ($F_{3,86} = 14.89$, $p < 0.01$, $\eta^2 = 0.32$; $F_{3,86} = 5.36$, $p < 0.02$, $\eta^2 = 0.04$; Table 2). The resistance of forbs was generally lower in plots treated with soil inocula addition compared to control plots, and had the lowest resistance with forest inocula (Figure 2c). In addition, forbs grown in plots treated with sterile

Table 1. Effects of Different Types of Soil Inocula Origin (Inoculum, I), Soil Sterilization (Sterilization, S) on the Resistance, BN-recovery (Baseline-normalized recovery) and IN-recovery (Impact-normalized recovery) of the Dune Plant Community to Drought

	Variance								
	Inoculum			Sterilization			I × S		
	F	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Resistance	**3.49**	**0.02**	**0.10**	1.93	0.17	0.02	2.08	0.11	0.06
BN-Recovery	**10.44**	**< 0.01**	**0.23**	**5.77**	**0.02**	**0.04**	**3.97**	**0.01**	**0.09**
IN-Recovery	**5.72**	**< 0.01**	**0.16**	2.54	0.11	0.02	1.55	0.21	0.04

F, F-value; P, p-value; η^2, the effect size of treatment. Significant effects ($p < 0.05$) are presented in bold.



◀**Figure 1.** Effects of soil inocula origin and sterilization on plant community resistance **(A)**. Effects of soil inocula origin and sterilization on the BN-recovery of plant community (Baseline-normalized recovery, BN-recovery = Living_Cover $_{\text{End of recovery}}$ / Living_Cover $_{\text{End of drought}}$) **(B)**. Effects of soil inocula origin and sterilization on plant community IN-recovery (Impact-normalized recovery, IN-Recovery = Living_Cover $_{\text{End of recovery}}$/ (Living_Cover $_{\text{End of drought}}$ + Dead_Cover $_{\text{End of drought}}$) **(C)**. Different lowercase letters indicate significantly different effects of soil inocula types, as revealed by a one-way ANOVA on soil inocula types, including control, followed by a post-hoc test ($p < 0.05$). *$p < 0.05$, **$p < 0.01$. The absence of asterisks denotes no significant effects. The black bar indicates plots with living soil inocula, and the grey bar indicate plots with sterile soil inocula.

inocula had a lower resistance compared to those grown in plots treated with living inocula (Figure 2c). The BN-recovery of forbs was also significantly influenced by the different types of soil inocula origin ($F_{3,86} = 4.82$, $p < 0.01$, $\eta^2 = 0.13$; Table 2) and sterilization treatment ($F_{3,86} = 7.97$, $p < 0.01$, $\eta^2 = 0.07$; Table 2). The BN-recovery of forbs was higher when grown with forest soil inocula (Figure 1d). In addition, we also observed that forbs had higher BN-recovery when grown with sterile soil inocula than with living soil inocula. None of the treatments significantly affected IN-recovery of forbs (Table 2). Altogether, none of the soil treatments had any significant influence on the IN-recovery on any of the plant functional groups (Table 2).

Impacts of Different Types of Soil Inocula and Soil Sterilization on the Response of Individual Species During Drought and Recovery

The PRC analysis showed that 19.62% of the total variation in species composition was explained by the different time periods of analysis (Table 3) and 10.70% could be attributed to the soil treatments. The first canonical axis of the PRC captured a significant part (49.64%) of the variance explained by the treatments (Monte Carlo permutation test, 999 permutations, $p = 0.001$). During the different periods, there was large variation in the responses of species to the experimental treatments (Figure 3). For example, the cover of *A. vulneraria*, *H. pubescens* and *D. carota* showed a positive response to the soil inoculation treatments. In contrast, there were negative relationships between species, such as *E. repens*, *S. inaequidens* and *P. lanceolata*, and the

Table 2. Effects of Different Types of Soil Inocula Origin (Inoculum, I), Soil Sterilization (Sterilization, S) on the Resistance and Recovery of Plant Functional Groups to Drought

		Variance								
		Inoculum			Sterilization			I × S		
	Functional Groups	*F*	*P*	η^2	*F*	*P*	η^2	*F*	*P*	η^2
Resistance	**Grasses**	1.90	0.14	0.05	2.31	0.13	0.02	**4.39**	**< 0.01**	**0.12**
	Legumes	**3.65**	**0.02**	**0.11**	1.54	0.22	0.02	2.14	0.10	0.06
	Forbs	**14.89**	**< 0.01**	**0.32**	**5.36**	**0.02**	**0.04**	1.31	0.28	0.03
BN-Recovery	**Grasses**	0.26	0.85	0.01	2.74	0.10	0.03	1.97	0.13	0.06
	Legumes	0.21	0.89	0.01	3.33	0.07	0.05	0.72	0.55	0.03
	Forbs	**4.82**	**< 0.01**	**0.13**	**7.97**	**< 0.01**	**0.07**	1.12	0.34	0.03
IN-Recovery	**Grasses**	0.17	0.92	0.01	1.10	0.30	0.01	0.68	0.57	0.02
	Legumes	0.20	0.89	0.01	1.71	0.20	0.02	1.22	0.31	0.04
	Forbs	0.95	0.42	0.03	2.09	0.15	0.02	0.27	0.85	0.01

F F-value P p-value η^2*, the effect size of treatment. BN-recovery (Baseline-normalized recovery), IN-recovery (Impact-normalized recovery). Significant effects (p < 0.05) are presented in bold.*

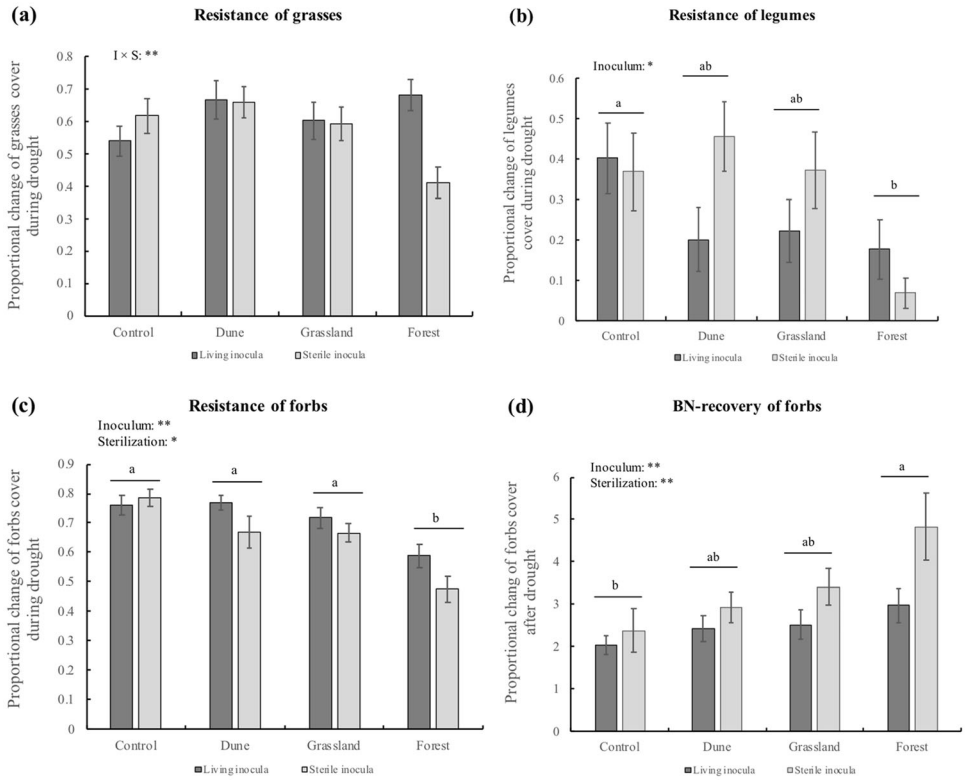


Figure 2. Interactive effects of soil inocula origin and sterilization on the resistance of grasses **(A)**, legumes **(B)** and forbs **(C),** and BN-recovery (Baseline-normalized recovery) of forbs **(D)**. Different lowercase letters indicate significantly different effects of soil inocula types, as revealed by a one-way ANOVA on soil inocula types, including control, followed by a post-hoc test ($p < 0.05$). *p < 0.05, **$p < 0.01$. The absence of asterisks denotes no significant effects. The black bar indicates plots with living soil inocula, and the grey bar indicate plots with sterile soil inocula.

Table 3. Statistics of the Principal Response Curve (PRC) Analysis

PRC-Statistics						
Monte Carlo permutation test on significance of the 1st canonical axis of the PRC				% of the total variance explained by		% of the variance explained treatment captured by the 1st canonical axis of the PRC
Eigenvalue	5.74	*p*-value	0.001	Time	Treatment	49.64
F-Ratio	13.26			19.62	10.70	

The PRC-Statistics show Eigenvalue, F-ratio and p-value of the Monte Carlo permutation test (999 permutations) on significance of the 1st canonical axis of the PRC and the explanatory content. Furthermore, the part of the total variance explained by time and by treatment and the part of the variance explained by treatment that is captured by the 1st canonical axis of the PRC is given.

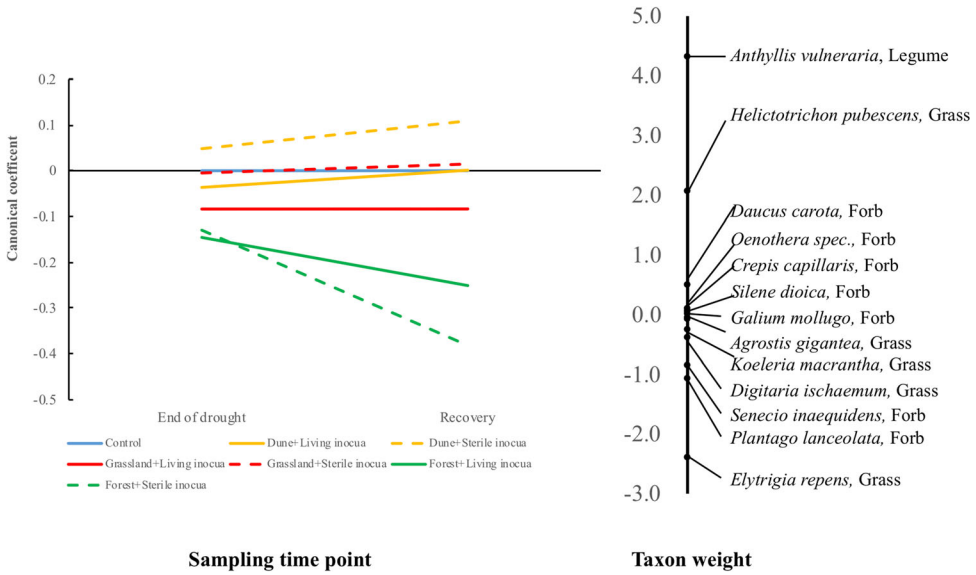


Figure 3. First component of the PRC, examining the impacts of soil treatments on individual plant species. The colored lines connect two sample points in the figure. The control treatment (no soil inocula), used as an internal reference. The species weights shown in the right part of the diagram represent the affinity of each species to the community response pattern shown in the diagram. For clarity, only species with total cover greater than 100 are shown.

treatments. This result indicates that under the same experimental treatments, plant species had different responses to drought due to the shifts in plant soil interactions. Overall, individual species exhibited a variety of responses to the soil treatments during different periods which is consistent with the response patterns found for the plant functional groups.

Discussion

Plant communities of later successional stages exhibit higher levels of stability to environmental disturbance (Hurd and others 1971; Howard and others 2020). The contribution of distinct mechanisms to this phenomenon and especially the role of soil biota community composition therein, so far, remained poorly understood. In this study, we experimentally investigated whether soil biota from later-successional stages of dune ecosystems influence the stability of sown early-successional plant communities when they were exposed to drought. A positive influence would suggest that additions of soil community could be used in nature restoration practices to promote establishment of target ecosystems (Wubs and others 2016) enhancing their resistance to environmental stresses.

In contrast to our expectations, soil biota from later successional stages did not improve the total

plant community responses to drought. We explain this negative effect by the fact that there were only few late-successional plant species (Table S3). Hence, there may be mismatches between soil biota from the inoculum and presence of associated plant species.

For plant communities grown in plots with forest soil inocula, the resistance of the plant community decreased less in non-sterilized plots (that is, subjected to living soil biota) compared to sterilized plots. Plant communities grown in plots with sterilized soil inocula, especially with sterile inocula originating from the dune forest, recovered faster (both BN-recovery and IN-recovery), suggesting that soil biota from later-successional soil inocula may impede plant post-drought recovery in dune ecosystems. The lowest recovery in plots with living inocula, particularly with later-successional (dune forest) inocula, could potentially be explained by increased densities of soil-borne pathogens (Kardol and others 2006). Soil pathogens themselves may have better recovery during drought events than other microbes, as they can adapt quickly to drought (Newton and others 2011). Thus, drought-resistant soil pathogens may have affected the resistance and recovery of primary-successional plant communities.

Nutrient competition between plant communities and soil communities may also exert effects on the responses of plant communities to drought. Our results contrast prior studies in which the addition of soil biota positively affected plant stability under drought through soil microbial symbionts (Prudent and others 2020; Yang and others 2021). However, because our study was conducted in an extremely nutrient-limited early-successional dune system (Table S4), competition for limited nutrients between plant and soil biota after drought may have outweighed the beneficial effects of mutualistic microorganisms, as soil biota sequester a large proportion of nutrients (Schimel and Bennett 2004; Liu and others 2020). This view is supported by our finding that plants grown in plots with sterile later-successional soil inocula had a higher recovery than those grown with living inocula. The living soil inocula from dune forest significantly reduced the recovery of the plant community (Figure 1b, c), further suggesting that there may be stronger nutrient competition between plant community and later-successional soil communities. Additionally, the results of higher resistance and recovery in plant community grown in plots with sterile forest soil inocula highlight the crucial role of soil nutrients in mediating plant drought responses (Gessler and others 2017; Mackie and others 2019).

The sensitivity of individual species and functional groups to drought was idiosyncratic and did not contribute to the drought responses of the plant community. For instance, sterile forest inocula promoted the recovery of plant communities as a whole and the functional group of forbs while it had no significant influence on legumes or grasses. Furthermore, the responses of plant species were distinct even within the same functional groups, such as *Helictotrichon pubescens* (grass) versus *Elytrigia repens* (grass), and *Dacus carota* (forbs) vs. *Plantago lanceolata* (forbs) (Figure 3). This suggests that the response pattern of the plant community as a whole was not underpinned by the concerted responses of functional groups. Instead, there might be compensation among the mixed interactions of the soil community and the different functional groups and plant species.

Such compensation pattern may also explain the difference in the recovery of plant functional groups (Table 2) versus the plant community (Table 1). We found that soil treatments significantly affected the recovery of plant community while they had less influence on the recovery of individual plant functional groups. This suggests that after drought all functional groups responded relatively similarly to soil treatments while the magnitude of the individual responses was low (see the non-significant p-values and low effect sizes in Table 2) and thus only detectable at the community level. In addition, the presence of added soil biota also significantly influenced the BN-recovery of plant community as a whole, whereas among functional groups only fobs showed similar response patterns. Overall, our findings suggest that the effects of soil inoculation treatments on plant community sensitivity to drought and especially so of additions of soil biota are idiosyncratic across plant functional groups. Generalizations with respect to positive impacts of the soil community in mediating stability of plant communities to drought are premature.

Conclusions

Using a comprehensive field experiment, we show that soil biota from later successional stages of ecosystem do not improve total plant community resistance and recovery subjected to drought. Instead, soil biota from later-successional soil inocula, like those originating from dune forest soil, may impede plant community post-drought recovery. Additionally, we found that soil inocula had differential influences on the drought sensitivity of functional groups and individual species. However,

the sensitivity of individual species and functional groups to drought was idiosyncratic and did not contribute to the overall stability of the plant community. Together these results suggest that impacts of the complexity of soil biota on the stability of plant communities in face of drought are highly context dependent.

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