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Tree seedling vitality improves with functional diversity in a Mediterranean common garden experiment

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ABSTRACT

Reforestation with multiple tree species is a promoted strategy to mitigate global change and to improve forest resistance against natural hazards. Dryland reforestation often fails because seedlings suffer from harsh conditions in degraded areas. Positive species interactions can overcome recruitment drawbacks by ameliorating environmental stress, but there is a strong need to advance functional insights from well-designed experiments.

We studied the vitality of 19,712 tree seedlings from 12 species in a Mediterranean common garden experiment (Sardinia). Vitality was assessed as an integrated index of foliage discoloration and defoliation measures, which are in dry areas potential indicators of early plant performance. The experimental design properly replicated all monocultures and a selection of mixed communities with different levels of species richness (SR) and functional diversity (FD). From the second year onwards, a water availability treatment (irrigated *versus* non-irrigated) was added to the design.

In the second year, seedling vitality was strongly determined by species identity and irrigation, but ecological interactions between trees were not relevant. In the third year, however, broad-leaved species were significantly more vigorous in mixed assemblages. Importantly, FD was identified as a seven times stronger predictor compared to SR. This suggests that a certain degree of trait diversification is essential to benefit from facilitative interactions. The positive FD effects were principally mediated by the presence of pines (*P. pinea*, *P. pinaster* and *P. halepensis*) in the neighborhood of broad-leaved trees. The latter had, on average, a 23% greater likelihood to have the highest vitality score in mixture with pines. The creation of a favorable physical and biotic neighborhood by pines is likely caused by their fast juvenile growth and adequate crown light transmission. FD effects on seedling vitality were positive, but contrary to the stress-gradient hypothesis, they were of similar magnitude in both irrigated and non-irrigated blocks.

We conclude that local neighborhood facilitation provides essential assistance for broad-leaved trees passing a critical seedling stage in semi-arid regions. This knowledge can contribute to increased success rates in forest rehabilitation in these regions.

1. Introduction

After the Paris Agreement, the world's nations are committed to undertake sufficient actions for limiting global warming well below 2 °C (Rockström et al., 2017; UNFCCC, 2015). A substantial role is dedicated to ecosystem-based mitigation actions. For instance, the negative emission potential from reforestation and forest restoration is, without exceeding biophysical constraints, estimated to 480 Gt CO_2 by 2100 (IPCC, 2014; SEI, 2016). Arid, semi-arid and dry-subhumid regions (hereafter: drylands) aggregately represent 41% of terrestrial land area

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and provide livelihood to 38% of the world's human population (Reynolds et al., 2007). Excellent opportunities for meeting ecosystem-based mitigation targets are found in these drylands. Due to intensive anthropogenic impacts, approximately 10–20% of land surface is severely affected by degradation (MEA, 2005). In the Mediterranean Basin, for instance, native forests once covered extensive areas but are nowadays compromised in their structure and functioning, or evolved to early-successional shrublands (Nocentini and Coll, 2013). Via raising temperatures and shifting precipitation patterns, climate change will further accelerate ecosystem vulnerability to desertification (Maestre et al., 2012). Many dryland restoration projects failed because seedlings could not pass a critical phase of plant settlement (Gómez-Aparicio, 2009; James et al., 2013). Such failure weights on financial budgets, but moreover, it demotivates land owners to invest in ecosystem restoration.

Difficulties to re-establish native dryland forest is best understood by considering a system with alternative stable states (Holmgren and Scheffer, 2001; Scheffer et al., 2001). The dryland forest state is dynamic, but quite inert to environmental modifications (i.e. strong ecosystem resilience). This changes once a critical point is reached, either following gradual stress accumulation or because of a dramatic event such as fire or clear-cut. The dryland forest state collapses and abruptly switches into another alternative state, e.g. a dry landscape dominantly covered by grasses, shrubs and/or bare soil (Holmgren and Scheffer, 2001). The backward transition is extremely difficult and requires conditions to be reversed beyond the critical point of ecosystem collapse, a phenomenon known as hysteresis (Scheffer et al., 2001). A strong feedback loop between biotic and abiotic components is chiefly stabilizing the degraded vegetation state (Kéfi et al., 2016). For instance, loss of canopy cover increases direct solar irradiation, temperature, evapotranspiration, water runoff and soil erosion. Tree seedlings are highly sensitive to dehydration because of their emerging rooting system and limited capacity to store water and carbohydrates (Aerts et al., 2007; O'Brien et al., 2014; Valladares and Sánchez-Gómez, 2006).

Where negative feedback loops stabilize the degraded vegetation state, positive species interactions can pave a way for transition back into forest. It has been demonstrated that nurse plants, for instance small pioneer shrub species or legumes (Gómez-Aparicio et al., 2004), promote native seedling performance via the reduction of environmental stress at microsite scale (Aerts et al., 2007; Castro and Zamora, 2004; Rey et al., 2008). Besides favouring water and temperature balance of the nursed trees, they also provide protection from grazing, reduce soil erosion and improve nutrient cycling. Conditions generally get better with accumulated biomass (i.e. positive feedback loop) and the thresholds hampering forest succession are surpassed (Kéfi et al., 2016). Once well established, native trees easily withstand harsh conditions.

The interest in restoration pathways via positive nurse plant – seedling interactions aligns with a growing research on the functional significance of biodiversity under climate change (Cardinale et al., 2012; Tilman et al., 2014). It was reported that the adoption of polyculture plantations, instead of conventional large-scale monocultures, provides long-term benefits for dealing with climatic uncertainties (Pawson et al., 2013). First, mixed forests benefit from greater spatial and temporal stability; a consequence of asynchrony in species responses to environmental fluctuations (Jactel et al., 2017; Thompson et al., 2009). Second, ecosystem functioning (e.g. productivity, litter decomposition) is favoured in mixed stands through resource complementarity (Madrigal-gonzález et al., 2016) or through the regulation by higher (Castagneyrol et al., 2014) or lower trophic levels (Laforest-lapointe et al., 2017).

As the relationship between biodiversity and forest functioning is primarily explored in mature systems, facilitative interactions in the early forest stages are far less understood, notably in the context of restoration success. To meet these shortcomings, research started manipulating tree species composition and diversity at scales relevant to policy and management (Verheyen et al., 2015). In these so-called *tree diversity experiments*, contrasting results have yet been found about the effects of tree diversity on seedling performance. Negative effects are observed by Yang et al. (2013), neutral effects by Potvin and Gotelli (2008) and Yang et al. (2017), and species-dependent diversity effects by Van de Peer et al. (2016). Also in the IDENT-Macomer experiment (Sardinia, Italy) seedlings are planted in monocultures and mixtures following a well-balanced design (Tobner et al., 2014). Interestingly, it is the only tree diversity experiment dealing with dry (Mediterranean) conditions. The experiment comprises 12 woody species assembled in 308 communities at different levels of species richness and functional diversity. It furthermore includes an irrigation treatment (irrigated *versus* non-irrigated) to examine shifts in species interactions with drought stress (Tobner et al., 2014). With insights into the autecology of dryland tree species and into mechanisms governing inter-specific interactions, it is possible to merge fundamental biodiversity-ecosystem functioning research with forest restoration ecology.

In this study we explored how tree species interactions are building-up in the Mediterranean IDENT-Macomer experiment and how they have an influence on seedling performance. Because seedling performance cannot be measured directly, growth measures are commonly used as a proxy. However, biomass allocation between aboveground and belowground plant structures differs greatly between species (e.g. the shoot:root biomass ratio is four times larger for seeders compared to resprouters; Verdu, 2000) as well as within species. Altered biomass allocation is usually a reaction to abiotic (water, nutrients and salinity) and biotic (vegetation competition) stress. Particularly in drought-prone or nutrient-poor environments, seedlings tend to disproportionally invest in root development to reach deeper and moister soil layers and to withstand droughts (Lloret et al., 1999; Padilla et al., 2007). Root biomass prioritizing is typical in environments where soil resources, rather than light, are constraining seedling establishment success. Assessing seedling performance with diameter/height measures may thus lead to some error, particularly for seedlings in harsh environments. Combining belowground and aboveground biomass data would be ideal, but belowground biomass is extremely difficult to estimate. The direct monitoring of tree physiological processes (e.g. leaf water potential, stomatal conductance or photosynthetic rate) may also provide valuable information, but these measures require sophisticated instruments and they are quite time consuming to take for many seedlings (Manzoni, 2014; Valladares and Sánchez-Gómez, 2006).

Foliage condition offers an alternative, time-efficient strategy to compare the performance of plants in different environments. The idea goes back to 1985. Since then, crown condition is annually assessed in the ICP Forests program (International Co-operative Program on Assessment and Monitoring of Air Pollution on Forests (Fischer and Lorenz, 2011). Following this standardized protocol, crown defoliation and discoloration is visually estimated and compared with a healthy reference tree. Intensive training and repeated control systems allow to create an objective vitality indicator. Vitality then reflects the integrated effects of site characteristics, intrinsic factors (e.g., age, phenology), biotic stresses, meteorological conditions and air pollutants (Bussotti and Pollastrini, 2017; De Marco et al., 2014).

Also in this study, seedling vitality was assessed as a combined index of foliage discoloration and defoliation measures. We hypothesized that (i) seedling vitality is principally determined by species identity and irrigation, because functionally dissimilar tree species respond differently to (drought) stress; (ii) seedling vitality is positively affected by tree species mixing due to facilitative plant interactions or due to the regulation by different trophic levels; (iii) some nurse trees (i.e. species firmly shaping the suitable physical or biotic micro-environment for other trees) substantially improve the vitality of their neighbors and, finally, (iv) positive interactions gain functional relevance under stress (the stress-gradient hypothesis), here tested by comparing irrigated with non-irrigated conditions.