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Local filters limit species diversity, but species pools determine composition

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ABSTRACT

In a series of three experiments, we tested for effects of species pools, resource stress, and species interactions on four aspects of community structure: species richness, evenness, species composition, and functional group composition. We also examined whether the impacts of species interactions on the community varied with resource availability or species pool. Communities of sand dune annuals grew from seed bank samples collected from two sites in three different years, so that the species pool differed at two levels: the source site and the year of seed bank collection. Communities experienced one of three irrigation treatments and a range of sowing densities, which varied resource supply (stress) and the potential for species interactions, respectively.

Species richness and evenness were most affected by local factors: higher densities and lower water availability decreased species diversity. In contrast, species composition was influenced most by the species pool. Functional group composition had an intermediate response, and was affected by both species pools and local filters.

Resource stress and species interactions strongly filtered species from the community, but the identity of species remaining was variable. Furthermore, the magnitude of species interaction effects on richness and evenness varied with species pools. Thus, the outcome of species sorting among biotic and abiotic environments was dependent on the pool of available species. Contrary to predictions from theory, the effects of species interactions on the community did not vary consistently with resource levels.

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Introduction

The community assembly process has been described as a series of successive filters, each of which limits the set of species in a community (Keddy, 1992; Zobel, 1997; Götzenberger et al., 2012). This concept of community assembly begins with a pool of species present in a region, only a subset of which is able to disperse to a habitat to form the local species pool. Abiotic conditions, such as resource shortage, and biotic interactions, such as competition, eliminate additional species, ultimately leaving the species that form the community. A current challenge in community ecology is to quantify the relative contributions of species pools and various abiotic and biotic filters in structuring communities and to understand how these interact to produce patterns in community structure across environments (Algar et al., 2011; Grace et al., 2011; Belmaker and Jetz, 2012; Götzenberger et al., 2012).

By examining patterns in natural field vegetation for a community of desert sand dune annuals, we previously showed that species pools, resource availability, and species interactions all affect species richness at different temporal and spatial scales (Rajaniemi et al., 2006). Previous experiments in the same system demonstrated that all three factors significantly affect fitness of individuals (Goldberg et al., 2001) as well as species composition (Rajaniemi et al., 2009). However, we did not quantify the relative magnitudes of effects of the different factors in those reports and therefore could not assess their relative importance. Here, we describe an experiment in which we simultaneously manipulated species pools, resources, and intensity of species interactions to measure their relative effects on multiple aspects of community structure: richness, evenness, species composition, and functional group composition.

In addition to their separate direct effects, species pools and abiotic and biotic filters may also interact in their effects on community structure. The effects of species interactions, in particular, may depend on resource levels. Alternative theories hold that the effects of interactions do not vary along resource gradients (Tilman and Pacala, 1993), are strongest when resources are abundant (Grime, 1977), are strongest when resources are low

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(Goldberg et al., 1999, 2001), or switch from mostly facilitative to mostly competitive as resource stress decreases (Bertness and Callaway, 1994; Maestre et al., 2009). Few previous studies have directly assessed the community-level effects of competition along resource gradients (Rajaniemi et al., 2003; Lenssen et al., 2004). The effects of species interactions may also vary with species pool: the traits of species in the pool form a biotic background or an “interaction milieu” with which an individual must interact (McGill et al., 2006), and different pools should provide different biotic backgrounds.

We studied the effects of species pools, resources, and species interactions on communities of annual plants grown from field-collected seed banks, using a series of three similar experiments. Species pool varied in two ways: seed banks came from two source communities representing two different pools, and each experiment used a seed bank collected in a different year, so the identity of the available species varied depending on differential reproductive success of adults in the previous year and survival in the seed bank over multiple years. Resource level was varied by irrigation treatments mimicking rainfall in the two source communities, as well as an intermediate level of rainfall. Finally, we used a community density series (Goldberg et al., 1995, 2001) to vary the intensity of species interactions.

The source communities, experiments, and experimental treatments we analyzed reflect the community assembly process in our study site. The two source communities draw species from a single regional pool, but differ in composition due to the effects of long-distance dispersal and climate patterns (Rajaniemi et al., 2006). In any given year, the species pool in the seed bank reflects reproduction across microsites that vary widely in shoot density and in microclimate (Rajaniemi et al., 2006); therefore, seed banks collected in different years are influenced more by random selection from the source community pool than by particular filters. Within a year, the actual community that emerges in a plot results from abiotic (resource) and biotic (species interactions) filters acting on the species pool present in the seed bank.

We addressed the following two questions:

- What are the relative magnitudes of the effects of species pool, resources, and species interactions on different aspects of community structure (richness, evenness, species composition, and functional group composition)?
- Does the magnitude of the effect of species interactions depend on resource level and/or species pool?

Methods

System

The system consisted of annual plants occurring at two semi-stabilized sand dune sites in Israel – one desert and one coastal community (source sites). Both sites have a Mediterranean climate with a winter growing season. Mean annual precipitation (30-year average, Israeli Meteorological Service) is 110 mm at the desert site (Holot Mashabim, 31°00'N 34°44'E), and 550 mm at the Mediterranean coastal site (Caesarea 32°30'N 34°55'E).

At both source sites, in September before the sowing of each experiment, we collected seed bank from the top 2 cm of sand from at least 60 random plots (Experiment 1) or along three 50-m transects (Experiments 2 and 3). The transects were established from randomly located starting points with randomly chosen directions within each source site. Samples were taken continuously along the transects, with the constraint of maintaining >30 cm margin from the edge of shrubs. Shortly after collection, the samples from within

each source site were combined and then passed through a series of sieves to eliminate the sand. The smallest fraction (<500 μm) contained almost no seeds (verified by germination tests) and was not used. The rest of the seed bank was thoroughly mixed to use as the concentrated seed bank, and stored in dry laboratory conditions.

The annual plant communities from the two source sites were grown in a common garden constructed at the Blaustein Institute for Desert Research at Sede Boqer (30°48'N 34°48'E; MAP 98 mm). The garden comprised multiple trenches (2 m \times 10 m; 1 m deep), each accommodating eight 1 m² plots and eight 0.5 m \times 0.5 m plots, filled with sterile sand. More detailed information on the common garden system can be found in Goldberg et al. (2001).

Experimental design

We conducted three experiments initiated in three different years; two lasted a single growing season and one lasted two seasons. The basic design for each experiment was a factorial with three to eight different initial community densities \times three irrigation treatments (low, intermediate, and high) \times two source communities (desert and coastal), with replication in multiple blocks (Table 1).

A range of initial sowing densities was established by sowing different amounts of homogenized, concentrated seed bank on the surface of the plots, from 1/16 \times to 8 \times average natural density (referred to as 1 \times). This approach allowed us to change the seed density while keeping the initial relative abundances of species constant. The 1 \times natural density plots were sown with the mean mass of seed bank that was collected from the equivalent area in the field and were intended to achieve the mean natural density. Increasing sowing density increases the probability that two plants compete for light by shading each other or compete for soil resources by drawing from the same soil volume. It also increases the opportunity for plants to ameliorate stresses by shading the soil to decrease temperatures or reduce evaporation.

Three irrigation treatments were imposed that mimicked aspects of the precipitation regimes of the two source sites, and an intermediate regime. Long-term rainfall records indicate that, on average, the desert and coastal sites receive, respectively, 1.1 and 5.8 times the annual precipitation of the experimental garden site at Sede Boqer. After each naturally occurring rainfall event at Sede Boqer, additional watering was done to maintain these proportional differences, with the intermediate treatment receiving the midpoint of these extremes (3.45 \times precipitation at Sede Boqer).

Because irrigation treatments could only be assigned to entire trenches, we used a nested block design, with three trenches in each block. One trench of each block was assigned randomly to each irrigation regime and the combinations of source and density treatments were then assigned randomly within each trench. Because of limited amounts of available seed bank it was necessary to have different plot sizes. The higher seed bank densities were sown into small (0.5 m \times 0.5 m) plots and the lower densities were sown in the larger (1 m²) plots (Table 1). In Experiments 1 and 3, natural densities (1 \times) were sown in both large and small plots to assess effects of plot size.

All plots were sown in November by spreading the appropriate amount of seed bank uniformly across the surface of the sand of each plot. The seed bank was then covered by 1 cm of sterile sand and lightly watered with an equivalent of 5 mm of rainfall to prevent loss of seed by wind.

Percent cover of each species in the two-year Experiment 3 was estimated at the end of the first season in April 1995, after cessation of natural rainfall and as most species were just beginning to dry after ripening seeds. In May 1995, plots were covered

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