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The importance of plant cover and predation in shaping a desert community

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ABSTRACT

The classical paradigm describe desert communities as being controlled by abiotic conditions and therefore it was assumed that predation had a limited role in the determination of desert community structure and that only one effective trophic level was expected. In the Negev desert, the desert isopod (*Hemilepistus raeumuri*) is common in the less productive habitats but almost absent from the more productive wadis. In the present study we tested whether predation by ectothermic predators has a role in controlling isopod populations in wadis. We hypothesized that plant cover provides a refuge for these predators from secondary endothermic predators. We addressed this hypothesis by comparing isopod survivorship with and without predation exclusion, and with and without plant cover removal. Isopods protected from predation had a sustainable population whereas unprotected isopods had an unsustainable sink population. Removal of plant cover did not affect the survivorship of predator-protected isopods, however it did increase the survivorship and reduced predation pressure when not protected from predators, for at least four years. Hence, we conclude that predation controls isopod population and causes an unsustainable sink population in wadis. We have shown that plant cover mediates predation and that some habitats in the desert have an effective third trophic level, suggesting that energy is not the major limiting factor in determining the length of food chains.

1. Introduction

One of the central issues in community ecology is the relative importance of bottom up (*e.g.,* water) limitation and top-down (*e.g.,* consumers) control in shaping terrestrial communities (Hopcraft et al., 2010). It has been suggested that, in terrestrial communities, there is a positive correlation between productivity and the number of effective trophic levels (Fretwell, 1977; Oksanen et al., 1981). A trophic level was defined as effective if it effectively controls the trophic level below it (Fretwell, 1977) suggesting that the effect of removal of one trophic level will cascade to lower trophic levels. Accordingly, Fretwell (1977) recognized two different states in terrestrial communities, namely, a “green” state, where the number of trophic levels is odd (*i.e.,* one or three) and consequently plants are resource limited, and a “brown” state, where the number of trophic levels is even (*i.e.,* two or four) and plants are herbivore-controlled (Hairston et al., 1960; Oksanen et al., 1981; Oksanen and Oksanen, 2000; Bond, 2005). In resource-poor hot deserts, only one effective trophic level is expected (*i.e.,* deserts represent a “green” state) and plants are water limited and therefore herbivores and predators are expected to play a minor role in shaping hot desert communities (Noy-Meir, 1973, 1985; Shmida, 1985; Megias et al., 2011).

However, an alternative explanation suggests that deserts could have more trophic levels and that predation can play an important role in shaping hot desert communities (Polis, 1991; Moore et al., 2004; Borer et al., 2005; Ayal, 2007). Hot deserts accumulate detritus which is more predictable and long lasting food source for primary consumers, especially macrodetritivorous arthropods (Noy-Meir, 1979). The macrodetritivorous arthropods serve as a major conduit transferring energy from primary producers to higher trophic levels (Crawford, 1981; Ayal et al., 2005). The abundant macrodetritivores can support two additional trophic levels, namely, primary ectothermic predators (*e.g.,* arachnids and reptiles) and secondary endothermic predators (*i.e.,* mammals and birds). Ayal (2007) suggested that the distribution of the primary

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ectothermic predators is determined by predation intensity of the endothermic secondary predators that is affected by plant cover: primary predators are abundant in more productive habitats where they are rather protected by plant cover, but rare in less productive habitats where they are exposed to heavy predation from secondary predators (Fig. 1). Therefore, macrodetritivores suffer high predation pressure in high plant cover habitats by the abundant primary predators, and rather low predation in low plant cover habitats where primary predators are rare and their foraging is limited (Groner and Ayal, 2001; Ayal, 2007). One of the most abundant primary consumers in deserts are isopods and in the Negev desert one of the most abundant species is the desert isopod *Hemilepistus raeumuri*. This species is less abundant in the lower areas of the desert water sheds (wadis) than in the adjacent slopes (Shachak et al., 1976). In the present study we explore Ayal (2007) theory in experiments that manipulate the distribution of the desert isopod *Hemilepistus raeumuri*. Specifically, we tested whether the low abundance of isopods in more productive wadi habitats is due to predation by ectothermic predators. This was tested by (a) protecting isopods in plant covered wadi plots from predation by ectothermic predators, and (b) by removing the plant cover and monitoring the densities and predation intensity on isopods.

2. Methods

2.1. Study area

The study was carried out in a wadi (ephemeral riverbed) in the Negev Desert Highlands approximately 10 km north of Sede Boqer Campus of the Ben Gurion University (30º51′N, 34º57′E). The study site is a hilly limestone area with an average annual precipitation of 92 mm with extreme values of 34 mm and 167 mm. For a detailed description of the study area and vegetation see Ayal and Merkl (1994). Isopod burrows were present on slopes adjacent to the wadi and in low densities in the wadi.

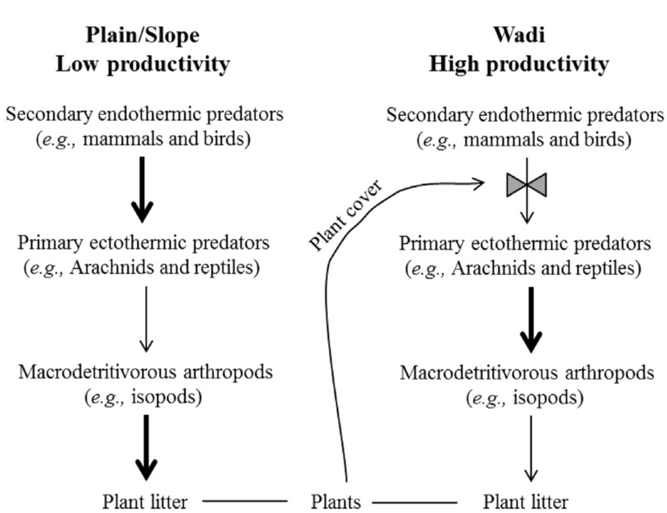

Fig. 1. The suggested features of the trophic control in the Negev Highlands (after Ayal et al., 2005). The direction of the arrows point on the affected group and their width on the intensity of the interactions. Secondary predators efficiency is higher in the low productivity habitat than in the wadi due to plant cover. Hence, in the low productivity habitat secondary predators efficiency controls primary predators and macrodetritivores are released from predation and become food limited. In the wadi primary predators find refuge in the plant cover, maintain high densities and efficiently control the macrodetritivores.

2.2. Study organism

The desert isopod, *Hemilepistus reaumuri*, is an annual semi-social isopod that is common throughout the arid parts of North Africa and the Middle East (Coenen-Stass, 1984). They live in monogamous family units in burrows that, at the end of the growing season, may reach about 50 cm deep. From February to March the isopods leave their family burrows and the females search for a new settling site up to several hundred meters from their original burrow (Shachak and Brand, 1991; Baker, 2004). Males search for established females, court them, and if accepted form a couple defending the burrow from any other isopods. The isopods continue to grow and mature during April. Young hatch in May and during the first month of their life, stay in the burrow while their parents provided them with food collected next to the burrow. In mid-June, the young start to forage independently and together with the parents continue to dig the burrow all along the season. The isopods forage for plant litter and soil crust till October when they cease above ground activity and stay in the family burrow until next February.

The major predators of the isopod in our study area are different ectothermic predators, mainly arachnids (Shachak and Brand, 1983; Baker et al., 1998), centipedes and skinks (Segoli, personal observations).

2.3. Plant cover manipulations

In the first year (2003), we chose three 750 m^2 plots (Fig. 2). We removed the plant cover (*i.e.*, above ground woody vegetation and dense herbaceous vegetation) from two of the plots, taking extra care to minimize damage to the soil crust and detritus. One of the plots was used for this experiment (Removed). The other plot was intended to check the effect of artificial woody vegetation and was not included in this experiment. The third plot was left as a control

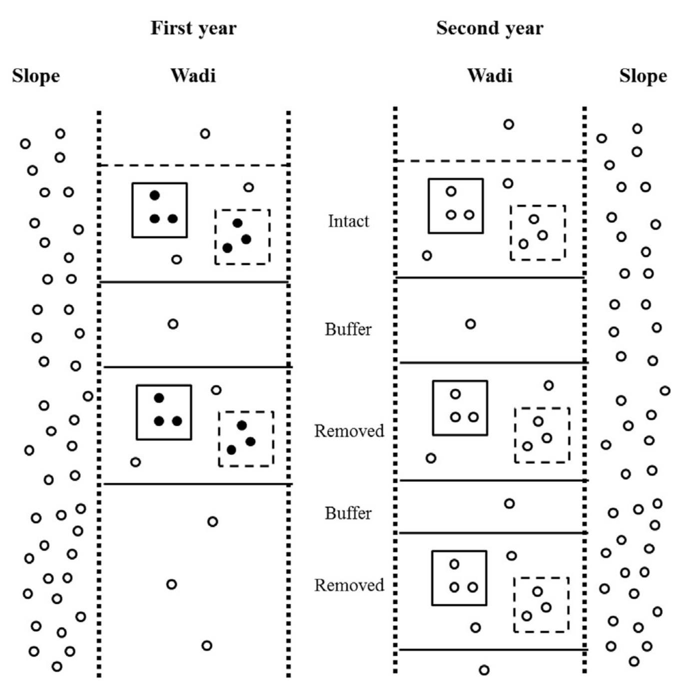

Fig. 2. A schematical representation of the experimental design. Intact & Removed plots are 750 m^2, Protected and Unprotected sub-plots are 25 m^2. Solid lines represent fences that reduce movement of predators (see Fig. A1 & A2). Solid circles represent isopods that were transferred in the first year. Hollow circles represent natural occurring isopods.