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Temperature-specific competition in predatory mites: Implications for biological pest control in a changing climate

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ABSTRACT

Climate change is affecting the future of sustainable agriculture, because increasing temperatures may interfere with the functioning of natural enemies that are used in biological pest control. In this work, we examined the role of abiotic conditions in shaping the structure of a simple agricultural community that is dominated by two species of predatory mites (i.e., *Eusieus stipulatus* and *Eusieus* scutalis) competing for resources. Population and community dynamics experiments were carried out at two abiotic conditions mimicking local climates in a Mediterranean region, to estimate the population carrying capacity (k) and interspecific competition (α) for each predatory mite species. Subsequently, we used this data to parameterize a competition model, thereby predicting species dominance at each abiotic condition. To test our model predictions, we sampled several orchards located in areas influenced by each of the local climates, to determine the abundance of each species of natural enemy. Results showed that the outcome of the competitive interactions between predatory mites was strongly affected by abiotic conditions, leading to temperature-dependent changes in the community structure. Furthermore, the pattern of species dominance found in the field agreed with the model predictions built upon our laboratory experiments. We therefore emphasize that, in a changing climate, if we are to guarantee the successful use of biocontrol agents, we need to account for the effect of temperature upon biotic interactions.
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1. Introduction

The impact of climate change on ecological and agricultural communities (Warren et al., 2011; Woodward et al., 2010) is expected to become larger over time (Dawson et al., 2011; Walther et al., 2002) because of the non-linear trend in the global temperature increase (IPCC, 2013). A recent review uncovered that environmental warming is affecting virtually all existing ecological interactions (Tylianakis et al., 2008), but such effects are highly variable, as the effect of abiotic factors upon species interactions depends on species identity (Dunson and Travis, 1991; Peñuelas et al., 2013; Tylianakis et al., 2008; Voigt et al., 2003). Interspecific competition, either exploitative (Tilman, 1982) or by interference (Schoener, 1983), is an important ecological interaction that can affect the presence, distribution and abundance of species (Gause, 1934; Hutchinson, 1965). The outcomes of competitive interactions among species, i.e., exclusion or coexistence, depend on the degree of niche overlapping between species, and on the degree to which species differ in competitive ability (Gause, 1934). However, the patterns of persistence and exclusion in competing species can differ according to the abiotic environment (Park, 1954). Abiotic environmental conditions and interspecific competition interact in the form of "condition-specific competition" (Dunson and Travis, 1991; Gilman et al., 2010; Krassoi et al., 2008). Abiotic-ecological interactions of that nature can facilitate the invasion of exotic species and subsequent exclusion of native species (Carmona-Catot et al., 2013), or be the limiting factor for the expansion of exotic species (Alcaraz et al., 2008; Holway et al., 2002; Thomas and Holway, 2005). When abiotic variability occurs over small spatial scales, the existence of

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a trade-off between competitive ability and abiotic stress tolerance may allow inferior competitors to coexist in areas where they would otherwise be excluded (Gilman et al., 2010).

Recent European policies explicitly demand a reduction in the use of pesticides in agriculture, to avoid environmental impacts and to protect human health (OJEU, 2009). To comply with sustainability in agriculture growers need to redirect pest management from chemical to biological pest control (BPC), i.e., the management of natural enemies to reduce pest densities. Accordingly, the percentage of the world's land under cultivation that is applying BPC is increasing (Van Lenteren, 2012), and it has even totally replaced chemical control in some areas (Calvo et al., 2012). However, climate change may become a crucial limiting factor for the persistence and future expansion of sustainable practices in agriculture, as warming may provide pests with increasing chances to escape predator control because sensitivity to rising temperatures usually increases with trophic level (Cagnolo et al., 2002; Preisser and Strong, 2004; Voigt et al., 2003). Indeed, adverse environmental conditions have already caused herbivore natural control disruption (Montserrat et al., 2013a), and failure in biological control strategies (Montserrat et al., 2013b; Roy et al., 2003; Stavrinides et al., 2010).

In south-eastern Spain, in the coastal areas of the province of Malaga in the region of Andalusia, more than 70% of the production of avocado (*Persea americana* Mill., Lauraceae) is pesticide-free (González-Fernández et al., 2012). The arthropod community of the Andalusian avocado agro-ecosystems is composed of a few mite species: the persea mite *Oligonychus perseae* (Acari: Tetranychidae), an invasive herbivore pest species that builds nests made of dense strands of silken webbing on the underside of avocado leaves, and three species of predatory mites (Acari: Phytoseiidae): *Neoseiulus californicus*, a commercially available specialist predator of tetranychid mites that forages inside the nests of *O. perseae* (Montserrat et al., 2008); and *Euseius stipulatus* and *E. scutalis*, two omnivores that mainly forage on pollen (González-Fernández et al., 2009) but also attack mobile stages of *O. perseae* wandering outside the nests (Montserrat et al., 2008). The two species of *Euseius* are currently being managed through conservation BPC methods for the control of three tetranychid mite pest species in two agro-ecosystems, *Tetranychus urticae* Koch and *Panonychus citri* (McGregor) in citrus (Aguilar-Fenollosa et al., 2011), and *O. perseae* in avocado (González-Fernández et al., 2009; Maoz et al., 2011). *E. stipulatus* is the dominant species in orchards of the western shores of the Mediterranean basin, where abiotic environmental conditions are relatively mild, whereas *E. scutalis* dominates in those of the eastern shores, where abiotic environmental conditions are hotter and dryer (Moraes et al., 2004). However, both species have been found in specific locations within the regions dominated by their respective sister species (Ferragut and Escudero, 1997).

Because *E. scutalis* is better adapted to heat stress (Kasap and Sekeroglu, 2004) than *E. stipulatus* (Ferragut et al., 1987), and because in the presence of a shared resource the two species do not engage in predator-prey interactions (i.e., intraguild predation) (Guzmán, 2014), we hypothesized that temperature-specific competition could explain the presence of the eastern species, *E. scutalis*, in the western Mediterranean shores. To test this, we performed laboratory experiments at the population and community level, to estimate population parameters for both species. These parameters were subsequently used in a simple competition model to explore whether abiotic conditions only were able to explain the patterns of species dominance. Lastly, we checked in the field if the observed patterns matched those predicted by the model. The ultimate goal was to ascertain that, in the present scenario of climate change, the structure of agricultural communities will increasingly be shaped by ecological-abiotic interactions rather than by ecological interactions only, which ultimately may influence the successful undertaking of species that provide important ecological services, such as natural enemies.

2. Methods

2.1. Phytoseiid mite cultures and experimental arenas

Cultures of the predatory mites *E. stipulatus* and *E. scutalis* were started in 2006 and 2009 from c.a. 300 and 100 individuals collected from coastal avocado trees located in the Experimental Station "La Mayora" and in a private inland orchard of the province of Málaga, respectively. Both species were cultured in separate climate chambers at $25 \pm 1\,^{\circ}$C, 65 ± 5% HR and 16:8 h L:D (Light: Dark). Rearing units consisted of three bean plants (*Phaseolus vulgaris* L.), with 6–10 leaves, positioned vertically in contact with sponges ($30 \times 20 \times 5$ cm, approx.) covered with cotton wool, with a plastic sheet (27×17 cm, approx.) on top, and placed inside water-containing trays (8 l, $42.5 \times 26 \times 7.5$ cm). The aerial parts of the plant were touching each other, forming a tent-like structure. Some leaves contained cotton threads that served as oviposition sites for the mites. Mites were fed ad libitum twice a week with pollen of *Carpobrotus edulis* (L.), spread on the leaves with a fine brush. Pollen of *C. edulis* was obtained from male flowers dried in a stove at $37\,^{\circ}$C for 48 h, then sieved (350 μm).

Experimental arenas were constructed as follows (Fig. 1): a circular hole (12 cm ø) was made in the middle of the base of Petri dishes (14 cm ø) with a welder. The inside and outside of the margin of the inner circle of Petri dishes was covered with a plasticine ring. An avocado leaf disc (13 cm ø) was placed in the base of each Petri dish, the borders glued to the plasticine, and the underside facing outdoor through the hole of the base of the Petri dish. A disc of foam of 13 cm ø was wrapped with wet cotton wool and it was placed inside the base of Petri dishes, and in contact with the leaf discs. Petri dish lids were then placed upon the foam, and both the lid and the base were wrapped with parafilm®. Arenas were then turned upside down (i.e., the lid being the base of the arena, and the underside of the life discs being in the open). To stop individual mites from escaping, Tanglefoot® was applied in the outside area of contact between the plasticine ring and the leaf disc. A few threads of cotton were glued to the leaf disc to serve as an oviposition site. Water was added to the foam with a syringe every day. The experimental arenas were designed to create two abiotic environments isolated from each other. The lower abiotic environment (contained within the Petri dish) was kept humid to help maintain turgidity in the avocado leaf-discs. The upper environment with the plasticine ring and leaf provided the

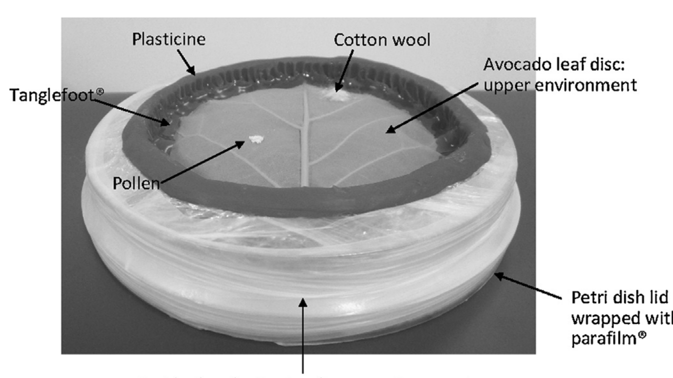

Fig. 1. Arenas for population and community dynamics experiments, designed to confine two abiotic environments isolated from each other: the lower abiotic environment was kept humid to help maintain turgidity of the avocado leaf-discs; the upper environment was defined by the experimental treatments, and it encompassed the area containing the tested populations or communities.

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