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## Does global warming induce segregation among alien and native beetle species in a mountain-top?

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**Abstract** The last few centuries have seen an increase in the mean air temperature of the planet, a phenomenon that is called “global warming”. One of the most sensitive habitats to the effects of global warming is the high-elevation mountain environments, because these habitats are characterized by low temperature. Cushion plants are one of the best-adapted growth forms in this habitat, generating more suitable sites for other plants and insects. In the present study, we experimentally evaluated the effects of global warming by open-top chambers on the abundance and interaction of two ladybirds at 3,600 m, growing over cushions of the *Azorella monantha* species in the Andes of central Chile. Additionally, we measured variation in temperature, water content, and food availability by the presence of open-top chambers as possible mechanisms of spatial segregation between ladybirds. Without open-top chambers, the abundance of native and alien beetles was similar; but with open-top chambers, the native beetle species is spatially segregated by alien species, decreasing in abundance. The open-top chambers increase temperature and food availability, but not water content. We suggest that under the global warming scenario, the native insects will decrease in abundance or become extinct by the presence of alien insects, at least in the high-elevation mountain environments.

**Keywords** Alien species · Cushion plants · Global warming · High-elevation mountain environments · Ladybirds · Open-top chambers

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### Introduction

The mean air temperature of the planet has increased about 1°C over the last 100 years (Walther 2003; IPCC 2007), and several models predict that this increase will be between 2 and 5°C over the next 50–100 years (IPCC 2007). Although global warming will affect all the ecosystems of the world, it has been suggested that some will be more sensitive than others to these climatic modifications (Welker et al. 2004).

High-elevation habitats are among the most sensitive ecosystems to global warming (Körner 2003). These habitats are characterized by very stressful climatic conditions for both plants (Körner 2003) and animals (Margraf et al. 2003). The low temperatures of air and soil, strong winds, and short growing seasons are the main characteristics of these habitats (Körner 2003). Several authors have suggested that due to this climatic harshness, high-elevation habitats are less prone to biological invasions compared to those with more benign habitats (McDougall et al. 2005). Hence, any modification of these harsh conditions (e.g., increases of temperature due to global warming) will have important consequences for the invasibility of these habitats (Warren et al. 2001). Indeed, it has been suggested that global warming could promote the invasion of alien species (Dukes and Mooney 1999). Although biological invasions and climatic changes are recognized as major threats to biodiversity (Sala et al. 2000), few studies have evaluated how global warming will affect the interactions between alien and native species (Dukes and Mooney 1999).

Most of the ecological studies related to the effects of global warming in high-mountain areas have been conducted in the northern hemisphere, and mainly using plant species (Loik et al. 2004). However, the possible effects of global warming on animal species interactions at the local scale remain poorly explored (Kreman et al. 1993). Further, as far as we are aware, there are no studies assessing the effects of global warming on

interactions among native and alien insect species in a mountain-top habitat.

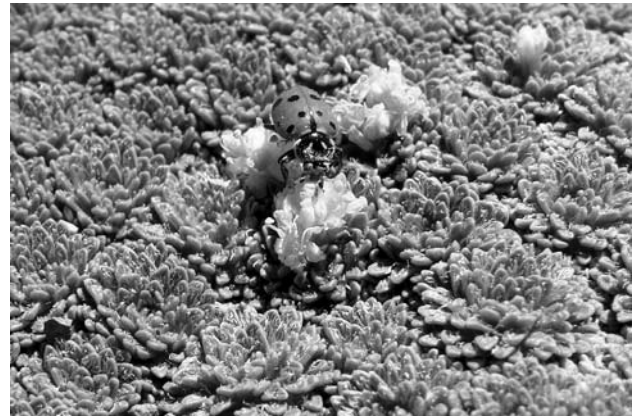
In previous studies, we have shown that the cushion plants *Azorella madreporica* and *Laretia acaulis* act like microclimatic shelters for ladybird beetle species at 3,200 m in the Andes of central Chile. Due to their low stature and compact form, cushion plants are particularly efficient heat-traps, decoupling their temperature from the surrounding air, generating more suitable environments for other plant (Cavieres et al. 2006, 2008) and insect species (Molina-Montenegro et al. 2006). For instance, the abundance of the native ladybird beetle species *Eriopis connexa* (native beetle) as well as that of the alien ladybird beetle species *Hippodamia variegata* (alien beetle) is several times higher inside cushions of *Azorella madreporica* compared to bare ground areas (Molina-Montenegro et al. 2006). This suggests that the population dynamics of beetle species in high-mountain habitats is enhanced by the amelioration of low temperatures performed by the cushion species. It is well known that life-history traits such as developmental time, fecundity, and fertility are important for successful invasion (Lanzoni et al. 2004). Further, all these traits are related and mediated by temperature (Labrie et al. 2006). For instance, developmental time decreased as the temperature increased, and developmental time of the alien beetle is shorter than the native for the eggs and larval instars (Labrie et al. 2006). Thus, with warmer conditions, we could expect higher abundances of beetle species in an alpine environment, especially with the alien beetle species.

## Materials and methods

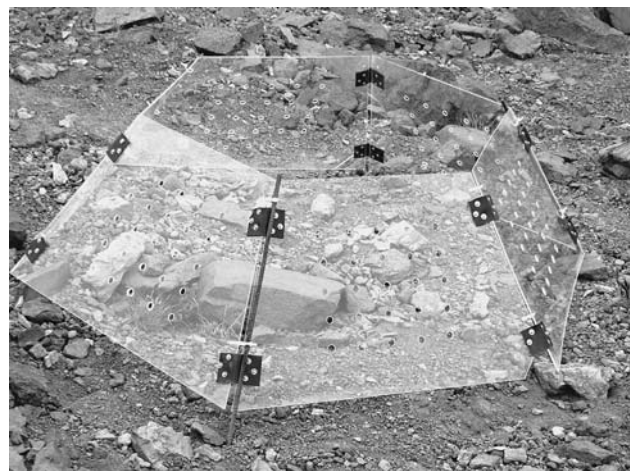
### Study site and target species

This study was conducted in the Andes of central Chile, near the ski resort of Valle Nevado (33°20'S, 70°16'W), located 50 km east of the city of Santiago. The study site is located in the summit of Co. Franciscano at 3,600 m a.s.l. The climate is typically alpine, with strong influence of the Mediterranean-type climate that prevails in lowlands (Di Castri and Hajek 1976). Mean annual air temperature during growing season (December–March) is 6.8°C, with a mean minimum of 0.1°C and with a mean maximum of 16.4°C (Cavieres et al. 2007). Mean annual precipitation ranges from 500 to 900 mm, which occurs mainly as snow during winter months (Santibañez and Uribe 1990).

Vegetation on this site is highly patchy, and the most abundant species is the cushion plant *Azorella madreporica* (Apiaceae) (Fajardo et al. 2008). This species is a very flat and tightly knit cushion species, distributed from 33°S to 55°S, and grows above 3,200 m elevation in the Andes of central Chile (33°S) and close to sea level at 55°S (Hoffman et al. 1998) (Fig. 1). *Eriopis connexa* (Germ.) and *Hippodamia variegata* (Goeze) are the only species of Coleoptera inhabiting this zone. *E. connexa* is



**Fig. 1** *Hippodamia variegata* (Coleoptera, Coccinellidae) individual on *Azorella monantha* cushion plant at 3,600 m a.s.l. at the study area



**Fig. 2** Open-top chamber (OTC) used to increase the temperature on the surface of cushion plants at 3,600 m a.s.l.

a native species of neotropical origin and very abundant in the northern and central zones of Chile. This ladybird species has a spherical shape, is about 5 mm long, and has an orange color with clear spots, and its principal food sources are aphids and mites distributed within vegetation (Milléo et al. 2007). On the other hand, *H. variegata* is an alien species, originating in the palae-arctic region and introduced into Chile in the 1960s for the biological control of cereal aphids. This species is slightly elongated in shape, about 4–6 mm long, and is well known as a common predator of aphids.

### Global warming simulation

Hexagonal chambers of transparent punched walls 50 cm in height and 120 cm in diameter and open at the top were used as passive warming systems (Fig. 2). These devices are called OTCs (open-top chambers) and have been widely used in global warming experiments in

alpine and arctic tundra (Henry and Molau 1997). The basic mechanism of warming by OTCs is the prevention of heat lost by convection, and it has been shown in several studies that air temperature inside these chambers is 4–5°C higher than the surrounding environment (Molau and Molgaard 1996). Twelve cushions of *A. madreporica* of similar size (ca. 1 m diameter) were randomly selected. On six of these cushions, an OTC was placed so as to completely include the cushion inside the OTC. The other six selected cushions were marked with a metallic sticks. All OTCs were placed at early of October 2005. Surface temperature on each cushion with and without OTCs was recorded with an infrared thermometer (IR-Thermometer, Tegam, HO, USA) every 2 h from 0800 to 2000 hours, in November, January, and March.

### Soil moisture

Soil moisture was estimated through the soil matrix potential. For this, we selected 12 *A. monantha* cushions of similar size different to those used for the warming treatment, in order to avoid effects on the ladybird abundance. On six of the selected cushions we placed open-top chambers (OTC) as described above. At each cushion with and without OTC, a soil-tensiometer (2725 Series Jet Fill Tensiometer; Soil Moisture Equipment Corp., Santa Barbara, CA, USA) was dug into the soil to a depth of 10 cm. Tensiometers were placed at 1200 hours, and after a stabilization period of 1 h, the soil matrix potential was recorded.

### Abundance of ladybirds

We estimated the abundance of *Eriopis connexa* and *Hippodamia variegata* in *Azorella monantha* cushions with and without OTCs. For this, on each cushion with OTC and those marked cushions without OTC the number of individuals of each ladybird species for a period of 10 min was recorded at midday (period of highest activity for ladybirds). The abundance of ladybird species in cushions with and without OTC was recorded once per month during the growing season (from November 2005 to March 2006).

### Abundance of arthropods

In March of 2006, 125 g of soil and 125 g of vegetal tissue were collected from six cushions with and six without OTCs. Samples were placed in sealed plastic bags, and sent to the Laboratory of Systematics of Coleoptera in the Universidad the Concepción. Samples were analyzed by the Barlesse funnel method with an illumination source of 60 W and after 48 h, all insect individuals were fixed in alcohol 70°. Collected individuals were observed under a binocular microscope and all specimens were identified at the lowest taxonomic level possible.

### Statistical analyses

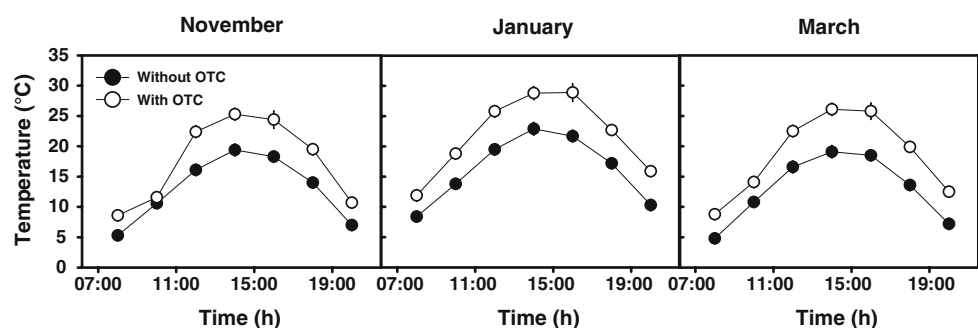
Differences in surface temperature between cushions with and without OTCs, during the growing season and along the day were analyzed using three-way repeated-measures ANOVA. Differences in the abundance between *E. connexa* and *H. variegata* with and without OTCs were assessed throughout the growing season using three-way repeated-measures ANOVA. Soil moisture between cushions with and without OTC was compared with a one-way ANOVA.

## Results

### Global warming simulation

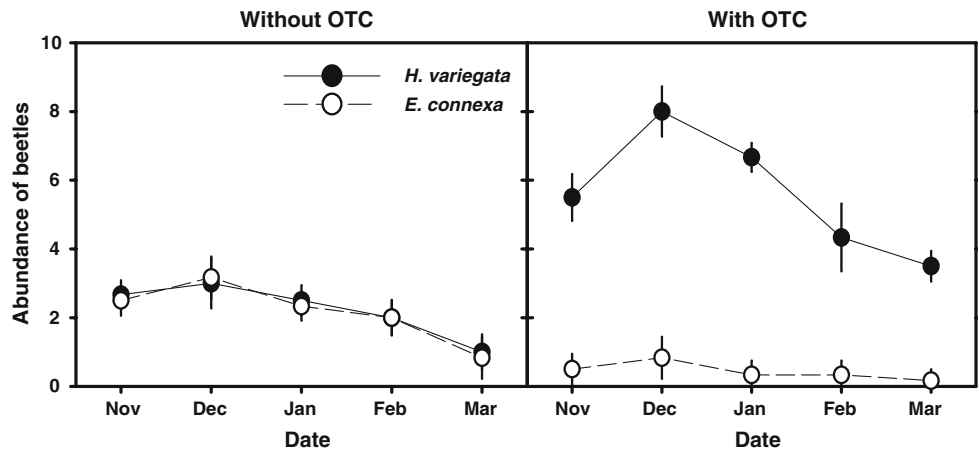
Each month, the maximum temperatures on the cushion's surface both with and without OTCs were recorded at midday (1200 at 1600 hours), whereas minimum temperatures were detected at 0800 and 2000 hours (Fig. 3). Repeated-measures ANOVA indicated differences in surface temperatures with and without OTCs ( $F_{1,30} = 714.92$ ;  $P < 0.0001$ ) as well as along the day ( $F_{6,180} = 12,590.61$ ;  $P < 0.001$ ). Surface temperatures on January both with and without OTC were significantly higher than on November and March ( $F_{2,30} = 218.16$ ;  $P < 0.001$ ). The interaction effect Treatment  $\times$  Hours was significant ( $F_{6,180} = 66,9726.79$ ;  $P < 0.001$ ), indicating that although cushions with and without OTCs increased the temperature at midday, this was more evident in cushions with OTCs (Fig. 3). The

**Fig. 3** Mean temperature ( $^{\circ}\text{C} \pm 2 \text{ EE}$ ) detected each hour over cushions with open-top chambers (open circles) and over cushions without open-top chambers (black circles) at 3,600 m a.s.l.





**Fig. 4** Abundance average of *Eriopis connexa* (open circles) and *Hippodamia variegata* (closed circles) on cushions of *Azorella monantha*, without (a) and with (b) open-top chambers (OTCs) treatments and along growing season at 3,600 m a.s.l. (Are showed  $\pm 2$  EE)



interaction effect Treatment  $\times$  Month was not significant ( $F_{2,30} = 1.58$ ;  $P = 0.24$ ).

#### Ladybird abundance

The abundance of ladybird individuals (including both the native and the alien invasive species) was significantly higher in cushions with OTCs ( $F_{1,20} = 51.97$ ;  $P < 0.001$ ). On the other hand, while there were no differences in the average abundance between *Eriopis connexa* and *Hippodamia variegata* on cushions without OTCs, in cushions with OTCs the abundance of *H. variegata* (alien ladybird) was 2.5 times more abundant whereas the abundance of *E. connexa* (native ladybird) was 5 times less abundant ( $F_{1,20} = 533.52$ ;  $P < 0.001$ ; see Fig. 4) compared with cushions without OTCs. The abundance of *H. variegata* was 13 times greater than the abundance of *E. connexa* in cushions with OTCs (Fig. 4).

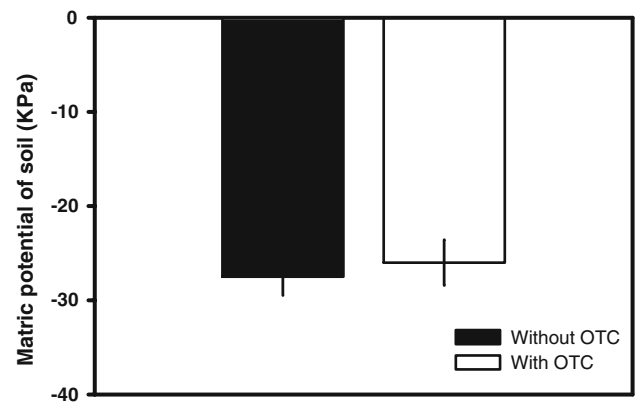
Ladybird beetle abundance was significantly greater during the first months of the growing season than in later months ( $F_{4,80} = 38.95$ ;  $P < 0.001$ ). The interaction effect Treatment  $\times$  Month did not affect abundances ( $F_{4,80} = 2.27$ ;  $P < 0.68$ ). On the other hand, the interaction effect Treatment  $\times$  Species  $\times$  Month was significant ( $F_{4,80} = 8.55$ ;  $P < 0.001$ ), where *H. variegata* was more abundant than *E. connexa*, but only during the first months of the warming treatment (Fig. 4).

#### Soil moisture

Soil matrix potential did not differ between cushions with OTCs and cushions without them ( $F_{1,10} = 0.92$ ;  $P = 0.36$ ) (Fig. 5).

#### Abundance of arthropods

Overall, 122 individuals were collected from samples of cushions with and without OTC and were classified in eight arthropod species belonging to four orders (Acari,



**Fig. 5** Soil matrix potential within cushions with (empty bar) and without (filled bar) open-top chambers at 3,600 m a.s.l. (Are showed  $\pm 2$  EE)

Aracnidae, Coleoptera, and Homoptera) and two classes (Arachnida and Insecta). Approximately 77% of the individuals were found on cushions with OTCs, while the remaining 23% were found on cushions without OTCs (Table 1). Only samples from cushions with OTC contained all the taxa recorded, while in cushions without OTC, only three taxa were recorded (Table 1).

#### Discussion

Our results suggest that global warming will affect the abundance of both native and alien beetle species in alpine habitats, where the abundance of the alien beetle species increased with warming and the abundance of the native species decreased. These results suggest that the alien species may segregate the native one causing or facilitating the local extinction of the native species under a global warming scenario.

The higher temperatures related to global warming might benefit the alien beetle species because insect alien species have been shown to maintain high activity in a variety of temperatures. For instance, it has been shown that alien insects can be more adaptive in their behavior

**Table 1** Abundance of arthropods cover in samples from the surface of cushion plants with and without open-top chambers at 3,600 m a.s.l.

Class	Order	Family	Species	Origin	With OTC	Without OTC
Arachnida	Acari	Camisiidae	<i>Camisia segnis</i>	A, NE	21	0
		Scheloribatidae	<i>Scheloribates monttensis</i>	N, E	11	5
		Opipiidae	<i>Globoppia intermedia</i>	A, NE	12	7
		Pherioldidae	<i>Pherioldes</i> sp.	A, NE	18	9
		Nothridae	<i>Novonthrus</i> sp.	A, NE	10	6
		Aracnidae	<i>Salticidae</i> sp.	A, NE	8	1
		Salticidae	<i>Salticidae</i> sp.	A, NE	8	1
Insecta	Coleoptera	Staphilinidae	<i>Aleocharinae</i> sp.	A, NE	5	0
	Homoptera	Aphididae	<i>Aphis</i> sp.	A, NE	9	0

A Alien, N Native, E Endemic, NE Not endemic

and metabolism than native species (Agrawal 2001), adjusting well to a wide range of thermal environments (Nice and Fordyce 2005). Human and Gordon (1996) reported that with an increase in the air temperature, the invader Argentine ant (*Linepithema humile*) showed a detrimental effect on native ant species. Alien Argentine ants maintain their foraging with the increase of temperature, while native ants decreased, resulting in a spatial segregation of the native ant colonies by alien ants. Beetles are ectotherms and depend on environmental temperatures during all phases of their life cycles. Several processes are affected by temperature, including life-span duration, diapause, dispersal, mortality, and genetic adaptation (Patterson et al. 1999). Additionally, Lombardero et al. (2000) suggested that temperature has a broad effect on the physiology and behavior of the majority of insects in all developmental stages and also influences metabolic rate, flight activity, reproduction, nutrition, development, and hence, survival. For instance, Mori et al. (2005) showed that temperature strongly affects the developmental and reproductive performance of alien ladybird species, enhancing their role as a biocontrol agent. Indeed, after 5 years of its introduction, it led to a decline of populations of two native species (Howarth 2000).

Another attribute that may be related to the alien success with OTC is their food-search strategies (Lanzoni et al. 2004; Osawa 2000). The food-search strategies resulting in the most successful prey capture can favor individuals of a species and influence the numerical and developmental responses of them (Dixon 2000). In this regard, it is supposed that an invasive species will have better searching strategies that result in higher predation efficiency than native ones (Kimberling 2004). For instance, Labrie et al. (2006) suggested that the alien ladybird *Harmonia axyridis* is a polyphagous feeding species and it is more efficient in food search than the native species. Considering that, under experimental global warming conditions the food availability was enhanced and the possible higher predation efficiency of alien than native beetle species could be the result of the spatial exclusion or segregation by alien beetles.

Although in this study the mechanisms of the segregation of the native ladybird species by the alien one remain unraveled, variation in feeding or time develop-

ment that would affect to final abundance should not be ruled out. Additionally, increases in the abundance of all arthropods under the experimental global warming scenario highlight a general response for those insects inhabiting the alpine zones (see Table 1). Nevertheless, the majority of these arthropods are alien species, thus possible segregations of other native species under a future scenario of global warming should not be discarded, at least in the alpine environments.

We are aware of the lack of knowledge about the effects of color, shape, or light reflection by OTCs on the behavior or other indirect effects on ladybirds, affecting a differential abundance among them. We consider that this is unlikely because in a previous study both ladybird beetles showed considerable differences in abundance induced by variation in temperatures. Nevertheless, more experiments considering warming devices with other shapes and colors could be helpful in future studies.

Several models predict that global warming will decrease the generation time of insects, increase their winter survival, and shift their distribution ranges (Cannon 1998). Although these models predict that insects will shift their ranges in response to global warming, changes in the distribution or abundance of key plant species (e.g., cushion plants) could restrict their potential habitat (Sutherst et al. 1995). In a revision made by Dukes and Mooney (1999) about global climatic change effects on biological invaders, they suggested that “specialist” species that rely on a particular plant community for food or shelter are more likely to be negatively affected by climatic change phenomenon than “generalist” species that can survive in a variety of plant communities. Since invasive animal species are more likely to be generalists than specialists, they thus might be more successful than natives at adapting to new climates (Dukes and Mooney 1999).

While some authors think that nearly 24% of the species could become extinct under a global warming scenario for the year 2050 (Thomas et al. 2004), others’ more apocalyptic projections estimate that more than half of the current species could become extinct (Smith et al. 1993), decreasing biodiversity at a global scale. In the current literature the outcome of long-term consequences of such climate changes on biodiversity is not clear (Sax and Gaines 2003). Nonetheless, there is a

general agreement that, in the short-term, the consequences will be a decrease in global diversity at least for native beetles in the alpine environments.

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