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Noxious invasive *Eupatorium adenophorum* may be a moving target: Implications of the finding of a native natural enemy, *Dorylus orientalis*

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Eupatorium adenophorum is a noxious invasive weed that is distributed throughout subtropical areas worldwide. Enemy release may be at least one of the reasons underlying its success as an invader. In this study, we observed damage to the epidermis, cortex, phloem, cambium, and xylem tissues of roots and stems around the root collar of *E. adenophorum* growing in an experimental field in Yunnan Province, southwest China. The damage was caused by *Dorylus orientalis*, a polyphagous ant feeding on the weed and resulted in the death of the plants by interrupting nutrient exchange between shoots and roots. This ant showed selectivity for the invader to some extent. The finding of *D. orientalis* and other native enemies indicate that *E. adenophorum* may gradually naturalize in introduced landscapes. In addition, this ant may have potential for use as a biocontrol agent against the invader.

biological control, *Dorylus orientalis*, *Eupatorium adenophorum*, invasive alien plant, native enemy

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Eupatorium adenophorum Sprengel (Asteraceae; hereafter *Eupatorium*) is native to Central America, but is a noxious invasive perennial weed distributed in subtropical areas worldwide [1]. It spread into Yunnan Province, southwest China, from Burma in the 1940s, and is now distributed in six provinces of southwest China. It invades a diverse range of habitats including roadsides, agricultural fields, disturbed grasslands, and abandoned fields, causing great economic and biodiversity losses [2]. The mechanisms underlying its invasion success are still poorly understood, although there have been several studies on its ecology and physiology [1,3,4]. Invasive plant species generally have lower herbivore loads in introduced ranges than in native ranges, and the "enemy release" hypothesis has been proposed to explain successful invasions of introduced plants [5,6]. In its native range in Mexico, *Eupatorium* is consumed by more than 30 phytophagous insect species, and is affected by several pathogens (Fritz Heystek, personal communication), many more than are generally observed for this species in China. Such release from enemies may allow *Eupatorium* to compete with reduced ecological restrictions, which in turn may promote evolutionary changes. For example, invasive *Eupatorium* has evolved reduced nitrogen allocation to cell walls (defense) and increased allocation to photosynthesis (growth), contributing to increased photosynthesis and photosynthetic nitrogen-use efficiency, and therefore to invasiveness [1]. The successful biocontrol of *Eupatorium* by *Procecidochares utilis* Stone (a gall fly native to Mexico) in some countries indicates that enemy release may be at least one of the reasons for the success of the invader [7–9]. In China, however, *P. utilis* does not significantly affect the invader [10], but several natural enemies for *Eupatorium*

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have been found recently. Here we report an effective native natural enemy of *Eupatorium*, *Dorylus orientalis* Westwood (Hymenoptera: Formicidae; hereafter *Dorylus*).

In early May 2009, we found two dead and three dying plants of *Eupatorium* in a 100-m^2 experimental field in Kunming, Yunnan Province, southwest China, in which 200 seedlings of the invader were grown in August 2008. Small soil hills (ant hills) were found around these plants (Figure 1). After uncovering the soil, we found evidence that these plants had been attacked by soil animals (Figure 2(a) and (b)). Epidermis, cortex, phloem, cambium and xylem tissues were damaged, and in 3 of the 5 plants, a 4–6 cm portion of the root and stem around the collar was completely destroyed. To determine which pest was responsible for the damage, we searched the surrounding soil, ant hills, and plants and found that many individuals (tens to hundreds) of *Dorylus* were eating the roots or stems of *Eupatorium* (Figure 2(c) and (d)). Generally, the feeding behavior of the ant was to first eat the roots in the uppermost 3–5 cm of topsoil, piling up soil around the plant stems, and then to eat the stems under the ant hill. When most or all of a 3–8-cm portion of the roots and stems around the collar was damaged, the ants left for another plant through a tunnel located 5–10 cm below the soil surface. Forty days after the ant was first observed, all the *Eupatorium* plants grown in the experimental field had died as a result of *Dorylus* attack, which interrupted nutrient exchanges between roots and shoots.

Dorylus also showed selectivity for *Eupatorium* to some extent. It did not attack other plant species grown in or around our experimental field, including many pasture species such as *Brachiaris decumbens* Stapl, *Setaria anceps* Stapf ex Massey, and *Medicago sativa* Linn. To test the selectivity of this ant further, we grew 25 individuals each of *E. adenophorum*, *E. chinense* L., *E. japonicum* Thunb, *E. heterophyllum* D C., *E. stoechadosmum* Hance, *Solanum melongena* L., *Ipomoea batatas* Lam., and *Solanum tuberosum* L. in the experimental field and observed the feeding

Figure 1 Ant hill of *Dorylus orientalis* around *Eupatorium adenophorum* plant.

Figure 2 Plants of *Eupatorium adenophorum* damaged by *Dorylus orientalis*. (a) and (b) Ants left for other plants through tunnels located 5–10 cm below soil surface when epidermis, cortex, phloem, cambium, and xylem tissues of a 3–8-cm portion of root and stem had been damaged. (c) and (d) Ants feeding on roots and stems of *E. adenophorum* plants.

behavior of *Dorylus*. All of the *E. adenophorum* individuals were damaged by *Dorylus*, but none of the native species. This pattern of selectivity for *E. adenophorum* was confirmed in another experiment, which was conducted 200 m away from above experimental field in July 2009, with potted *E. adenophorum*, *E. chinense*, *E. japonicum*, *E. heterophyllum* and *E. stoechadosmum*. Similar results were also found in another experiment conducted nearby, in which *E. adenophorum* was grown alongside native *E. japonicum*, *E. heterophyllum*, *E. chinense*, and *E. stoechadosmum* under two nitrogen levels and two irradiances. The selectivity of this ant is consistent with the fact that it favors foods with fishy and fragrant odors [11]. The strong odor of *E. adenophorum* may act as a chemical signal for the ant.

Because we did not conduct detailed host range tests following the current international standardized protocols, we cannot conclude that *Dorylus* is a specialist enemy of *Eupatorium*. In fact, *Dorylus* is a polyphagous insect and agricultural pest [12–14]. More studies are required to test the suitability of *Dorylus* as a biocontrol agent for *Eupatorium*. However, our results indeed suggest that *Dorylus* may significantly affect the *Eupatorium* population dynamics and invasiveness in the future. Like *Eupatorium*, *Dorylus* is distributed across a wide range of habitats in tropical and subtropical areas in South and Southeast Asia, including China, Myanmar, Nepal, India, Sri Lanka, Indonesia, and Malaysia [12–15]. *Dorylus* has 3 progenitive peaks per year [11,14]; ant queens lay many eggs when there is ample food supply, and their life span ranges from 10 years to several decades [13]. *Dorylus* appears to be an effective enemy for *Eupatorium*. It has a greater effect on the invader than that of introduced biocontrol agents. This ant can kill plants, whereas introduced biocontrol agents generally only impair target plants to some extent [16]. For example, in China, parasitic activity of the gall fly *Procecidochares utilis* decreases growth of the parasitized branches of *Eupatorium*, but does not kill the whole plant, or even the parasitized branch.

Toxic substances in invasive plant species may deter generalist herbivores (novel defense hypothesis). Alternatively, generalists may avoid the invading plant species simply because of their feeding habits (behavioral *constraint hypothesis*) [17]. In the latter case, invaders may be potentially edible food sources for generalists. Many studies have found that native enemies can feed on invasive plants in introduced ranges [17–20], and the number of native enemies gradually increases for invasive plants. In addition, invasive plants may increase resource allocation to defenses after reassociation with natural enemies [21], reducing competitive ability. The behavioral constraint hypothesis may explain the small number of native enemies for *Eupatorium* in China. The invader does not show higher resistance to generalists than to native congeners in both selection and non-selection feeding trials (unpublished data). *Acrydium japonicum* Bolivar (Orthoptera: Tettigidae), *Callimorpha albipuncta* Wileman (Lepidoptera: Arctidae), *Agriolimax* sp. (Stylommatophore: Agriolimacidae), a species of Limacodidae (Lepidoptera), a species of Tortricidae (Lepidoptera), and a species of Geometridae (Lepidoptera) have also been found to attack *Eupatorium* in another experimental site nearby a nursery garden located in Qujing, Yunnan Province. In the nursery, pesticides are regularly applied, and pesticide application may force the above mentioned insects to feed on *Eupatorium*, which they have never been observed to do in field situations. Thus, the gradual accumulation of native enemies including *Dorylus* and introduced *Procecidochares utilis* may reduce the competitive ability of *Eupatorium* in terms of ecology (herbivory) and evolution (increased allocation to defenses). Our results indicate that *Eupatorium* may gradually naturalize into introduced landscapes, although at present it causes great economic loss and damage to biodiversity worldwide.

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