

ECOLOGICAL DOMINANCE BY *PARATRECHINA LONGICORNIS* (HYMENOPTERA: FORMICIDAE), AN INVASIVE TRAMP ANT, IN BIOSPHERE 2

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ABSTRACT

Tramp ants are invading disturbed ecosystems worldwide, exterminating untold numbers of native species. They have even invaded Biosphere 2, a 1.28-hectare closed greenhouse structure built in the Arizona desert as a microcosm for studying ecological interactions and global change. Invertebrate surveys within Biosphere 2 from 1990 to 1997 have revealed dramatic changes in faunal composition, including an almost complete replacement of the ant fauna by a single tramp ant species.

In 1990-91, surveys in Biosphere 2 found no one ant species dominant. By 1993, populations of the crazy ant, *Paratrechina longicornis* (Latreille), a tramp species not found in 1990-91, had increased to extremely high levels. In 1996, virtually all ants (>99.9%) coming to bait were *P. longicornis*. We observed *P. longicornis* foragers feeding almost exclusively on the sugary excretions (honeydew) produced by vast numbers of Homoptera, primarily scale insects and mealybugs, found on many of the plants. High densities of ants were associated with high densities of homopterans. In 1997, soil and litter surveys found that the only invertebrates thriving in Biosphere 2, besides *P. longicornis* and homopterans, were either species with effective defenses against ants (well-armored isopods and millipedes) or tiny subterranean species that can escape ant predation (mites, thief ants, and springtails). A convergent pattern of biodiversity occurs in disturbed tropical and subtropical ecosystems dominated by tramp ants.

Key Words: ants, invasive species, microcosms, *Paratrechina longicornis*

RESUMEN

En todo el mundo, hormigas vagabundas han estado invadiendo ecosistemas perturbados, eliminando grandes números de especies nativas. Han invadido hasta la "Biósfera 2", una estructura cerrada estilo invernadero de 1.28 hectáreas que fue construida en el desierto de Arizona como un microcosmo para el estudio de interacciones ecológicas y de cambios globales. Censos de los invertebrados dentro de "Biósfera 2" de 1990 a 1997 han revelado cambios dramáticos en la composición faunística, incluyendo un reemplazo casi total de la fauna de las hormigas por una sola especie de hormiga vagabunda.

En 1990-91, censos dentro de "Biósfera 2" indicaron que ni una sola especie de hormiga era dominante en sus números. En 1993, la población de la hormiga *Paratrechina longicornis* (Latreille), una especie vagabunda que no se había encontrado en 1990-91, había aumentado a niveles extremadamente altos. En 1996, virtualmente todas las hormigas (>99.9%) que habían visitado los cebos eran de la especie *P. longicornis*. Observamos que estas hormigas se alimentaban casi exclusivamente de las secreciones azucaradas (miel de rocío) producidas por grandes números de Homoptera, principalmente escamas y cochinillas harinosas, que se encontraban en muchas de las plantas. Densidades altas de hormigas estaban asociadas con densidades altas de homópteros. En 1997, se descubrió en censos de suelo y de hojarasca que los únicos invertebrados que estaban prosperando en "Biósfera 2", además de *P. longicornis* y homópteros, eran especies con defensas eficaces en contra de las hormigas (isópodos y milpiés con buenas armaduras) o pequeñísimas especies subterráneas que escapan de la depredación por las hormigas (ácaros, hormigas robadoras y colémbolos). Un patrón convergente de biodiversidad existe en ecosistemas tropicales y subtropicales perturbados y dominados por hormigas vagabundas.

Biosphere 2 is a 1.28-hectare closed greenhouse structure built in the Arizona desert north of Tucson as a model for a self-contained space colony and used as a microcosm for understanding ecosystem dynamics and global change. Biosphere 2 contains not only human residences and an agricultural area, but also "wilderness" areas designed to model natural biomes, including a desert, a savanna, a rain forest, a marsh, and an ocean (Alling et al. 1993, Nelson et al. 1993). Eight people lived sealed in Biosphere 2 for two years, from 1991 to 1993, and 7 more lived inside for 6.5 months in 1994. These experiments indicated that maintaining a balance of atmospheric gases suitable for human life was difficult in this closed system. For example, in the fifteen months after initial closure in September 1991, the oxygen level dropped from 21 percent to 14 percent, requiring oxygen to be added to the system (Broecker 1996, Cohen & Tilman 1996). In addition to atmospheric changes, many ecological changes within Biosphere 2 were noted (Broecker 1996, Cohen & Tilman 1996).

The plants and animals living in Biosphere 2 at the time of initial closure came from many sources (Alling et al. 1993, Nelson et al. 1993). Planners imported hundreds of species of plants and animals and integrated them into Biosphere 2 in an attempt to recreate self-sustaining artificial ecosystems. Many species were selected to fill specific community functions, e.g., bees and hummingbirds were introduced to serve as pollinators. Other species, such as chickens and bananas, were included as sources of human food. As Biosphere 2 was being constructed, many local Arizona plant and animal species also took up residence in the structure (Alling et al. 1993, Nelson et al. 1993). In addition, accidental species arrived in building material and in soil and plant samples.

It has been widely reported anecdotally that the crazy ant, *Paratrechina longicornis* (Latreille), has taken over Biosphere 2 and that little else of the original fauna remains. For example, Cohen & Tilman (1996) made the widely repeated but undocumented observation that in Biosphere 2, "the majority of the introduced insects went extinct, leaving crazy ants (*Paratrechina longicornis*) (sic.) running everywhere, together with scattered cockroaches and katydids." Indeed, at present, *P. longicornis* swarm in exceedingly high numbers in many parts of Biosphere 2, but other insects occur in very high densities as well. For example, plant-feeding Homoptera, primarily scale insects (Families Coccidae, Diaspididae, and Asterolecaniidae) and mealybugs (Family Pseudococcidae), are extremely common in Biosphere 2.

Homopterans feed by piercing plant tissue with their hypodermic-like mouthparts and ingesting the phloem liquid. Homopterans pass large volumes through their digestive tracts, excreting a sugary liquid called honeydew. Homopterans are major agricultural pests, in both the field and in greenhouses, causing damage both through sapping plants of nutrients and by increasing the occurrence of diseases, including viral and fungal infections (Power 1992, Miller & Stoetzel 1997). Many species of ants, including *P. longicornis*, feed on the honeydew produced by homopterans (Hölldobler & Wilson 1990). In turn, ants protect homopterans from attack by predators and parasites, boosting homopteran population levels. Homopteran exudate appears to be an important source of food for many ants. Due to the tremendous economic impact of homopterans in agricultural systems, a vast literature exists on the relationship between homopterans and their attendant ants (Hölldobler & Wilson 1990).

In the present study, we documented *P. longicornis*' rise to dominance in Biosphere 2 and its relationship with homopterans. Further, we surveyed the current invertebrate biodiversity. These analyses may provide novel insights into ecological dynamics in highly-disturbed "natural" ecosystems.

MATERIALS AND METHODS

Ant and Homopteran Introductions

We sought all records of intentional introductions of ants and homopterans to Biosphere 2, searching internal reports of Biosphere 2.

Ant Surveys

We conducted surveys of ants on numerous occasions between 1990 and 1997. Between August 1990 and March 1991, D. E. W. conducted visual surveys of Biosphere 2, hand collecting ants. In August 1990, C. A. O. conducted surveys using hand collecting, sweep nets, and pitfall traps. From April to August 1993, during the first human enclosure experiment (Mission 1), M. N. ran ~25 pitfall traps once a month throughout the wilderness biomes. From 27 September to 4 October 1993, immediately after the end of Mission 1, S. E. M., D. A. P., J. L., and S. Buchmann conducted surveys using hand collecting, aerial and sweep netting, Malaise traps, ultraviolet lights, ant baits (honey, peanut butter and tuna-based cat food), pitfall traps, Berlese funnel samples of soil and leaf litter, and yellow pan traps (for ground-dwelling and low-flying insects). In January 1994, C.A.O. surveyed the desert area. In November 1996, J. K. W., I. W. A., K. R. H., M. P., E. L. H., and J. G. made visual ant surveys and collected ants at 174 bait stations (tuna in oil and "Keebler Pecan Sandies" cookies) set out at 5 m intervals along every trail throughout the wilderness areas.

Soil and Leaf Litter Surveys

In June 1997, J. K. W., A. G. H., M. M. Y, and C. E. D. collected 18 1-liter soil and leaf litter samples from 18 widely separated parts of "wilderness" areas on Biosphere 2 (6 each from the desert, savanna, and rain forest biomes). We placed the samples in Berlese funnels for 48 hours to extract ants and other invertebrates.

Homopteran-tending by Ants

Between September 1996 and March 1998, J. K. W. searched for the food source of foraging *P. longicornis* in Biosphere 2 during numerous visits, tracing hundreds of foraging trails to their origins.

In November 1996, J. K. W, I. W. A., M. P., E. L. H., and J. G. counted ants foraging on 24 large *Thalia geniculata* L. leaves, each on a different plant in order to document the association between ants and homopterans. The number of ants present on each leaf was assessed 3 times at 10 minute intervals on one day, and 3 times again 2 days later. The leaves were visually ranked according to density of scale insects, and all scale insects were counted on the 17 lowest-ranked leaves and the one highest. Ant visitation rate was compared for the 8 low-, 8 medium-, and 8 high-ranked leaves.

RESULTS

Ant and Homopteran Introductions

Between August 1990 and August 1991, before Biosphere 2 was sealed, W. Scott recorded 1 or more colonies of 11 ant species intentionally introduced by S. Schneider and others: *Camponotus sexguttatus* (Fabr.), *Camponotus ustus* (Forel), *Camponotus festinatus* (Buckley), *Camponotus mina* Forel, *Camponotus* sp., *Dorymyrmex insanus* (Buckley) (formerly *Conomyrma insana*), *Crematogaster steinheili* (Forel), *Crematogaster* sp., *Cyphomyrmex minutus* Mayr, *Forelius pruinosus* Roger, and *Pheidole* sp. 1. These species were selected, based on advice from J. Longino and others, to serve a variety of vital functions such as seed-dispersal and recycling of dead plant and animal material. None of these deliberately-introduced ant species was recorded in any subsequent surveys (Table 1).

We found no records of intentional introductions of homopterans into Biosphere 2.

Ant Surveys

Between August 1990 and March 1991, invertebrate surveys conducted to document pre-closure conditions recorded 9 ant species (A in Table 1), including local native ants, as well as "tramp" ants, i.e., species dispersed worldwide by human commerce and associated with human disturbance (Hölldobler & Wilson 1990). No single ant species showed clear dominance.

Between April 1993 and January 1994, surveys conducted during and immediately after the first human enclosure experiment recorded 6 ant species (B in Table 1), including 2 tramp ant species not recorded before closure in 1991. One of these species, *Paratrechina longicornis*, now occurred in high numbers. The five other ant species occurred in very low numbers.

In November 1996 and June 1997, surveys recorded 10 ant species (C in Table 1), including 7 species not recorded previously and only 1 species found in surveys before

TABLE 1. ANTS OF BIOSPHERE 2. SURVEY: A = 1990-91; B = 1993-94; C = 1996-97. STATUS: N = LOCAL NATIVE SPECIES, T = TRAMP SPECIES.

Species	Survey	Status
<i>Odontomachus clarus</i> Roger	A	N
<i>Crematogaster opuntiae</i> Buren	A	N
<i>Linepithema humile</i> (Mayr)	A	T
<i>Paratrechina bourbonica</i> (Forel)	A	T
<i>Pheidole</i> sp. 2	A	?
<i>Pheidole hyatti</i> Emery	AB	N
<i>Solenopsis xyloni</i> (MacCook)	AB	N
<i>Cardiocondyla ectopia</i> Snelling	AB	T
<i>Hypoponera opaciceps</i> (Mayr)	ABC	T
<i>Paratrechina longicornis</i> (Latreille)	BC	T
<i>Tetramorium bicarinatum</i> (Nylander)	BC	T
<i>Solenopsis molesta</i> Say	C	N
<i>Forelius mccooki</i> (McCook)	C	N
<i>Cardiocondyla wroughtoni</i> (Forel)	C	T
<i>Monomorium floricola</i> (Jerdon)	C	T
<i>Tapinoma melanocephalum</i> (Fabr.)	C	T
<i>Paratrechina vividula</i> (Nylander)	C	T
<i>Strumigenys rogeri</i> Emery	C	T

initial closure in 1991. Among the extremely large numbers of ants observed foraging above ground, every one was *P. longicornis*, except small numbers of *Monomorium floricola* (Jerdon) on 5 plants, and *Cardiocondyla wroughtoni* (Forel), *Tapinoma melanocephalum* (Fabr.), *Tetramorium bicarinatum* (Nylander), and *Paratrechina vividula* (Nylander) each on a single plant. Of the 28,827 ants collected at baits, all were *P. longicornis*, except 1 *T. bicarinatum* specimen.

Soil and Leaf Litter Surveys

Soil and leaf litter surveys in June 1997 found that only a few types of invertebrates predominate in Biosphere 2, though many other invertebrates occurred in low numbers. Of the 1193 ants extracted from the 18 soil and leaf litter samples, there were 987 *P. longicornis*, 200 *Solenopsis molesta* Say, 3 *Hypoponera opaciceps* (Mayr), 1 *M. floricola*, 1 *Strumigenys rogeri* Emery, and 1 *Forelius mccooki* (McCook). In addition to ants, we extracted 1271 mites (Acari), 323 Isopoda, 74 millipedes (Diplopoda), 39 springtails (Collembola), 12 earthworms (Oligochaeta), 8 Homoptera, 7 spiders (Araneae), 7 webspinners (Embioptera), 5 snails (Gastropoda), 4 termites (Isoptera), 3 cockroaches (Blattaria), 3 beetles (Coleoptera), 2 wasps (Hymenoptera), 1 caterpillar (Lepidoptera), 1 lacewing (Neuroptera), and 1 Diplura.

Although we found few specimens in our soil and leaf litter samples, cockroaches remain conspicuous throughout Biosphere 2, especially at night. The only other large insect to maintain a noticeable population in Biosphere 2 was the katydid *Scudderia mexicana* (Saussure) (Orthoptera: Tettigoniidae), which we consistently observed in low numbers on vegetation in the savanna and desert areas.

Homopteran-tending by Ants

Trails of foraging *P. longicornis* on plants in Biosphere 2 invariably led to homopterans. High densities of ants on plants were always found to be tending high densities of homopterans, such as scale insects that heavily encrusted the trunks, branches, and leaves of many *Piper* trees, and mealybugs that covered the branches of many mangrove trees. Ants returning from these sources to their nests were bloated with liquid.

Surveys of ants on *Thalia geniculata* L. leaves demonstrated a strong positive association between ants and scale insects. Leaves with few scales (3 to 23) averaged 0.5 ± 0.8 ants per survey, leaves with an intermediate number of scales (27 to 314) averaged 3.9 ± 3.5 ants per survey, and leaves with the most scales (534 to 5755 scales) averaged 51.8 ± 28.5 ants per survey (Kruskal-Wallis Test for differences between means, $H = 24.0$, $df = 2$, $p < 0.0001$).

DISCUSSION

In the few years since arriving in Biosphere 2, the crazy ant, *Paratrechina longicornis*, has quickly become the ecologically dominant ant species. *Paratrechina longicornis* is called the "crazy" ant because of its fast, jerky movements. It is of Old World origin, but is now found throughout the tropics and subtropics, usually associated with disturbance, e.g., in highly-disturbed natural environments, in cities, in greenhouses, and even on ships (Weber 1940, Smith 1965, Wilson & Taylor 1967, Trager 1984, Hölldobler & Wilson 1990, Yamauchi & Ogata 1995, Wetterer 1998). One strikingly parallel example of ecological dominance by *P. longicornis* occurs in the Dry Tortugas, the highly-exposed, outermost islands of the Florida Keys (Hölldobler & Wilson 1990). Here, *P. longicornis* "is an overwhelmingly abundant ant and has taken over nest sites that are normally occupied by species of *Camponotus* and *Crematogaster*, which are absent from the Dry Tortugas; and open soil, normally occupied by crater nests of *Conomyrma* (now *Dorymyrma*) and *Iridomyrma* (now *Forelius*), which genera are also absent from the Dry Tortugas" (p. 433; Hölldobler & Wilson 1990).

Besides *P. longicornis*, the only common ant now in Biosphere 2 is a tiny subterranean thief ant belonging to the *S. molesta* species group. In California, *S. molesta* is the most common native ant persisting in areas invaded by the tramp Argentine ant, *Linepithema humile* (Mayr) (formerly *Iridomyrma humilis*) (Human & Gordon 1997). Thief ants also persist in areas invaded by the highly-destructive red imported fire ant (*Solenopsis invicta* Buren) (Stein & Thorvilson 1989).

In Biosphere 2, *P. longicornis* foragers appear to obtain almost all their carbohydrates from honeydew produced by homopterans. The extremely high densities of homopterans in Biosphere 2 appear to be essential for maintaining the high populations of ants. The same may be true in many "natural" ecosystems. Tramp ants most commonly invade and dominate disturbed communities (Wilson & Taylor 1967, Hölldobler & Wilson 1990, Yamauchi & Ogata 1995, Wetterer 1998), possibly because they depend on honeydew produced by plant-feeding homopterans that thrive on secondary-growth plants (Tennant & Porter 1991).

Although earlier anecdotal reports only noted cockroaches and katydids among the insect species remaining in Biosphere 2, this observation probably reflected not so much the numbers, but the visibility of these large insects. In contrast, the vast numbers of Homoptera covering the plants and mites in the soil are much less conspicuous. The present invertebrate diversity in Biosphere 2 is strikingly skewed in a way that suggests heavy influence of ants. Although a wide diversity of invertebrates persist in low numbers in Biosphere 2, the only ones that now thrive are species that are: 1) ant mutualists (homopterans tended by ants), 2) ant resistant (well-armored isopods and millipedes), or 3) or escape ant attack by being very small and subterranean (mites, thief ants, and springtails). Researchers have documented similar patterns of invertebrate diversity in disturbed tropical and subtropical ecosystems dominated by tramp ants (Stein & Thorvilson 1989, Porter & Savignano 1990, Cole et al. 1992, Williams 1994, Human & Gordon 1997). Several of us were struck by how much the character of the plant and animal community within Biosphere 2 resembled that of disturbed lowland areas in Hawaii. Thus, Biosphere 2, a 1.28-hectare habitat island surrounded by desert, appears to be a fairly good ecological analog for a small, highly-disturbed, subtropical island. As we understand more of the ecological dynamics in Biosphere 2, the results may provide important insights into the workings of simplified ecosystems that are useful for the conservation and restoration of Earth's increasingly disturbed habitats. Future research in Biosphere 2 can examine more closely the interactions among ants, homopterans, and plants and study the impact of biological introductions, particularly introductions of natural enemies of ants and homopterans.

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