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Author(s): W. Bond and P. Slingsby

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COLLAPSE OF AN ANT-PLANT MUTUALISM: THE ARGENTINE ANT (*IRIDOMYRMEX HUMILIS*) AND MYRMECOCHOROUS PROTEACEAE¹

W. BOND²

Saasveld Forest Research Station, Private Bag X6531, George, 6530, South Africa

AND

P. SLINGSBY

Box 108, Kleinmond, 7195, South Africa

Abstract. Many plant species in Cape fynbos shrublands have seeds dispersed by ants. *Iridomyrmex humilis*, the Argentine ant, has recently invaded areas of fynbos and displaced the dominant native ants. The consequences of the invasion for seed dispersal were studied. *Iridomyrmex* differed from native ants in being slower to discover the seeds (morphologically achenes) of ant-dispersed *Mimetus cucullatus* (Proteaceae), in moving them shorter distances, and in failing to store them in nests below the soil. Seeds left on the soil surface were eaten by vertebrate and invertebrate predators.

To study seedling emergence, seed depots were established and then the area was burned. Emergence was 35.3% in sites not infested by *Iridomyrmex* and 0.7% in infested sites. Seedlings in naturally occurring stands of *M. cucullatus* burnt in the same fire were widely distributed in noninfested sites, but were fewer and were confined within the canopy radius in infested sites. We suggest that continued invasion of fynbos by *Iridomyrmex* may eventually lead to extinction of many rare, endemic Cape Proteaceae by slow and subtle attrition of seed reserves.

Key words: Cape fynbos; coevolution; dispersal; *Iridomyrmex humilis*; keystone mutualist; mutualism; myrmecochory; Proteaceae; seed predation.

INTRODUCTION

Pollination and seed dispersal are often mutualistic interactions between animals, which gain a source of food, and plants, which gain a pollen vector or seed-dispersal agent. Though many studies have demonstrated coevolution between flowers and their pollinators, less is known about both the benefits and the specificity of interactions between plants and their dispersers (Howe and Smallwood 1982). In some cases, seed dispersal may be both required for germination and accomplished by a single partner; extinction of the animal disperser will cause extinction of the coevolved plant species (Temple 1977). Alternatively, the loss of a whole guild of dispersers may merely lead to new dispersers taking over, or to passive seedfall beneath the parent, with recruitment continuing and with little change in plant distribution or abundance (Janzen and Martin 1982).

Plants that have seeds dispersed by ants (myrmecochores) may be particularly sensitive to changes in the disperser community. Ants are attracted by elaiosomes, food bodies attached externally to the seed, and carry the seed to their nests. The elaiosome is eaten and the seed is left planted in the nest or is discarded nearby in ant middens (Sernander 1906, Berg 1975,

van der Pijl 1982). Though ants usually transport seeds only short distances, myrmecochory may increase seedling recruitment in several ways (e.g., seeds may escape from competitors or predators, or seedling growth may be enhanced in nutrient-enriched ant-nest soils) (Culver and Beattie 1978, Handel 1978, Heithaus et al. 1980, O'Dowd and Hay 1980, Davidson and Morton 1981, Westoby et al. 1982). The benefits a seed gains from dispersal depend on the behavior of the ant species that finds it and therefore on the composition of the ant community. Pudlo et al. (1980), for example, were able to relate different densities and dispersion of myrmecochorous woodland herbs to changes in ant communities.

In this paper, we address the question of what happens to a plant population when one guild of ground-foraging, seed-dispersing ants is replaced by another. *Iridomyrmex humilis*, the Argentine ant, has recently invaded fynbos shrublands of the southwestern Cape, South Africa. *Iridomyrmex* probably reached South Africa at the turn of the century (Prins 1978) but has been collected in undisturbed fynbos only recently (Mostert et al. 1980, D. Donnelly, *personal communication*, W. Bond and P. Slingsby, *personal observations*). As in other parts of the world, *Iridomyrmex* has replaced the dominant indigenous ants, radically altering the diversity and composition of native ant communities (Hattingh 1945, Skaife 1961, Crowell 1968). Myrmecochory is extremely common in the evergreen sclerophyllous shrublands of the Cape (Slingsby and

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² Present address: Department of Biology, University of California at Los Angeles, Los Angeles, California 90024 USA.

Bond 1981, Bond and Slingsby 1983). If the success of myrmecochorous plants depends on association with a coevolved guild of ants, then the *Iridomyrmex* invasion may have devastating effects on the Cape flora.

Fynbos is burnt by fires at intervals of 3 to >60 yr; shrubs survive either by stump-sprouting or as seeds (Kruger 1977). Seedling establishment is virtually confined to the immediate postfire period (Kruger 1977), so it is relatively easy to follow the influence of dispersal on population growth. This study was designed to test the hypothesis that the Argentine ant, by replacing indigenous ants, disrupts a coevolved dispersal system and reduces seedling establishment. We concentrated particularly on the importance of seed predation in the absence of effective seed burial and dispersal. We studied the end effect of ant dispersal by observing patterns of seedling distribution and survival after fire in areas infested by *Iridomyrmex humilis*.

STUDY AREA

Fynbos in the vicinity of the Oudebos settlement in the Kogelberg State Forest has been invaded by *Iridomyrmex* and was used as a study site. Oudebos, which has been occupied by humans sporadically since the 1930s, lies on the southern boundary of Kogelberg in the Palmiet River Valley (34°20'S, 18°58'E). It is a broad, low-lying (<150 m) valley with gentle slopes enclosed by the steep flanks of surrounding mountains. It has a mediterranean climate with relatively mild temperatures and an annual rainfall of 700–800 mm concentrated in the winter months. The geology is varied; much of the valley lies on shaleband and has hard, loamy, yellowish-brown soils. The steeper mountain slopes are on quartzitic sandstones and tillites and have shallow, rocky, pale, sandy soils.

The vegetation includes areas of old cultivation and pine and eucalypt windbelts, especially on shaleband soils, and undisturbed fynbos communities. Boucher (1978) has given detailed descriptions of climate, soils, geology, and vegetation of the area. *Mimetes cucullatus* (L.) R. Br. (Proteaceae) is a common and widespread species that usually survives fires by sprouting from an underground lignotuber. The fruit of *M. cucullatus* is an achene (hereafter referred to as a seed) ≈6 mm long and with an elaiosome at both distal and proximal ends.

METHODS

Influence of Iridomyrmex on seed dispersal

We used ant and rodent exclosures to assess rates of predation in the absence of dispersal. Exclosure experiments were replicated at five sites. Three sites were in habitats infested with Argentine ants and two were in noninfested habitats. Sites 1 and 2 had native ant faunas and were located in low, ericoid-restioid shrubland on shallow, stony pale sands. Sites 3, 4, and 5 were infested with *Iridomyrmex*. Site 3 was in tall er-

icoid-graminoid shrubland and road-verge on hard, moderately deep, yellowish-brown loam. Sites 4 and 5 were in medium-height ericoid shrubland with scattered Proteaceae on shallow, stony pale sands. Experiments began on 4 April 1982 at site 3 and 5 April 1982 at all the other sites, and ended on 7 April 1982.

At each site, we established a grid in which two lines, spaced 10 m or more apart, each had four stations at 5 m intervals. Sites 1 (native ants only) and 3 (Argentine ants present) included both vertebrate and ant exclosure treatments. A 15-mm wire mesh cage the size and shape of an inverted wastepaper basket was placed at each of the eight stations at each of these two sites. The cages were secured to the ground by iron pegs. The cages excluded birds and small mammals, but allowed free passage to ants carrying seeds. Two wooden boards were placed under each exclosure. Five fresh seeds of *Mimetes cucullatus* were placed loosely on one board; five more fresh seeds were glued to the second board with a glue that was colorless and odorless (to humans) when dry. The loose seeds were accessible to ants but not to small mammals; the glued seeds were inaccessible to both ants and mammals, and were used as a control on the efficiency of the exclosures. A third board was placed 2 m from the cages, and five seeds were glued to it. This board excluded ants but was accessible to vertebrate predators.

The three remaining sites had only two treatments, one with seeds free and one with seeds glued to the wooden board at each station. Vertebrates were not excluded.

Grids were checked at least once daily for numbers and fate of seed remaining in each exclosure. A circle of radius 0.5 m around each station was searched for seed or seed remnants.

Influence of Iridomyrmex on seedling emergence and distribution

We studied the effect of the Argentine ant on seedling recruitment by feeding seeds to ants shortly before a fire. Fresh seed depots were established on 12 April in three separate areas. Area A was infested by *Iridomyrmex*; area B did not contain *Iridomyrmex*; area C straddled the boundary between infested and noninfested habitats. In area A and area B we laid out six depots of 25 seeds each in two parallel rows 25 m apart, with three depots in each row spaced 25 m apart. Area C had four depots of 25 seeds each spaced 25 m apart in two parallel rows. The closest proximity of any naturally occurring *M. cucullatus* to any depot group was >100 m.

All three experimental areas were burnt in a prescribed fire on 5 May. After the fire, we mapped seedling distribution and densities at the experimental areas and also under naturally occurring *M. cucullatus* shrubs in both infested and noninfested habitats. We report results of seedling censuses up to 21 July.

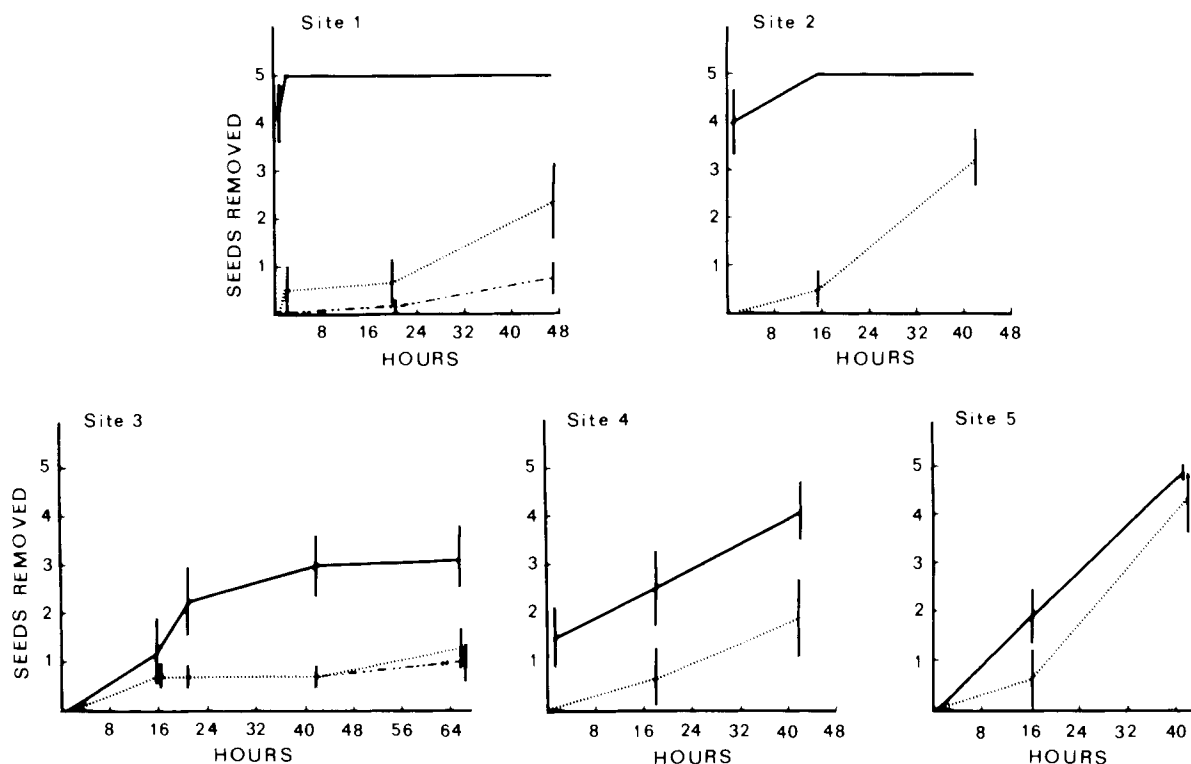


FIG. 1. Seed removal rates in enclosure trials. The horizontal axis is time after initiating the experiment; the vertical axis is mean number of seed removed from eight depots of five seeds each. Vertical bars are ± 1 SE. — loose seed under 15-mm wire mesh cages at sites 1 and 3; - - - seed glued to wooden boards under 15-mm wire mesh cages (ants and vertebrates excluded); seed glued to wooden boards outside enclosures (accessible to rodents but not to ants). *Iridomyrmex* was absent in site 1, which had rodent enclosures, and site 2. *Iridomyrmex* was present in site 3, which had rodent enclosures, site 4, and site 5. Error bars = ± 1 SE.

Distribution of *Iridomyrmex*

To disrupt seed dispersal significantly, *Iridomyrmex* would have to dominate or replace native elaiosome-gathering ants. The distributions of *Iridomyrmex* and native ants were mapped from their incidence at meat baits placed in transects throughout the study area.

RESULTS

Influence of Iridomyrmex on seed dispersal

Removal rates.—Seed removal by native ants was very rapid. Eighty percent of the loose seed was removed <30 min after we set up the enclosure experiments; 100% was removed by the end of the first day. Ants were recruited in large numbers and seed was transported to the nests. Only one of two species—*Anaplolepis custodiens* or *Pheidole capensis*—was active at each depot. *A. custodiens* dominated at site 1 (6 out of 8 stations), and *P. capensis* dominated at site 2 (6 out of 8 stations).

Seed removal in habitats infested by *Iridomyrmex* was much slower (Fig. 1), and we seldom observed any seed removal by this species. Only 44% (range 37.6–

50%) of the loose seed was removed (by both ants and seed predators) during the first day.

Fate of loose seed.—We observed ants removing seeds and burying them from all except one station (five seeds) in the Argentine-free areas. All the seeds we were able to follow were buried, and we therefore assume 100% burial. In later observations, we did not find any seeds in the vicinity of the nests. (In comparable experiments with *Leucospermum* [W. Bond and P. Slingsby, *personal observations*], up to 25% of the seeds taken into a nest were ejected within 48 h.)

In *Iridomyrmex*-infested areas, seed typically was carried <5 cm from a board. The ants made no attempt to carry the seeds to a nest. Instead they dragged them into shallow hollows between roots or under leaves on the soil surface or, most frequently, under the wooden boards themselves.

Fate of seed glued to wooden boards outside the cages.—The amount of seed eaten by predators varied greatly among different sites (Tables 1, 2, and 3). Shrew and rodent predation was recognized by the presence of fragments or neatly opened seed husks similar to those found during laboratory feeding trials. Invertebrate predation was characterized by ragged-edged holes

TABLE 1. Seed loss from depots where ants or both ants and vertebrates were excluded. Five seeds per depot were presented at each of eight stations at each site. The proportion of depots with husks chewed by rodents or shrews is in parentheses. + = *Iridomyrmex* present; - = *Iridomyrmex* absent.

Depot group	<i>Irido- myrmex</i>	Number of days			P†
		0	1	2	
Vertebrates and ants excluded		No. seeds remaining			
a (Site 1)	-	40 (0)	39 (0)	34 (0)	NS (a, b)
b (Site 3)	+	40 (0)	38 (0)	38 (0)	
Ants excluded					
c (Site 1)	-	40 (0)	35 (0)	21 (.25)	** (a, c)
d (Site 2)	-	40 (0)	36 (0)	14 (0)	** (a, d)
e (Site 3)	+	40 (0)	38 (0)	38 (0)	NS (a, e)
f (Site 4)	+	40 (0)	35 (.13)	25 (.25)	* (a, f)
g (Site 5)	+	40 (0)	35 (.13)	6 (.75)	** (a, g)

† Fisher's Exact Test between the depot groups indicated in parentheses. NS = $P > .05$, * $P < .05$, ** $P < .01$.

chewed through the pericarp of the seed. Piecemeal attack was typical of invertebrates; vertebrates typically removed all seeds from the wooden board. Millipedes were seen feeding on seeds. Other invertebrates, such as beetles, were not seen but were probably involved. Sources of predation were measured by direct physical evidence only, and loss due to vertebrates was probably underestimated (e.g., site 2, Table 1).

The maximum loss of glued-down seed due to invertebrate predators (Table 3) was 37.5% in noninfested habitat (site 2) and 27.5% with *Iridomyrmex* present (site 3). Maximum seed loss due to vertebrate predators was 22.5% in noninfested habitat (site 1) and 72.5% in infested habitat (site 5). The differences probably reflect local small-mammal densities unrelated to the presence or absence of *Iridomyrmex*.

The fates of seed available to ants and of seed not available to ants are shown in Tables 2 and 3. In most of the trials with Argentine ants present, some seeds

could not be accounted for (labelled "Fate unknown" in Tables 2 and 3). Perhaps these seed were dispersed and buried and will escape predation. Since the mean proportion of loose seed unknowns in the three *Iridomyrmex* localities was only 22.5% of the seed (range 10–40%), dispersal by Argentine ants is, at best, less than one-half as effective as dispersal by indigenous ants.

Influence of Iridomyrmex on seedling establishment

The size of seedling populations was strongly dependent on the presence or absence of the Argentine ant. Only one seedling (0.67% of seeds offered in depots) emerged in the infested area, whereas 53 seedlings (35.3%) emerged in the noninfested area. The mean number of seedlings per replicate was 8.8 (SD = 2.32) in the noninfested area; it was 0.2 (SD = 0.41) with *Iridomyrmex* present ($P < .001$, t test).

Iridomyrmex humilis and *Tetramorium quadrispinosum* were both present in area A. The latter is an indigenous ant that seems capable of an uneasy co-existence with *I. humilis*. It has been observed taking elaiosome-bearing seed but is slow-moving and lacks the large colony structure of the dominant seed-dispersing ants.

Common ants in area B were *Anaplolepis steingroeveri*, *Pheidole capensis*, *T. quadrispinosum*, and *Camponotus niveosetosus*. No *Iridomyrmex* was present. Seedlings occurred in groups, and each group was associated with ant nests or nest holes. The 53 seedlings fell into 18 groups. Twelve groups (42 seedlings) were associated with *A. steingroeveri* nests and 6 groups (11 seedlings) with *P. capensis* nests.

Area C straddled the boundary of Argentine-infested habitat. No seedlings emerged on the *Iridomyrmex* side. On the indigenous-ant side, five seedlings emerged, apparently originating from one depot, and all from a *P. capensis* nest.

TABLE 2. Fate of seed exposed and accessible to ants. At each site, loose seeds ($n = 40$) were placed in a grid of eight stations with five seeds at each station. Differences between numbers of seeds dispersed and buried (or fate unknown) and numbers of seeds not buried or eaten were significant for all comparisons between site 1 and sites 3, 4, and 5 ($P < .01$, Fisher's Exact Test).

Area	Number of seeds					Fate un- known
	Dis- persed + buried > 50 cm	Dispersed + not buried		Eaten		
		0 cm	< 10 cm	by verts.	by in- verts.	
<i>Iridomyrmex</i> absent						
Site 1	40	0	0	0	0	0
Site 2	40	0	0	0	0	0
<i>Iridomyrmex</i> present						
Site 3	0	15	8	0	1	16
Site 4	0	6	20	5	5	4
Site 5	0	1	10	22	0	7

TABLE 3. Fate of seed ($n = 40$) glued to wooden blocks and therefore unavailable to ants. Experimental layout as in Table 2.

Area	Number of seeds			
	Not removed	Eaten		Fate unknown
		by verts.	by in-verts.	
<i>Iridomyrmex</i> absent				
Site 1	21	9	3	7
Site 2	14	0	15	11
<i>Iridomyrmex</i> present				
Site 3	29	0	11	0
Site 4	25	10	5	0
Site 5	6	29	2	3

Observations on naturally occurring populations of *Mimetes* burnt in the same fire further demonstrated the disruptive effect of *Iridomyrmex* on seed dispersal and seedling establishment (Fig. 2). In the infested habitat, seedlings were found only in the area that, before the fire, was below the crown of the parent plant, where there would be little chance of surviving in competition with sprouting parents. The hypocotyls of 30 excavated seedlings were each shorter than 12 mm, suggesting germination occurred from seed in the unburnt litter layer. In the noninfested habitat, seedlings were both better dispersed (only 25% were found below the crown) and more abundant. The average hypocotyl length of 30 excavated seedlings was 43 mm, suggesting that most seed germinated below the soil surface. Ants found in the area included *Anaplolepis steingroeveri* and *Pheidole capensis*.

Distribution of *Iridomyrmex*

Iridomyrmex has colonized 38 ha of the Kogelberg Valley and has completely displaced the dominant indigenous ants: *Pheidole capensis*, *Anaplolepis steingroeveri*, and *A. custodiens*. None of these species was recorded at baits within the infested area, but all were common on baits outside it, so the boundary between infested and noninfested habitats could be precisely drawn (Table 4).

TABLE 4. Distribution of *Iridomyrmex* and native ants inside and outside the infested area. The data are number of baits (out of 240) at which a species was recorded in transects traversing the Oudebos Valley (Dash = not recorded.) *C. transvaalensis* is an arboreal nester.

Species	Inside infested area	Outside infested area
<i>Iridomyrmex humilis</i>	104	...
<i>Tetramorium quadrispinosum</i>	6	2
<i>Crematogaster transvaalensis</i>	5	45
<i>Pheidole capensis</i>	...	56
<i>Anaplolepis steingroeveri</i>	...	9
<i>A. custodiens</i>	...	3

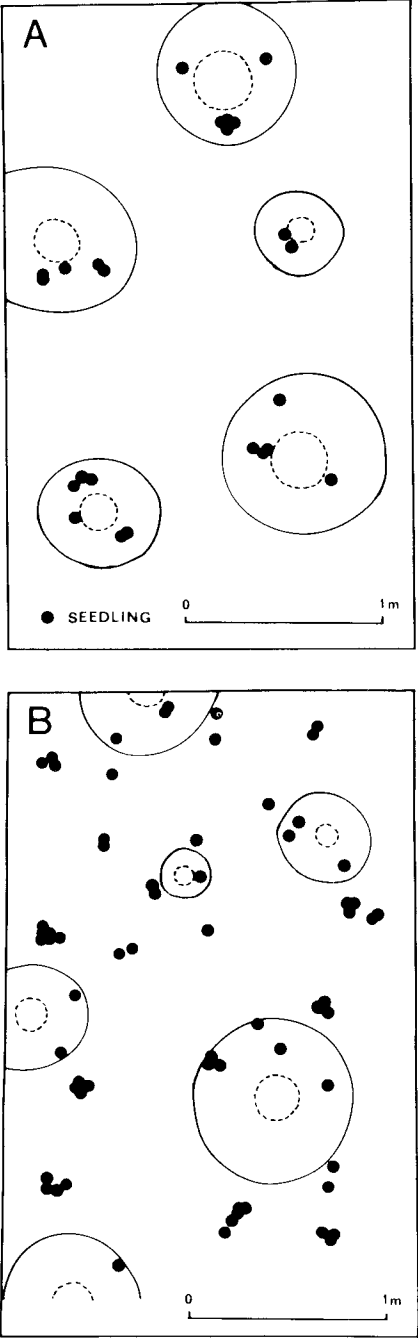


FIG. 2. Seedling dispersion in *Mimetes cucullatus* populations after a burn. A, *Iridomyrmex* present; B, *Iridomyrmex* absent. Solid lines delineate the approximate spread of burned branches; dashed lines, the spread of the rootstock.

DISCUSSION

The importance of mutualism in structuring communities is still poorly understood (Boucher et al. 1982). Gilbert (1980) has postulated the existence of “key-stone” mutualists whose demise would lead to major

community change. The invasion of Cape fynbos by *Iridomyrmex* provides an extreme example of disruption of a mutualism involving many plant species and only a small number of ant species. The keystone concept can be examined by observing how plant species respond to the replacement of their seed dispersers by *Iridomyrmex* and how the ant may effect the collapse of the interaction.

Our data show that *Mimetes cucullatus* seedling recruitment is significantly affected by the invasion of *Iridomyrmex*. *Mimetes* seedling densities shortly after germination were 50-fold higher in native ant sites than in sites infested by *Iridomyrmex*. The difference is probably due to seed escape from predators or to favorable nest conditions for germination rather than to more vigorous seedling growth in nutrient-enriched ant nests (cf. Davidson and Morton 1981, Culver and Beattie 1983). Effects of the latter would be more delayed. In similar studies with *Leucospermum glabrum* Phill. and *Mimetes pauciflorus* R. Br., seed loss to predators when ants were excluded varied from 25 to 90% over a 48-h period, increasing to 100% if experiments were repeated at the same site (W. Bond and J. Breytenbach, *personal observations*). All myrmecochorous Proteaceae with relatively large seeds (e.g., *Leucospermum*, *Leucadendron*, *Paranomus*, *Orothamnus*, *Mimetes*) share a dispersal process similar to that for *Mimetes cucullatus* (Slingsby and Bond 1981). The effects of *Iridomyrmex* invasion reported here may therefore be applicable to many of the >170 species of ant-dispersed Cape Proteaceae.

Differences in behavior between *Iridomyrmex* and its indigenous competitors, especially *Anaplolepis* and *Pheidole*, suggest three critical aspects of the ant-plant interaction that are essential for successful seedling recruitment. First, indigenous ants respond extremely rapidly to seeds that have elaiosomes. In contrast, the Argentine ant was slow at finding seed, and this resulted in greater rates of seed predation. There is some evidence that seeds release a signal that attracts coevolved ants and that *Iridomyrmex* fails to recognize this signal. Fynbos rodents have been shown in laboratory experiments to be significantly better at finding seeds with elaiosomes than at finding seeds without elaiosomes (J. Breytenbach, *personal communication*). Furthermore, *Anaplolepis custodiens* populations in semidesert shrubland and savannah (both of which have no contact with ant-dispersed Proteaceae) ignore artificially introduced Proteaceae elaiosomes (G. Burger, *personal communication*, W. Bond, *personal observations*).

Second, native ants transported seeds to their nests before feeding on the elaiosomes. In contrast, *Iridomyrmex* moved seeds for very short distances (mostly <10 cm) and did not take them into nests. Instead, they left seed exposed on the soil surface or transported seed under leaves, into shallow hollows between superficial roots, or (as shown in several of our experi-

ments) under the wooden blocks. Thus seeds remained vulnerable after dispersal.

Third, both *Anaplolepis* and *Pheidole* build subterranean nests with galleries and channels well suited to seed storage away from fire and predators (Steyn 1954, Skaife 1961, Bond and Slingsby 1983) and in which seeds germinate and seedlings become established. In contrast, *Iridomyrmex* builds superficial nests beneath stones and logs, under decaying vegetation, or in the mass of roots at the foot of shrubs (Skaife 1961, W. Bond and P. Slingsby, *personal observations*) from which very few seedlings emerge.

Both the speed of seed discovery by native fynbos ants and the subsequent transport of seeds to their nests are possible evidence of coevolution. Any benefits of nest structure, however, are probably fortuitous. *Anaplolepis* nests are similar over large parts of southern Africa (Steyn 1954), but myrmecochory is common only in the Cape (Bond and Slingsby 1983).

Our data suggest that the ant-plant interaction is mutualistic, that myrmecochory is obligatory, and that plants benefit primarily through lessened seed predation. Only complete displacement of the indigenous ants by another ant with quite different habits shows the dependence of the plant populations on the dispersal process and reveals the keystone nature of the dispersal agents.

We know too little of the biology of *Iridomyrmex* or of seed longevity in the soil to predict future areas of invasion or rates of local plant extinction. Censuses of *Iridomyrmex* at Kogelberg and elsewhere in the southwestern Cape (Skaife 1961, D. Donnelly, *personal communication*), demonstrate that *Iridomyrmex* can oust the native ant fauna in a variety of fynbos habitats. There is good circumstantial evidence that myrmecochorous Proteaceae seed may remain viable in the soil for at least 15 yr (Rourke 1976). The effects of the Argentine ant on seedling recruitment thus may only appear decades after invasion. This study merely suggests the possible magnitude of those effects. Unless the spread of the Argentine ant is checked, we believe that by slow and subtle attrition of seed reserves many ant-dispersed species, including a large proportion of the Cape's most spectacular, rare, and endemic Proteaceae, will be driven to extinction.

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