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COMPETITIVE DISPLACEMENT AMONG INSECTS AND ARACHNIDS*

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■ **Abstract** Competitive displacement is the most severe outcome of interspecific competition. For the purposes of this review, we define this type of displacement as the removal of a formerly established species from a habitat as a result of direct or indirect competitive interactions with another species. We reviewed the literature for recent putative cases of competitive displacement among insects and arachnids and assessed the evidence for the role of interspecific competition in these displacements. We found evidence for mechanisms of both exploitation and interference competition operating in these cases of competitive displacement. Many of the cases that we identified involve the operation of more than one competitive mechanism, and many cases were mediated by other noncompetitive factors. Most, but not all, of these displacements occurred between closely related species. In the majority of cases, exotic species displaced native species or previously established exotic species, often in anthropogenically-altered habitats. The cases that we identified have occurred across a broad range of taxa and environments. Therefore we suggest that competitive displacement has the potential to be a widespread phenomenon, and the frequency of these displacement events may increase, given the ever-increasing degree of anthropogenic changes to the environment. A greater awareness of competitive displacement events should lead to more studies documenting the relative importance of key factors and developing hypotheses that explain observed patterns.

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INTRODUCTION

The prevalence and importance of interspecific competition has been one of the most intensely debated topics in ecology. Historically, interspecific competition was considered a fundamental mechanism in structuring communities (30, 55, 101). However, the importance of interspecific competition in the organization of communities was disputed during the 1970s and 1980s, especially for phytophagous arthropods (23, 173, 176). In part, this debate arose from the difficulty in demonstrating that competitive interspecific interactions had occurred, or continued to occur other than under simplified field or laboratory conditions (151).

Such arguments have stimulated more research that has shown interspecific competition to be a widespread phenomenon among species of almost all taxa, including arthropods (93). Recent reviews (29, 35, 165) provide compelling evidence that supports the importance of interspecific competition as a mechanism structuring phytophagous arthropod communities despite assumptions that food is not limiting for these species (55). Likewise, there is strong empirical support for the presence of interspecific competition in other arthropod communities, such as parasitoids (118), omnivores (72), and predators (68).

Given that interspecific competition can and does operate in arthropod communities, numerous outcomes for these interspecific interactions are possible. In the most severe asymmetric form of interspecific competition, a species will be unable to occupy the same spatio-temporal habitat as a superior competitor. If a superior competitor invades the habitat of an inferior species, the inferior species will be displaced (i.e., competitive displacement occurs).

Over three decades ago, DeBach (31) reviewed underlying principles and cases of competitive displacement. He defined competitive displacement as "the elimination, in a given habitat, of one species by another where one possesses the identical ecological niche of the other." At that time there were relatively few well-documented cases. However, recent events in a variety of different systems, as outlined below, suggest that competitive displacement among insects and arachnids is a more frequent, and perhaps common, phenomenon than has been recognized.

Such displacement events have practical and theoretical importance. Practical concerns arise from the environmental and economic impact when one species displaces another. Beyond the proximate outcome of one species being displaced, displacement events form natural experiments, which can be used to demonstrate the impact of interspecific competition on communities and how competition can alter the evolutionary history of the interacting species, as well as other associated species. Furthermore, the frequency of these displacement events likely will increase, given the ever-increasing degree of anthropogenic changes to the environment (e.g., increasing numbers of introductions and invasions of exotic species, global climate change) (53, 120). As such, a review and analysis of competitive displacement appears timely.

The objectives of our review are to examine the relevant literature for cases in which competitive displacement is thought to have occurred or is occurring, determine what mechanisms of interspecific competition may contribute to these displacements, and assess the impact of such displacements. In so doing, we update and extend the database of DeBach (31). Although many of the species we discuss have been introduced or occur in other regions of the world than those we present, we limit the discussion to situations where displacements have been documented best. A major complication with an analysis of competitive displacement is that many accounts are anecdotal and incomplete (161). The process has rarely been documented adequately, let alone empirically examined. This lack of rigorous attention, although understandable, is unfortunate because such situations provide natural experiments for testing competition theories and examining mechanisms of competition. These situations also provide a framework for understanding and mitigating the impact of introduced species.

For each putative case of displacement, we address the following questions: (*a*) Is there evidence that displacement has occurred through competition? (*b*) If so, what mechanisms are responsible for displacement? (*c*) What is the extent of the displacement? (*d*) What impact has the displacement had on the species and systems involved?

METHODS

For the purposes of this review, we modify DeBach's definition (31) and define competitive displacement as the removal of a formerly established species from a habitat through superior use, acquisition, or defense of resources by another species. In doing so, we wish to emphasize the value of considering mechanisms of competition that lead to displacement. Although competition encompasses many types of interactions, from symmetric to asymmetric forms, we focus on asymmetric competition leading to displacement. As DeBach (31) points out, the displacement of an established species is more likely to occur than its complete exclusion. He also recognized that displacement is not necessarily a "black and white" issue. The habitat where displacement occurs may be a subset of habitats that each species can occupy, and the interactions can be mediated by other noncompetitive factors. As displacements are historical processes, there is a temporal as well as spatial component inherent in the definition. Because timescales for arthropods differ among species and from those of humans, the temporal component cannot be explicitly defined.

We reviewed ecological and entomological literature published since DeBach's seminal 1966 review (31) for putative cases of competitive displacement. To determine if displacement in these cases resulted from competition, we assessed the status of each species before and after displacement, mechanisms of competition involved, and other mediating factors that could influence competitive interactions and displacements.

Competitive mechanisms can be categorized broadly as either exploitation or interference (5). In exploitation competition, individuals of one species acquire resources to a greater extent than individuals of another species. Interference competition results from members of one species limiting or denying individuals of another species access to resources. Collectively when such interactions between members of competing species are predominantly asymmetric, they can lead to displacement of populations. These types of competition are not mutually exclusive, and more than one type could be operating in individual cases.

A prerequisite for the occurrence of competitive displacement is that a system has undergone an alteration from a previous state to allow the displacement to occur. In many cases, the alteration involves colonization by a new (superior) competitor that displaces and excludes a previously established species. Other scenarios are possible, including alterations of biotic factors that shift the competitive balance between previously coexisting species or the evolution of coexisting species that allows one to displace the other.

By definition, active cases of competitive displacement (i.e., those in progress) comprise a small proportion of all cases because most cases have gone to completion. Because these events are unplanned natural experiments, reliable data collected before and after the displacement are scarce. Circumstances of unstudied historic cases that have gone to completion cannot be reconstructed conclusively although hypotheses about the causal factors may be reasonably inferred. We recognize that portions of the existing data are post-hoc or anecdotal, and causal factors must be inferred with caution. Experimental results that address mechanisms are available for certain systems. Therefore we present evidence for and against probable mechanisms where appropriate.

The extent of the displacement encompasses the scale to which one species has been displaced and excluded. The most dramatic form is when a species is displaced from multiple habitats across a broad geographic area. However, displacements can occur on other scales. Species may be displaced from a particular microhabitat or a particular host, as in the case of polyphagous species. Multivoltine species may be displaced from a habitat at certain times by superior competitors but may persist in that same habitat during other seasons.

Displacement can occur at these scales, rather than just across large geographic areas, if species are distributed as metapopulations, which then allows for a degree of persistence by the displaced species (58). Populations in favorable environments will be more likely to persist than those in less favorable environments. Because displacement is an ongoing process, emigrants may recolonize areas only to be displaced.

RESULTS

Mechanisms of Competition Leading to Displacement

Most displacements that we have identified were triggered by the introduction or invasion of an exotic species (78%), although other environmental factors may predispose a species to being displaced (e.g., 50, 57, 123). Polyphagy and the lack of natural enemies often characterize invasive species that have large impacts on communities. Such invasive species typically have their greatest impact on simple and anthropogenically disturbed habitats (97).

We identified eight general mechanisms of interspecific competition that have contributed to the cases of displacement. Because competitive ability is an assessment of an interspecific relationship rather than an inherent species characteristic, competitive displacement is dynamic and results from differences between species in the context of the environments where they interact. We also identified four factors that mediate these competitive interactions that lead to displacement. Schreiber & Gutierrez (152) provide a physiological ecology model that predicts the outcome of competitive interactions between invading and established species. They define a metabolic compensation point as the ratio of prey biomass to consumer demand at which prey assimilation compensates for metabolic costs. Hence, the species with the lower metabolic compensation point will displace the other. When competing species have shared predators, the prediction is that the species with the lower ecological compensation point (i.e., the ratio of prey biomass to total consumer demand when the prey-consumer-predator food chain is at equilibrium) will displace the species with the higher ecological compensation point. This model provides a framework to generate hypotheses concerning displacement and can be applied to the general mechanisms that we identified in the following cases of displacement.

DIFFERENTIAL RESOURCE ACQUISITION In this form of exploitation competition, all individuals have potential access to resources. However, when individuals of one species garner sufficient resources while individuals of another species cannot obtain sufficient resources, the latter species will be displaced. This differential resource acquisition is not driven by agonistic interactions, but by the intrinsic abilities of the species to obtain resources. These differences can be manifested as differences in resource harvesting (see 65) or differential growth rate and survivorship (67).

DIFFERENTIAL FEMALE FECUNDITY When one species has greater realized fecundity than a competitor, that competitor will be displaced (34). This mechanism applies not just to numbers of offspring, but also to the ability to produce proportionately more females from the same resources. However, distinguishing interspecific differences in the number of eggs produced versus the number of offspring recruited into the population can be difficult because differences in realized fecundity may reflect other factors that affect offspring survival and not just intrinsic differences in the reproductive capacity of each species. For example, escape from natural enemies confers a significant reproductive advantage to many exotic species (49, 117).

DIFFERENTIAL SEARCHING ABILITY Differential searching ability is a form of exploitation competition where superior searchers locate and exploit resources faster than competitors. Thus over time, the superior searchers reduce the resource pool available to competitors. Differential searching behavior can occur between species in their location of ephemeral or discrete resources (e.g., ants locating baits, predators locating prey, or parasitoids locating hosts). Generally there is a trade-off in competitive skills; often a species with higher searching abilities is inferior in contest type competitions (20, 137), although this is not always the case (73, 77).

RESOURCE PREEMPTION Resource preemption occurs when a species utilizes critical resources before they become available to a competitor. This type of competition is not limited to species of a particular feeding guild, or to a particular resource. For example, by attacking younger life stages of a common host than stages attacked by competitors, one parasitoid species diminishes the potential number of hosts available to its competitors and can displace those competitors (100, 118). Likewise, a phytophagous species that consumes host plants before the foliage is suitable for another species (153), or before fruit has set (11, 25), can displace that species. Resource preemption also includes instances when species gain a competitive advantage by having an earlier seasonal phenology compared with competitors.

RESOURCE DEGRADATION Another factor leading to competitive displacement is the degradation of a resource by one species below the requirements for another. Unlike differential resource acquisition or resource preemption, a resource (e.g., food or breeding site) is still present but has been qualitatively degraded or altered by the actions of one species so that the development of individuals of another species is inhibited (41, 47, 75, 86). Therefore recruitment decreases, and over time, the inferior species is displaced.

AGONISTIC INTERFERENCE COMPETITION Agonistic interactions are a form of interference competition where direct physical interactions occur between individuals, and the winner gains control of contested resources. Contests can be over discrete food resources, foraging sites, territory, or oviposition sites, and can occur between larvae or adults. The intensity of interactions lies on a continuum from nonlethal interactions (e.g., ritualized displays) to use of repellent chemicals, nonlethal combat, or lethal fighting. For example, larval competition is one mechanism leading to the competitive displacement of parasitoids introduced in classical biological control programs. In these cases, larvae attack one another, with the superior fighter gaining control of the host (e.g., 16, 39, 106, 136). Ants commonly fight for access to resources or territory. While these interactions often involve lethal combat, other Hymenoptera may contest foraging sites in a nonlethal manner. Given enough of these interactions, displacement of an inferior competitor occurs.

REPRODUCTIVE INTERFERENCE A form of interference that does not involve direct mortality is reproductive interference. In these cases, displacement is driven by a lack of courtship and mating discrimination between species. For reproductive interference to lead to competitive displacement, one of the following situations must be present. Males of one species do not discriminate between conspecific and heterospecific females as much as males of a second species. Alternatively, females of one species discriminate against interspecific matings more than females of another species (90). In either event, one species, in effect, competes with the other for mates. When such a bias in interspecific courtship and mating behavior occurs, females of one species are rendered less fecund and displacement results (119, 130, 167, 183). McLain (113) cites a case where aggressive mating tactics of male *Neacoryphus bicrucis* (Heteroptera: Lygaeidae) led other herbivores to abandon *Senecio smallii* as a host plant. Although displacement occurs, it is not through competition because the interactions are independent of actual resource use.

INTRAGUILD PREDATION Another form of interference competition contributing to displacement is intraguild predation. This type of interaction involves predation among species at the same trophic level (37, 139, 146). Intraguild predation occurs when a predator attacks another predator (68, 103). Intraguild predation also includes when facultative hyperparasitoids, which can parasitize herbivores, alternatively parasitize primary parasitoids of that herbivore (146, 181), or when phytophages consume plant material that contains another phytophage (2).

Factors That Mediate Displacement

LACK OF ALTERNATIVE HOST/FOOD SOURCES The lack of alternative hosts effectively renders polyphagous species monophagous and therefore increases the intensity of competition. When species compete under such circumstances, the species better adapted to the common host or habitat should displace the other. Therefore, introduced species, especially introduced biological control agents intended to target a single pest species, may be prone to displacement because they lack refugia from superior competitors (see 35).

DIFFERENTIAL IMPACT OF NATURAL ENEMIES Exotic species typically are not introduced with their natural enemies (33). This escape from natural enemies confers a tremendous advantage when exotic species compete with native species, which still must contend with their natural enemies. This advantage is expressed as an increase in realized fecundity of the exotic species, or alternatively, as enabling a species to allocate more resources to aggressive interactions.

METAPOPULATION STRUCTURE When a species has a metapopulation structure, subpopulations are distributed across variable habitats and are linked by dispersal (58). Some subpopulations will be in habitats to which they are well adapted; others will be in less favorable habitats. In these cases, population sinks (i.e., where mortality and emigration exceed reproduction) only persist through immigration from source populations located in favorable habitats. If interspecific competition becomes intense by the introduction of a superior species, recruitment and dispersal will be reduced, increasing the probability of displacement of population sinks.

ADAPTATIONS TO LOCAL CONDITIONS The outcome of interspecific competitive interactions can be contingent on many abiotic or other environmental factors. Therefore displacements can be limited, or even reversed, as conditions vary. Conditions that mediate competitive interactions include differences in climatic tolerances, abilities to contend with host defenses, or anthropogenically produced conditions such as insecticide use leading to resistance.

Displacements and Their Extent

Of the putative cases of competitive displacement we examined, there is evidence to support interspecific competition in 42 cases (Table 1, see the Supplemental Material link at www.annualreviews.org). In six other cases, interspecific competition likely accounts for changes in species status. The 42 cases of competitive displacement that we identified are taxonomically diverse. Half of these occurrences were between species of the same genus, with the others occurring between species of different genera, families, or orders (Table 1, see the Supplemental Material link at www.annualreviews.org). In eight cases, multiple species were displaced by one species.

Not surprisingly, numerous cases (33%) involve exotic species displacing native species, but more cases (55%) involve the displacement of a previously established exotic by another exotic. These events include cases where the exotic species coexist sympatrically in their native habitats. Only 14% of the cases involve the displacement of one native species by another. The remaining cases comprise laboratory or field experiments that demonstrate potential cases of displacement among natural populations.

Displacements were not confined to any particular feeding guild. We found support for competitive displacement among parasitoids, predators, phytophages, and omnivores. The dataset described below is probably biased toward relatively conspicuous species and economically important systems. However, the widespread taxonomic distribution of the species lends support for competitive displacement being a widespread and prevalent phenomenon.

DISPLACEMENT IN BIOLOGICAL CONTROL Some of the most spectacular cases of displacement have occurred in classical biological control programs, especially those targeting exotic Homoptera (see 43, 44, 85 for discussion of competitive exclusion in classical biological control). In perhaps the best-known case of competitive displacement, *Aphytis melinus* displaced *Aphytis lingnanensis* as the primary parasitoid of *Aonidiella aurantii* in California citrus groves [case 37] (numbers in square brackets refer to respective Table 1 entries). This displacement followed the earlier displacement of *Aphytis chrysomphali* by *A. lingnanensis*. Both *A. lingnanensis* and *A. melinus* were introduced for control of *A. aurantii* but were imported from separate regions of Asia (31, 34). Both the displacement of *A. chrysomphali* and of *A. lingnanensis* occurred rapidly, within ten years of the introduction of their superior competitor. *A. melinus* displaced *A. lingnanensis* through resource preemption because it utilizes smaller hosts for production of female progeny than *A. lingnanensis* (100, 118). Therefore, the pool of potential hosts for *A. lingnanensis* is severely limited by *A. melinus*. In addition *A. melinus* produces proportionately more females from larger hosts, thereby increasing its recruitment and further depleting future resources for *A. lingnanensis*. As in other cases, the lack of alternative hosts contributed to the inability of *A. lingnanensis* to persist in this novel habitat.

In a situation with similar results but different mechanisms, two South American parasitoids were introduced into central and southern Africa for biological control of the exotic cassava mealybug, *Phenacoccus manihoti*, but only one of these parasitoids, *Apoanagyrus lopezi*, became established [case 38]. Although the two species are sympatric in South America (138), *A. lopezi* has competitively displaced and excluded *Apoanagyrus diversicornis* through at least three mechanisms in Africa (54, 136). *A. lopezi* larvae are superior competitors in multiply parasitized hosts and destroy larvae of *A. diversicornis* (136). *A. lopezi* also have greater searching efficiency for hosts and, like *A. melinus*, are able to produce females from smaller hosts than their competitor. Finally, *A. diversicornis* lacks any alternative hosts in Africa to aid its establishment in the presence of *A. lopezi* (138).

In another case of displacement occurring in a classical biological control program, *Bathyplectes anurus* has displaced *Bathyplectes curculionis*. Both are species introduced to North America for control of the exotic weevil *Hypera postica* [case 34]. *B. curculionis* was the first released and spread rapidly throughout the North American range of *H. postica* (87). *B. anurus* was released later but spread slowly despite being released in 38 states. However, as *B. anurus* established in eastern North America, it displaced *B. curculionis* (59, 89). The displacement was predicted by Dowell & Horn (39) and has been driven by multiple competitive differences between *B. anurus* and *B. curculionis*. In part, *B. anurus* is a more efficient searcher and has a greater reproductive potential (59). In addition, its larvae are able to eliminate competing heterospecifics (39) while escaping encapsulation by the host (59). Ironically, *B. anurus* prefers to attack hosts older than those attacked by *B. curculionis*, but these older hosts are more likely to escape fungal infections that are deleterious to the parasitoids. Likewise, *Aphidius ervi* has displaced *Aphidius smithi* as the predominant parasitoid of the aphid *Acyrthosiphon pisum* in North America [case 31]. In this case *A. smithi* was introduced first; however, between 1972 and 1981, populations of *A. smithi* declined rapidly in British

Columbia (102) with a concomitant increase in *A. ervi* populations. This displacement is driven through direct and indirect larval interactions and possibly superior searching by *A. ervi* females in mixed populations (16, 106). Similar increases in *A. ervi* populations in other regions are correlated with declines in *A. smithi* and other introduced *Aphidius* spp. (18, 20). In another similar case, the specialist parasitoid *Cotesia rubecula* has displaced the oligophagous *Cotesia glomerata* [case 32] as the predominant parasitoid of *Pieris rapae* in western North America (9, 180). In multiply parasitized *P. rapae* hosts, *C. rubecula* larvae eliminate *C. glomerata* (91). The specialist *C. rubecula* has a further advantage because *P. rapae* is a poor host for *C. glomerata* (13), and there are no alternative hosts for *C. glomerata* in North America.

Other widespread displacements of native parasitoids caused by introduced biological control agents have occurred. In Florida, *Aphytis holoxanthus* displaced *Pseudhomalopoda prima* as the predominant parasitoid of the scale *Chrysomphalus anoidum* [case 36], apparently through larval resource acquisition and resource degradation (157). Because *P. prima* is not a natural parasitoid of *C. anoidum*, this displacement represents a range contraction after its adoption of *C. anoidum* as a factitious host (8). In at least one case, a biological control agent introduced against one species has effectively utilized an alternative host and displaced biological control agents of that pest species. *Lysiphlebus testaceipes* was introduced into the Mediterranean region for biological control of *Aphis spiraecola* in citrus [case 33]. Since its introduction, it also has utilized *Toxoptera aurantii*, another citrus pest, as a host. In so doing, *L. testaceipes* has been displacing *Lysiphlebus confusus* and *Lysiphlebus fabarum* as parasitoids of *T. aurantii* (105, 169). Again, multiple interspecific biological differences, including *L. testaceipes*' greater longevity and proportion of female offspring produced, appear to account for this displacement (24). In a similar case, the egg-larval parasitoid *Copidosoma floridanum*, introduced into New Zealand for control of *Chrysodeixis eriosoma*, has displaced native egg parasitoids in the genus *Trichogrammatoidea* (see 76).

Williams (181) cites examples where the establishment of heteronomous aphelinid hyperparasitoids has led to the displacement of conventional aphelinid parasitoids through intraguild predation [case 35]. In testing the hypothesis that hyperparasitoids displace conventional parasitoids and disrupt biological control, Williams (181) demonstrated that the hyperparasitoid *Encarsia tricolor* eliminates the conventional parasitoid *Encarsia inaron*, and *E. inaron* cannot establish in existing populations of *E. tricolor*. The hyperparasitoid preferentially oviposits male eggs in heterospecific (i.e., conventional) parasitoid hosts rather than in conspecifics. The presence of the heterospecific larvae results in excess production of male *E. tricolor*, and this characteristic precludes the use of *E. tricolor* as a biological control agent.

Other possible cases of competitive displacement have been mentioned briefly in the literature but have not been investigated extensively. For example, Schuster & Dean (155) suggest *Anagyrus antoninae* has been displaced by its ecological homologue *Neodusmetia sangwani* [case 39]. The life histories of these introduced biological control agents of scales suggest that resource preemption could have driven the displacement (154).

As with parasitoids, certain predaceous coccinellids have been introduced as biological control agents and have displaced other predators. The widespread release and establishment of *Coccinella septempunctata* for aphid control has been associated with displacement of native Coccinellidae [case 16], such as *Coccinella novemnotata* across North America (45, 112, 178, 179). In apple orchards of West Virginia, *C. septempunctata* was first found in 1983 (15). It became the predominant species of Coccinellidae until *Harmonia axyridis* became established in 1994 and displaced it. *H. axyridis* displaces *C. septempunctata* [case 17] through intraguild predation (68, 168). Other increases in exotic coccinellids are correlated with declines in native species, such as *C. novemnotata* (178, 179). Therefore, more intraguild predation could be responsible for more competitive displacements.

DISPLACEMENT OF PHYTOPHAGOUS INSECT SPECIES Other broad-scale ecological displacements have occurred between exotic Homoptera. General characteristics of homopteran life history suggest this order is predisposed to strong interspecific competition (35). Several species that colonize perennial systems (e.g., orchards and tree farms) have been involved in displacement events. *A. aurantii*, the target host for *Aphytis* spp., displaced *Aonidiella citrina* in citrus groves of Southern California through exploitation mechanisms [case 13]. Both of these scales are exotic to California and were first reported in the late nineteenth century. Originally *A. citrina* was more predominant and widespread in Southern California (32). However, by 1930, populations of *A. aurantii* had begun increasing, and by 1970, *A. citrina* populations were displaced from Southern California. In an analysis of historical records and a series of laboratory experiments, DeBach et al. (32) concluded that *A. aurantii* has a higher reproductive rate, survivorship, and a broader feeding range on citrus than does *A. citrina*. They found no evidence of differential susceptibility to insecticides, natural enemies, or other environmental factors that would lead to the replacement of *A. citrina* by *A. aurantii*. Both species coexist in their native habitat (33), but in a simplified novel environment, such as citrus, displacement occurs because *A. citrina* does not have a refuge plant as it does in its native range.

In apple orchards of eastern North America, *A. spiraecola* has displaced *Aphis pomi* [case 10] as the primary aphid pest (14, 135). Because *A. spiraecola* was not recorded prior to the mid-1980s (135), this displacement must have occurred rapidly, possibly within ten years, and might have been mediated by human activities, as well as biological differences between the species (14, 70, 71). *A. spiraecola* has greater fecundity and is less susceptible to insecticides than *A. pomi* (70, 71). Despite the apparent shift in the aphid complex, both species have similar effects on apple trees so the impact of displacement has been neutral (83).

Similar widespread displacements of exotic Homoptera in perennial systems include the displacement of *Nuculaspis* (=*Tsugaspidiotus*) *tsugae* by *Fiorinia* *externa* [case 14] on eastern hemlock, *Tsuga canadensis*, in eastern North America (107). *F. externa* displaces *T. tsugae* because it colonizes trees earlier in the season than *N. tsugae* and monopolizes younger nitrogen-rich needles. *N. tsugae* is forced to use older nitrogen-poor needles and consequently suffers higher mortality. The negative effects of competition on *N. tsugae* are enhanced by parasitism from *Aspidiotiphagus citrinus*, which in turn is mediated by the interspecific competition. The larger summer populations of the univoltine *F. externa* are heavily parasitized by *A. citrinus*. As a result, there are disproportionately more second-generation parasitoids, produced from *F. externa*, available to parasitize the fall generation of the bivoltine *T. tsugae*.

The native *Pineus coloradensis* has been displaced from many red pine (*Pinus resinosa*) plantations in the northeastern United States by its Asian congener *Pineus boerneri* [case 11], which has become a serious pest (110). Feeding by *P. boerneri* severely damages pines and reduces host quality for *P. coloradensis*. This damage forces *P. coloradensis* to less suitable feeding sites, where it has low survivorship (109). *P. boerneri* is less affected by reductions in host quality and therefore establishes numerical dominance. *P. boerneri* represents another example of the transient nature of competitive displacement. Another exotic pest of red pine, *Matsucoccus resinosae*, became established in eastern North America after *P. boerneri*. Since its introduction, *M. resinosae* has displaced *P. boerneri* [case 12] in the same regions where *P. boerneri* displaced *P. coloradensis* and has done it through similar mechanisms (111).

Other cases of displacement by exotic Homoptera species have occurred in annual cropping systems. The highly polyphagous whitefly, *Bemisia argentifolii* [case 9], has displaced its congener *Bemisia tabaci* (7, 132). *B. argentifolii* was first reported as a different strain of *B. tabaci* in Florida and the southeastern United States during the mid-1980s (143). Once it was recognized as a separate species (7, 132), *B. argentifolii* had already displaced *B. tabaci* across the southwestern United States. This displacement has continued over large geographic areas, from Florida, through Texas, Arizona, to California, within a relatively short period of time (131). *B. argentifolii* has greater reproduction on common hosts and a broader host range than does *B. tabaci* (7, 130, 132). In addition, males of *B. argentifolii* court female *B. tabaci* more aggressively than *B. tabaci* males court *B. argentifolii* females. Therefore in mixed populations, fewer successful *B. tabaci* matings may occur, resulting in lower reproduction.

Rapid displacements between phytophagous insects whose larvae feed internally on plant tissues have been reported. Among stemborers of grains, the exotic *Chilo partellus* has been displacing the native *Busseola fusca* [case 27] in southern Africa (86). *C. partellus* emerges earlier and has more rapid development. In addition, *C. partellus* feeding damage deters *B. fusca* oviposition, conferring a further competitive advantage to *C. partellus*.

The Mediterranean fruit fly, *Ceratitis capitata*, has been displaced from most cultivated and feral host plants in Hawaii by *Bactrocera dorsalis* [case 22]. *C. capitata* was the first of these species to be introduced, in 1910, and became a common pest of fruits throughout the islands of the state. After the introduction of *B. dorsalis*, approximately in 1945, *C. capitata* became rare in the lowlands of Hawaii but it persists in abundance at higher elevation habitats not exploited by *B. dorsalis* (172). *B. dorsalis* has a higher net reproductive rate on certain hosts (171), and its larvae outcompete *C. capitata* through scramble competition and inhibit development of *C. capitata* (84). However, this competition is host mediated, to an extent; *C. capitata* persists in lowlands on coffee, a host plant to which it is better adapted (172).

There is also evidence for displacement between externally feeding phytophagous insects. On Guam, the exotic Lepidoptera, *Penicillaria jocosatrix*, almost completely displaced several native Lepidoptera, including *Anisodes illepidaria* [case 30], by exploiting food resources before they became suitable for the native species (153). A successful biological control program for *P. jocosatrix* has allowed populations of the displaced species to recover, demonstrating the influence of natural enemies as a mediating factor.

In several cases, changes in phytophagous species occurrence have been noted, but no direct evidence in support of competitive displacement has been reported. These cases warrant further investigations on the underlying mechanisms of displacement. For example, following its introduction from Florida, the leafmining fly *Liriomyza trifolii* rapidly replaced *Liriomyza sativae* [case 24] as the predominant leafminer of vegetables and ornamentals in California and other regions of the western United States (128, 170). Although *L. trifolii* populations were less susceptible to many insecticides (128, 144), no other biological differences were identified that would account for the replacement. More recently, *Liriomyza huidobrensis* has replaced *L. trifolii* [case 25] as the primary leafminer in Central California (38; S.R. Reitz & J.T. Trumble, unpublished data). This replacement correlates with a worldwide spread of *L. huidobrensis* that began in the late 1980s (see 177). Genetic variation among populations of *L. huidobrensis* suggests that possibly a new and more competitive strain was introduced recently into Central California (116). As with displacements of similar types of herbivores (e.g., *C. capitata*), differences in host plant utilization could contribute to this shift of *Liriomyza* species. *L. huidobrensis* and *L. trifolii* have overlapping host ranges but differ in their reproductive success on various hosts (S.R. Reitz & J.T. Trumble unpublished data). In addition, displacement could be driven by scramble competition among the larvae (133) and mediated by differential susceptibility to insecticides (177) and parasitoids (124).

In a similar manner, *Phoracantha semipunctata*, an exotic cerambycid borer of *Eucalyptus*, is being replaced in California by *Phoracantha recurva* [case 18]. This species shift combines elements of interspecific competition as well as natural enemy–mediated apparent competition (127; T.D. Paine, personal communication). Not only does *P. recurva* develop faster and have an earlier seasonal phenology than *P. semipunctata*, it is not extensively parasitized by *Aventianella longoi*, an introduced egg parasitoid responsible for suppressing *P. semipunctata* populations in California (56). Given the close taxonomic relationship of these *Phoracantha* species, the possibility of mating interference also exists.

Drosophila subobscura, a Palearctic species, has become established in South and North America (142). The establishment of *D. subobscura* [case 23] correlates with declines of the Nearctic *Drosophila pseudoobscura* (122, 129). This situation is anomalous because, in laboratory experiments, *D. pseudoobscura* is a superior competitor to *D. subobscura* (125, 129), and any displacement is not a result of parasitoid-mediated apparent competition (88). This situation may arise from microhabitat differences rather than from competition. Theoretical modeling suggests that interspecific competition between drosophilids can be locally intense, but competitive displacement and exclusion would not occur over larger spatial scales (160).

DISPLACEMENTS OF MEDICALLY IMPORTANT SPECIES Various Diptera of human health importance also have been involved in competitive displacements, including several species of mosquitoes. For example, *Aedes albopictus* [case 20] was introduced into the southeastern United States through refuse automobile tires imported from Japan (145, 164). In this region and others, *Ae. albopictus* has displaced *Aedes aegypti* (69, 74, 145). Similar declines of *Aedes triseriatus* [case 19] populations in disturbed or artificial treeholes in Texas correspond with the establishment of *Ae. albopictus* (164). Several types of interactions contribute to the displacement of *Ae. aegypti* and possibly other species by *Ae. albopictus* (41, 96, 119). Larvae of *Ae. albopictus* inhibit egg hatch of *Ae. aegypti* to a greater extent than the converse (41). Likewise *Ae. albopictus* males are more likely to inseminate *Ae. aegypti* females than the converse (119). Although *Ae. albopictus* seasonally displaces *Ae. aegypti* in rural habitats of Thailand, *Ae. aegypti* predominates in urban habitats of Southeast Asia (115). However, this situation results from these urban habitats being unsuitable for *Ae. albopictus* rather than from interspecific competition (see 3).

Anthropogenic habitat changes also have brought two vectors of St. Louis encephalitis, *Culex quinquefasciatus* and *Culex tarsalis*, into more competitive interactions at larval breeding sites (163). With this increased level of interaction, *Cx. quinquefasciatus* has largely displaced *Cx. tarsalis* [case 21] in the southern San Joaquin Valley of California through competition for larval resources and by degrading larval breeding sites.

Another case with Diptera of human health importance involves tsetse flies. *Glossina palpalis palpalis* [case 26] reportedly is displacing *Glossina fuscipes quanzensis* in the Congo (52). *G. p. palpalis* has been extending its range since the 1950s. This displacement has been triggered by anthropogenic alterations in habitat that brought these species into contact and results from several different types of competitive interactions, including differential effects of heterospecific copulations and reproductive differences.

DISPLACEMENTS BY SOCIAL HYMENOPTERA Interspecific competition is a significant factor in the community ecology of ants (Hymenoptera: Formicidae) (72). It is not surprising that numerous cases of competitive displacement have been documented among ants, especially with several species that have been transported readily, in association with humans, throughout the world. Among these tramp species that have displaced native ants and have become serious pests in their new habitats are *Linepithema humile, Solenopsis invicta,* and *Wasmannia auropunctata* (22, 48, 73, 77, 78, 99, 140), as well as other tramp species (64).

L. humile [case 41] has been the most prevalent invader among these three species. It has successfully invaded habitats in numerous Mediterranean climate zones (77, 174, 175) but is not limited to these. Species that forage above ground are most vulnerable to displacement by *L. humile,* especially when interactions occur in disturbed habitats (174). *L. humile* uses a variety of competitive strategies to eliminate competitors and does not have a trade-off between exploitation and interference competitive abilities (73). *L. humile* individuals initiate encounters with heterospecifics, and this interference contributes to decreased foraging success of other ant species (78). Not only is it more aggressive, but also in introduced habitats, *L. humile* recruits to food sources faster, in greater numbers, and for longer periods of time than native species (77). This advantage partly results from the lack of natural enemies, which reduce its foraging efficiency in native habitats (126). However, the lack of natural enemies is not the only reason *L. humile* has displaced other species. *L. humile* displaced *Pheidole megacephala,* another invasive species, throughout most of Bermuda, after that species had displaced other native species. These species have since reached an equilibrium in which both are predominant species and have displaced most other endemic species (64).

W. auropunctata [case 43] is a tramp ant species that has invaded numerous regions through human transport, including the Galapagos Islands. Its workers are relatively small but recruit in large numbers to food sources and are aggressive toward other species, resulting in the displacement of native ant species (22, 99).

S. invicta began its invasion of North America around 1930 and is well established throughout the southern United States (17). In the southern United States, *S. invicta* forms both polygynous and monogynous colonies, with the polygynous form being more disruptive (140). The abundance of native ants has been reduced and several species displaced by *S. invicta* [case 42]. Displacement by *S. invicta* can occur over a relatively long time period after the initial invasion. After the initial invasion front passes through a region, *S. invicta* colonies proliferate, and these colonies displace remaining colonies of native species (141). The increased biomass of ants and reduced arthropod species richness in these areas suggests that *S. invicta* can displace other scavenger species as well (140). Although individual *S. invicta* workers are less efficient at gathering resources compared with other ants (80), *S. invicta* discovers food sources faster than native ants (140) and maintains dominance at food sources through aggressive behavior and numerical superiority. These interactions reduce populations of competing ants, eventually leading to their displacement. In part, *S. invicta* achieves numerical superiority because of a lack of natural enemies in North America. In their native habitat, *S. invicta* are hindered in two ways by parasitic flies. Although mortality from parasitism reduces overall colony growth, defensive behavior in response to parasitoids severely reduces colony foraging time (117).

Past displacements also can be used to test potential competitive mechanisms of current interspecific interactions. The recent invasion of southern California by *S. invicta* has brought it into contact with *L. humile* (California Department of Food and Agriculture, 1999, http://pi.cdfa.ca.gov/rifa_plan/). Although both species occur in the southeastern United States, the Mediterranean climate of Southern California could favor the long established *L. humile*. Because these species use similar competitive advantages to displace other ants, the outcome of encounters between *S. invicta* and *L. humile* in California will be interesting.

Not all displacements between ant species involve invasive species. In Brazil the native *Atta sexdens* [case 44] has displaced another native species, *Atta robusta* (50). This displacement apparently has been triggered by human activities that brought the two species into contact in disturbed habitats. *A. sexdens* is better adapted to foraging across variable habitats including disturbed sites (36). Therefore its overall population recruitment is greater than that of *A. robusta* (50).

Other social Hymenoptera have been involved in competitive displacements. *Vespula germanica* first arrived in New Zealand in the 1940s. Some 30 years later, *Vespula vulgaris* [case 45] became established and displaced *V. germanica* in many habitats (150). Despite this displacement in novel habitats, neither species is known to exclude the other in their native European habitats. Potentially better adaptations to local conditions coupled with superiority in agonistic interactions over certain food resources allow *V. vulgaris* to predominate (62).

Likewise in New Zealand, *Polistes chinensis antennalis* has been displacing *Polistes humilis* [case 46]. *P. humilis* is an exotic that had become established over most of New Zealand since its arrival some 120 years ago from Australia, whereas *P. chinensis antennalis* is a recent (<25 years ago) arrival. However, *P. chinensis* has increased its range and is now the predominant *Polistes* species in New Zealand (21). Although *P. humilis* still occurs throughout the North Island of New Zealand, anecdotal evidence suggests that it has been displaced from certain localized habitats through agonistic interactions with *P. chinensis*.

Since the honey bee, *Apis mellifera*, was intentionally imported from Africa into South America, feral "Africanized" bees (offspring of African and previously introduced European strains) have spread throughout the Americas, which has led to concern over the loss of native pollinators [case 47]. Circumstantial evidence for the displacement of native pollinators by *A. mellifera* (European or African) has been reported (149). Roubik (147) found experimental evidence for displacement of native pollinators (stingless bees: *Melipona* spp. and *Trigona* spp.) by Africanized *A. mellifera* in Panama. Additional studies demonstrate that the presence of *A. mellifera* alters foraging behavior of native *Melipona* spp. and *Trigona* spp. in Panama, which could lead to their localized extinction (148).

DISPLACEMENTS AMONG ARACHNIDS There is also evidence for broad-scale and localized competitive displacement among arachnids. The web-building spider

Lactrodectus katipo is native to New Zealand beach habitats, whereas *Steatoda capensis* [case 1] is a recent arrival from South Africa (57). Following a series of environmental disturbances that decimated populations of *L. katipo*, *S. capensis* was able to invade *L. katipo* habitats and usurp limited web sites for immatures through scramble competition. Since then, *S. capensis* has continued to monopolize that resource through interference, thus preventing recolonization by *L. katipo*. Because *L. katipo* recruitment is limited by *S. capensis* and it lacks adaptations to other habitats, remnant populations of *L. katipo* have been displaced. Hann (57) has proposed that in its native coastal dunes, *L. katipo* is competitively superior to *S. capensis* and was able to exclude it until storms decimated *L. katipo* populations. In a similar manner, *Steatoda bipunctata*, a Eurasian web-building species introduced to eastern North America, has been displacing the native *Steatoda borealis* [case 2]. Although this displacement is geographically widespread, it is locally restricted to synanthropic environments (123). In undisturbed forest habitats, *S. borealis* has not been displaced.

The distribution of the phytophagous mite *Panonychus mori* [case 7] in peach orchards across Japan is limited to northern sections of the country, although *P. mori* is physiologically capable of developing in more southerly regions. This range restriction results from competitive displacement and exclusion by *P. mori's* congener *Panonychus citri* through reproductive interference (51). Males of both species will attempt to copulate with heterospecific females. However, *P. citri* males have more extensive and detrimental copulations with *P. mori* females than reciprocal copulations between *P. mori* males and *P. citri* females (167). Alternatively, the northerly distribution of *P. citri* is not limited by competition but by climatic conditions (159).

Two experimental demonstrations of competitive displacement have involved phytophagous mites. Interactions between *Tetranychus urticae* and *Panonychus ulmi* [case 8] can be mediated by the presence of phylloplane fungi (6). In the presence of the fungi, *T. urticae* displaces *P. ulmi*, whereas in the absence of the fungi, *P. ulmi* is competitively superior. In another case, early season feeding by *Eotetranychus willamettei* [case 6] on grapevines induces plant resistance that suppresses later season populations of *Tetranychus pacificus* (47).

Localized displacements of predatory mites used in augmentative biological control programs have been observed numerous times, with concomitant implications for biological control. In a series of studies, mutual predation occurred among predatory mites released for control of pest mites in apple trees. When both species are released as control agents, *Typhlodromus pyri* displaces *Metaseiulus occidentalis* [case 3] through intraguild predation (27). Macrae & Croft (104) suggest that *T. pyri* has a more generalized diet than *M. occidentalis*, which allows it to switch to preying on *M. occidentalis* in the presence of greater densities of alternative prey. *T. pyri* has a further advantage in being able to develop at lower temperatures. Localized displacement of *M. occidentalis* by *Zetzellia mali* [case 5] can also enhance biological control by *Amblyseius andersoni* (26, 27). Although *Z. mali* is the most competitive of the three species, *A. andersoni* provides the best control of pest mites, and its colonization is lowest when *M. occidentalis* is present. In Italian vineyards, Duso et al. (40) found that *Kampimodromus aberrans* typically displaces *T. pyri* [case 4] within one year through intraguild predation when augmentative releases of both are made.

DISPLACEMENTS BETWEEN TAXA OF DIFFERENT FEEDING GUILDS The previous examples have occurred between relatively closely related species with similar feeding habits. However, displacements have occurred between taxa of different feeding guilds. The monarch butterfly, *Danaus plexippus* [case 28], displaced the milkweed bug, *Oncopeltus sandarachatus*, on Barbados through competition for food resources although the two species belong to different guilds (11). Both of these phytophagous species are exotic having colonized Barbados after the introduction of their common host *Asclepias curassavica* and a second host of *D. plexippus*, *Calotropis procera*, in the eighteenth century. *D. plexippus* has virtually eliminated *A. curassavica* thereby removing the only food source for *O. sandarachatus*. *D. plexippus* persists because it has an alternative food source, *C. procera*, that *O. sandarachatus* lacks.

An analogous case of competitive displacement on a localized scale occurs between *Tyria jacobaeae* [case 29] and *Pegohylemyia seneciella* (25). Both species feed on ragwort, *Senecio jacobaea*. *T. jacobaeae* feeding removes *S. jacobaea* flower heads, which are the breeding site for larvae of *P. seneciella*. However, only large stands of *S. jacobaea* support *T. jacobaeae*. Therefore, isolated plants still support *P. seneciella* because such plants do not provide sufficient resources for reproduction of *T. jacobaeae*.

Another case of localized displacement involving unrelated phytophagous insects is that of *Sitophilus zeamais* displacing *Sitotroga cerealella* [case 15] in laboratory cultures of stored grain (2). This displacement results from interference competition when adults of *S. zeamais* feed on corn kernels containing immatures of *S. cerealella*, thereby eliminating those immatures. Such interactions could explain the geographical range limits of *S. cerealella* in the southern United States (19). Conversely, the range of *S. zeamais* is limited by abiotic factors.

Impacts of Competitive Displacement

From an ecological perspective, displacements provide opportunities to examine mechanisms of interspecific competition. However, competitive displacements can have varied impacts. The majority of displacements cause negative impacts. As the term displacement implies, the most obvious impact is the loss of biodiversity when an invasive species displaces a native one (Table 1, see the Supplemental Material link at www.annualreviews.org). In most cases, we found a one-to-one change in species numbers (i.e., one species displaced one species) perhaps because the number of ecologically similar species in a particular habitat is limited. The major exception to this result is among the ants, where multiple ecologically similar species occur in a given habitat. Therefore, one invasive ant species can displace multiple native or previously established species. The increased biomass of ants and generally reduced arthropod species richness in these areas suggests that invasive ants can displace other scavenger (140) or predatory species (22, 99).

Complex interactions are possible when species are less ecologically similar. Displacement of keystone species (species with critical influence on community structure) has adverse impacts for other native species. The displacement of native seed-dispersing ants in South Africa by *L. humile* threatens the existence of native plants that depend on those ants (12). Comparable insect-plant mutualisms would be at risk if *A. mellifera* displaces native pollinators (148). More extensive information on food webs is needed to understand comprehensive effects of competitive displacement.

The effect of competitive displacement on species diversity impacts classical biological control programs. The introduction of multiple natural enemies may not always produce beneficial results. Competitive displacement has been implicated as a cause of low rates of establishment of introduced natural enemies (42). Yao & Chant (182) and Williams (181) have demonstrated that superior competitors could displace superior biocontrol agents. Even in cases where biological control is not disrupted, a superior competitor that displaces other natural enemies may not enhance biological control (45). In addition, introduced biological control agents have been implicated for displacing competing parasitoid species (8, 76, 169). Therefore the possibility that one biocontrol agent will displace another should be considered in developing biocontrol programs. As a corollary, competitive displacement has other ramifications for applied ecology in terms of pest management. Often a more significant pest displaces another (e.g., 86). In other cases, the species involved may have similar effects on agroecosystems (e.g., 83), or displacement could have beneficial effects by eliminating more pestiferous species (47, 158).

Competition is a dynamic ongoing process. Therefore interspecific competition that leads to displacement has profound evolutionary consequences for the interacting species. Two species may coexist over time, but then one may evolve superior competitive abilities, leading to the displacement of the other (114). Such rapid evolution could contribute to the sudden shift in *Liriomyza* species. Other reversions of displacements could reflect evolution and adaptations of “displaced” species to their new environmental conditions. Such a scenario could account for the equilibrium reached by *P. megacephala* and *L. humile* in Bermuda (64). Alternatively, displacement of certain populations could isolate other populations and lead to their speciation. Furthermore, interspecific mating asymmetries may favor ancestral species over some derived species, thus allowing the former to displace the latter should they come into contact (183). Evolutionary changes brought about through competition are historic and not necessarily predictable. Therefore competitive interactions between different populations of the same species can have different outcomes (81, 94). Given the ecological, environmental, and evolutionary outcomes, there is an urgent need to understand competitive interactions leading to displacement and their effects.

CONCLUSIONS

We found evidence for competitive displacement across a variety of taxa and ecological systems. In many cases more than one competitive mechanism is responsible for displacement. Within specific taxonomic groups certain themes do emerge. Of the 42 cases of competitive displacement identified, 14% involve species of Homoptera. Denno et al. (35) attribute the prevalence of interspecific competition between Homoptera to species characteristics such as rapid reproduction, aggregated and sedentary lifestyle, and feeding on a common phloem resource. Competitive displacements among the Homoptera usually involve differences in resource acquisition. Displacements of mandibulate phytophages also tend to result from exploitative competition. In contrast, displacements within the parasitic Hymenoptera mostly have been driven through interference competition among larvae. These cases typically involve introduced parasitoids of exotic pests; therefore, competition is intensified by the lack of alternative hosts or superior adaptations to novel environments. Among the social Hymenoptera, interference competition and territorial behavior generally drive displacements. Displacements among actively hunting predators typically involve intraguild predation. An unexpected finding was the extent to which displacements have been driven by reproductive interference. Although mechanisms may not always be apparent and may not be discernable from laboratory studies (e.g., 10), the similarity of factors contributing to displacements within taxonomic groups suggests that those same factors contribute to other displacements among similar taxa.

Another important theme is how competitive relationships are mediated by other factors. The release from natural enemies is perhaps the most significant advantage for exotic species when competing with native ones. Perhaps more significantly, many documented cases of displacements have occurred in anthropogenically disturbed habitats, including agroecosystems and synanthropic environments. Elton (46) considered disturbed habitats to be more susceptible to invasions because they have less “biotic resistance.” Although the phrase “disturbance enhances invasions” does not provide a basis for generating testable hypotheses (97), Petran & Case (134) argue that anthropogenic habitat changes, especially the reduction of habitat complexity, do facilitate establishment of invasive species and displacement of resident species. Their contention is supported by the cases where a native species is displaced by an exotic species in synanthropic or anthropogenically modified habitats but persists in less disturbed habitats (Table 1, see the Supplemental Material link at www.annualreviews.org).

Displacements have occurred at a variety of spatial scales from large geographic areas to localized habitats, either where a species has been displaced from a particular host or habitat, or displaced temporally. Obviously, species of importance to humans are more likely to be studied, as are ones that produce dramatic shifts in the environment (162). However, the emergence of conservation biology has focused more attention on the impact of invaders on invaded communities and habitats.

Although competition is thought to be subtle and difficult to demonstrate (98), it may be critically important, especially in regard to higher trophic levels (92). There are inherent problems with the study of interspecific competition and determining if competitive displacement has occurred. The historic nature of displacement means that underlying mechanisms may never be established with confidence (79), and therefore alternative explanations are possible for these cases. However, invasions and displacements represent natural experiments, which if found at the appropriate time and empirically examined in depth can provide insight into competitive processes, ecological impacts, and evolutionary change.

Certain systems we cite have been studied in depth [e.g., cases 3, 14, 19, 37, 38, 41, 42 (for other taxa, see references 66, 134)], and these examples serve as templates for future studies. In these examples, observational data have been combined with appropriate experimental studies to demonstrate whether the phenomenon of competitive displacement has occurred and, as importantly, the underlying processes. These in-depth studies are valuable and necessary for testing alternative or complementary hypotheses to explain changes in the status of species. These types of in-depth studies also reveal the complexity of ecological interactions and how other noncompetitive mechanisms influence the outcome of interspecific interactions. For example studies by Juliano (82) & Barrera (3) point to the need for experiments to be as realistic as possible so key interactions will not be missed. Ongoing tests of complementary hypotheses, such as the studies of displacement of ants by the Argentine ant, *L. humile* (case 41), have shown elegantly how multiple competitive mechanisms can operate within one system. Likewise, such in-depth studies would reveal cases of species replacement where interspecific competition was not a contributing factor. Without such attention, opportunities to document scientifically displacement events will be missed, and we will continue to rely on anecdotal and circumstantial evidence.

Our hope is that this review shows the importance of competitive displacement in communities. The economic, ecological, and evolutionary implications of competitive displacement should stimulate further study of these phenomena as new situations arise. Interactions leading to competitive displacement are complex and often involve multiple mechanisms and mediating factors. A greater awareness of competitive displacement events should lead to more studies that allow better documentation to determine the relative importance of key factors and to develop hypotheses that explain observed patterns.

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