

## ■ Research Paper

# Traits Underlying the Capacity of Ant Colonies to Adapt to Disturbance and Stress Regimes

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How do groups of social agents organize themselves to cope with stress and disturbances? We address this question by looking at ant colonies. We review the suites of traits that allow ant species to adapt to different disturbance and stress regimes, and changes in these regimes. Low temperatures and low nest site and food resource availability are important stresses that affect ant abundance and distribution. Large-scale habitat disturbances, such as fire, grazing and mining, and small-scale disturbances that more directly affect individual colonies, such as predation, parasitism and disease, also affect ant abundance and distribution. We use functional groups to study the social and individual traits underlying different responses to temperature stress, large-scale habitat disturbance and competition from other ants. Specific individual and colony traits, such as colony size, queen number and worker specialization, seem to underlie adaptation to various stress and disturbance regimes. Copyright © 2008 John Wiley & Sons, Ltd.

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## INTRODUCTION

Organisms are adapted to survive under particular sets of disturbance and stress regimes. Furthermore, species differ in their ability to adapt to changing stress and disturbance regimes at various temporal scales. Anthropogenic change in many cases represents a particularly extreme and rapid change in disturbance and

stress regimes that affect the resilience of ecological systems (Scheffer *et al.*, 2001). In ecology, there have been significant efforts to understand the impact of disturbance regimes, especially on the diversity of species in particular ecosystems (Turner *et al.*, 2003; Shea *et al.*, 2004). However, most efforts are focussed on the description of the response of communities to disturbance, and less on the mechanisms underlying the response of particular species or groups of species (Shea *et al.*, 2004). Alternatively, we are interested in the traits of specific organisms that underlie their responses to stress and disturbance.

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In particular, we focus on organisms that are organized into social-ecological systems. The response of such systems is dependent not only on the response of individuals, but also on social organization and the response of groups of individuals. In this paper, we use ants as a study system because they are extremely diverse in terms of life history and have been fairly well studied (e.g. Hölldobler and Wilson, 1990). At the end, we discuss the possible relevance of our findings to other social-ecological systems (e.g. human social systems).

Ants are ubiquitous and ecologically dominant in nearly all terrestrial habitats in which they exist (Hölldobler and Wilson, 1990). Ants are also an extremely diverse and evolutionarily successful group, with over 10 000 described extant species (Bolton, 1995). Within this diversity of species is found a correspondingly diverse array of life histories and colony traits. For example, many species are scavengers, but others are predators, granivores or herbivores (Hölldobler and Wilson, 1990; Bourke and Franks, 1995). Colony size ranges from a few individuals to over a million in some leaf-cutting and army ant species to hundreds of millions in some species with supercolonies (Bourke, 1999). Some colonies have monomorphic workers with little division of labour, and others have age-based, size-based or morphology-based division of labour, with specialized worker subcastes, such as soldiers (Oster and Wilson, 1976; Hölldobler and Wilson, 1990). Some ant species have individual-based foraging, while others have complex foraging strategies based on rapid recruitment or maintained trunk trails (Traniello, 1989; Anderson and McShea, 2001). In addition, an important colony trait—colony queen number—ranges from one to many, or in some cases, there is no specialized queen caste, but colonies consist of a small number of workers that all have the potential to mate and reproduce (Heinze and Tsuji, 1995).

In this paper, we specifically ask, what are the traits of ant species underlying their adaptation to different stress and disturbance regimes and changes in these stress and disturbance regimes? We first describe different stresses and disturbances that are important in determining ant abundance and diversity, and we introduce

the variety of levels at which ant colonies can respond to stress and disturbance. We then describe functional groups that have been defined based on trade-offs among tolerance of stress, tolerance of disturbance and competitive ability. We review what stress and disturbance regimes these functional groups are adapted to and the major traits that are adaptations. We especially focus on traits that affect social organization and describe specific traits that underlie adaptation. Finally, we discuss changing disturbance and stress regimes and possible traits that enable response to these changing conditions.

## STRESSES AND DISTURBANCES FOR ANTS

Definitions of stress and disturbance usually focus on ecosystem-, habitat- or community-wide effects on diversity and abundance (e.g. Grime, 1979; Turner *et al.*, 2003; Shea *et al.*, 2004). Our goal is to explore the effects of a wide range of factors on a specific group of organisms, ants, so we use broad definitions of stress and disturbance that together include all abiotic and biotic environmental factors acting at a variety of scales that limit ant colony or population growth (see Table 1). We define stress as any factor that limits organisms' growth or productivity, the accumulation of biomass (e.g. extreme temperatures) and we define disturbance as any factor that acts to directly remove biomass (e.g. fires, predation) (see Grime, 1979; Andersen, 2000, although these authors study abiotic disturbance and stress on a biogeographic scale) (Grime, 1979; Andersen, 2000). Disturbances are usually discrete events whereas stresses are usually long-term pressures.

There is some ambiguity and overlap in these definitions of stress and disturbance when applied to specific organisms such as ants. For example, stresses and disturbances can act on the whole ecosystem at once, on specific food or nest resources used by ants, or only on specific ant colonies or individual workers. In addition, factors may act as disturbances at first and as stresses over longer time periods (Table 1). For example, predators may kill and eat a number of workers (a disturbance) but the long-term effect

Table 1. Biotic and abiotic environmental factors that act as stresses and disturbances on ant colonies

Biotic or abiotic environmental factor	Disturbance or stress to ant colony?	Frequency of occurrence	Predictably occurs during generation time of colony?
Low temperatures	Stress	Potentially constant	Yes
Low soil humidity	Stress	Potentially constant	Yes
High complexity of foraging surface	Stress	Potentially constant	Yes
Low nest/food resources	Stress	Potentially constant	Yes
Competition with neighbouring colonies	Disturbance–stress	Daily–weekly-(potentially constant)	Yes
Attack by predators/parasites/pathogens	Disturbance–stress	Daily–monthly-(potentially constant)	Yes
Normal habitat disturbance (e.g. fire, drought)	Disturbance–stress	Monthly–decades	Yes
Extreme habitat disturbance (e.g. hurricane)	Disturbance	Decades–centuries	No
Climate change	Stress	Decades–centuries	No
Invasive species	Disturbance–stress	Does not occur naturally	No

Some factors can act as a disturbance over short time periods and a stress over longer periods. The frequency of occurrence and predictability of factors determines how likely it is for ant colonies to adapt to these factors.

of predation on the colony may be that the colony ceases foraging when predation pressure is high, decreasing colony growth (a stress).

### Stress

Ants as a group are thermophilic, and variation in temperature determines ant abundance, distribution and diversity (Kaspari *et al.*, 2000). Variation in temperature at a macrogeographic scale (e.g. biogeographic, latitudinal or elevational gradients) mainly controls species range and abundance (Kaspari *et al.*, 2000). Factors are usually described as stresses based on their effects over large scales, such as whole groups of ants (i.e. factors that limit ant abundance and diversity on a habitat or macrogeographic scale), and stresses are usually measured based on their effects on community productivity. However, factors also can act as stresses on smaller scales, such as individual ant colonies. For example, variation in temperature at a microgeographic scale (e.g. in open areas that receive more insolation compared to closed areas that receive less insolation) affects local species composition and abundance, as well as growth rates of individual colonies. Finally, variation in

temperature over time (e.g. daily and seasonal cycles or long-term climatic change) also can affect ant communities. For example, ant species differ in temperature tolerance, and an important way in which different taxa coexist is by partitioning their foraging activities based on daily temperature cycles (Andersen, 1992). In general, low temperatures are stressful to ants, and ant abundance and diversity decrease over space and time as temperature decreases (Kaspari *et al.*, 2000). Extremely high temperatures also can be stressful to ants, but some taxa have physiological and behavioural adaptations that enable them to forage at temperatures that are lethal to most other insects (Christian and Morton, 1992).

The most productive habitats for ants, characterized by the presence of behaviourally dominant species (see section on trade-offs), couple high thermal energy with high metabolic energy in the form of a carbohydrate supply of sugary plant or insect secretions (Yanoviak and Kaspari, 2000; Majer *et al.*, 2004). Thus, in some cases, food availability (range of types and abundance) may limit ant abundance, especially for species with specialized diets (Andersen, 2000). Similarly, nest site availability (range of types and abundance) can be a stress that limits ant abundance,

especially for species with specialized nesting requirements (Andersen, 2000). At the microgeographic scale of an individual colony, competition with neighbouring nests may act predominantly as a stress by limiting food resources or nesting sites, thus limiting colony growth.

The structural complexity of the foraging surface can limit the ability of ants to efficiently locate and capture food resources and may act as a stress, limiting ant productivity (Andersen, 2000). Finally, soil moisture can be a key environmental factor limiting the distribution of some species (e.g. Holway, 1998). Dry soil is an important stress for some species but, as with high temperatures, it is not stressful for ants in general, and many taxa have adapted to dry, desert conditions.

### Disturbance

Disturbance (the removal of biomass) is also an important factor that determines ant distribution and abundance, but the effects of disturbance on ants are complex, and the distinction between whether a factor acts predominantly as a stress or disturbance is not always clear (Hoffmann and Andersen, 2003). We believe it is useful to distinguish between two types of disturbance: large-scale disturbances that affect whole habitats (e.g. fire and grazing, which involve the removal of vegetation biomass) and small-scale disturbances that affect individual colonies or small groups of colonies (e.g. predation and disease, which involve the actual removal of ant biomass) (see Majer *et al.*, 2004).

Disturbances are usually defined based on their effect on vegetation and the habitat in general, but these large-scale habitat disturbances typically do not have a strong effect on ants in terms of actual removal of ant biomass (Andersen, 2000; Hoffmann and Andersen, 2003). Most ants live in the ground and are largely protected from the direct effects (i.e. loss of ant biomass) of habitat disturbances. Furthermore, ant colony growth rates are often high relative to plant growth rates, and ant colonies quickly replace the biomass lost as a direct result of the disturbance (Andersen, 2000; Hoffmann

and Andersen, 2003). Instead, large-scale habitat disturbances often affect ant communities more through their effect on environmental stresses experienced by individual ants and ant colonies, such as extreme temperatures. For example, the most important effect that fire has on ant communities is that it removes shrubs that shade the ground and improves habitat quality. Shade is generally stressful to ants, because their activity decreases with decreasing insolation and temperature (Hoffmann and Andersen, 2003). In addition, habitat disturbances often strongly affect the types and abundance of nest sites and available food resources. The effect of large-scale habitat disturbance on any particular taxon in any particular habitat also depends on what habitat that taxon is adapted to. For example, while some disturbances such as fire may improve the habitat for many ant taxa (even taxa that are generally intolerant of habitat disturbance), leaf-litter inhabiting taxa are strongly negatively impacted by fire (Hoffmann and Andersen, 2003). The effect of several of these large-scale disturbances, such as fire, grazing, mining, on ants have been fairly well studied (reviewed by Hoffmann and Andersen, 2003).

Besides these large-scale habitat disturbances, smaller-scale disturbances caused by other organisms (e.g. predation, parasitism and disease) act on the microgeographic scale of an individual colony or small groups of colonies and can be important in shaping community structure and colony traits. For example, predation by social, insect-consuming army ants is thought to be a major factor affecting ant community structure and colony traits in the neotropics (Kaspari and O'Donnell, 2003). Attack by parasitoid phorid flies also has strong effects on ant foraging patterns and, potentially, ant community structure (Feener, 2000). Pathogens are another source of disturbance that affects colony traits (Hart and Ratnieks, 2002; Naug and Camazine, 2002). Predation, parasitism and disease all act as small-scale disturbances, directly removing ant biomass, but these factors may also further act as stresses that limit colony productivity, because their presence may alter the behaviour of individual ants and whole colonies in the short or long term (Feener, 2000).

Another biotic factor thought to be very important in structuring ant communities at macrogeographic and microgeographic scales is competition with other ants (Andersen, 1992, 2000). Like plants, ant nests are relatively stationary and stable over time, and competition among colonies for food and nest resources largely determines the spatial structure of ant communities. For example, ant colonies are often distributed in a mosaic pattern, with colonies of the most highly competitive species evenly spaced and colonies of subordinate species interspersed between them (Levings and Trianello, 1981, but see Ribas and Schoereder, 2002). Competition for food resources also interacts with daily and seasonal temperature patterns to temporally structure ant communities (Andersen, 1992). As with predation, parasitism and disease, competition can act as both a disturbance (e.g. if battles between neighbouring colonies results in worker or colony mortality) but on longer time scales may be more important as a stress (e.g. competition for food and nest resources is likely to limit colony growth).

Finally, another important and well-studied source of disturbance that acts on whole communities as well as individual colonies is the introduction of non-native, invasive ants (e.g. Holway, 1999). As with competition with other native ants, competition with invasive ants can act as both a disturbance and a stress.

#### SCALES OF STRESS AND DISTURBANCE AND LEVELS OF RESPONSE

As discussed in the previous section, stress and disturbance can affect ants at multiple spatial and temporal scales. In addition, ant colonies have different levels of organization, from the individual to the whole colony, that can respond to and adapt to stress and disturbance regimes over several temporal scales (Table 2). Individual ants can exhibit an immediate behavioural or physiological response to a stress or disturbance and over a longer period may exhibit a different response. Groups of individuals may communicate and have a collective behavioural response that occurs immediately or over a longer

time period (e.g. Wilson, 1986). Nests and whole colonies may also respond to stresses or disturbances through task allocation, decisions about resource allocation to colony growth or reproduction (Oster and Wilson, 1976). Communities of interacting ant colonies may also respond to stress and disturbance (Feener, 2000; Holway *et al.*, 2002). Traits at the individual, group and colony levels affect the adaptation of ant species to different stress and disturbance regimes and the potential to respond to changes in stress and disturbance regimes (Table 2). Ultimately, if an individual-, group- or colony-level trait of a population is to adapt to a stress or disturbance regime, it must evolve. In order for a population to have the capacity to adapt in the short term, it must have genetic variation for whatever trait is to respond to selection.

#### BIOGEOGRAPHIC PATTERNS OF TRADE-OFFS IN ADAPTATION TO EXTREME TEMPERATURES, HABITAT DISTURBANCE AND COMPETITIVE ABILITY

A variety of stresses and disturbances are important in determining ant species distribution and abundance. Following Grime's (1979) approach for plants, Andersen (1992, 2000) defines ant functional groups based on trade-offs in adaptation to three factors: extreme temperatures, habitat disturbance and competition with other ants. This functional group scheme focusses on the responses of taxonomic groups (e.g. genera) to important stresses and disturbances on a biogeographic scale (Andersen, 1992, 2000). This functional group scheme was developed in Australia but has also been applied to North American and Neotropical ants. Although there are limitations to any taxonomically based functional group scheme (i.e. because of the diversity of ant life histories at nearly all taxonomic scales), we believe Andersen's (1992, 2000) functional group scheme provides a useful organizing framework for identifying important individual and colony traits that seem to underlie trade-offs between adaptation to important stresses and disturbances.

Table 2. Responses of ants at different levels that occur over a range of temporal scales

Temporal scale <sup>a</sup>	Level	Response	Example	Reference
Seconds and hours	Individual ants	Immediate behavioural change	Switching tasks in response to threshold stimuli	Beshers and Fewell (2001)
	Groups or teams	Formation and response of groups and teams	Teams of individuals form to transport large food items	Anderson and Franks (2001)
	Colony	Emergent properties of responses of individuals and groups or teams	Recruitment of large numbers of ants to a food source or cessation of foraging in response to rain or predation	Anderson and McShea (2001), Beshers and Fewell (2001)
Days	Individual ants	Progression through series of age-related tasks (temporal polyethism) depending on social environment	Young ants care for brood, and old ants forage	Odonnell and Jeanne (1995), Beshers and Fewell (2001)
	Colony	Emergent properties of division of labour	Resiliency of division of labour when worker caste ratios are altered	Wilson (1984)
Months	Colony	Colony ontogeny and change in investment in reproduction versus colony maintenance or different forms of reproduction	Production of mostly workers when the colony is small or young and production of mostly reproductive individuals when the colony is large or mature	Porter and Tschinkel (1986), Mailleux <i>et al.</i> (2003)
Seasons	Community	Change of community structure in response to environmental (biotic or abiotic) change	Introduction of invasive species or degradation of habitat	Holway (1999), Holway <i>et al.</i> (2002), Mailleux <i>et al.</i> (2003), Tsutsui and Suarez (2003)
Generations	Population	Genetic change	Evolution of individual-, group- and colony-level traits	Frumhoff and Ward (1992), Bourke (1999), Peeters and Ito (2001)

<sup>a</sup>Note that temporal scales can overlap.

The functional group scheme is largely focussed on four taxonomically based functional groups: Dominant Dolichoderinae, Generalized Myrmicinae, Opportunists and Climate Specialists (Andersen, 1992, 2000). Dominant Dolichoderinae are adapted to high-quality habitats (in terms of the conditions which maximize ant abundance) that are open and well insulated (i.e. low temperature stress). They do not tolerate

major habitat disturbance or temperature stress but are highly competitive with highly aggressive and active individuals (Andersen, 1992, 2000). Generalized Myrmicinae are more tolerant of temperature stress and habitat disturbance than Dominant Dolichoderinae and can compete with them in some situations due to their rapid recruitment of food sources, although Generalized Myrmicinae individuals are not highly

active or aggressive (Andersen, 1992, 2000). Opportunists are tolerant of high levels of habitat disturbance and some stress (e.g. narrow range of nest or food resources) but are unspecialized in terms of competitive ability and tolerance of extreme temperature stress (Andersen, 1992, 2000). Climate Specialists are adapted to climates that are stressful in terms of extreme temperatures but do not tolerate high levels of habitat disturbance and cannot compete with Dominant Dolichoderinae and Generalized Myrmicinae in less stressful environments (Andersen, 1992, 2000).

#### SUITES OF TRAITS OF FUNCTIONAL GROUPS AS POSSIBLE ADAPTATIONS TO STRESS AND DISTURBANCE REGIMES

In this section, we review the stress and disturbance regimes that each functional group seems to be adapted to and identify colony- and individual-level traits that seem to be adaptations to these stress and disturbance regimes. Table 3 summarizes the main characteristics of the functional groups. Because of the high degree of variation in life-history traits of ants at the genus level (the taxonomic level that is generally used in the functional group scheme) there are many notable exceptions to these generalizations.

#### Disturbance Specialists: Opportunists

The Opportunist functional group includes a wide variety of ant taxa with fairly similar life-history characteristics. They are the disturbance specialists of all the functional groups and predominate when habitat disturbances are too severe or frequent for other ants to exist (Andersen, 2000). Traits of Opportunists that allow them to exist in regularly disturbed environments include many traits that could be considered to be consistent with an 'r-selected life-history strategy' (Pinanka, 1970; Reznick *et al.*, 2002), including small colony size, behaviourally and morphologically unspecialized workers, unspecialized nest sites and diets, polygyny and polydomy (Table 3, see discussion

of r- and K- selection as applied to ants in Bourke and Franks, 1995).

#### Stress Specialists: Climate Specialists

Climate Specialists are adapted to environments that are predictably stressful in terms of temperature extremes. They have unspecialized foraging strategies and consequently are non-competitive relative to ants that are adapted to more favourable conditions (Andersen, 2000). However, Climate Specialists have individual and colony adaptations to deal with stressful environmental conditions. For example, some cold Climate Specialist *Formica* species have large colonies with specialized nests that can maintain a temperature several degrees higher than the ambient temperature (Hölldobler and Wilson, 1990). Colony size of ants increases with increasing latitude (Kaspari and Vargo, 1995), and one reason may be that large colonies have more workers to collect food and thus are buffered against seasonal starvation (Kaspari and Vargo, 1995). Similarly, worker size also increases with increasing latitude in one species (Heinze *et al.*, 2003). Other species have additional individual-level physiological and behavioural adaptations to deal with temperature stress (Table 3) (e.g. Christian and Morton, 1992; Heinze, 1993).

#### Competition Specialists: Dominant Dolichoderinae and Generalized Myrmicinae

Dominant Dolichoderinae and Generalized Myrmicinae can be considered competition specialists. Dominant Dolichoderines are found only in predictably high-quality environments (unstressful in terms of temperature and without most habitat disturbances), but they are highly competitive and can dominate ant communities (Andersen, 2000). Generalized Myrmicinae are less competitive but have a higher tolerance of a variety of stress and disturbance (Andersen, 2000). Hoffmann and Andersen (2003) found that the abundance of Generalized Myrmicinae in habitats was negatively correlated with the

Table 3. Colony- and individual-level traits that seem to characterize species with tolerance of disturbance, tolerance of stress (extreme temperatures) or high competitive ability

Level	Trait <sup>a</sup>	Tolerance of disturbance	Tolerance of stress (extreme temperature)	High competitive ability		Invasive species
				Interference competition	Exploitative competition	
			Opportunists <sup>a</sup>	Dominant Dolichoderinae <sup>a</sup>	Generalized Myrmicinae <sup>a</sup>	
Individual	Worker behavioural specialization	No	Sometimes	Yes	Yes	Yes
	Small worker size	No <sup>b</sup>	Sometimes	Sometimes	Yes	Yes
	Fast worker speed	No <sup>b</sup>	No <sup>b</sup>	Yes	No <sup>b</sup>	Sometimes
	Short queen lifespan	Yes	No	No	No	Yes
	Worker sterility	No <sup>b</sup>	No	No	Yes <sup>b</sup>	Yes
	Large colony size	No	No <sup>b</sup>	Yes	Yes	Yes
	Worker polymorphism	No	No <sup>b</sup>	No <sup>b</sup>	Yes	No <sup>b</sup>
	Mass recruitment	No	No <sup>b</sup>	Yes	Yes	Yes
	High tempo	No	No <sup>b</sup>	Yes	No <sup>b</sup>	Sometimes
	Polygyny	Yes	Sometimes	Yes	Sometimes	Yes
Colony	Polydomy	Yes	Sometimes	Sometimes	Sometimes	Yes
	Reproduction through budding	Sometimes	No <sup>b</sup>	No <sup>b</sup>	No	Yes
	Frequent colony migration (unspecialized nest sites)	Yes	No <sup>b</sup>	No	No	Yes
	Strong interspecific aggression	No	Sometimes	Yes	Yes	Yes
	Loss of mating flight	Sometimes	No	No	No	Yes <sup>b</sup>

Sources: (Hölldobler and Wilson, 1990; Passera, 1994; Bourke and Franks, 1995; Andersen, 2000; Tsutsui and Suarez, 2003).

<sup>a</sup>Generally corresponds to one of Andersen's (1992) functional groups.

<sup>b</sup>There are notable exceptions to this trait generalization.

abundance of Opportunists. One possible explanation is that Generalized Myrmicinae are adapted to a range of disturbances; but if the disturbances are too extreme, only Opportunists can exist. Both Dominant Dolichoderines and Generalized Myrmicinae typically have individual- and colony-level traits that could be considered to be consistent with a 'K-selected life-history strategy' (Pinanka, 1970; Reznick *et al.*, 2002), such as large colony size, morphologically specialized queens and behaviourally specialized workers (Table 3). One difference between the two groups is that Dominant Dolichoderinae typically have large, highly active and aggressive workers, while Generalized Myrmicinae typically have smaller workers that move more slowly, but the colony has efficient mass recruitment and can dominate food found close to the nest (Andersen, 2000). Holway (1999) found that native ants had a trade-off between competitive ability through interference and exploitative competition. Specifically, like Dominant Dolichoderinae, species with large, highly active and aggressive individuals can compete largely through interference competition (i.e. by discovering and collecting food items before their competitors). Alternatively, species like Generalized Myrmicinae have smaller, slower individuals and colonies with small foraging ranges. These species do not compete through interference competition but through exploitative competition (Holway, 1999). Large food items found near the nest site can be monopolized because of the mass recruitment of large numbers of small foragers. *Pheidole*, one of the three genera included in the Generalized Myrmicinae functional group, is extraordinarily successful, as demonstrated by its abundance in many habitats and its hyperdiversity (Wilson, 2003). This genus has two distinct worker subcastes, normal-sized workers and large soldiers with disproportionately large heads. Dimorphic workers enable *Pheidole* colonies to have a morphologically based division of labour in which a large number of easily produced small workers (minors) carry out most of the colonies' tasks, while a small number of large workers (majors) specialize in tasks such as nest defense or breaking open seeds (Wilson, 2003).

### Invasive Species: Competition and Disturbance Specialists?

Another group of ants that can provide information about traits important to trade-offs between competitive ability and adaptation to other stresses and disturbances is invasive ants. Invasive ants usually out-compete native ants in habitats that are highly disturbed by human activity, but are less successful in more pristine habitats (Holway, 1998; Holway *et al.*, 2002). Traits common to invasive ant species include large colony size, small and usually monomorphic workers, strong interspecific aggression and weak intraspecific aggression, polygyny with unicoloniality, short queen lifespan, worker sterility, mating in the nest with colony reproduction via budding, and unspecialized nest sites and food requirements (Table 3) (Passera, 1994). These traits enable invasive ants to be highly competitive and tolerant of disturbed habitats. Holway (1999) found that the invasive Argentine ant, *Linepithema humile*, unlike native ants, had high competitive ability through both interference and exploitative competition. However, like other invasive ants, *L. humile* is adapted to a narrow range of environmental conditions and cannot tolerate stresses such as low temperatures or low soil moisture (Holway, 1999). In addition, escape from natural enemies, such as predators, parasites and pathogens, may facilitate the competitive advantage that invasive ants have over native ants in some habitats (Holway *et al.*, 2002).

### CORRELATES OF COLONY SIZE AS ADAPTATIONS TO DISTURBANCE, STRESS AND COMPETITION

Several authors have highlighted the importance of colony size for social organization and social complexity (Karsai and Wenzel, 1998; Bourke, 1999; Anderson and McShea, 2001). Colony size is also an important factor in terms of adaptation to different stress and disturbance regimes. In fact, most of the factors distinguishing the different functional groups (see Table 3) are

correlated in one way or another with colony size.

### Colony Size and Disturbance

Colony size is directly implicated as an important factor for adaptation to different disturbance regimes. Life-history theory predicts that frequent severe disturbance, such as high rates of predation on colonies, will select for smaller average colony size (Kaspari and O'Donnell, 2003). Theoretically, there is a trade-off between colony size and generation time such that species with smaller mature colony sizes have shorter generation times. Species adapted to high levels of habitat disturbance, such as Opportunists, then may use an 'r-selected strategy' of small colony size and short generation time so that they reproduce before being hit by a habitat disturbance. This life-history strategy may also be used in response to frequent biotic disturbances such as predation (see Kaspari and O'Donnell, 2003). There is also a trade-off between colony size and worker behavioural specialization (Oster and Wilson, 1976; Anderson and McShea, 2001). Species with larger colonies have more specialized workers and sometimes even have a division of labour based on worker polymorphism. In addition, queen-worker dimorphism seems to increase with colony size (Frumhoff and Ward, 1992). Species with small colonies have behaviourally generalist workers and little queen-worker dimorphism. In fact, some species do not have a queen caste, but instead have workers that can mate (Heinze and Tsuji, 1995). This could be selectively favoured with frequent disturbance because if any egg-laying queens are killed, other workers begin egg-laying. More generally, polygyny is queen redundancy and could be an adaptation to frequent disturbance. In summary, possible adaptations to frequent disturbance include small colony size with fast generation time, unspecialized workers and polygyny. Note that there are likely alternate strategies for dealing with some disturbances. For example, in response to pressure from large predators or competition from other mature colonies, some species may invest all resources

in colony growth instead of reproduction in order to grow large relatively quickly to deal with predators or competitors.

Wilson (1984) experimentally studied the effects of disturbance on colony organization and worker behavioural specialization by removing a portion of the colony and observing how individual workers and the colony as a whole responded. When all small workers were removed from a *Pheidole* colony, the large soldiers, which normally carried out a few specialized tasks, carried out tasks normally completed by small workers, although they were not as efficient at those tasks. Wilson (1984) discussed the 'elasticity' of individuals in response to major disturbances and 'resiliency' of the colony as a whole. Wilson's experiments revealed that species with specialized workers can respond to major disturbances, but presumably, species with a small number of unspecialized workers can better respond to disturbance. It is interesting to note that most ant species go through a stage in early colony development in which there are a small number of workers. Instead of producing a smaller number of large, morphologically or behaviourally specialized workers, colonies at this stage produce many small, monomorphic, unspecialized workers (Porter and Tschinkel, 1986; Tschinkel, 1993; Mailleux *et al.*, 2003). Incipient colonies are especially vulnerable to disturbance from neighbouring colonies, parasites, etc., and the optimal colony strategy seems to be one that maximizes the ability of the colony to be resilient to disturbance by generating a large number of smaller workers, rather than relying on the larger, protective, specialized workers.

### Colony Size and Stress

Large colony size may facilitate tolerance of stress because as colony size increases the ability to maintain homeostasis increases (Kaspari and Vargo, 1995). However, in extremely stressful habitats, such as the arctic, only ants with small colonies exist. These ants have individual-level physiological adaptations to extreme cold temperatures as well as colony-level adaptations,

such as multiple queens and generalized nest site preference (Heinze, 1993; Heinze *et al.*, 2003).

### Colony Size and Competition

When all else is equal, large colonies are competitively superior to small colonies simply because they can field more workers to collect food resources or battle neighbours (McGlynn, 2000). As discussed above, there is a trade-off between colony size and worker behavioural specialization, worker polymorphism and queen-worker dimorphism (Frumhoff and Ward, 1992). Worker polymorphism may enable a colony to be competitively superior due to an efficient division of labour (Oster and Wilson, 1976). However, most invasive ants are monomorphic with many, small workers, and worker polymorphism is clearly not necessary for high competitive ability (McGlynn, 1999). Queen-worker dimorphism is positively correlated with colony size (Frumhoff and Ward, 1992). One reason is that in order to have high egg-laying rates, queens must have physiological and morphological adaptations, which are not expressed in workers. In general, colony size is correlated to social complexity: as colony size increases, colony tempo increases, the amount of worker polymorphism decreases, the amount of worker reproduction decreases (Bourke, 1999; Anderson and McShea, 2001).

### Evolution of Colony Size

Throughout this section, we have highlighted that colony size is often involved in adaptations to disturbance, stress and competition. It is interesting to note that colony size seems to be fairly evolutionarily labile, with closely related species having widely different colony sizes (Bourke, 1999). Small changes in individual-level traits such as queen fecundity may have large impacts on colony size, and positive feedback loops may exist between these individual-level traits and colony size (Bourke, 1999). The optimal, mature colony size of a species is likely to be determined largely by environmental

conditions (Bourke, 1999). For example, as discussed above, species experiencing frequent disturbance may be selected to have small colony size with early age at reproduction. Exactly how evolutionarily labile colony size and correlated traits are related to changing environmental stress and disturbance regimes determines whether a species can persist in the face of long-term environmental change.

### ADAPTATION TO CHANGING STRESS AND DISTURBANCE REGIMES

Ants are insects with limited behavioural responses to environmental change, and there is a limit to how fast ants can evolve to tolerate new stress and disturbance regimes. This can be demonstrated by the fact that while humans have drastically modified the environment, especially over the past century, only a handful of 'tramp' ant species can be called human commensals (Passera, 1994; Holway *et al.*, 2002). These species do not seem to have evolved to the environments inhabited by humans, rather these species had several preadaptations that allowed them to thrive in habitats disturbed by human activity (Passera, 1994). Similarly, ant species commonly found in habitats highly disturbed by human activity such as suburban lawns and sidewalks are species that are adapted to live in grasslands (e.g. Wheeler and Wheeler, 1963), which might experience similar disturbance regimes. In general, ant species seem to be adapted to a particular disturbance and stress regime, and they thrive only within this narrow environmental range (Meier, 1994; Holway, 1998; Holway *et al.*, 2002).

Ultimately, if a population is to adapt to changing stress and disturbance regimes, individual- and colony-level traits that underlie tolerance of stress and disturbance must have genetic variation so that these traits can respond to selection. Overall, there is very little known about levels of genetic variance and rates of evolution for these individual- and colony-level traits in ants. For example, only two studies have estimated the genetic variance for traits of ant populations (Li and Heinz, 1998). However, as

discussed above, there are reasons to believe that some important traits are more evolutionarily labile than others. For example, colony-level traits important to social organization and tolerance of disturbance, such as colony queen number and colony size, seem to be relatively evolutionarily labile (Bourke, 1999). In the red fire ant, *Solenopsis invicta*, a single gene seems to largely determine whether colonies are monogynous or polygynous, and this difference has cascading effects on colony organization, reproductive strategy and tolerance of disturbance (Krieger and Ross, 2002). It is interesting to note that many populations of invasive ants seem to differ from the native populations from which they arose in traits such as worker size, queen number and reproductive strategy (McGlynn, 1999; Tsutsui and Suarez, 2003). These differences seem to involve genetic differences and may be associated with founder events such as population bottlenecks. It may be that only a small portion of populations of invasive ants are successful because only a small portion has the requisite genetic changes (Tsutsui and Suarez, 2003).

It is interesting to consider the relative difficulty for ants to adapt to changing stress and disturbance regimes. Stresses such as daily and seasonal temperature extremes are relatively predictable and change over long time periods. Adaptations to these temperature-related stresses involve complex individual-level physiological and behavioural traits or colony-level traits such as specialized nests. These adaptations seem to be exhibited in a limited number of taxonomic groups (Andersen, 2000). For example, only a handful of ant genera have the necessary individual- and colony-level adaptations to tolerate extremely cold temperatures (Heinze, 1993; Heinze *et al.*, 2003). Similarly, traits connected to tolerance of low availability of nest sites and food resources, are specific to groups of species, and these traits may not be very evolutionarily labile. In contrast, as discussed above, traits connected to tolerance of disturbances seem to be relatively evolutionarily labile. Traits such as colony size, colony queen number and reproductive strategy often differ between closely related species and even among popu-

lations within a species (Bourke and Franks, 1995; Bourke, 1999). A wide variety of ant taxa have traits associated with tolerance of disturbance (Andersen, 2000). Thus, ants may be more capable of adapting to changing disturbance regimes than changing stress regimes.

## DISCUSSION

The purpose of this paper was to identify important individual- and colony-level traits that underlie trade-offs among adaptations to disturbance, adaptations to stress and competitive ability. We chose ants as a study system because of their extreme diversity in terms of life history at nearly all taxonomic levels. In addition, a functional group scheme based on groups of taxa that seem to be differentially adapted to habitat disturbance, temperature stress and competition has already been developed (Andersen, 2000; Hoffmann and Andersen, 2003). Unfortunately, ants' extreme diversity limits the utility of taxonomically based functional groups. While we were able to identify some traits that seemed to be common within the various functional groups, there were also many notable exceptions (see Table 3). We suggest that in the future it may be useful to define functional groups based not on taxonomy, but on the presence of particular life-history traits. Considering a variety of scales of stress, disturbance and responses to these factors is useful. Clearly, much more research into this topic is needed (Bourke and Franks, 1995).

More generally, the study of ants provides some insights into possible adaptation of social organisms to disturbances and stress regimes. Within the literature on robustness of systems, three key factors are mentioned that make systems able to cope with changes: redundancy, modularity and diversity (Kirschner and Gerhart, 1998; Csete and Doyle, 2002; Low *et al.*, 2003; Staber and Sydow, 2002; Krakauer, 2003; Sole *et al.*, 2003). While all ant colonies have some of these system characteristics (Hölldobler and Wilson, 1990), our review of functional groups that cope with disturbances in different ways highlights the importance of some of these

characteristics. For example, Opportunists and Invasive species often have redundancy of queens (polygyny) and modularity of nests (polydomy). Species with large colonies that are more competitive usually have more complex societies with levels of organization above the level of the individual worker and communication among these levels. There is often diversity among workers (behavioral and morphological task specialization) and worker groups. There is also some degree of redundancy because when the colony is disturbed, groups of workers can switch tasks. In addition, species with large colonies often have multiply mated queens (polyandry), which, along with queen number, determine the genetic diversity of colonies.

Tolerance of high levels of disturbance may require small, relatively homogeneous populations that can reproduce relatively fast. Adaptation to stress may often require physiological traits such as tolerance of extreme temperatures, which can only evolve over many generations. Such stress adaptations refer to highly optimized adaptation of complex systems, which are robust within a certain regime, but are fragile to regime change (Carlson and Doyle, 2002). Systems of high social complexity and specialized individuals seem likely to evolve only in environments with a relatively stable and mild disturbance and stress regime. Such ant colonies can be very competitive and invest resources to build up redundancy and diversity to deal with modest disturbances. In case of more frequent and severe disturbances, high social complexity is costly for survival.

What can the insights on ant species contribute to anthropogenic social-ecological systems? From the anthropological studies on adaptation it is known that humans in harsh environments with high levels of disturbances and stress, like hot/cold climates, or high rainfall variability, communities are organized to be very mobile with low capital investments. These types of human adaptations are disappearing due to the emergence of highly competitive capital intensive forms of humans to organize themselves. Some scholars argue that civilization could only take off during a period of a very benign climate (Fagan, 2004). Although we make some crude

simplifications, especially since humans are affected by cultural evolution more than genetic evolution, it resembles some of the differences we seen among ant species. Since human activities are changing the spatial and temporal variability by, for example, climate change, disturbing the global biogeochemical cycles, the introduction of invasive species and genetic modified organisms, we wonder how *H. sapiens* may respond to this in an effective way. Some scholars are focussing on social memory and functional roles of various individuals (Berkes *et al.*, 2003). We suggest that it might be worthwhile to focus on the organization of human activities at a higher level. Will future disturbance and stress regimes shifts require human societies to be less capital intensive and more mobile? Given the current human-induced changes in disturbance and stress regimes, and the expected increased volatility of disturbance regimes, there is an interesting open question how *H. sapiens* can best culturally adapt to and anticipate those regime shifts.

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