Out of Oz: Opportunities and Challenges for Using Ants (Hymenoptera: Formicidae) as Biological Indicators in North-Temperate Cold Biomes

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Aaron M. Ellison
Harvard University
Harvard Forest
324 North Main Street
Petersham, Massachusetts 01366 USA
e-mail: aellison@fas.harvard.edu

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Abstract

I review the distribution of ant genera in cold biomes of the northern hemisphere, and discuss opportunities and challenges in using ants as environmental, ecological, and biodiversity indicators in these biomes. I present five propositions that, if supported with future research, would allow ants to be used as biological indicators in north-temperate cold biomes: (1) distribution of individual species or species groups are leading (early-warning) indicators of climatic warming at tundra/taiga or taiga/broadleaf forest boundaries; (2) mound-building species in the *Formica rufa* LINNAEUS, 1758 group are ecological indicators for land-use changes in European taiga and broadleaf forests; (3) relative abundance (evenness) is a leading indicator of environmental changes whereas high species richness is an indicator of past or ongoing disturbance; (4) presence or social parasites and slave-making species are better indicators of ecological integrity than presence or abundance of their hosts alone; (5) occurrence of non-native or invasive species is an indicator of reduced ecological integrity. Important aspects of long-term sampling, surveying, monitoring, and experimenting on ants are discussed in light of future research needs to test these propositions and to further develop ants as indicators of changing environmental conditions in north-temperate cold biomes.

Key words: disturbance, ecological indicator, ecosystem integrity, indicator species, leading indicator, reference state, restoration, umbrella species.

Prof. Dr. Aaron M. Ellison, Harvard University, Harvard Forest, 324 North Main Street, Petersham, Massachusetts 01366 USA. E-mail: aellison@fas.harvard.edu

Introduction

Invertebrates have been used as biological indicators of environmental conditions in aquatic ecosystems for over 100 years, but it is really only in the last 30 years that arthropods – most notably ants, beetles, and butterflies – have been developed as biological indicators in terrestrial ecosystems (e.g., reviews by ROSENBERG & al. 1986, MCGEOCH 1998, ANDERSEN & MAJER 2004). Ants have been promoted as particularly useful biological indicators, especially for detecting colonization of exotic and potentially invasive species, identifying success or failure of land management and restoration schemes that cannot be determined by monitoring vegetation change alone, and monitoring lasting effects of changes in land use and land cover (e.g., reviews by ALONSO 2000, KASAPRI & MAJER 2000, ANDERSEN & MAJER 2004, UNDERWOOD & FISHER 2006, CRIST 2009, PHILPOTT & al. 2010). The utility of ants as biological indicators has been demonstrated most frequently in Australia (reviewed by ANDERSEN & MAJER 2004), the rangelands of southwest North America and South America (BESTELMEYER & WIENS 1996, 2001), and in both wet and dry tropical forests (e.g., ROTH & al. 1994, PERFECTO & SNELLING 1995, PERFECTO & al. 1997) (Fig. 1).

Perhaps unsurprisingly, the majority of localities for which ants have been used successfully as biological indicators have warm climates. Temperature is strongly associated with increases in ant diversity and abundance (SANDERS & al. 2007), seasonal patterns of foraging activity (DUNN & al. 2007) and behavior (RUANO & al. 2000), and the strength of competitive hierarchies among species (CERDA & al. 1997, HOLWAY & al. 2002). The rates of many ecosystem processes that can be mediated by ants, such as decomposition, nutrient cycling, and primary production (HÖLLDOBLER & WILSON 1990, FOLGARAIT 1998), also increase with temperature; ant activity may accelerate these responses (PEAKIN & JOSENS 1978, PĘTAL 1978). Because of their sensitivity to temperature, ants should respond rapidly to such climatic changes and how ants respond to climatic change, especially to local and regional changes in temperature, could have dramatic consequences for associated taxa and ecosystem dynamics (LENSING & WISE 2006, MOYA-LARANO & WISE 2007, CRIST 2009). Responses of ants to climatic changes also may be especially apparent at ecotonal or habitat boundaries.

Cold temperate biomes (Table 1; Fig. 2) are underrepresented in studies and syntheses of ants as biological indicators (Fig. 1) despite the fact that two of the four cold temperate biomes in the northern hemisphere – Arctic tundra and taiga / boreal forest – together account for ≈ 50% of the land surface of the Earth. Ants may not be as diverse in cold climates as they are in the tropics, but the climates of cold temperate biomes are changing much more rapidly than those of warm temperate and tropical biomes – for example, projections suggest a 3 – 6 ^{o}C warming of land surface temperatures by the end of the 21st century for the Arctic tundra (FENG & al. 2011) – and ants are likely to respond rapidly to these changes (PELINI & al. 2011a).

In this paper, I discuss the use of ants as environmental, ecological, and biodiversity indicators in north-temperate cold biomes. I highlight opportunities for the use of ants as leading (or early warning) indicators of environmental change, especially at northern and southern boundaries of the boreal forest; explore the utility of different functional group classifications of ants in cold climates; discuss unique aspects of sampling, surveying, and monitoring ants in these regions; and suggest future directions for research on ants in these currently cold, but rapidly warming, biomes.

Can ants be useful indicators in north-temperate cold biomes?

I follow MCGEOCH (1998) in distinguishing three types of biological indicators – environmental, biodiversity, and ecological indicators – and add one additional type of indicator: leading indicators of impending environmental change (also called critical thresholds, state changes, or regime shifts; SCHEFFER & al. 2009). In brief: environmental indicators illustrate a *response* to environmental change; leading indicators *anticipate* environmental change; biodiversity indicators *represent* other taxa in the same environment; and ecological indicators both respond (or anticipate) to environmental change *and* represent other taxa (Fig. 3; Box 1).

ANDERSEN (1999) identified five criteria for deciding if a taxon can be a useful biological indicator. First, the group should be taxonomically stable and species (or functional groups) should be readily identifiable. Second, it should be abundant enough to sample reliably. Third, it should be functionally important at least in its local ecosystem. Fourth, the potential indicator should be sensitive to environmental change. Finally, responses to environmental change should be interpretable as real responses distinct from expected random variation in temporal patterns.

Ant taxonomy is relatively stable (nomenclature throughout this review follows BOLTON & al. 2007 and associated web updates posted through 1 January 2012). The north temperate myrmecofauna is known well enough that reliable checklists and keys are already available (e.g., WHEELER & WHEELER 1963, 1977, FRANCOEUR 1997, PFEIFFER & al. 2006, SEIFERT 2007, RADCHENKO & ELMES 2010, ELLISON & al. 2012) or can be constructed from on-line sites such as antweb.org, antdata.org, or antbase.net. In the next section, I describe the primary environmental threats to each of the north-temperate cold biomes, provide examples of how ants respond to some of these threats, and discuss whether ants can meet the second, third, and fourth criteria of biological indicators for each of the biomes. Although it is a necessary precondition to demonstrate experimentally that a potential indicator taxon responds to environmental perturbation (criterion four), only sustained experimental treatments ("press experiments" sensu BENDER & al. 1984) with appropriate controls coupled with long-term monitoring (LOVETT & al. 2007) can allow for reliable separation of a putative indicator's "signal" from background "noise" (ANDERSEN 1999). Thus in the penultimate section, I discuss whether ants can meet ANDERSEN's (1999) fifth criterion for north-temperate cold biomes, along with requirements and challenges of sampling, surveying, monitoring, and conducting experiments on ants in these regions. I close with a short agenda of future research needs to more fully develop ants as biological indicators in north-temperate cold climates.

North-temperate cold biomes: environmental threats and their ants

This review focuses on the four biomes that cover the vast majority of the northern hemisphere: Arctic tundra; taiga and boreal forest; temperate broadleaf forests; and temperate grasslands (Table 1; Fig. 2). For the latter two biomes, discussion is restricted to regions north of the approximate extent of the Pleistocene glacial maximum in Eurasia and North America (blue line in Fig. 2). The southern extent of Pleistocene glaciation is a notable boundary for ants in North America; army ants (Ecitoninae: *Neivamyrmex* BORGMEIER, 1940), leaf-cutter ants (Myrmicinae: *Trachymyrmex* FOREL, 1893), harvester ants (*Pogonomyrmex* MAYR, 1868 and *Messor* FOREL, 1890), and *Forelius* EMERY, 1888 and other dominant Dolichoderinae (sensu ANDERSEN 1997a) do not extend north of this line (Wheeler & Wheeler 1963, Watkins 1985, Coovert 2005). Southern hemisphere temperate broadleaf/mixed forests and temperate grasslands/savannas/ shrublands, with their unique vegetation types and diverse ant faunas, are well-represented in the ants-as-indicators literature and also are excluded from this review. Finally, I do not discuss the extensive temperate coniferous forests (temperate rain forests) of western North America, and their isolated counterparts in western Ireland, Scotland and Wales, western Norway, southern Japan, and the Caspian Sea region of Turkey, Georgia, and northern Iran, as these forests have a distinctly warmer and wetter climate than the other four north-temperate cold biomes. The climate of north-temperate cold biomes is changing rapidly (Feng & al. 2011), which not only provides a unique opportunity to observe and study responses of ants to unprecedented environmental changes but also suggests new possibilities for using ants as leading indicators of global environmental change.

Arctic tundra (Fig. 4). The primary environmental threats to Arctic tundra are habitat fragmentation and destruction from oil and gas exploration, drilling, and oil spills (e.g., Kumpula & al. 2011; Fig. 4); pollutants derived from wet and dry atmospheric deposition (e.g., Vingarzan 2004, Derome & Lukina 2011, Sokolik & al. 2011); and thawing of the permafrost and encroachment of woody vegetation as regional temperatures warm (e.g., Chapin & al., 1995, 1996, Hudson & Henry 2009, Sun & al. 2011). Local and regional warming will provide opportunities for ants to extend their range northward (Alfimov & al. 2011).

The temperature regime of the tundra is well below the temperature optima for all but a handful of ants (Berman & al. 2010). Thus, ants are few and far between in the Arctic tundra, and generally are collected only very close to the tundra/taiga boundary. Supplementing Gregg's (1972) records of ants collected in Churchill, Manitoba (Canada) with additional collections from the tundra/taiga boundary of Québec (55 to > 58 ^{o}N), Francoeur (1983) identified five ant species that occur near the tree-line in North America – *Myrmica alaskensis* Wheeler, 1917, *Leptothorax acervorum* (Fabricius, 1793), *Leptothorax* cf. *muscorum* (Nylander, 1846), *Camponotus herculeanus* (Linnaeus, 1758) (Fig. 5), and *Formica neorufibarbis* Emery, 1893 – and one species – *F. aserva* Forel, 1901– for which stray individuals, but not colonies, have been collected. Weber (1950, 1953) recorded *F. fusca* Linnaeus, 1758 from the mouth of the Mackenzie River in Canada, and suggested based on historical evidence that it would eventually be found in Arctic Alaska. Based on a subsequent collection in the Yukon (Francoeur 1997), I would attribute this species to *F. gagatoides* Ruzsky, 1904, but confirmation will require additional collections. *Formica gagatoides, F. lemoni* Bondroit, 1917, and *L. acervorum* all have been recorded at the tundra/taiga boundary in the Central Altai Mountains of Russia, near the joint border of Russia, China, Mongolia, and Kazakhstan (Chesnokova & Omelchenko 2011). In the Kamchatka region of Russia, *Myrmica kamtschatica* Kupyanskaya, 1986 nests in moss atop the permafrost (Berman & al. 2010) and is the most cold-tolerant species of the Palearctic *Myrmica* Latreille, 1804 discussed by Radchenko & Elmes (2010)

Although ants are rare to absent deep in the tundra, their predictable occurrence at the tundra/taiga boundary suggests that they could be a reliable leading indicator of rapid environmental change at this ecotone. As the climate warms and permafrost thaws, woody vegetation is expanding into the tundra (e.g., Walker & al. 2006, Feng & al. 2011), and species such as *Camponotus herculeanus*, which is among the most cold-tolerant ants (Berman & al. 2010) but requires dead wood for nest sites (Francoeur 1983), could rapidly extend its range northward. Although one could simply monitor plant cover as an indicator of environmental change, simply seeing plants is not in itself sufficient evidence of wholesale ecosystem change. In other words, the plants could be there, but herbivores, omnivores, and predators might not. The presence of ants, which fill many roles in the ecosystem other than primary production, provides better evidence than plants alone for systemic ecological changes. *Formica exsecta,* the least cold-tolerant of the tundra/taiga-boundary ants (Berman & al. 2010), is already moving north (Alfimov & al. 2011), and other cold-tolerant ants such as *Leptothorax acervorum* and *F. gagatoides* likely will follow. However, none of these ants are abundant enough or have substantial impacts on ecosystem functions in the tundra to be considered more broadly as ecological or biodiversity indicators.

Taiga and the boreal forest (Fig. 6). The primary environmental threats to taiga include: habitat fragmentation and loss from extensive logging (e.g., Boucher & Grondin 2012); flooding due to development of large hydroelectric projects (e.g., Kumari & al. 2006, Mallik & Richardson 2009); exploration and extraction of oil and natural gas reserves (e.g., Robertson & al. 2007); mining for minerals and peat (e.g., Maljanen & al. 2010, Petit & al. 2011); fire (e.g., Jiang & Zhuang 2011); and widespread loss of tree canopies from insect outbreaks (e.g., Simard & al. 2011). The extent and frequency of fire and insect outbreaks across the taiga also have increased rapidly in recent decades as the climate has warmed (e.g., Gustafson & al. 2010, Beck & al. 2011), and all of these factors interact synergistically and cumulatively, often resulting in far more environmental damage than any one of them alone (Yamasaki & al. 2008). Ant responses to these disturbances can be very variable.

At least 25 Holarctic ant genera (Table 2) and >100 species can be found in taiga (Azuma 1955, Vespsäläinen & Pisarski 1982, Savolainen & al. 1989, Reznikova 2001, Pfeiffer 2006, Herbers 2011, Ellison & al. 2012), including cold-climate specialists, cryptic species, opportunities, generalized Myrmicinae (Fig.7), and specialist predators (functional groups sensu ANDERSEN 1997a). Individual ant species and groups of colonies can be very abundant in taiga, where they often have strong and persistent effects on ecosystem processes (e.g., FROUZ & al. 2005, RUBASHKO & al. 2011) and where their distribution and abundance can be dramatically altered by human actions.

The most extensive ecological research on the relationships between ant assemblages and environmental changes in the taiga has been done in northwestern Europe, where competitively dominant, mound-building wood ants in the *Formica rufa*-group are prevalent (e.g., SAVOLAINEN & al. 1989) and may be good indicators of logging and subsequent succession (e.g., PUNTILLA 1996, KILPELÄINEN & al. 2005) or other land-use changes. In Eurasia, as human land use of the taiga has changed from historical patterns, such as by decreasing extent of clear-cut logging or increasing intensity of repeated land use (e.g., PUNTTILA & al. 1994, PUNTTILA 1996, DOMISCH & al. 2005, KILPELÄINEN & al. 2005), distribution and abundance of *Formica rufa*-group ants, notably *F. aquilonia* YARROW, 1955 and *F. lugubris* ZETTERSTEDT, 1838 has changed in parallel. For example, in Finnish forests, *Formica aquilonia* generally is more abundant in old-growth forests and large parcels of older forests, whereas *F. lugubris* and the *F. sanguinea*-group ant *F. sanguinea* LATREILLE, 1798, favors younger forests and smaller fragments (PUNTTILA 1996, PUNTTILA & al. 1996). Historical legacies are important; 20-year-old monocultures of Scots pine (*Pinus sylvestris* LINNAEUS, 1753) planted in clearcuts after which the site had been ploughed before replanting lack *F. rufa*-group mounds (DOMISCH & al. 2005).

Curiously, although many *F. rufa*-group ants occur in North America, only a handful builds large mound-nests (JURGENSEN & al. 2005). Of these, only *F. obscuripes* FOREL, 1886 may extend its range into taiga in northern British Columbia, Canada (LINDGREN & MACISAAC

2002). Two other *F. rufa*-group species that build small, thatch-covered mounds can be found in North American taiga: an undescribed species near *F. fossaceps* BUREN, 1942 (ELLISON & al. 2012) and *F. dakotensis* EMERY, 1893 (FRANCOEUR 1997). However, two North American *F. fusca*-group species – *F. podzolica* FRANCOEUR, 1973 and *F. glacialis* WHEELER, 1908 – build substantial mounds in the southern taiga and northern reaches of the temperate broadleaf forests (FRANCOEUR 1973). Like *F. exsecta* in northeastern Siberia, *F. podzolica* and *F. glacialis* have potential to be developed as leading indicators of climatic change at the southern boundary of the taiga.

In both European and North American taiga, however, overall ant species richness is much lower in mature forests than in either recently logged areas or in early successional forests (JENNINGS & al. 1986, PUNTTILA & al. 1991, LOUGH 2003), suggesting that high ant species richness *per se* is a better indicator of present or past disturbance than of baseline, “natural” environmental conditions. Similarly, ant species richness in taiga is not likely to be a good surrogate for species richness of other groups in this biome (JONSSON & JONSELL 1999, SCHULDT & ASSMANN 2010). There are no data available suggesting that ants could be leading indicators of any particular environmental changes within taiga, as opposed to at its margins.

Particular taiga species have very narrow habitat requirements and could be developed as indicators of habitat decline or restoration success. For example, in North America, open peatlands within the taiga host unique ants, including *Myrmica lobifrons* PERGANDE, 1900 (Fig. 7; FRANCOEUR 1997) and *Leptothorax sphagnicola* FRANCOEUR, 1986 (FRANCOEUR 1986). The ecology of Palearctic bog-dwelling *Myrmica*, a common and diverse group of taiga-dwelling ants, is covered in detail by RADCHENKO & ELMES (2010). High abundance of such habitat specialists could serve as indicators that mined peatlands throughout the have been restored, whereas their absence could indicate some degree of disturbance or environmental stress. Experiments and additional observations are needed, however, to support this assertion.

Finally, many environmental monitoring programs look for indicators of "ecosystem health" or "ecosystem integrity." For example, the Canada National Parks Act (S.C. 2000, c. 32, as amended 10 December 2010; Department of Justice Canada 2012) states that "maintenance or restoration of ecological integrity, through the protection of natural resources and natural processes, shall be the first priority of the Minister when considering all aspects of the management of parks" (S.C. 2000, c.32, Section 8). Ecological integrity is interpreted to mean that "ecosystems have their native components intact, including abiotic components, biodiversity, and ecosystem processes" (Parks Canada 2009). An oft-neglected characteristic of intact biodiversity is the presence of parasites. A number of taiga ant species, including *Myrmica quebecensis* Francoeur, 1981, *M. lampra* Francoeur, 1968, *Harpagoxenus canadensis* Smith, 1939, and *Formica rufa*-group and *F. exsecta*-group species are temporary social parasites or slave-makers. Given appropriate habitats and abiotic conditions, the presence of such parasites could indicate a more "intact" assemblage of ants than one lacking them.

Temperate broadleaf (deciduous) forests (Fig. 8)**.** Temperate deciduous forests have been settled and used by people for millennia (e.g., Foster & Aber 2004), and there are virtually no environmental threats that are not present in this biome. Changes in land use and land cover from centuries of urbanization, forestry, agriculture, mining, and hydroelectric power development, and global commerce also have provided extensive opportunities for colonization and spread of non-native ant species (e.g., Pećarević & al. 2010).

There are nearly 40 ant genera that nest in north-temperate broadleaf forests (Table 2). Most genera found in taiga are also found in broadleaf forests, but they are more speciose in the latter (e.g., PISARSKI 1978, GOTELLI & ELLISON 2002, ELLISON & al. 2012). Functional groups and Holarctic genera present in north-temperate forests, but absent from tundra and taiga, include the generalist Myrmicinae *Crematogaster* LUND, 1831, *Monomorium* MAYR, 1855, and *Pheidole* WESTWOOD, 1839, and the specialist predators *Polyergus* LATREILLE, 1804 and *Pachycondyla* F. SMITH, 1858 (Table 2).

Ant abundance and species richness is higher in temperate broadleaf forests than in taiga – notably many more species in cryptic genera (Table 2) occur in temperate broadleaf forests – but there are surprisingly few data on responses of ants to environmental pressures or climatic changes in this biome (PELINI & al. 2011a, 2011b). In northeastern North America, species evenness is highest at intermediate temperatures, but there is little effect of a ±1 ^{o}C change in temperature on other measures of ant species diversity or ant foraging activities (PELINI & al. 2011a). In northwest Belgium, abundance of colonies of *F. rufa* and *F. polyctena* have been declining steadily as their open-forested habitat matures and closes in, is converted to intensive agriculture, is used heavily for recreation, or is destroyed for urbanization (DEKONINCK & al. 2010). A key reason for their decline is the lack of co-occurring *F. fusca*, which the social-parasite *F. rufa*-group species use as hosts; in North America *F. fusca*-group species are enslaved by species in the *sanguinea* group (Fig. 9). This further illustrates the need to consider multiple taxa in the context of overall ecological integrity in developing ants as indicator taxa.

Mature broadleaf or mixed-deciduous forests also have fewer ant species than early-successional ones. For example, the hemlock-oak-maple forests of eastern North America are rapidly losing their late successional dominant, eastern hemlock (*Tsuga canadensis* (L.) CARRIÈRE, 1855) due to infestation by the non-native hemlock woolly adelgid (*Adelges tsugae* [ANNAND, 1924]) (ORWIG & al. 2002). Ant assemblages in hemlock-dominated forests are species poor – *Temnothorax longispinosus* (ROGER, 1863), *Aphaenogaster picea* (WHEELER, 1908), *Camponotus novaeboracensis* (FITCH, 1855), and *C. pennsylvanicus* (DEGEER, 1773) are the most abundant taxa – but the death of hemlock opens up canopy gaps, creates localized warm spots in the forest matrix, and initiates successional processes that favor a wide range of *Formica fusca*-group and *Lasius* FABRICIUS, 1804 species, among other cold-climate specialists and opportunists (ELLISON & al. 2005, SACKETT & al. 2011). As in taiga, high ant species richness or nest density in temperate broadleaf forests likely is a better indicator of present or past disturbance or successional status than of undisturbed forests (HERBERS 2011). In further support of this proposition is the observation that non-native ant species in this biome tend to favor disturbed or urbanized areas (e.g., GRODEN & al. 2005, CREMER & al. 2008, PEĆAREVIĆ & al. 2010, ELLISON & al. 2012), where they may either increase species richness while at low densities or decrease species richness when they reach high densities and outcompete native species.

Temperate grasslands (Fig. 10). Grasslands have been modified extensively by humans, who have used these areas for agriculture and livestock production for hundreds-to-thousands of years. For example, nearly all of the North American prairies have been replaced with crop monocultures (primarily maize or soybean) or exotic grasses for extensive grazing, and many Eurasian steppes have been similarly impacted (e.g., CREMENE & al. 2005). Restoration of North American remnant prairies is a high priority (e.g., KINDSCHER & TIESZEN 1998, MARTIN & al. 2005), but methods and appropriate species remain controversial (e.g., HOWE 1994) and ecosystem recovery is slow (e.g., MCLACHLAN & KNISPEL 2005, HILLHOUSE & ZEDLER 2011). In Central Europe, agricultural intensification is as much an environmental issue for steppes as is agricultural abandonment; grasslands have been maintained for so long that many species of contemporary conservation concern are restricted to traditionally-managed grasslands (CREMENE & al. 2005).

Of the four biomes under consideration here, grasslands have the most diverse ant fauna because the comparatively warm and dry climate is more favorable to ants (Fig. 11). All but one of the grassland genera occur in the other biomes as well (Table 2), but species diversity of genera and groups such as the *Formica rufa*-group tends to be higher in grasslands. In Eurasia, the endemic genus *Strongylognathus* MAYR, 1853 is probably restricted to grasslands (REZNIKOVA 2003). What is unclear, however, is whether current ant faunas of grasslands and steppes (e.g., WHEELER & WHEELER 1963, REZNIKOVA 2003) represent the "true" fauna of these areas or whether they represent the fauna of a biome long modified by human land use (e.g., ELLISON 2012). This issue is likely to be resolved at best only for North America, as virtually no areas not modified by humans exist in Eurasia.

Many ant species, including species in *Lasius* and *Formica*, have large and demonstrable effects on local ecosystem processes. In North America, *Formica rufa*-group ants attain their highest diversity in grasslands and open woodlands and would be the first group to look at for potential ecological indicators of land-use changes. However, the taxonomy of the North American *F. rufa*-group is in desperate need of revision and very little is known about what environmental factors are related to their patterns of distribution and abundance or how competitive interactions with *Camponotus* species may limit their distribution in ways that differ from their European counterparts (JURGENSEN & al. 2005). On the other hand, as restoration efforts proceed in North America and Eurasia, some ant species may emerge as leading indicators of successful restoration of native prairies and steppes.

Developing ants as biological indicators in north-temperate cold biomes

The above survey and overview of north-temperate cold biomes and their associated ants suggests several possibilities for using ants as biological indicators in these areas, but in light of data currently available, each of these should be treated as proposals to be tested, not as foregone conclusions:

1. Distribution and abundance of individual ant species (e.g., *Camponotus herculeanus*, *Formica exsecta*) or species groups (such as mound-building *F. rufa*-group or *F. fusca*-group species) are leading indicators of climatic change at tundra/taiga or taiga/broadleaf forest boundaries in North America, Europe, and North Asia;
2. Mound-building *F. rufa*-group ants are ecological indicators for land-use changes in European taiga and broadleaf forests;
3. Relative abundance (evenness), not species richness, is a leading indicator of local warming or other climatic changes in north-temperate cold biomes, whereas high species richness is likely to be an indicator of disturbed areas, not reference conditions, if the latter exist;
4. Presence of social parasites and slave-making species are better indicators of ecological integrity than even high abundance of their hosts;
5. Presence of non-native species are indicators of reduced ecological integrity.

Testing these propositions will require reliable samples, robust surveys, and long-term experiments and monitoring programs (Box 2) to ensure that observed responses of ants to environmental changes, and how well these responses reflect broader ecosystem dynamics, can be interpreted as a true ecological "signal" separate from environmental background "noise" (McGeoch 1998, Andersen 1999). Although I have focused this review on large scale, biome-wide patterns, ants (and other invertebrates) are much more appropriately used as biological indicators at regional or local scales (ANDERSEN 1997b). As MCGEOCH (1998) pointed out, many studies of the relationship between indicator species and their broader environment appear to be predictive, but in fact are conducted at the wrong spatial or temporal scale to provide reliable indications of environmental impacts or change. Elaborating all the elements of design and implementation for long-term monitoring schemes, sampling and surveying programs, and experiments would require several book-length treatments (useful references include MEAD 1988, UNDERWOOD 1997, MANLY 2000, and THOMPSON 2002). Box 2 highlights key elements of good monitoring programs, reliable long-term observations and experiments, and core principles of designing studies that will provide useful information on ants so that signals can be differentiated from noise; additional features of successful development of ants as biological indicators include appropriate observational and experimental controls, replication, and reference states (Box 3).

Future research on ants as indicators in north-temperate cold biomes

Ants have great potential to be developed as ecological indicators of ongoing and impending environmental change in north-temperate cold biomes, but research to date on ants-as-indicators has not been as extensive or focused as comparable research in warmer climates and Australia. My list in the preceding section of five propositions about how north-temperate cold climate ants could be developed as biological indicators provides a starting point for targeted research, but it is not meant to be an exclusive list. In addition to testing those propositions, a number of other areas merit renewed attention in studies of north-temperate cold biome ant assemblages:

- **Functional groups.** ANDERSEN & al. (2002) showed that using functional groups instead of individual species simplifies and facilitates the use of ants as indicator taxa. Although functional group assignments of Australian genera can be mapped onto genera of warm climate genera in North America (ANDERSEN 1997), the range of functional groups in north-temperate cold biomes is much smaller (Table 2). Finnish myrmecologists have developed a different functional classification based on competitive hierarchies (SAVOLAINEN & al. 1989) that has proven useful in myrmecological studies throughout northern Europe and Asia. Assessment of the utility of the Finnish approach in colder regions of North American is needed because *F. rufa*-group species in North America are rarely aggressive or territorial. The advantage of using functional groups is that they can be used to identify broad-scale patterns in the responses of ants to changing environments, and to compare these responses across environments. Such observations can help distinguish true responses from background variation, as well as to augment data from large-scale observational or uncontrolled studies (Box 3). On the other hand, the smaller number of species in cold-temperate biomes suggests that specific species, rather than functional groups, could be developed as biological indicators, but then identification becomes much more time-consuming.
- **Umbrella species.** In most warm climates, species richness of ants is not a good surrogate for species richness of other groups at small spatial scales (LAWTON & al. 1998, ALONSO 2000, but see MAJER & al. 2007), but ants are a better surrogate taxon in Western Europe at larger spatial scales (SCHULDT & ASSMANN 2010). This result may be due to the large increase in species richness southern Europe with its Mediterranean climate. Do these steep latitudinal gradients persist at smaller geographical scales (cf.

GOTELLI & ELLISON 2002), are there similar patterns in North America, or are they related to patterns in other potential indicator species of north-temperate cold biomes, such as carabid beetles and lichens (JONSSON & JONSELL 1999)?

- **Reference states**. If ants are developed as indicators of restoration success, we need to have baselines or reference states against which to evaluate observed changes (Box 3). Digitized records of specimens in museum collection may reveal historical patterns of distribution and abundance of ants, and provide data from which to establish appropriate baselines.
- **Standard protocols for long-term monitoring.** Measurement and assessment of distribution and abundance of ants has been standardized for warm climates (AGOSTI & al. 2000), and modifications have been suggested for temperate broadleaf forests (ELLISON & al. 2007). Neither of these, however, addresses the challenges uniquely associated with long-term monitoring (Box 2): habitat alteration by investigators; frequent disturbance of nests attendant to regular censuses; excessive colony depredation by, and unacceptable by-catch in, pitfall traps; and ensuring permanent access to long-term research sites. A community-wide effort to address these issues, on a par with AGOSTI & al. (2000), would be welcome.
- **Regional checklists and accessible keys.** Australian land managers have keys and pointers to functional groups of ants that facilitate their use as biological indicators (ANDERSEN & MAJER 2004). Similar resources need to be created, field-tested, and provided to conservation professionals in north-temperate regions (e.g., ELLISON & al. 2012).

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Box 1: Different kinds of biological indicators.

All indicators are not alike. Thus, it is important first to clearly identify what kind of ecological state or process is of interest and second to ensure that there is sufficient evidence that the proposed indicator can actually be used. Following McGeoch (1998), we identify five different kinds of biological indicators.

Environmental indicators are either a single species or a group of closely related or functionally similar species that *occur* in a particular site or region and *respond in a predictable way* to some change in environmental conditions. Observations demonstrate occurrence, and short-term experiments provide evidence for predictable responses to environmental conditions. Most published examples of ants as biological indicators provide evidence for ants only as environmental indicators (reviews in UNDERWOOD & FISHER 2006, PHILPOTT & al. 2010).

Leading (or early-warning) indicators of abrupt environmental change are species (or species groups) whose population dynamics illustrate dramatic changes in temporal variance as environmental change approaches and whose population sizes following small environmental perturbations recover slowly relative to pre-perturbation conditions (SCHEFFER & al. 2009, BESTELMEYER & al. 2011). Only long-term studies can reveal if ants will be useful as leading indicators (ALFIMOV & al. 2011).

Biodiversity indicators are groups of closely-related species whose richness in a given site or habitat is well-correlated with the species richness of many other groups of conservation or management interest (NOSS 1990). Identification of biodiversity indicators, also known as umbrella taxa, has had mixed success at best. Ants, along with ground beetles (Carabidae) and vascular plants, have been found to be good representatives of overall invertebrate, vertebrate, and plant diversity at regional and country-wide scales in Western Europe (SCHULDT &

ASSMANN 2010), but at smaller scales (e.g., within sites or localities), ants are considered to be poor biodiversity indicators (LAWTON & al. 1998, ALONSO 2000, ENGLISCH & al. 2005, but see MAJER & al. 2007 for a study where ants perform reasonably well as biodiversity indicators).

Ecological indicators combine attributes of all of the other types of biological indicators. They represent the effects of environmental change on the broader ecological system and themselves are usually of particular concern or conservation interest. In Australia and in the humid tropics, there are many examples where there are sufficient data to use ants as ecological indicators (ANDERSEN & MAJER 2004, MAJER & al. 2007). Examples are sparser in north-temperate cold biomes, and emphasize species in the *Formica rufa*-group (DEKONINCK & al. 2010, GILEV 2011).

Box 2: The essentials of strong, long-term monitoring programs of ants.

Long-term monitoring is crucial for accumulating data on temporal changes in the environment and concomitant changes in the distribution and abundance of ants. Environmental monitoring is defined as "the collection of time-series of physical, chemical or biological variables at one or more locations in order to address questions and hypotheses about environmental change" (LOVETT & al. 2007). Six essential characteristics of successful monitoring programs are (modified and expanded from LOVETT & al. 2007):

1. Develop clear, interesting, compelling, and motivating questions.
2. Monitor only variables of crucial interest and take care with the measurements; time, labor, and money are always limiting, so not every variable can or should be monitored.
3. Ensure and control long-term access to monitored sites.
4. Examine, check, interpret, and present the data regularly. Note especially that quality control – e.g., are temperature sensors drifting or stable? Are repeated measurements of mound or colony size consistent from year to year or when field technicians change? – is an often overlooked aspect of ecological research but is critical in long-term studies.
5. Evolve the monitoring program over time. Trends observed in sampling programs and experiments will support some predictions, fail to support others, eliminate some hypotheses, and suggest new directions. Monitoring programs should evolve in tandem.
6. Archive the data publicly, document the data, and maintain both electronic databases and paper files (e.g., GOTELLI & ELLISON 2004: chapter 8, MICHENER & JONES 2012).

Long-term studies on ants require particular care in determining sampling design and methods. Most field scientists know that observations taken close in space or time are less likely to be independent of one another than observations taken further apart in space or at longer intervals. Polydomous colonies confound spatial sampling even further. Because spatial and temporal autocorrelation cannot really be eliminated, it is crucial to document the patterns of spatial autocorrelation, temporal autocorrelation, and other forms of non-independence and incorporate them explicitly into the analysis. On the plus side, temporal or spatial autocorrelation themselves are the key variables of interest in deciding whether a potential leading indicator is indicating a shift in environmental conditions (e.g., SCHEFFER & al. 2009, BESTELMEYER & al. 2011). Note that a lengthy time series is a series of regularly-spaced observations, not simply a relatively small number of repeated samples made over a long span of time. The latter are much more readily available in the myrmecological literature (e.g., KIPELÄINEN & al. 2005, DEKONINCK & al. 2010, ALFIMOV & al. 2011, HERBERS 2011), but we need the former to determine if ants can be reliable biological indicators of environmental change.

Additional attention to sampling methods also is required because repeated long-term visits to plots or nests can have unintended or unanticipated effects on the system. Obvious examples of observer impacts in both short- and long-term studies of ants include: soil compaction from repeatedly walking the same paths to reach a sampling station, colony, or nest; disturbance of nests through repeated sampling of individuals; and potential reduction of colony size below sustainable levels following repeated disturbances or sample collection bouts. For these and several other reasons, I do not recommend using pitfall sampling for long-term sampling or monitoring. First, digging holes for pitfall traps causes extensive disturbance to soil; the impacts of this disturbance on ant activity or population dynamics is rarely studied (GREENSLADE 1973, MAJER 1978). Second, if pitfall traps are placed on an active foraging trail, one or more entire colonies can be unintentionally collected, changing local population densities. At the same time, pitfall traps accumulate many other species (“by-catch”), few of which may be of interest to the investigators (Buchholz & al. 2011), some of which may be of significant conservation concern (New 1999), and many of which may be strong interactors with local ant colonies. Finally, in north-temperate cold biomes, pitfall traps are not as effective at sampling overall species diversity as the combination of hand- and litter-sampling (Ellison & al. 2007). Hand- and visual sampling also are much more appropriate if the focus is on a particular species or species group that is readily apparent (such as mound-building ants).

Because large-scale surveys and experiments can be expensive and labor-intensive to set up, there is a temptation to measure everything one can think of. This temptation must be resisted or there will be so many disturbances to study areas and ant nests that monitoring artifacts overwhelm the signals of interest. Thus, the most important principle of good design is that the monitoring activities should not contaminate the data by altering the processes being studied: the data should reflect only the effects of the imposed treatments or chosen comparisons, and not the monitoring activities themselves.

Box 3: Controls, replication, and reference states**.**

Ecological studies need adequate replication and appropriate controls. Designs may be replicated in space, in time, or in both. Sometimes space is substituted for time, as in simultaneous examination of temporal responses of ants following logging (e.g., PUNTTILA & al. 1991). Study designs may have no manipulation (purely observational), a controlled (by the investigator), experimental intervention, or an uncontrolled intervention. Experimental manipulations provide for controls, but manipulative experiments and there controls are expensive and difficult to implement across large spatial scales (see PELINI & al. 2011b for a resolution of both of these issues). Uncontrolled interventions are a good compromise between controlled experiments and monitoring studies that lack controls. Uncontrolled interventions can be accidental (e.g., air pollution and subsequent deposition) or deliberate (e.g., logging of forests); sometimes replicates are available, other times they are not. If the intervention is unplanned, it also is rarely possible to collect any data before the intervention occurs, and baselines or reference states may be otherwise unavailable.

Most studies can be easily classified based on their type of replication and type of manipulation. For example, long-term monitoring of the number of ant mounds at one or more locations are temporally replicated without manipulation (e.g., ALFIMOV & al. 2011). A snapshot comparison of ant assemblage structure in multiple areas with and without logging (e.g., JENNINGS & al. 1986) is a spatially replicated, uncontrolled intervention. An experimental investigation of the responses of ants to changes in forest canopy structure (e.g., ELLISON & al. 2007, SACKETT & al. 2011) is a controlled, spatiotemporally replicated manipulation

A controversial problem in the design of ecological studies is “pseudoreplication”: observations that are not independent of one another because sample plots have not been replicated or randomly placed, or temporal observations that are too close in time to be truly independent (HURLBERT 1984). Studies of polydomous ant colonies will be pseudoreplicated if related colonies are treated as independent replicates. The best ways to avoid pseudoreplication are to: (1) collect replicated observations that are sufficiently separated in time and space to be considered independent (or are deliberately temporally autocorrelated if leading indicators are being assessed); (2) treat observations that must be collected on very small spatial or temporal scales as subsamples and make sure the statistical design (e.g., a nested analysis of variance) reflects any non-independence; (3) replicate and spatially intersperse treatments or plots whenever possible; and (4) record the time and the spatial coordinates of every observation so that spatial and temporal autocorrelation structure can be included in any statistical model.

Finally, if ants are to be used as indicators of environmental change or restoration success, we also need reference states: the expected patterns of distribution and abundance of ants in the environment which we are trying to restore. In North America, these may be environments more-or-less representative of times before humans significantly altered the landscape. In Eurasia, these may be environments representing particular cultural practices. Identification of baseline assemblages in either type of reference state is likely to be inferred only from historical chronicles and information gleaned from labels in museum collections. Such reconstructions have been done repeatedly for marine ecosystems (e.g., KNOWLTON & JACKSON 2008, MONTES & al. 2008) but rarely for terrestrial ecosystems (CARILLI & al. 2009). As far as I know, similar reconstructions have not yet been attempted for ant assemblages.

Tab 1: Climate, vegetation, and soils of, and primary environmental threats to, the four north-temperate cold biomes. Biome names follow Olson & al. (2001); climatological details after Breckle (2002) and Feng & al. (2011).

Biome	Temperature regime	Average annual precipitation	Soils	Permafrost	Dominant vegetation
Arctic tundra	Average monthly temperatures ≤ 10 ^{o}C; at least one month > 0 ^{o}C.	< 250 mm	Peaty	Present ≥ 1m below surface, often only 25 cm below surface	Small shrubs, grasses, sedges, mosses, and lichens. Trees are absent
Taiga/boreal forest	Average annual temperature –5 to +5 ^{o}C; At least 4 months > 10 ^{o}C; coldest month ≤ –10 ^{o}C; daily range –50 to +30 ^{o}C;	200 – 750 mm; sometimes > 1000 mm	Rocky, acidic, nutrient-poor; some peat	Generally absent, but may be present ≥ 1m below surface	Conifer trees, with cold-tolerant deciduous trees including birches (*Betula* Linneaus, 1753), aspen (*Populus* Linneaus, 1753), and willows (*Salix* Linneaus, 1753). Mosses (*Sphagnum* Linneaus, 1753 and *Polytricum* Hedwig, 1801) in bogs
Temperate broadleaf (deciduous) forests	Average annual temperature 3 – 16 ^{o}C;, 4 – 7 months > 10 ^{o}C; coldest month < 0 ^{o}C;	600 – 1500 mm	Variable, but richer than taiga	Absent	Deciduous oaks (*Quercus* Linneaus, 1753), beech (*Fagus* Linneaus, 1753), and maples (*Acer* Linneaus, 1753)
Temperate grasslands (north of southernmost extent of Late Pleistocene glaciation)	Average annual temperatures 0 – 20 ^{o}C; daily range –40 to +40 ^{o}C;	250 – 500 mm, often seasonal	Generally rich	Absent	Grasses (family Poaceae) and forbs (flowering herbs)

Tab. 2: Genera of ants, their assignment to functional groups (sensu ANDERSEN 1997a), and their expected position in a competitive hierarchy (sensu VEPSÄLÄINEN & PISARSKI 1982) known to occur in taiga, or temperate deciduous forests or grasslands north of the southern limit of the Pleistocene glaciation.

Functional group and genus	**Competitive hierarchy**	**Present in**		
		Taiga	**Temperate deciduous forest**	**Temperate grassland**
Subordinate Camponotini				
Camponotus MAYR, 1861	Aggressive, non-territorial	X	X	X
Cold-climate specialists				
Dolichoderus LUND, 1831	Aggressive but not territorial	X	X	X
Anergates FOREL, 1874	Aggressive but not territorial	X	X	X
Formicoxenus MAYR, 1855	Aggressive but not territorial	X	X	X
Harpagoxenus FOREL, 1893	Aggressive but not territorial	X		
Leptothorax MAYR, 1855	Submissive	X	X	X
Manica JURINE, 1807	Aggressive but not territorial		X	X
Myrmecina CURTIS, 1829	Submissive	X	X	X
Protomognathus WHEELER 1905	Aggressive but not territorial	X	X	
Stenamma WESTWOOD, 1839	Submissive	X	X	X
Formica LINNAEUS, 1758 (*exsecta* group)	Aggressive but not territorial	X	X	X
Formica (*microgyna* group)	Aggressive but not territorial	X	X	X
Formica (*rufa* group)	Aggressive & territorial	X	X	X
Lasius FABRICIUS, 1804 (in part)	Aggressive & territorial; Aggressive but not territorial; or Submissive (depending on species group or subgenus)	X	X	X
Prenolepis MAYR, 1861	Submissive	X	X	X
Strongylognathus MAYR, 1853	Aggressive but not territorial			X

Functional group and genus	Competitive hierarchy	Present in		
		Taiga	Temperate deciduous forest	Temperate grassland
Cryptic species				
Amblyopone ERICHSON, 1842	Submissive	X	X	X
Ponera LATREILLE, 1804	Submissive	X	X	X
Proceratium ROGER, 1863	Submissive		X	X
Pyramica ROGER, 1862	Submissive		X	X
Solenopsis WESTWOOD, 1840	Submissive		X	X
Vollenhovia MAYR, 1865	Submissive (?)		X	X
Brachymyrmex MAYR, 1868	Submissive	X	X	X
Plagiolepis MAYR, 1861	Submissive		X	
Lasius (in part)	Aggressive & territorial; Aggressive but not territorial; or Submissive (depending on species group or subgenus)	X	X	X
Opportunists				
Tapinoma FOERSTER, 1850	Aggressive but not territorial	X	X	X
Aphaenogaster MAYR, 1853	Aggressive but not territorial	X	X	X
Cardiocondyla EMERY, 1869	Submissive		X	X
Myrmica LATREILLE, 1804	Submissive; In North America; invasive *M. rubra* may be aggressive and territorial	X	X	X
Temnothorax MAYR, 1861	Submissive	X	X	X
Tetramorium MAYR, 1855	Aggressive but not territorial	X	X	X
Formica (*fusca* group)	Submissive	X	X	X
Formica (*sanguinea* group)	Aggressive but not territorial	X	X	X
Nylanderia EMERY, 1906	Submissive		X	X
Generalized Myrmicinae				
Crematogaster LUND, 1831	Aggressive but not territorial		X	X

Functional group and genus	Competitive hierarchy	Present in		
		Taiga	Temperate deciduous forest	Temperate grassland
Monomorium MAYR, 1855	Aggressive but not territorial		X	X
Pheidole WESTWOOD, 1839	Aggressive but not territorial		X	X
Specialist predators				
Pachycondyla F. SMITH, 1858	Aggressive & territorial		X	
Polyergus LATREILLE, 1804	Aggressive but not territorial		X	X
Hot-climate specialist				
Cataglyphis FOERSTER, 1850	Aggressive but not territorial		X	X

Figure Legends

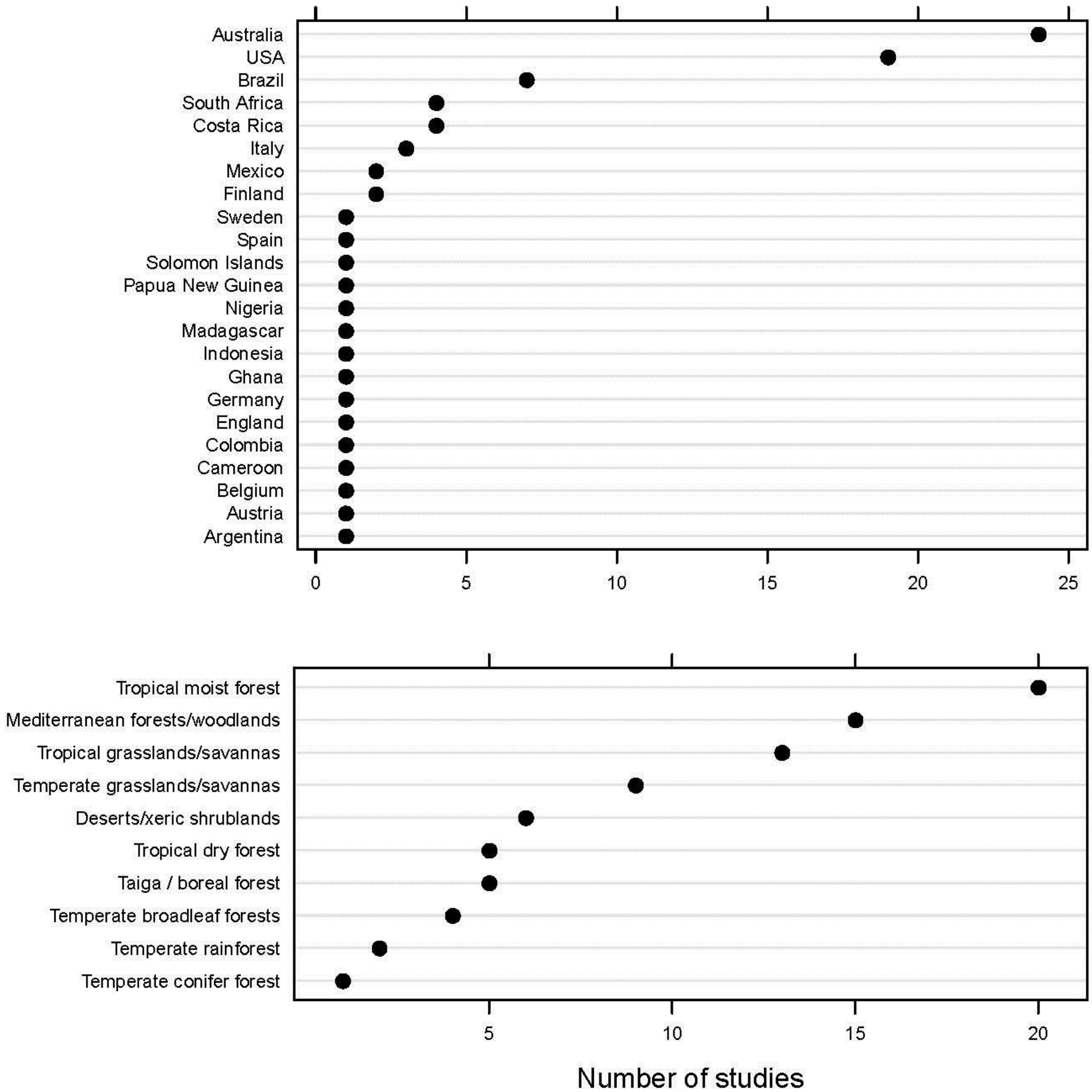
Fig. 1: Where (top), and in what biome (bottom), ants have been used in monitoring of logging, grazing, mining, fire, and land conversion and fragmentation. Data summarized from UNDERWOOD & FISHER (2006) and additional references after 2005 from a targeted search in Science Citation Index (complete list of citations available from the author on request). Naming of biomes follows OLSON & al. (2001).

Fig. 2: Geographic range of biomes discussed in this review, showing tundra (brown), taiga (dark green), temperate broadleaf forests (light green), and temperate grasslands (yellow), and the extent of the Pleistocene glaciation (blue lines). Biome names as in OLSON & al. (2001); digital data on biomes from WWF (2012); Pleistocene glaciation boundary based on information in ARKHIPOV & al. (1986), RICHMOND & FULLERTON (1986), and ŠIBRAVA (1986), and digitized from projected maps provided by Ron Blakely, Colorado Plateau Geosystems, Inc.

Fig. 3: Relationships among the four types of biological indicators.

Figs. 4-11. The north-temperate cold biomes and representative ants. First row: Arctic tundra (Barrow, Alaska, USA) is threatened by oil and gas exploration and extraction; *Camponotus herculeanus* is the most cold-tolerant ant species and may extend its range northward as the climate warms. Second row: Taiga (Bergen, Norway) is dominated by conifers and glacially-derived kettle ponds and bogs are a common feature of the landscape; the bog-specialists *Myrmica lobifrons* is used as an indicator of ecological integrity in North American bogs, where it is also one of the most common prey of many carnivorous plants, including this sundew (*Drosera rotundifolia*, LINNEAUS, 1753). Third row: Temperate broadleaf (deciduous) forests (Hamden, Connecticut, USA) have a diversity of trees and shrubs and are known worldwide for their spectacular autumn foliage; here, a colony of *Formica subsericea* is raided by *F. pergandei*.

Bottom row: Temperate grasslands (Wisconsin, USA) are dominated by grasses and flowering herbs (forbs); *Aphaenogaster treatae* FOREL, 1886 is abundant throughout North American prairies and grasslands. All photographs by the author.


Australia
USA
Brazil
South Africa
Costa Rica
Italy
Mexico
Finland
Sweden
Spain
Solomon Islands
Papua New Guinea
Nigeria
Madagascar
Indonesia
Ghana
Germany
England
Colombia
Cameroon
Belgium
Austria
Argentina
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5
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20
25
Tropical moist forest
Mediterranean forests/woodlands
Tropical grasslands/savannas
Temperate grasslands/savannas
Deserts/xeric shrublands
Tropical dry forest
Taiga / boreal forest
Temperate broadleaf forests
Temperate rainforest
Temperate conifer forest
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20
Number of studies

Fig. 1

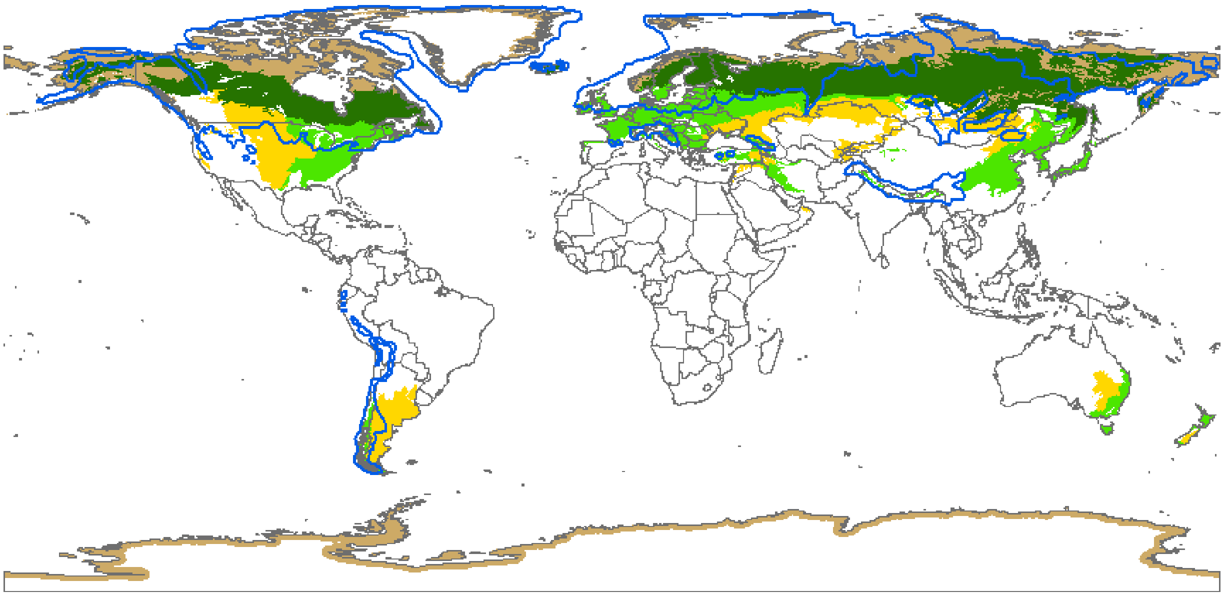

Fig. 2

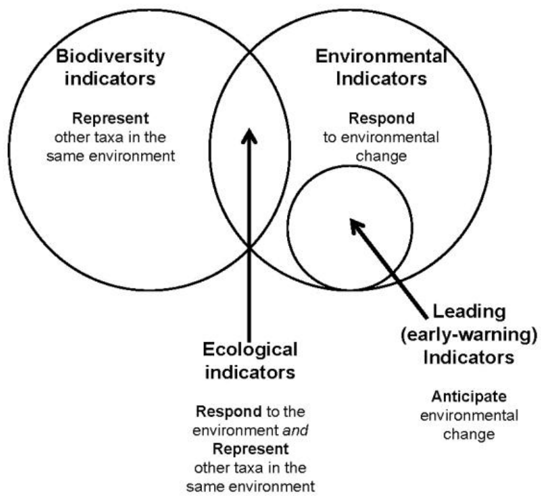
Biodiversity indicators
Represent other taxa in the same environment
Environmental Indicators
Respond to environmental change
Ecological indicators
Respond to the environment *and* Represent other taxa in the same environment
Leading (early-warning) Indicators
Anticipate environmental change

Fig. 3

Figs. 4-11