



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

Citation

Ellison, Aaron. Forthcoming. Out of Oz: Opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological indicators in north-temperate cold biomes. *Myrmecological News*.

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1 Out of Oz: Opportunities and challenges for using ants (Hymenoptera: Formicidae) as biological
2 indicators in north-temperate cold biomes

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

13

14 Number of manuscript pages: 54

15 Number of words: 12 470

16 Number of Figures: 11

17 Number of Tables: 2

18

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20 indicators in north-temperate cold biomes

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23

24 **Abstract**

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

40

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

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47 **Introduction**

48 Invertebrates have been used as biological indicators of environmental conditions in aquatic
49 ecosystems for over 100 years, but it is really only in the last 30 years that arthropods – most
50 notably ants, beetles, and butterflies – have been developed as biological indicators in terrestrial
51 ecosystems (e.g., reviews by ROSENBERG & al. 1986, MCGEOCH 1998, ANDERSEN & MAJER
52 2004). Ants have been promoted as particularly useful biological indicators, especially for
53 detecting colonization of exotic and potentially invasive species, identifying success or failure of
54 land management and restoration schemes that cannot be determined by monitoring vegetation
55 change alone, and monitoring lasting effects of changes in land use and land cover (e.g., reviews
56 by ALONSO 2000, KASAPRI & MAJER 2000, ANDERSEN & MAJER 2004, UNDERWOOD & FISHER
57 2006, CRIST 2009, PHILPOTT & al. 2010). The utility of ants as biological indicators has been
58 demonstrated most frequently in Australia (reviewed by ANDERSEN & MAJER 2004), the
59 rangelands of southwest North America and South America (BESTELMEYER & WIENS 1996,
60 2001), and in both wet and dry tropical forests (e.g., ROTH & al. 1994, PERFECTO & SNELLING
61 1995, PERFECTO & al. 1997) (Fig. 1).

62 Perhaps unsurprisingly, the majority of localities for which ants have been used
63 successfully as biological indicators have warm climates. Temperature is strongly associated

64 with increases in ant diversity and abundance (SANDERS & al. 2007), seasonal patterns of
65 foraging activity (DUNN & al. 2007) and behavior (RUANO & al. 2000), and the strength of
66 competitive hierarchies among species (CERDA & al. 1997, HOLWAY & al. 2002). The rates of
67 many ecosystem processes that can be mediated by ants, such as decomposition, nutrient cycling,
68 and primary production (HÖLLDOBLER & WILSON 1990, FOLGARAIT 1998), also increase with
69 temperature; ant activity may accelerate these responses (PEAKIN & JOSENS 1978, PETAL 1978).
70 Because of their sensitivity to temperature, ants should respond rapidly to such climatic changes
71 and how ants respond to climatic change, especially to local and regional changes in temperature,
72 could have dramatic consequences for associated taxa and ecosystem dynamics (LENSING &
73 WISE 2006, MOYA-LARANO & WISE 2007, CRIST 2009). Responses of ants to climatic changes
74 also may be especially apparent at ecotonal or habitat boundaries.

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

83 In this paper, I discuss the use of ants as environmental, ecological, and biodiversity
84 indicators in north-temperate cold biomes. I highlight opportunities for the use of ants as leading
85 (or early warning) indicators of environmental change, especially at northern and southern
86 boundaries of the boreal forest; explore the utility of different functional group classifications of

87 ants in cold climates; discuss unique aspects of sampling, surveying, and monitoring ants in these
88 regions; and suggest future directions for research on ants in these currently cold, but rapidly
89 warming, biomes.

90

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

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

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

105 Ant taxonomy is relatively stable (nomenclature throughout this review follows BOLTON
106 & al. 2007 and associated web updates posted through 1 January 2012). The north temperate
107 myrmecofauna is known well enough that reliable checklists and keys are already available (e.g.,
108 WHEELER & WHEELER 1963, 1977, FRANCOEUR 1997, PFEIFFER & al. 2006, SEIFERT 2007,
109 RADCHENKO & ELMES 2010, ELLISON & al. 2012) or can be constructed from on-line sites such

110 as antweb.org, antdata.org, or antbase.net. In the next section, I describe the primary
111 environmental threats to each of the north-temperate cold biomes, provide examples of how ants
112 respond to some of these threats, and discuss whether ants can meet the second, third, and fourth
113 criteria of biological indicators for each of the biomes. Although it is a necessary precondition to
114 demonstrate experimentally that a potential indicator taxon responds to environmental
115 perturbation (criterion four), only sustained experimental treatments (“press experiments” sensu
116 BENDER & al. 1984) with appropriate controls coupled with long-term monitoring (LOVETT & al.
117 2007) can allow for reliable separation of a putative indicator’s “signal” from background
118 “noise” (ANDERSEN 1999). Thus in the penultimate section, I discuss whether ants can meet
119 ANDERSEN’s (1999) fifth criterion for north-temperate cold biomes, along with requirements and
120 challenges of sampling, surveying, monitoring, and conducting experiments on ants in these
121 regions. I close with a short agenda of future research needs to more fully develop ants as
122 biological indicators in north-temperate cold climates.

123

124 **North-temperate cold biomes: environmental threats and their ants**

125 This review focuses on the four biomes that cover the vast majority of the northern hemisphere:
126 Arctic tundra; taiga and boreal forest; temperate broadleaf forests; and temperate grasslands
127 (Table 1; Fig. 2). For the latter two biomes, discussion is restricted to regions north of the
128 approximate extent of the Pleistocene glacial maximum in Eurasia and North America (blue line
129 in Fig. 2). The southern extent of Pleistocene glaciation is a notable boundary for ants in North
130 America; army ants (Ecitoninae: *Neivamyrmex* BORGMEIER, 1940), leaf-cutter ants (Myrmicinae:
131 *Trachymyrmex* FOREL, 1893), harvester ants (*Pogonomyrmex* MAYR, 1868 and *Messor* FOREL,
132 1890), and *Forelius* EMERY, 1888 and other dominant Dolichoderinae (sensu ANDERSEN 1997a)

133 do not extend north of this line (WHEELER & WHEELER 1963, WATKINS 1985, COOVERT 2005).
134 Southern hemisphere temperate broadleaf/mixed forests and temperate grasslands/savannas/
135 shrublands, with their unique vegetation types and diverse ant faunas, are well-represented in the
136 ants-as-indicators literature and also are excluded from this review. Finally, I do not discuss the
137 extensive temperate coniferous forests (temperate rain forests) of western North America, and
138 their isolated counterparts in western Ireland, Scotland and Wales, western Norway, southern
139 Japan, and the Caspian Sea region of Turkey, Georgia, and northern Iran, as these forests have a
140 distinctly warmer and wetter climate than the other four north-temperate cold biomes. The
141 climate of north-temperate cold biomes is changing rapidly (FENG & al. 2011), which not only
142 provides a unique opportunity to observe and study responses of ants to unprecedented
143 environmental changes but also suggests new possibilities for using ants as leading indicators of
144 global environmental change.

145 **Arctic tundra** (Fig. 4). The primary environmental threats to Arctic tundra are habitat
146 fragmentation and destruction from oil and gas exploration, drilling, and oil spills (e.g.,
147 KUMPULA & al. 2011; Fig. 4); pollutants derived from wet and dry atmospheric deposition (e.g.,
148 VINGARZAN 2004, DEROME & LUKINA 2011, SOKOLIK & al. 2011); and thawing of the
149 permafrost and encroachment of woody vegetation as regional temperatures warm (e.g., CHAPIN
150 & al., 1995, 1996, HUDSON & HENRY 2009, SUN & al. 2011). Local and regional warming will
151 provide opportunities for ants to extend their range northward (ALFIMOV & al. 2011).

152 The temperature regime of the tundra is well below the temperature optima for all but a
153 handful of ants (BERMAN & al. 2010). Thus, ants are few and far between in the Arctic tundra,
154 and generally are collected only very close to the tundra/taiga boundary. Supplementing
155 GREGG's (1972) records of ants collected in Churchill, Manitoba (Canada) with additional

156 collections from the tundra/taiga boundary of Québec (55 to > 58 °N), FRANCOEUR (1983)
157 identified five ant species that occur near the tree-line in North America – *Myrmica alaskensis*
158 WHEELER, 1917, *Leptothorax acervorum* (FABRICIUS, 1793), *Leptothorax* cf. *muscorum*
159 (NYLANDER, 1846), *Camponotus herculeanus* (LINNAEUS, 1758) (Fig. 5), and *Formica*
160 *neorufibarbis* EMERY, 1893 – and one species – *F. aserva* FOREL, 1901– for which stray
161 individuals, but not colonies, have been collected. WEBER (1950, 1953) recorded *F. fusca*
162 LINNAEUS, 1758 from the mouth of the Mackenzie River in Canada, and suggested based on
163 historical evidence that it would eventually be found in Arctic Alaska. Based on a subsequent
164 collection in the Yukon (FRANCOEUR 1997), I would attribute this species to *F. gagatoides*
165 RUZSKY, 1904, but confirmation will require additional collections. *Formica gagatoides*, *F.*
166 *lemoni* BONDROIT, 1917, and *L. acervorum* all have been recorded at the tundra/taiga boundary
167 in the Central Altai Mountains of Russia, near the joint border of Russia, China, Mongolia, and
168 Kazakhstan (CHESNOKOVA & OMELCHENKO 2011). In the Kamchatka region of Russia, *Myrmica*
169 *kamtschatica* KUPYANSKAYA, 1986 nests in moss atop the permafrost (BERMAN & al. 2010) and
170 is the most cold-tolerant species of the Palearctic *Myrmica* LATREILLE, 1804 discussed by
171 RADCHENKO & ELMES (2010)

172 Although ants are rare to absent deep in the tundra, their predictable occurrence at the
173 tundra/taiga boundary suggests that they could be a reliable leading indicator of rapid
174 environmental change at this ecotone. As the climate warms and permafrost thaws, woody
175 vegetation is expanding into the tundra (e.g., WALKER & al. 2006, FENG & al. 2011), and species
176 such as *Camponotus herculeanus*, which is among the most cold-tolerant ants (BERMAN & al.
177 2010) but requires dead wood for nest sites (FRANCOEUR 1983), could rapidly extend its range
178 northward. Although one could simply monitor plant cover as an indicator of environmental

179 change, simply seeing plants is not in itself sufficient evidence of wholesale ecosystem change.
180 In other words, the plants could be there, but herbivores, omnivores, and predators might not.
181 The presence of ants, which fill many roles in the ecosystem other than primary production,
182 provides better evidence than plants alone for systemic ecological changes. *Formica exsecta*, the
183 least cold-tolerant of the tundra/taiga-boundary ants (BERMAN & al. 2010), is already moving
184 north (ALFIMOV & al. 2011), and other cold-tolerant ants such as *Leptothorax acervorum* and *F.*
185 *gagatoides* likely will follow. However, none of these ants are abundant enough or have
186 substantial impacts on ecosystem functions in the tundra to be considered more broadly as
187 ecological or biodiversity indicators.

188 **Taiga and the boreal forest** (Fig. 6). The primary environmental threats to taiga include:
189 habitat fragmentation and loss from extensive logging (e.g., BOUCHER & GRONDIN 2012);
190 flooding due to development of large hydroelectric projects (e.g., KUMARI & al. 2006, MALLIK &
191 RICHARDSON 2009); exploration and extraction of oil and natural gas reserves (e.g., ROBERTSON
192 & al. 2007); mining for minerals and peat (e.g., MALJANEN & al. 2010, PETIT & al. 2011); fire
193 (e.g., JIANG & ZHUANG 2011); and widespread loss of tree canopies from insect outbreaks (e.g.,
194 SIMARD & al. 2011). The extent and frequency of fire and insect outbreaks across the taiga also
195 have increased rapidly in recent decades as the climate has warmed (e.g., GUSTAFSON & al.
196 2010, BECK & al. 2011), and all of these factors interact synergistically and cumulatively, often
197 resulting in far more environmental damage than any one of them alone (YAMASAKI & al. 2008).
198 Ant responses to these disturbances can be very variable.

199 At least 25 Holarctic ant genera (Table 2) and >100 species can be found in taiga
200 (AZUMA 1955, VESPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & al. 1989, REZNIKOVA 2001,
201 PFEIFFER 2006, HERBERS 2011, ELLISON & al. 2012), including cold-climate specialists, cryptic

202 species, opportunities, generalized Myrmicinae (Fig.7), and specialist predators (functional
203 groups sensu ANDERSEN 1997a). Individual ant species and groups of colonies can be very
204 abundant in taiga, where they often have strong and persistent effects on ecosystem processes
205 (e.g., FROUZ & al. 2005, RUBASHKO & al. 2011) and where their distribution and abundance can
206 be dramatically altered by human actions.

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

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

225 2002). Two other *F. rufa*-group species that build small, thatch-covered mounds can be found in
226 North American taiga: an undescribed species near *F. fossiceps* BUREN, 1942 (ELLISON & al.
227 2012) and *F. dakotensis* EMERY, 1893 (FRANCOEUR 1997). However, two North American *F.*
228 *fusca*-group species – *F. podzolica* FRANCOEUR, 1973 and *F. glacialis* WHEELER, 1908 – build
229 substantial mounds in the southern taiga and northern reaches of the temperate broadleaf forests
230 (FRANCOEUR 1973). Like *F. exsecta* in northeastern Siberia, *F. podzolica* and *F. glacialis* have
231 potential to be developed as leading indicators of climatic change at the southern boundary of the
232 taiga.

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

241 Particular taiga species have very narrow habitat requirements and could be developed as
242 indicators of habitat decline or restoration success. For example, in North America, open
243 peatlands within the taiga host unique ants, including *Myrmica lobifrons* PERGANDE, 1900 (Fig.
244 7; FRANCOEUR 1997) and *Leptothorax sphagnicola* FRANCOEUR, 1986 (FRANCOEUR 1986). The
245 ecology of Palearctic bog-dwelling *Myrmica*, a common and diverse group of taiga-dwelling
246 ants, is covered in detail by RADCHENKO & ELMES (2010). High abundance of such habitat
247 specialists could serve as indicators that mined peatlands throughout the have been restored,

248 whereas their absence could indicate some degree of disturbance or environmental stress.
249 Experiments and additional observations are needed, however, to support this assertion.

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

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

269 There are nearly 40 ant genera that nest in north-temperate broadleaf forests (Table 2).
270 Most genera found in taiga are also found in broadleaf forests, but they are more speciose in the

271 latter (e.g., PISARSKI 1978, GOTELLI & ELLISON 2002, ELLISON & al. 2012). Functional groups
272 and Holarctic genera present in north-temperate forests, but absent from tundra and taiga, include
273 the generalist Myrmicinae *Crematogaster* LUND, 1831, *Monomorium* MAYR, 1855, and *Pheidole*
274 WESTWOOD, 1839, and the specialist predators *Polyergus* LATREILLE, 1804 and *Pachycondyla* F.
275 SMITH, 1858 (Table 2).

276 Ant abundance and species richness is higher in temperate broadleaf forests than in taiga
277 – notably many more species in cryptic genera (Table 2) occur in temperate broadleaf forests –
278 but there are surprisingly few data on responses of ants to environmental pressures or climatic
279 changes in this biome (PELINI & al. 2011a, 2011b). In northeastern North America, species
280 evenness is highest at intermediate temperatures, but there is little effect of a ± 1 °C change in
281 temperature on other measures of ant species diversity or ant foraging activities (PELINI & al.
282 2011a). In northwest Belgium, abundance of colonies of *F. rufa* and *F. polycтена* have been
283 declining steadily as their open-forested habitat matures and closes in, is converted to intensive
284 agriculture, is used heavily for recreation, or is destroyed for urbanization (DEKONINCK & al.
285 2010). A key reason for their decline is the lack of co-occurring *F. fusca*, which the social-
286 parasite *F. rufa*-group species use as hosts; in North America *F. fusca*-group species are enslaved
287 by species in the *sanguinea* group (Fig. 9). This further illustrates the need to consider multiple
288 taxa in the context of overall ecological integrity in developing ants as indicator taxa.

289 Mature broadleaf or mixed-deciduous forests also have fewer ant species than early-
290 successional ones. For example, the hemlock-oak-maple forests of eastern North America are
291 rapidly losing their late successional dominant, eastern hemlock (*Tsuga canadensis* (L.)
292 CARRIÈRE, 1855) due to infestation by the non-native hemlock woolly adelgid (*Adelges tsugae*
293 [ANNAND, 1924]) (ORWIG & al. 2002). Ant assemblages in hemlock-dominated forests are

294 species poor – *Temnothorax longispinosus* (ROGER, 1863), *Aphaenogaster picea* (WHEELER,
295 1908), *Camponotus novaeboracensis* (FITCH, 1855), and *C. pennsylvanicus* (DEGEER, 1773) are
296 the most abundant taxa – but the death of hemlock opens up canopy gaps, creates localized warm
297 spots in the forest matrix, and initiates successional processes that favor a wide range of *Formica*
298 *fusca*-group and *Lasius* FABRICIUS, 1804 species, among other cold-climate specialists and
299 opportunists (ELLISON & al. 2005, SACKETT & al. 2011). As in taiga, high ant species richness or
300 nest density in temperate broadleaf forests likely is a better indicator of present or past
301 disturbance or successional status than of undisturbed forests (HERBERS 2011). In further support
302 of this proposition is the observation that non-native ant species in this biome tend to favor
303 disturbed or urbanized areas (e.g., GRODEN & al. 2005, CREMER & al. 2008, PEĆAREVIĆ & al.
304 2010, ELLISON & al. 2012), where they may either increase species richness while at low
305 densities or decrease species richness when they reach high densities and outcompete native
306 species.

307 **Temperate grasslands** (Fig. 10). Grasslands have been modified extensively by humans,
308 who have used these areas for agriculture and livestock production for hundreds-to-thousands of
309 years. For example, nearly all of the North American prairies have been replaced with crop
310 monocultures (primarily maize or soybean) or exotic grasses for extensive grazing, and many
311 Eurasian steppes have been similarly impacted (e.g., CREMENE & al. 2005). Restoration of North
312 American remnant prairies is a high priority (e.g., KINDSCHER & TIESZEN 1998, MARTIN & al.
313 2005), but methods and appropriate species remain controversial (e.g., HOWE 1994) and
314 ecosystem recovery is slow (e.g., MCLACHLAN & KNISPEL 2005, HILLHOUSE & ZEDLER 2011). In
315 Central Europe, agricultural intensification is as much an environmental issue for steppes as is
316 agricultural abandonment; grasslands have been maintained for so long that many species of

317 contemporary conservation concern are restricted to traditionally-managed grasslands (CREMENE
318 & al. 2005).

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

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

339

340 **Developing ants as biological indicators in north-temperate cold biomes**

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

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

358 Testing these propositions will require reliable samples, robust surveys, and long-term
359 experiments and monitoring programs (Box 2) to ensure that observed responses of ants to
360 environmental changes, and how well these responses reflect broader ecosystem dynamics, can
361 be interpreted as a true ecological “signal” separate from environmental background “noise”
362 (MCGEOCH 1998, ANDERSEN 1999). Although I have focused this review on large scale, biome-

363 wide patterns, ants (and other invertebrates) are much more appropriately used as biological
364 indicators at regional or local scales (ANDERSEN 1997b). As MCGEOCH (1998) pointed out, many
365 studies of the relationship between indicator species and their broader environment appear to be
366 predictive, but in fact are conducted at the wrong spatial or temporal scale to provide reliable
367 indications of environmental impacts or change. Elaborating all the elements of design and
368 implementation for long-term monitoring schemes, sampling and surveying programs, and
369 experiments would require several book-length treatments (useful references include MEAD
370 1988, UNDERWOOD 1997, MANLY 2000, and THOMPSON 2002). Box 2 highlights key elements of
371 good monitoring programs, reliable long-term observations and experiments, and core principles
372 of designing studies that will provide useful information on ants so that signals can be
373 differentiated from noise; additional features of successful development of ants as biological
374 indicators include appropriate observational and experimental controls, replication, and reference
375 states (Box 3).

376

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

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

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

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

- 411 • **Reference states.** If ants are developed as indicators of restoration success, we need to
412 have baselines or reference states against which to evaluate observed changes (Box 3).
413 Digitized records of specimens in museum collection may reveal historical patterns of
414 distribution and abundance of ants, and provide data from which to establish appropriate
415 baselines.
- 416 • **Standard protocols for long-term monitoring.** Measurement and assessment of
417 distribution and abundance of ants has been standardized for warm climates (AGOSTI &
418 al. 2000), and modifications have been suggested for temperate broadleaf forests
419 (ELLISON & al. 2007). Neither of these, however, addresses the challenges uniquely
420 associated with long-term monitoring (Box 2): habitat alteration by investigators;
421 frequent disturbance of nests attendant to regular censuses; excessive colony depredation
422 by, and unacceptable by-catch in, pitfall traps; and ensuring permanent access to long-
423 term research sites. A community-wide effort to address these issues, on a par with
424 AGOSTI & al. (2000), would be welcome.
- 425 • **Regional checklists and accessible keys.** Australian land managers have keys and
426 pointers to functional groups of ants that facilitate their use as biological indicators
427 (ANDERSEN & MAJER 2004). Similar resources need to be created, field-tested, and
428 provided to conservation professionals in north-temperate regions (e.g., ELLISON & al.
429 2012).

430

431 **Acknowledgements**

432 I thank Nick Gotelli for suggesting this review and the editors of Myrmecological News for
433 inviting me to write it. Ron Blakely (Colorado Plateau Geosystems, Inc.) kindly provided an
434 image of global coverage of the Pleistocene glaciation, from which Brian Hall digitized a data
435 layer. Brian also assisted with production of Fig. 2. Alan Andersen, Jens Dauber, Elizabeth
436 Farnsworth, and Florian Steiner provided constructive critiques on early versions of the
437 manuscript. The ideas for this review germinated while teaching an intensive field course on the
438 ants of New England at the Humboldt Field Research Institute in Steuben Maine and have been
439 nourished by ongoing research supported by grants from the US Department of Energy (DE-
440 FG02-08ER64510) and the US National Science Foundation (DEB 11-36646).

441

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805

806 Box 1: Different kinds of biological indicators.

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

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

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

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

829 ASSMANN 2010), but at smaller scales (e.g., within sites or localities), ants are considered to be
830 poor biodiversity indicators (LAWTON & al. 1998, ALONSO 2000, ENGLISCH & al. 2005, but see
831 MAJER & al. 2007 for a study where ants perform reasonably well as biodiversity indicators).
832 **Ecological indicators** combine attributes of all of the other types of biological indicators. They
833 represent the effects of environmental change on the broader ecological system and themselves
834 are usually of particular concern or conservation interest. In Australia and in the humid tropics,
835 there are many examples where there are sufficient data to use ants as ecological indicators
836 (ANDERSEN & MAJER 2004, MAJER & al. 2007). Examples are sparser in north-temperate cold
837 biomes, and emphasize species in the *Formica rufa*-group (DEKONINCK & al. 2010, GILEV
838 2011).

839

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

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

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

860 Long-term studies on ants require particular care in determining sampling design and
861 methods. Most field scientists know that observations taken close in space or time are less likely
862 to be independent of one another than observations taken further apart in space or at longer

863 intervals. Polydomous colonies confound spatial sampling even further. Because spatial and
864 temporal autocorrelation cannot really be eliminated, it is crucial to document the patterns of
865 spatial autocorrelation, temporal autocorrelation, and other forms of non-independence and
866 incorporate them explicitly into the analysis. On the plus side, temporal or spatial autocorrelation
867 themselves are the key variables of interest in deciding whether a potential leading indicator is
868 indicating a shift in environmental conditions (e.g., SCHEFFER & al. 2009, BESTELMEYER & al.
869 2011). Note that a lengthy time series is a series of regularly-spaced observations, not simply a
870 relatively small number of repeated samples made over a long span of time. The latter are much
871 more readily available in the myrmecological literature (e.g., KIPELÄINEN & al. 2005,
872 DEKONINCK & al. 2010, ALFIMOV & al. 2011, HERBERS 2011), but we need the former to
873 determine if ants can be reliable biological indicators of environmental change.

874 Additional attention to sampling methods also is required because repeated long-term
875 visits to plots or nests can have unintended or unanticipated effects on the system. Obvious
876 examples of observer impacts in both short- and long-term studies of ants include: soil
877 compaction from repeatedly walking the same paths to reach a sampling station, colony, or nest;
878 disturbance of nests through repeated sampling of individuals; and potential reduction of colony
879 size below sustainable levels following repeated disturbances or sample collection bouts. For
880 these and several other reasons, I do not recommend using pitfall sampling for long-term
881 sampling or monitoring. First, digging holes for pitfall traps causes extensive disturbance to soil;
882 the impacts of this disturbance on ant activity or population dynamics is rarely studied
883 (GREENSLADE 1973, MAJER 1978). Second, if pitfall traps are placed on an active foraging trail,
884 one or more entire colonies can be unintentionally collected, changing local population densities.
885 At the same time, pitfall traps accumulate many other species (“by-catch”), few of which may be

886 of interest to the investigators (BUCHHOLZ & al. 2011), some of which may be of significant
887 conservation concern (NEW 1999), and many of which may be strong interactors with local ant
888 colonies. Finally, in north-temperate cold biomes, pitfall traps are not as effective at sampling
889 overall species diversity as the combination of hand- and litter-sampling (ELLISON & al. 2007).
890 Hand- and visual sampling also are much more appropriate if the focus is on a particular species
891 or species group that is readily apparent (such as mound-building ants).

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

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

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

913 Most studies can be easily classified based on their type of replication and type of
914 manipulation. For example, long-term monitoring of the number of ant mounds at one or more
915 locations are temporally replicated without manipulation (e.g., ALFIMOV & al. 2011). A snapshot
916 comparison of ant assemblage structure in multiple areas with and without logging (e.g.,
917 JENNINGS & al. 1986) is a spatially replicated, uncontrolled intervention. An experimental
918 investigation of the responses of ants to changes in forest canopy structure (e.g., ELLISON & al.
919 2007, SACKETT & al. 2011) is a controlled, spatiotemporally replicated manipulation

920 A controversial problem in the design of ecological studies is “pseudoreplication”:
921 observations that are not independent of one another because sample plots have not been

922 replicated or randomly placed, or temporal observations that are too close in time to be truly
923 independent (HURLBERT 1984). Studies of polydomous ant colonies will be pseudoreplicated if
924 related colonies are treated as independent replicates. The best ways to avoid pseudoreplication
925 are to: (1) collect replicated observations that are sufficiently separated in time and space to be
926 considered independent (or are deliberately temporally autocorrelated if leading indicators are
927 being assessed); (2) treat observations that must be collected on very small spatial or temporal
928 scales as subsamples and make sure the statistical design (e.g., a nested analysis of variance)
929 reflects any non-independence; (3) replicate and spatially intersperse treatments or plots
930 whenever possible; and (4) record the time and the spatial coordinates of every observation so
931 that spatial and temporal autocorrelation structure can be included in any statistical model.

932 Finally, if ants are to be used as indicators of environmental change or restoration
933 success, we also need reference states: the expected patterns of distribution and abundance of
934 ants in the environment which we are trying to restore. In North America, these may be
935 environments more-or-less representative of times before humans significantly altered the
936 landscape. In Eurasia, these may be environments representing particular cultural practices.
937 Identification of baseline assemblages in either type of reference state is likely to be inferred
938 only from historical chronicles and information gleaned from labels in museum collections. Such
939 reconstructions have been done repeatedly for marine ecosystems (e.g., KNOWLTON & JACKSON
940 2008, MONTES & al. 2008) but rarely for terrestrial ecosystems (CARILLI & al. 2009). As far as I
941 know, similar reconstructions have not yet been attempted for ant assemblages.

942

943 Tab 1: Climate, vegetation, and soils of, and primary environmental threats to, the four north-
 944 temperate cold biomes. Biome names follow OLSON & al. (2001); climatological details
 945 after BRECKLE (2002) and FENG & al. (2011).

946

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

947

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

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

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

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

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953 **Figure Legends**

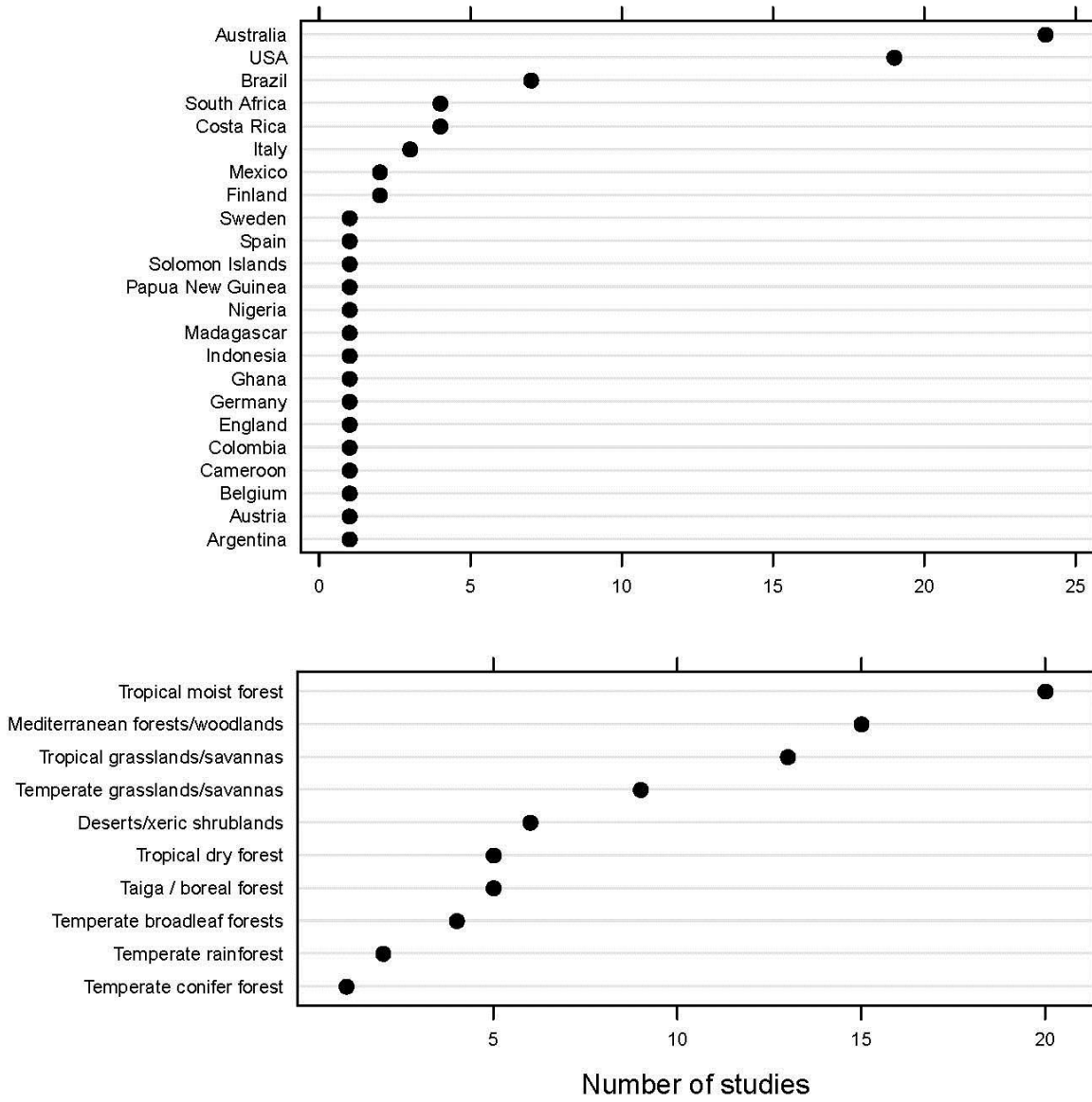
954 Fig. 1: Where (top), and in what biome (bottom), ants have been used in monitoring of logging,
955 grazing, mining, fire, and land conversion and fragmentation. Data summarized from
956 UNDERWOOD & FISHER (2006) and additional references after 2005 from a targeted search in
957 Science Citation Index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

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

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

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

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



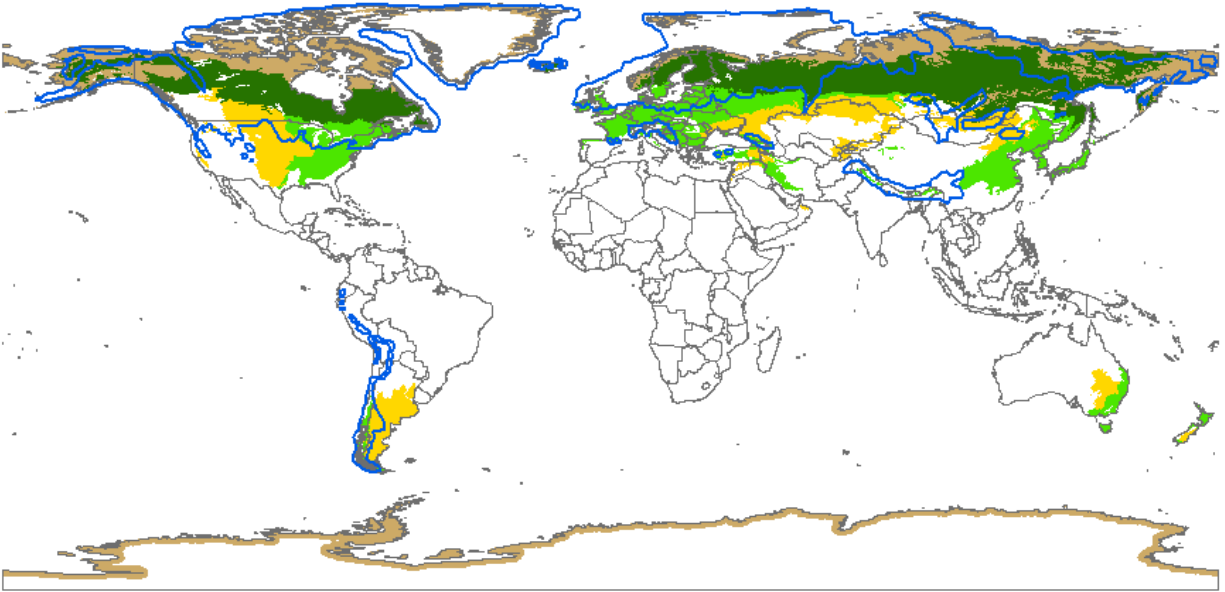
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Fig. 1

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Fig. 2

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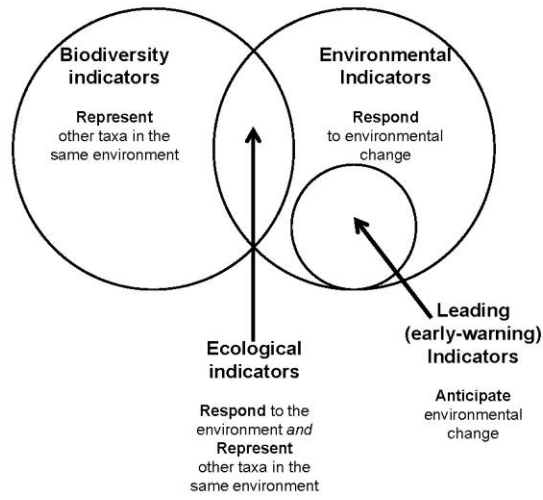


Fig. 3



Figs. 4-11