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Ground beetles (Coleoptera: Carabidae) as bioindicators

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Abstract. One of the primary goals of research on bioindicators is to identify species or other taxonomic units that would reliably indicate disturbances in the environment, and reflect the responses of other species or the overall biodiversity. However, there is no perfect bioindicator and selecting the most suitable one depends to a great extent on the goal of the survey. In this paper we examine the suitability of carabids as bioindicators. Carabids are frequently used to indicate habitat alteration. They have been used in grasslands and boreal forests where species number and/or abundances have been noted to change along a habitat disturbance gradient. A common trend is that large, poorly dispersing specialist species decrease with increased disturbance while small generalist species with good dispersal ability increase. Some species are not affected by moderate disturbance. There is, however, not enough research to determine how suitable carabids are for biodiversity studies, or how well they represent the response of other species. We conclude that carabids are useful bioindicators, but as crucial understanding of their relationship with other species is incomplete, they should be used with caution.

Introduction

Bioindicators have proved to be a useful tool for monitoring and detecting changes in the environment. Since the time when canaries were used to detect carbon monoxide in mines, the use of indicators has increased to span both aquatic and terrestrial ecosystems covering a wide range of habitat alteration, from local disturbance to global climatic change (Spellerberg 1993). Despite the long history of use of bioindicators, there still are no unanimous definitions or criteria for selection of bioindicators. A bioindicator can be loosely defined as a species or a species group that reflects the abiotic or biotic state of the environment, represents the impact of environmental change on a habitat, community or ecosystems, or indicates the diversity of other species (McGeoch 1998). Many species fulfil at least one of these criteria.

The use of bioindicators is based on a number of reasons. One of the most important ones is their cost-effectiveness. By using bioindicators it is possible to assess the impact of human activities on the biota, instead of examining the entire biota. Especially useful are species that provide early warning of change (Spellerberg 1993). Bioindicators are also a good way to monitor the effects of toxic materials on organisms (Bridgham 1988). This might be difficult to assess through direct toxicity level assessment in nature.

In biodiversity surveys, bioindicators are used to assess species richness of the community. Using only a few species groups and estimating diversity of total biota e.g. through extrapolation is a quick technique (Colwell and Coddington 1994). This is a great advantage especially in the tropics, where it is impossible to survey all species due to high species richness.

There are, however, several problems related to use of bioindicators (Landres et al. 1988). A difficult problem is the generalisation of results. For example, how well does one species or a species group represent the remaining biota? Species' ecological requirements can be very different, implying that the responses of species to certain environmental change might be opposite (Lawton et al. 1998; Jonsson and Jonsell 1999). As most species respond to changes in the environment, almost every terrestrial animal group has been used as some kind of indicator (e.g. Rosenberg et al. 1986; Roth 1993; Kremen et al. 1994). In many cases selection is based more or less on personal preference (Andersen 1999).

The objective of this study is to determine how suitable carabids (ground beetles, Coleoptera: Carabidae) are as bioindicators. Attention is paid to fragmentation and biodiversity studies, while geographically we focus on areas where most of the research has been done, i.e. grasslands (and cereal fields), and boreal and temperate forests. Also, surveys in tropical forests are reviewed. Carabids are examined because they are widely used as indicators. Their claimed advantages include easy and cheap sampling by the use of pitfall traps, and morphological and ecological diversity (Niemelä et al. 2000).

Classification of bioindicators

There are several ways of classifying bioindicators. McGeoch (1998) divides them into three classes: (1) environmental, (2) ecological, and (3) biodiversity indicators, while Lindenmayer et al. (2000) divide them into seven groups. The basic division is that environmental and ecological indicators are used to detect changes in the environment, while biodiversity indicators reflect the diversity of the overall biota. However, these are not mutually exclusive divisions. Some species responding to environmental change can also reflect diversity or response of other species.

Environmental change can cause different kinds of effects in the indicator, including physiological changes or changes in species number or abundance. The response of the species can be seen within the organism (e.g. heavy-metal concentrations), at the species level (species number and abundance) or at the community level (relations between species, e.g. pest–predator). Increase or decrease of species number or abundance might be directly caused by change in abiotic and/or biotic factors (Blake et al. 1996) or indirectly by change of species assemblage of other species (Haila et al. 1994).

Biodiversity indicators are a group of taxa or a functional group, the diversity of which (species richness, level of endemism, etc.) reflects diversities of other taxa

(McGeoch 1998). In addition, biodiversity indicators can be classified as: (1) species whose presence or absence indicates presence or absence of some other species, (2) species whose addition or loss leads to major changes in abundance or occurrence of at least one other species (keystone species), or (3) dominant species which provide a major part of the biomass or number of individuals (Lindenmayer et al. 2000).

Selecting suitable indicators

Several authors (e.g. Noss 1990; Pearson and Cassola 1992; Niemelä 2000) have defined the requirements that a useful indicator species should have. In short, a good bioindicator should have well-known taxonomy and ecology, be distributed over a broad geographic area, have specialisation to certain habitat requirements, provide early warning of change, be easy and cost-effective to survey, be relatively independent of sample size, its response should reflect the response of other species, one should be able to differentiate between natural cycles or trends and those induced by anthropogenic stress, and it should be of potential economic importance. Because of the wide range of desired characteristics, it is difficult to find species or species groups which would have all of the characteristics mentioned above (Noss 1990; Pearson and Cassola 1992). Requirements needed depend on the goal of the survey, which might be e.g. biodiversity survey, effects of climate change or consequences of habitat destruction. Furthermore, species suitable for monitoring are not always the best ones for inventory and vice versa. This is because indicators appropriate for monitoring should be sensitive to anthropogenic disturbance, while indicators for inventory should identify biogeographic zones, areas of endemism and community types (Kremen et al. 1993).

Because species have different ecological requirements, some species are better indicators than others (Dufrene and Legendre 1997). Some species are generalists occurring in a wide range of habitats and others are more specialised, demanding certain habitat characteristics. Specialist species are usually more sensitive to environmental factors than generalist species.

When selecting an indicator taxon, the above issues should be considered. After the selection of a suitable indicator, the proper spatial and temporal scale for study should be decided upon. This is because species number depends on the scale of observation, and some species are more uniformly and others more patchily distributed. Increasing the size of the survey area increases the probability of finding patchily distributed species (Weaver 1995). Furthermore, the temporal scale must be considered. In many animal species, activity and abundance vary throughout the year (Janzen and Shoener 1968). For instance, some species are abundant in spring, while others peak in the autumn. This kind of variation might have a great impact on results, if only a short time period is studied.

McGeoch (1998) has developed procedural steps, which aim at improving the selection of an appropriate environmental, ecological, and biodiversity indicator. This is a step-by-step procedure beginning with defining the objectives of bioindica-

Table 1. Examples of bioindicator studies of carabid beetles.

Goal of the survey	Habitat, country	Comments	Reference
Management practices (including cutting, grazing, fertilizers)	Grasslands, Scotland	Carabid faunas of managed grasslands were less species rich, less diverse and species were of smaller body size than in unmanaged land. Management tends to favour species preferring drier conditions.	Blake et al. (1996)
Fragmentation	Heaths, the Netherlands	Species with low dispersal power were virtually absent from small and isolated fragments. A decline of these species was apparent in areas smaller than 75 ha.	de Vries (1994)
Land use	Grasslands, Belgium	A few common species have become relatively more common at the expense of a larger number of rare species, which become even rarer.	Desender et al. (1994a)
Habitat classification	Grasslands, Europe	Each type (17 types) of grassland was characterised by a specific species assemblage. Important features affecting distribution of carabid species were soil water content and altitude.	Eyre and Luff (1990)
Assessment of environmental quality	Several habitats, e.g. riversides, woodlands, grasslands, UK, Ireland	Environmental quality was assessed by comparing numbers and abundances of rare and generalist species. High rarity score of the habitat was caused by presence of specialist or rare species.	Eyre et al. (1996)
Habitat fragmentation	Boreal forest, Canada	Response to forest edge depends on the sensitiveness of the species. Only a few species were sensitive to forest edge.	Spence et al. (1996)
Habitat fragmentation	*Eucalyptus* forest, SE Australia	Fragmentation did not alter species richness but did alter species composition. Abundances of some species changed (increased or decreased).	Davies and Margules (1998)
Size of the fragment	Boreal forest, Finland	Species richness of carabids was higher in small (0.5–3 ha) than in medium-sized (4–8 ha) or large (10–20 ha) forest fragments. No forest specialist species were found in the small forest fragments.	Halme and Niemelä (1993)
Forest cutting	Boreal forest, Finland	Responses of common species fell into three groups: (1) forest generalists were not dramatically affected, (2) species of open habitat appeared and/or increased in abundance, and (3) mature forest species disappeared or decreased in abundance	Niemelä et al. (1993)
Urbanization	Boreal forest, Helsinki, Espoo, Finland	Species diversity decreased with increasing urbanization (rural > suburban > urban). Urbanization had a negative effect on both carabid abundance and species richness.	Venn (2000)
Climate change	North America and Europe	Response of arctic carabids to climate change will be rapid and the geographic range of species will change. Species extinction is unlikely in arctic species but probable at more southern latitudes, because dispersal is blocked by human activities.	Ashworth (1996)
Biodiversity	Cultivated and seminatural areas	Ground beetles did not show correlation in species number but diversity indices (Shannon and Simpson) were correlated to those of other insect orders.	Duelli and Obrist (1998)

tion and ending with the rejection or acceptance of the indicator. During the procedure the relationship between the bioindicator and environmental data is compared under two or more different conditions. Below we first examine how well ground beetles meet requirements of bioindicator species mentioned above, and thereafter test the suitability of carabids as bioindicators by using the method proposed by McGeoch (1998).

Ground beetles as bioindicators

Carabids have been widely and successfully used for different kinds of indicator studies (Table 1). Most of the surveys focus on the response of the species to changing environmental conditions, e.g. forest fragmentation (e.g. Niemelä et al. 1988) or management practices (e.g. Rushton et al. 1990). In addition to these studies, ground beetles have been used in studies on urban ecology (Venn 2000), insecticides (Basedow 1990), effects of military tanks (Mossakowski et al. 1990), classification of habitat type (Eyre and Luff 1990) and assessment of site quality (Eyre et al. 1996).

Knowledge of carabid taxonomy and ecology, and distribution over geographic area

Carabid beetles are well known both taxonomically and ecologically (Lövei and Sunderland 1996; Niemelä 1996). This, however, mainly concerns the temperate region, as surveys are scarcer in the southern hemisphere (New 1998). Ground beetles are distributed over broad geographic ranges and inhabit all major habitats, except the driest parts of deserts (Lövei and Sunderland 1996).

Specialisation to habitat requirements

Carabids can be divided into geographically wide-ranging generalist (ubiquitous) species, species occupying a wide range of habitats (eurytopic), and specialists occurring in one or a few habitats (stenotopic) (Eversham et al. 1996). Each habitat type has certain species assemblage with generalist and specialist species. Thus, individual carabid species or species assemblages can be used as bioindicators (Niemelä et al. 2000). However, because of the high number of generalist species carabids have been criticised as bioindicators (Rykken et al. 1997).

Carabids depend on several abiotic and biotic factors. These include (1) temperature or humidity, (2) food conditions, (3) presence and distribution of competitors, and (4) life history and season, including migration between hibernation and reproduction habitat (Lövei and Sunderland 1996). The role of interspecific interaction, especially competition in affecting carabid communities, is not clear (Niemelä 1993a). Most vulnerable are the egg, larval, and pupal stages (Lövei and

Sunderland 1996). As these requirements are well known for many parts of the world, carabids appear reliable bioindicators.

Provide early warning of change

Management practices in grasslands and forests have shown that carabids respond quickly to habitat fragmentation, grazing, fertilisation, and forest cutting (Table 1). This is because they are sensitive to environmental factors such as temperature, humidity, vegetation, and size of the forest patch (Eyre and Luff 1990; Halme and Niemelä 1993; Butterfield 1996; Niemelä 2001). However, the ecological requirements of species vary, and consequently, some species are more sensitive to environmental changes than others (Niemelä et al. 1993).

Easiness and cost-effectiveness of survey

There are several collecting methods for surveying carabid assemblages. These include pitfall traps, sticky traps, sweep netting, Malaise traps, window traps, hand picking, litter washing, and beating (Spence and Niemelä 1994; Clark and Samways 1997). Pitfall trapping is the most commonly used field method because carabids can be easily and cost-effectively collected by these traps (Spence and Niemelä 1994). There are, however, some disadvantages associated with pitfall trapping. Catches from pitfall traps depend on the activity of the species, which varies between species and seasons (Luff 1975; Spence and Niemelä 1994). Therefore, pitfall catches reflect both the actual abundances and the activity of the species. Compared to other methods, such as litter washing, pitfall traps capture more large-sized individuals (Spence and Niemelä 1994), while hand collecting often yields species not found in pitfall catches (Niemelä et al. 1988).

Pitfall traps are easy to modify according to specific needs of the study (Spence and Niemelä 1994; Luff 1996). Selecting the best collecting method depends on the goal of the survey and environmental conditions, such as the type of vegetation in which collecting is conducted. Pitfall traps are suitable for studies in which assemblages of ground-dwelling species are compared, but not suitable for surveys of actual abundances or of arboreal species (Spence and Niemelä 1994).

Independence of sample size

Ground beetle surveys are not independent of sample size, because of the patchy distribution of the species. Therefore, survey results might depend on the number of sites studied (Atlegrim et al. 1997). Replication (several study sites) reduces this problem because increasing site number increases the probability to find patchily distributed species (Weaver 1995), and thereby increases the reliability of the results.

Reflect response of other species

The degree to which changes in carabid assemblages reflect the response of other species is poorly studied. There is some resemblance of change in carabid and spider species assemblages among habitat types (Rushton et al. 1989). Species of both taxa decreased in improved grassland sites (including e.g. pesticide treatment) which were dominated by invasive species. When carabids, spiders, and ants were collected along a forest succession gradient, carabids and spiders showed fairly similar responses, but did not covary with ants (Niemelä et al. 1996). Although changes in species assemblages were similar in the study, the causes of the change might differ (Niemelä et al. 1996).

Differentiation of natural cycles and anthropogenic stress

There are seasonal (Maelfait and Desender 1990; Niemelä et al. 1992) and year-to-year variations in carabid population sizes (Niemelä et al. 1993; Abildsnes and Tømmeros 2000). Because of this, surveys covering the whole activity season are recommended (Niemelä et al. 2000).

Weather conditions (Abildsnes and Tømmeros 2000) or human impact (Niemelä et al. 1993; Blake et al. 1996) can cause year-to-year variation. In most cases the use of control sites can separate these effects, but sometimes weather conditions can be different in nearby control and study sites (Luff 1990).

Economic importance

Economic importance of indicator species is significant, if they are needed to convince politicians of the importance of monitoring efforts (Pearson 1994). However, the use of only a few economically important species as indicators for monitoring ecosystem functions and biological diversity could be misleading (Landres et al. 1988). Ground beetles can be considered economically important, because they are significant predators of agricultural pests (Hance 1990).

Test of carabids as bioindicators

In the following, we examine the reliability of carabids as bioindicators by using the step-by-step procedure of selecting indicator species (McGeoch 1998). These procedural steps include testing of environmental, ecological, and biodiversity indicators (Table 2). In the procedure, two or three studies per type of indicator were selected to test the suitability of carabids as bioindicators. The studies were selected on the basis of the study question, dealing with bioindication or a closely related issue. We tried to avoid bias by selecting different kinds of studies and approaches. In fact, the studies examined here include most of the relevant studies conducted during the past few years. Three hypotheses were tested: (1) does fragmentation affect the carabid species assemblages (environmental indicator)?; (2) do responses of carabid assemblages to management practices resemble those of other species groups (ecological indicator)?; and (3) does carabid diversity reflect the diversity of other species groups (biodiversity indicator)?

Three studies (Halme and Niemelä 1993; Davies and Margules 1998; Abildsnes

Table 2. Procedural steps (McGeoch 1998) for testing suitability of carabid beetles as bioindicators.

Step 1. Broad objective	Environmental indicator[a]	Ecological indicator[b]	Biodiversity indicator[c]
Step 2. Objectives and endpoints	To detect the nature of disturbance (forest fragmentation) using an indicator (Davies and Margules 1998).	To determine the impact of disturbance (management practices) on spider and ant assemblages using an indicator (Rushton et al. 1989).	To assess the biodiversity (number of species) of biota using an indicator (Duelli and Obrist 1998).
Step 3. Potential indicator	Carabid beetles	Carabid beetles	Carabid beetles
Step 4. Accumulate data on indicator	In total 45 species were identified. Abundances of eight species were surveyed (Davies and Margules 1998).	In total 20 carabid (and 26 spider) species were identified (Rushton et al. 1989).	Limpach Valley in the Swiss central plateau, 19 study sites, 31 412 individuals of 98 carabid species collected. Most diverse areas (48 and 44 carabid species) were in wetlands and in grassland (45 species) (Duelli and Obrist 1998).
Step 5. Collect quantitative relational data	Three plot sizes (0.25, 0.875 and 3.062 ha) were surveyed. In four of the six replicates forest surroundings was cleared and planted with *Pinus radiata* (Davies and Margules 1998).	Four control (unimproved) and 15 study sites with different pesticide treatment, sward age and sown plant species (%) were surveyed (Rushton et al. 1989).	24 other insect groups with 222 species and 191 214 individuals (Duelli and Obrist 1998).
Step 6. Relationship between the indicator and the relational data	Of the 45 species, three were trapped only before and 12 since fragmentation. Abundances of eight species vary so that three species declined, three increased and in two species there was no response (Davies and Margules 1998).	There were less carabid and spider species in improved than in unimproved sites, and unimproved sites were dominated by highly invasive spider and carabid species (Rushton et al. 1989).	Two of the three areas with highest carabid diversities were also among the most diverse as regards the total species diversity. The most diverse area (semi-dry meadow) was the fourth diverse in carabid species number (Duelli and Obrist 1998).

Step 7. Accept or reject an indicator	There was a correlation between habitat fragmentation and species abundance in some, but not in all species (Davies and Margules 1998).	There was a correlation between habitat alteration and ground beetle species, and carabids also reflected the response of spiders (Rushton et al. 1989).	Shannon and Simpson diversity indices showed positive correlation between carabid species number and total species number, but number of carabid species did not correlate with overall species diversity (Duelli and Obrist 1998).
Step 8. Robustness of the indicator and testing appropriate hypothesis under different conditions	Testing the indicator in other surveys (Halme and Niemelä 1993; Abildsnes and Tømmeros 2000) proved that carabids respond to forest fragmentation.	Testing the indicator along a forest succession gradient showed some resemblance with spider species assemblages, but less with ant species (Niemelä et al. 1996).	Testing the indicator in the Swiss Jura mountains showed no correlation between threatened ground beetle diversity and threatened vascular plant, butterfly, gastropod and grasshopper species (Niemelä and Baur 1998).
Step 9. If the null hypothesis is rejected, make specific recommendations, based on the original objectives, for the use of the indicator	Carabids proved to be suitable indicators and the null hypothesis is rejected. Carabids can be used as bioindicators in fragmentation studies, although not all of the species are affected.	There are some correlations between carabids and other taxa, but there is inconclusive evidence that carabids would reflect the response of other taxa.	There is no clear correlation between species richness of carabid beetles and other species groups and the null hypothesis cannot be rejected. It is better to use ground beetles together with some other taxonomic groups to assess biodiversity.

[a]Defined by McGeoch (1998) as a species or species group that responds predictably, in ways that are readily observed and quantified, to environmental disturbance or to a change in environmental state. [b]Defined by McGeoch (1998) as a taxon that is sensitive to identified environmental stress factors, that demonstrates the effect of these stress factors on biota, and whose response is representative of the response of other taxa. [c]Defined by McGeoch (1998) as a taxon or functional group whose diversity (character richness, species richness, level of endemism) reflects the diversity of other taxa.

and Tømmeros 2000) indicated that carabids are suitable environmental indicators (Table 2). Although not all of the species responded to forest fragmentation under the studied conditions, most did. This was seen as changes in species assemblages.

There are fewer studies on the suitability of carabids as biodiversity indicators (Duelli and Obrist 1998; Niemelä and Baur 1998), or about how well they reflect the response of other species (ecological indicators) (Rushton et al. 1989; Abensperg et al. 1996). There is some evidence that they reflect the response of spiders (Rushton et al. 1989), but whether they also indicate some other species groups is not known.

In biodiversity surveys, carabids have not proved to be especially satisfactory indicators (Duelli and Obrist 1998; Niemelä and Baur 1998). According to these two studies there were some or no correlations between the species number of carabids and other taxonomic groups. However, this can be at least partly explained by the small number of sites surveyed (Niemelä and Baur 1998) or by the calculation technique (Duelli and Obrist 1998). A problem in Duelli and Obrist's (1998) study is that insect orders are correlated also to themselves, which means that species-rich groups benefit because they make up a bigger proportion of the species richness. When we recalculated the correlations by taking this into consideration, ground beetle diversity reflected the diversity of other species as well as the other groups do.

To conclude, carabids can be acceptable as environmental indicators, at least when fragmentation studies are concerned. However, this conclusion has been contested (e.g. Rykken et al. 1997). There is some evidence, but not conclusive, supporting the suitability of carabids as ecological and biodiversity indicators (Table 2). Below we review some additional studies on the use of carabids as indicators of habitat change, and their use as biodiversity indicators.

Carabids as indicators of habitat change

Carabids as indicators of grassland changes

Grasslands and cereal fields are the two most intensively studied habitat types as regards carabids (e.g. Desender et al. 1994b). One reason is that ground beetles are seen as important predators of agricultural pests (Hance 1990). Since 1950, there has been a severe loss of natural and semi-natural open habitats, while at the same time agriculture has intensified in Europe. Consequently, great changes have occurred in ground beetle abundances: a few common species have become relatively more common at the expense of a large number of rare species, which have become even rarer (Desender et al. 1994a).

Ground beetles are affected by several grassland management practices, including grazing, fertilising, cutting and other pasture improvement measures. A general principle seems to be that management practices and increasing disturbance decrease the numbers of species and individuals (Rushton et al. 1989, 1990; Blake et al. 1996; Kotze and Samways 1999). Similar results have been found for spiders (Rushton et al. 1989).

One reason for the above negative relationship between management intensity and carabid abundance may be the timing of reproduction. Breeding time is an important factor affecting the survival of a carabid population. Species that breed during the time of intensive management practices (spring) are affected more than species that breed during times of less disturbance (autumn) (Rushton et al. 1990). However, not all of the species decline subsequent to such disturbance. A species' response depends on its dispersal power and habitat preference. Management practices seem to favour species preferring dry conditions (Blake et al. 1996), and those that have high dispersal power (Rushton et al. 1989). In grasslands, ground beetles have also been used for assessment of environmental quality and classification of grasslands. It is possible to assess site quality by comparing abundances of rare and generalist species and giving rarity scores to different habitats (Eyre et al. 1996). Grasslands can be classified by differences in species assemblages (Eyre and Luff 1990), as different types of grasslands have unique species assemblages.

Compared to forest ecosystems, abundances of carabid species in agroecosystems are relatively independent of local small-scale habitat variations (Luff 1990). However, there might be great variation between years and this variation might be habitat specific (Luff 1990).

Although management practices have a strong impact on species abundances, it is sometimes difficult to pinpoint the primary cause of this impact. Species declines can be caused directly by management practices, but also indirectly by e.g. change in soil water content (Rushton et al. 1990). Whether direct or indirect, management practices have impacts on carabid assemblages.

Carabids indicating forestry practices in the boreal zone

Boreal forests cover most of the land area of northern Europe, Asia, and America. Their management is economically important, but at the same time many species have become threatened due to forestry. For instance, in Finland 30% of the threatened species are declining because of forestry (Rassi et al. 2000). Ecologically sustainable forestry practices are an important way to maintain populations of forest species, and ground beetles have been used to develop such methods (Koivula 2002).

Most of the studies in boreal forests are concerned with habitat fragmentation, edge effects and other forestry practices (e.g. Niemelä et al. 1993; Spence et al. 1996; Atlegrim et al. 1997; Heliölä et al. 2001). According to these studies there are clear differences between generalist species, which are not affected by forestry, and specialist species, which are affected by forestry practices. Open habitat species are favoured by clear cutting (Niemelä et al. 1993).

Boreal forest is a patchy environment and ground beetles occur there in aggregations (Niemelä 1990). Forest specialists, in particular, are associated with certain microhabitat types (Niemelä et al. 1990). For instance, abundance of deciduous litter is a sign of a high quality 'resource spot' for many carabids, and these spots may serve as source patches from which individuals move into lower-quality patches nearby (Haila et al. 1994). These spots of deciduous litter are especially important in forests with poor soils and humus layer (Koivula et al. 1999).

After forest clearance, specialised forest species, which are often large-sized and poor dispersers, decrease in number (Halme and Niemelä 1993; Niemelä et al.

1993). Because these species have poor dispersal ability they might not be able to move to suitable habitats over clear-cuts (Halme and Niemelä 1993). Additional decrease in number and size of remaining mature forest patches may cause local extinctions in these species (Koivula et al. 2002). Furthermore, there may be indirect effects on the specialised species, e.g. through decreased abundance of prey species (Haila et al. 1994).

Although forest management affects specialised forest species, the dominance structure of the most abundant species does not necessarily change. For instance, the carabid fauna of southern Finnish forests consists of very few abundant species (e.g. *Calathus micropterus* and *Pterostichus oblongopunctatus*) in all forest age-classes from 0- to over 100-year-old stands (Niemelä 1993b; Haila et al. 1994). Overall, it appears that 'adversity selection' is functioning in the boreal forest as regards carabids. This implies that only a few species are able to maintain high population sizes, while most species are scarce, probably due to the harsh conditions of the boreal forest environment (Niemelä 1993b).

To conclude, specialised forest species can be used as bioindicators of changes in the boreal forest caused by forestry practices. Furthermore, the abundances of forest generalists usually decrease, although they do not entirely disappear from harvested sites. In terms of carabid surveys, there are some recommendations. Because of the patchy distribution of carabids, it is important to sample over several sites (Atlegrim et al. 1997) and, because activity and abundances of species vary during the season (Niemelä et al. 1992), surveys covering the whole growing season are recommended (Niemelä et al. 2000).

Carabids in tropical forests

In the tropics, forest decline is one of the most important environmental problems. Most of the species in the world live in tropical forests and many of these are still unknown to science (May 1992). There are several studies on ground beetles in boreal forests and grasslands, but less surveys from tropical forests. Most surveys concern tiger beetles (Coleoptera: Cicindelidae) (e.g. Pearson and Cassola 1992) or the beetle order as a whole (e.g. Lawton et al. 1998).

Tiger beetles have been suggested as indicator species in the tropics, because they are specialised to certain habitat types and reflect diversity of birds and butterflies (Pearson and Cassola 1992). Studies on the impacts of forest disturbance on beetles in Cameroon (Lawton et al. 1998) and Brazil (Brown 1997) showed that complete clearance had negative impacts on beetle species diversity, but there were no clear correlations of response to other species along a disturbance gradient (Brown 1997; Lawton et al. 1998).

In tropical forests, there might be great differences in insect species richness in adjacent habitats (Janzen and Shoener 1968). Usually, there are more individuals/ species in the temperate and boreal regions than in the tropics (Erwin 1988), indicating that higher trapping effort is needed in the tropics for catching all or at least a representative proportion of the fauna. In the tropics the generally used trapping method for carabids, pitfall trapping, might fail because >30% of species are arboreal, exhibiting special morphological and behavioural adaptations (Stork

1987). Another problem is that not all species can be identified. Identifying species only to morphospecies partly remedies this problem (Kremen 1992). However, because of lack of surveys it is too early to assess the suitability of carabids as bioindicators in tropical forests.

Effects of fragmentation on carabids

Habitat fragmentation, and the associated loss of habitat, is the partitioning of a continuous habitat into many small remnants (Saunders et al. 1991; Haila 1999). Fragmentation is one of the greatest environmental problems all over the world, and it is one of the most important reasons for declining biodiversity (Pimm and Gilpin 1989).

According to Didham (1997) there are five fragmentation-related issues of importance for invertebrates: (1) area effects (size of the fragment), (2) edge effects, (3) shape of the fragment, (4) degree of spatio-temporal isolation, and (5) degree of habitat connectivity in the landscape. Furthermore, fragmentation changes temperature, light, moisture, and wind conditions in habitat patches. At least area effects, edge effects, shape of the fragment, and habitat connectivity in the landscape have impacted ground beetle assemblages (Niemelä 2001).

The size of the patch affects carabid assemblages by changing species composition, species number and/or species abundances. Depending on the study, species richness increased (Burke and Goulet 1998), remained the same (Davies and Margules 1998) or decreased (Halme and Niemelä 1993) with increasing forest fragment size. The high number of species found in small-sized (0.5–3 ha) fragments can be explained by the invasion of species from the surroundings of the fragments, and the diversity of vegetation which positively affects carabid species richness (Halme and Niemelä 1993). On the other hand, isolation has a negative effect on species richness (Burke and Goulet 1998).

Although species richness may remain the same between differently sized fragments, species abundances (Niemelä et al. 1988) or assemblage structure may change (Davies and Margules 1998). According to Halme and Niemelä (1993), forest fragments up to 21.5 ha did not support populations of strict forest specialist species, which were found only in contiguous forest. These species are in general large-sized, short-winged and they have limited dispersal ability.

Forest edges influence some, but not all species (Spence et al. 1996). Edges attract open habitat species, which increase in abundance and/or species number (Niemelä et al. 1993). However, edges may not affect populations of forest carabids near the edge (Heliölä et al. 2001).

Comparisons of fragments to their surroundings have shown that as the size of the fragment decreases, the resemblance of carabid fauna to the surrounding human-modified habitat increases (Niemelä 2001; Halme and Niemelä 1993). Furthermore, the shape of the fragment affects species richness so that forest fragments with high edge-to-area ratios contained more species because of a high invasion rate from the surroundings (Usher et al. 1993).

The impact that habitat connectivity has on beetle assemblages depends on species' dispersal power and flight ability, which varies between ground beetle species (den Boer 1990a). Flightless carabids can move up to a few hundreds of meters by walking (Thiele 1977; den Boer 1990b), and benefit from ecological corridors (Niemelä 2001). Species with good flight capability can move longer distances, and are therefore not that dependent on dispersal corridors (Niemelä 2001).

Fragmentation has caused several carabid species to become threatened in Europe (Desender and Turin 1989). Most vulnerable are strict forest species with limited ability to move, and species found in interiors of fragments (e.g. Halme and Niemelä 1993). General impacts of forest fragmentation on ground beetles are: (1) species composition changes although species number might remain the same (Davies and Margules 1998), (2) species abundance changes (increasing or decreasing) in some but not in all species (Spence et al. 1996; Abildsnes and Tømmeros 2000), and (3) specialist species decline and open habitat species increase (Halme and Niemelä 1993; Niemelä et al. 1993).

Carabids as biodiversity indicators

A biodiversity indicator is a taxon or a functional group the diversity of which (character richness, species richness, level of endemism) reflects diversity of other taxa (McGeoch 1998). The search for biodiversity indicators has intensified during the past years, as there is a general lack of time and resources to survey species diversity of whole communities (Raven and Wilson 1992). However, it has proved to be difficult to find reliable biodiversity indicators.

Some studies report correlations between species richness of different species groups, e.g. tiger beetles and birds (Pearson and Cassola 1992), butterflies and flowering plants (Kremen 1992), and several insect groups and overall species diversity (Duelli and Obrist 1998). However, there are also several studies where no or very few correlations between species richness of different taxonomic groups were found (plants, mosses, birds, butterflies, beetles etc.) (Kremen 1992; Prendergast et al. 1993; Oliver and Beattie 1996; Lawton et al. 1998; Jonsson and Jonsell 1999).

Sometimes there are correlations between pairs of species in some places but not elsewhere. For instance, Beccaloni and Gaston (1995) found a strong positive relationship between species richness of ithomiine (Nymphalidae: Ithomiinae) and the overall species richness of all other butterfly species across sites, countries and the Neotropics as a whole. However, opposite results were reported from Britain, where none of the butterfly families indicated in any consistent way the overall species richness of butterflies (Prendergast 1997).

Carabid beetles have not been commonly used as indicators of biodiversity (Greenslade 1997; Duelli and Obrist 1998; Niemelä and Baur 1998), although beetles in general or other beetle genera have been used in several studies (e.g. Oliver and Beattie 1996; Brown 1997; Jonsson and Jonsell 1999). According to biodiversity surveys (Greenslade 1997; Duelli and Obrist 1998; Niemelä and Baur 1998) there was little or no correlation between the diversity of carabids and other species groups (including several insect orders, gastropods and vascular plants).

However, results were not unambiguous because ground beetles did show a positive correlation with other insect orders in diversity indices (Shannon and Simpson) (Duelli and Obrist 1998). Carabid species richness has also shown a positive correlation to other beetle families (Scarabaeidae and Pselaphidae) (Oliver and Beattie 1996).

How can we know in advance whether or not there are significant correlations between species groups? There are no clear answers, but ecological requirements of the species and the scale of observation can provide some guidance. There may be no correlation between species groups with different ecological requirements (Lawton et al. 1998; Jonsson and Jonsell 1999), whereas correlation can be expected between species, which depend on the same ecological factors e.g. moisture, soil quality, and dead wood. Species richness also depends on the scale of observation (e.g. He et al. 1994; Weaver 1995). Species are distributed differently, some more patchily and others more uniformly, and therefore, increasing the sampling unit increases the species numbers at different rates (Weaver 1995). In some species groups there might be very little increase in species number compared to others (Weaver 1995).

Species richness might not be the best measure of the conservation value of an area, as areas of high biodiversity and amount of rare species may not coincide (Prendergast et al. 1993). However, protecting every hotspot for just one taxon might protect more than half of the species targeted and of species in every other group (Prendergast et al. 1993). In addition to reflecting species richness, a good indicator should also reflect the level of endemism and amount of rare or endangered species. The level of endemism is high in many tropical countries. In Madagascar, 80% of forest birds and all 32 species of primates are endemic (Harcourt and Thornback 1990; Langrand 1990). The level of endemism in carabids is not known for Madagascar, but new species are being reported constantly. For instance, of the 56 platynine species recorded from the 40000 ha Ranomafana National Park, 18 are new to science (E. Elsom and D.H. Kavanaugh, personal communication). This situation is common in many other tropical countries.

There are several factors affecting species diversity and it is rarely only one species or species group which would adequately predict the whole diversity of the biota. Nevertheless, there are some pairs of taxa that correlate at least in some places. However, as single species are unreliable indicators, it is better to use several species groups with different ecological requirements to indicate biodiversity (Niemelä and Baur 1998).

Conclusions

Although the use of bioindicators is somewhat problematic, as has been indicated above, bioindicators are a popular and cost-effective way to detect and monitor changes in the environment. Selecting the most suitable indicator depends on the goal of the survey and the characteristics of the indicator. In carabid beetles there are several species or species groups that have been used as indicators.

Selecting the proper indicator taxon is a compromise between advantages and disadvantages. The success of using carabid beetles is based on cost-effective data collection, sensitivity to different environmental factors and wide habitat requirements. Disadvantages of carabids as bioindicators include their seasonal variation, patchy distribution, high number of generalist species, and difficulty to predict species richness. However, these characteristics are common to most groups of organisms. To minimise the effect of seasonal variation, studies covering the whole growing season are recommended and a way to capture most of the patchily distributed species is to sample in several study sites (i.e. spatial replication). Both of these approaches increase survey time, but this might be remedied by shortening the sampling period and by using more efficient traps (Niemelä et al. 1990; Luff 1996).

Although generalist carabids make up most of the species assemblage, there are also specialist or sensitive species. A lack of specialist species might indicate disturbances in the environment (Halme and Niemelä 1993), and most generalist species also respond to habitat alteration (e.g. Blake et al. 1996; Davies and Margules 1998), or their species composition can be used e.g. for habitat classification (Eyre and Luff 1990).

Few studies have compared carabid beetle responses to responses of other taxonomic groups. According to Rushton et al. (1989) carabids and spiders showed a similar kind of response, i.e. decrease in species richness after pasture improvement. According to Niemelä et al. (1996) there were similar abundance variations in carabids and spiders across a forest succession gradient.

To conclude, we suggest some common principles of how carabid assemblages change after disturbance in grasslands and forests: (1) although species number may remain unchanged, species composition and species' abundances change, and (2) large-sized and poorly dispersing specialist species decrease, while small-sized, generalist species with good flight ability increase in number. Most important factors affecting carabid species number and abundances are fragmentation, soil water content (Eyre and Luff 1990) and vegetation (Halme and Niemelä 1993). In terms of conservation, eurytopic and ubiquitous species probably survive without protection, if the range of habitats they use is maintained (Eversham et al. 1996). Stenotopic species with more specific habitat requirements, however, are a more appropriate focus of conservation. These are the first species to suffer from forestry or habitat fragmentation, and their numbers have already started to decline. Knowledge of community changes following disturbance and the environmental sensitivity of carabids render them suitable bioindicators in studies on habitat alteration and disturbance. However, it is unclear how well they represent the response of other species groups, i.e. are they suitable biodiversity indicators. More studies are needed to answer these questions.

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