

# Carabid Beetles as Ecological Indicators

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## Abstract

This paper will examine the utility of carabid beetles and other invertebrates as bioindicators in coastal western hemlock forests. This work has been carried out as part of Weyerhaeuser's adaptive management program between 2001-present. We have been examining how invertebrates may inform us of fragmentation and edge effects, and how we may interpret their responses to various partial cutting methods to determine how well variable retention harvesting conserves biodiversity. In this presentation we address the effectiveness of pitfall trapping as a method to trap carabid beetles, the utility of the invertebrate by-catch, and we discuss why we believe ground beetles are a useful group for large-scale monitoring studies.

## Introduction

My presentation focuses on work that I have been carrying out for Weyerhaeuser as part of their adaptive management program since 2001. Under the Forest Project, Weyerhaeuser's adaptive management program is examining the effectiveness of retention systems and stewardship zoning in maintaining the forest attributes necessary to sustain biodiversity and essential ecosystem functions.

Biological processes are difficult to measure directly, but the adaptive management program has identified a range of indicator organisms and structures that might prove useful in assessing ecosystem health. Ideally, indicator organisms are individual species, groups of species or structures that perform critical ecosystem functions or are particularly sensitive to disturbances. I have been working since 2001 to assess the utility of carabid beetles as indicator species on Vancouver Island and to determine how we may interpret the responses of carabids to various partial cutting methods to determine how well variable retention harvesting conserves biodiversity?

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**Citation:** Pearsall, I.A. 2007. Carabid Beetles as Ecological Indicators. Paper presented at the "Monitoring the Effectiveness of Biological Conservation" conference, 2-4 November 2004, Richmond, BC. Available at: <http://www.forrex.org/events/mebc/papers.html>

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Some of the specific questions that I will address in this paper include:

- Why are ground beetles are a useful group for large-scale monitoring studies?
- How effective is pitfall trapping as a method to trap carabid beetles?
- Can carabids inform us of fragmentation and edge effects?
- Is the invertebrate by-catch informative?

## **Discussion**

Firstly we may address why we are using carabids as ecological indicators, then we will discuss the benefits and limitations of pitfall trapping as a method to catch carabids. Next we we will discuss some of the types of results that we have been obtaining over the past three years that we have been examining carabid beetles as focal species for Weyerhaeuser's adaptive management program and finally we will touch briefly on details regarding the possible utility of some of the by-catch.

### *Why Carabids?*

We are using carabid beetles as an indicator species in the Weyerhaeuser adaptive management program, in part because they show the following useful traits:

#### *Ubiquitous*

Ground beetles are abundant and diverse in most ecological systems and therefore serve as an appropriate group for which to make inter-regional comparisons.

#### *Predatory nature*

The majority of ground beetles are predatory. Thus carabids are good integrators of a substantial amount of ecological information about the biological communities to which they belong because they are may be primary or secondary predators in forest soils (Day and Carthy 1988).

#### *Amenable scale*

Different species of carabids are found in high numbers at various times of year, which likely coincides with periods of reproduction. Some of the carabids are highly mobile, and capable of moving large distances, but many do not have functional wings and can only walk out of blocks. Populations of carabids, and indeed arthropods as a whole, tend to be large in comparison to vertebrates and possibly even plants. These small insects have high reproductive potential and although in some cases, only one individual is trapped in a block, it may generally be assumed that there are more. Those species that cannot fly, and have fairly limited dispersal ability are most likely reproducing within that habitat. This is quite different than may be the case for larger vertebrates that may be moving through the area, and not necessarily reproducing in that specific habitat. Small size, small scales of movement and lifecycles, and high reproductive ability, make them an excellent candidate for work of this sort.

### *Abundant identification materials*

Much of the taxonomy of this family of beetles has been determined for North American species and there is a lot of research underway examining the use of carabids in monitoring the health of various habitats.

### *Sensitive to disturbance*

Associations of particular carabid species with broad habitat categories, such as 'forest' or "fields" have been established e.g. Lindroth 1961-69. Relationships with factors like soil form, soil moisture and plant species have been reported for ground beetle species and communities (Lindroth 1961-69, Niemela and Spence 1994, Rykken et al 1997, Walsh et al. 1993). Although there is some debate over habitat specificity within some species, there is little doubt that most carabids are found in association with very specific landscape features, and in narrowly defined microclimates (Duchesne and McAlpine 1994; Heijerman and Turin 1994).

Because carabids show different levels of habitat selectivity, ranging from specialists to generalists (Niemela 1990), carabid assemblages can be used to characterize disturbance in various habitats such as forests. Three aspects of carabid diversity are modulated by the environment: relative catches of each species within a particular forest site, absolute population size of individual species, and presence or absence of species within assemblages.

Carabids can be used as an indicator guild to quickly and cheaply assess the biotic sensitivity of a forest and are generally chosen much more frequently than most other groups of insects for use in surveys. Carabid beetles have been used as an indicator of soil diversity after disturbance caused by forest fire (Holliday 1991a, b), clear cutting (Sustek 1981, 1984, Lenski 1982, Jennings et al 1986, Langor et al 1991), scarification (Parry and Rodger 1986), pollutants (Stubbe and Tietze 1982, Kolbe 1988), land reclamation (Day and Carthy 1988), management of primeval or old growth forests (Niemela et al. 1988, Terrel-Nield 1990) and climate change (Elias 1991). The sensitivity of carabid beetles to environmental variation and their rapid responses to habitat change, shown by numerous studies make them suitable indicators for predicting and assessing effects of forest management practices.

### *Easy to trap*

Carabid beetles are easy to catch in relatively large numbers with the use of simple, inexpensive pitfall traps. The traps that I have been using are of a very simple design, and very inexpensive to put together. Specifically, the traps are made up of two 14oz plastic beer cups, one placed inside the other, and which are buried into the ground. The ground layer is made to be smooth and level with the top of the top plastic cup. This double cup method allows for sampling without undue disturbance to the trap-vegetation/soil complex. The insert cup may be easily removed, emptied and replaced independently of the lower trap. The insert cup is filled approximately to 1/3 of its volume with diluted propylene glycol to be used as a collection fluid and preservative. This is effective as a killing agent, but does not attract beetles or other fauna, and is cheap and readily acquired.

The traps are covered with elevated squares of coroplast (a type of corrugated plastic) to prevent flooding during rain and to protect from birds and mammals. Large sheets of coroplast are cut into 20 \* 20 cm squares. Three large nails are pushed through three corners of the square and pushed into the ground around the trap, making a rain cover to protect the trap.

Traps can be sampled in a couple of minutes. The inner cup is pulled out, leaving the outer cup still buried in the ground, and thus keeping the trap intact. The contents of the inner cup are poured through a small sieve and the organisms collected are placed into a collecting vial. The cup is replaced, after washing, into the trap, and the sieved fluid is poured back in. The trap over is then replaced over the top of the trap. They can easily be left out for one month periods if necessary with adequate preservation of contents.

### **Pitfall Trapping Issues**

Pitfall traps have been widely used to sample ground-dwelling arthropods (Southwood 1978), especially carabid beetles (e.g. Briggs 1961, Greenslade 1964, Luff 1975, 1986, Dennison and Hodkinson 1984, Waage 1985, Niemela et al. 1992). Data from pitfall traps have been used to describe annual activity patterns (e.g. Niemela et al 1992), spatial distributions (Hengeveld 1987), habitat associations (Niemela 1990, Niemela et al. 1992), and relative abundances of species (Kharboutli and Mack 1991, Niemela et al. 1992).

However, there has been a large amount of discussion in the literature concerning the problems associated with using this method of sampling. Catches are known to be affected by trap size, and shape (Luff 1975, Adis 1979, Spence and Niemela 1994) and material of construction (Luff 1975, Waage 1985), type of preservative (Luff 1968, Waage 1985), microclimate (Honek 1988), length of the trapping period (Niemela et al 1990) and the physical structure of the environment (Greenslade 1964). The latter concern is very important: Greenslade (1964) found that the type of vegetation surrounding a pitfall trap would significantly affect its trapping ability, as numbers of carabid entering a trap is highly associated with their activity. If there is a lot of thick ground cover, then movement of beetles may be impeded and catches will be low. Craig (1995) noted that in the case of forest successional stages, the understory vegetation (or in the case of clearcut areas, the vegetation) of all the forests was heterogenous, with areas of mosses, salal, barren rock, decaying wood, and exposed soil. Thus, even in one environment, the microhabitat variation may be enormous. Baars (1979) advised that if the microhabitat is very heterogenous, then it may be better to use numerous traps. Craig (1995), therefore, used a large number of traps which were randomly located within assigned grids, and thus a wide variety of microhabitats were sampled.

Pitfall trapping has been criticized on the grounds that it cannot be used to compare or estimate densities, since the capture rate is dependent upon both the activity level and on density of the beetles (Thiele 1977). However, the activity density is of interest itself, since the impact of a carabid species on its prey and on competition is a function of activity as well as density (Lenski 1982).

Because carabid activity is affected by environmental factors such as temperature and moisture (Mitchell 1963) some workers believe that sampling using pitfall traps is unreliable at estimating even relative abundances (Southwood 1978). However, Baars (1979) and den Boer (1986) suggest that it is reliable given that certain conditions are met. For intraspecific comparisons, it is suggested that trapping should be continuous for the complete activity period of the beetles, or for one year. Traps should remain in the ground in the same physical arrangement throughout this period.

To be able to calculate the absolute population size of any one species, you would need to know the relationship between species density and pitfall efficacy for each species (Baars 1979). Quadrat sampling methods such as a litter washing or sieving a measured area can be used to determine absolute carabid density, but in order to gather enough data for meaningful analysis these methods would likely be prohibitively labour intensive and habitat destructive (Thiele 1977, Spence and Niemela 1994).

Spence and Niemela (1994) examined a variety of methods of sampling – litter washing, five different types of pitfall trapping and Tullgren funnel extraction. In general, they found that pitfall trapping caught the larger bodied individuals whereas smaller sized species were caught in the litter washing. Craig (1995) also noted that in general pitfall traps do tend to collect more of the larger carabids and very small carabids tend to be under-represented. She also noted that smaller traps tend to catch more of the smaller carabids. Spence and Niemela (1994) warned that pitfall trapping must be viewed with caution if it is to be used to provide comparative estimates of species abundance across habitats (Greenslade 1964, Niemela et al. 1990). However, density estimates based on quadrat samples also showed biases in this study. The authors noted that direct, quantitative sampling of litter also does not take in to account the resting foraging or possible evasive behaviour of carabids, and consequently some important species may be underrepresented in the sample. Other methods, such as litter washing were very time consuming and interestingly, litter samples caught more of the smaller carabids, and larger ones tended to be under-represented in comparison with pitfall catches.

Spence and Niemela (1994) suggested that the choice of sampling method to be used will depend on question being asked. For example, in surveys of large geographical areas where the objective is qualitative inventory and comparison of assemblages, pitfall trapping is the only realistic alternative available (Niemela et al. 1990, 1993). This kind of work may include assessing and monitoring environmental problems by using carabids as an indicator group (Freitag et al. 1973, Niemela et al 1990).

Digweed et al. (1995) examined how depletion and disturbance may influence catches of ground beetles. The authors noted that commonly, catches of carabids in pitfall traps tend to decrease over time, mostly due to decreased activity of many species in midsummer. However, temporal variation in catches may not be fully explained by annual activity patterns. Catches have often been seen to be highest soon after pitfall traps are inserted into the ground. The following decrease in catches may be due to the pitfall traps depleting the local carabid population. Digweed et al. (1995) hypothesized that higher trap densities at smaller distances would result in local depletion of the carabid population and thus, lower catches. They examined the effect of different

spacing (10m, 25 or 50m apart) of traps and also the effects of disturbing, i.e. moving the traps on catch in a poplar-spruce mixed forest northwest of Edmonton. They found fewer carabids were captured in traps that were spaced only 10m and that this was no doubt due to depletion, i.e., populations of carabids decreased in abundance and could not be replaced quickly enough by immigration. They also found that low numbers of carabids were caught in permanent traps rather than traps that moved to new locations over time. This was suggested to be a disturbance effect, due to ground getting trodden down and the area generally disturbed due to constant visits. Permanent traps and those at the 10m spacing also were less sensitive to changes in activity over time. Digweed et al. (1995) recommended that traps be placed at least 25m apart, to reduce depletion effects, to increase sensitivity of phenology curves, to increase capture of rare species, and to ensure statistical independence.

Niemela et al. (1990) recommend that pitfall data may be used to compare relative abundances within species between habitats and to assess habitat effects on carabid diversity. Thus, for our needs, we have concluded that pitfall trapping is the easiest, cheapest, fastest, and most appropriate strategy.

## **Discussion of some of the results from our studies**

Over the past few years we have carried out pitfall trapping throughout Vancouver Island and mainland B.C. These studies have included examination of carabid communities in operational forest blocks of different ages from a number of site series throughout Vancouver Island, a comparison of carabid communities in two of Weyerhaeuser's experimental VR sites (group and dispersed treatments), and an examination of carabid communities in some of the oldest operational VR sites in West Vancouver Island. The work done during 2001-2004 has clearly identified that carabid beetles are a highly sensitive indicator species, with significantly different communities in clearcut, immature and mature forests. Overall, the most common species caught has been *Scaphinotus angusticollis*, which is a slug and snail eating species. Each year of study, significantly greater numbers of *S. angusticollis* were trapped in forested sites than in clearcuts.

Another forest specialist appeared to be *Zacotus matthewsii*, also encountered in significantly lowest numbers in clearcut blocks. This is a litter and soil predator, feeding primarily on millipedes and has been suggested as an old growth specialist in a number of other studies, for example in the HJ Andrews Experimental Forest in Oregon and by Craig (1995) for southern Vancouver Island. A number of generalist species have also been found, such as *Pterostichus lama*, *P. amethystinus* and *P. herculeanus*. We have also identified a number of disturbance specialist species, such as the tiny *Notiophilus sylvaticus*, and *Synuchus impunctatus*, which were most commonly trapped in clearcut blocks. Patterns of carabid abundance may be used to reflect differences in the prey base of these arthropods.

Using the above information, we were able to make a comparison of the effects of harvesting by group and dispersed variable retention (VR) in two experiments in Tsitika and Stillwater, respectively. Our results showed that group retention appeared to be a more effective method of preservation of forest specialist species than dispersed retention for a similar level of tree retention. One-year post-harvest, forest specialists

were similarly abundant in all group retention patches as in the original old-growth control at Tsitika and thus the patches all appeared to act as adequate source areas for carabids over the short-term.

We have begun to put together response curves in terms of changes in abundance of different carabid species to site age. These curves allow us to estimate how long the forest specialists require before they can re-establish in traditional clearcuts as they age. The rate of re-establishment may be compared with how quickly the cut matrices of VR blocks are re-established with forest species. We have also compared the communities found in old-growth throughout Vancouver Island. Some of our work in remnant patches of old growth in North Vancouver Island have shown that those carabid communities appeared to contain lower numbers of three forest specialists, *Zacotus matthewsii*, *Pterostichus crenicollis* and *Scaphinotus angusticollis*, than found in comparable contiguous patches of old-growth. There were also increased proportions of generalist species such as *Pterostichus lama* and *P. herculeanus*, and greater evenness within sites in terms of species composition. Thus, there is some evidence for altered community composition and changes in the relative abundance of forest specialists and generalists within remnant communities over time.

Other work done over the past few years examined the changes in communities across forest edges separating old-growth sites and differently aged clearcuts. Specific species responses across the forest-clearcut transition were apparent for *Scaphinotus angusticollis*, *Zacotus matthewsii* and *Pterostichus crenicollis*. All these forest specialists were caught in highest abundance in traps placed in old-growth, and both *Zacotus* and *Scaphinotus* displayed a possible edge effect of over 50 m into the clearcuts from the edge: catches of these species remained high until traps were at least 75m from the forest edge. If similar edge effects are apparent from the forest edge into interior old-growth, then this would suggest that patches set up for variable retention would need to be greater than 100m width at the narrowest points. Future work will be carried out during 2005 to address the required size and shape of patches.

### **Utility of Bycatch**

By-catch may be very useful, particularly catches of arachnids and staphylinids, as clear patterns have been evident among the different sites over the course of the study. Spiders have been generally most abundant overall in clearcuts, whereas staphylinids have rarely been trapped in these blocks. Staphylinids show high ecological specialization and are thus useful as bioindicators, although they have not been used as much as carabid beetles, due to difficulties in their identification (Bohac 1999). Spiders have also been identified as potential indicator species (Uetz 1991, Wise 1995, Mclver et al. 1992). Millipedes, such as the yellow spotted millipede, *Harpaphe haydeniana haydeniana* are thought to have high indicator potential (Mt. Hood National forest Invertebrate Inventory Project). This species has been listed as an old growth/ late successional forest related species in both the Appendix J2 of the Northwest Forest Plan and the 1993 report of the Scientific Analysis Team. We hope in future studies to begin to also examine the by-catch to the species level, and thus to obtain greater amounts of information from the trapping process.

## Summary

Overall, we have also shown that carabid beetles exhibit responses that are sensitive enough at small scales such that they may be used appropriately to indicate edge conditions, and to assess how quickly sites recover and re-establish typical old-growth communities. They are captured easily and in large numbers using inexpensive pitfall traps, the most abundant species are generally very easy to identify and sample sizes have been adequate for statistical analysis. The ground beetles as a group are highly sensitive to harvesting methods, and the results of our studies have indicated clearly that carabid beetles would be an ideal focal species to be used in forest biodiversity and adaptive management studies of this nature.

## Acknowledgements

I am very grateful to Glen Dunsworth and Bill Beese for providing the funding and interest in this project and to Jeff Sandford for all his help with location of blocks, loans of field equipment and advice and help with data and mapping needs. This work could not have been done without the great field assistance of Claudia Lake. Thank you very much to Jeff Jarrett for invaluable help with beetle identifications and to Karen Needham for allowing me space and time in the UBC George J. Spencer Entomological Museum. Many thanks to Dave Huggard for shrew identifications. Thanks to the Weyerhaeuser staff at North Island, West Island and South Island Timberlands, particularly Ally Gibson, Ken Epps, Brian Goosder, Dave Gatenby, Mike Dunn, Richard Player, Jonathan Flintoft and John Eden.

## References

- Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zool. Anzeig.* 202: 177-184
- Baars, M.A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41: 25-46
- Bohac, J. 1999. Staphylinid beetles as bioindicators. *Agric. Ecosyst. Env.* 74: 357-372
- Briggs, J.B. 1961. A comparison of pitfall trapping and soil sampling in assessing populations of two species of ground beetles (Coleoptera: Carabidae). *Rep. East. Malling Res. Stn. for 1960*: 108-112
- Craig, K.G. 1995. Variation in carabid community structure associated with coastal Douglas-Fir forest successional stages. M.Sc. Thesis, University of British Columbia.
- Day, K.R. and J. Carthy. 1988. Changes in carabid beetles communities accompanying a rotation of sitka spruce. *Agric. Ecosys. And Environ.* 24: 407-415
- den Boer, P.J. 1986. Carabids as objects of study. In *Carabid beetles: their adaptations*

- and dynamics. Gustav Fischer: New York, pp 539-551
- den Boer, P.J. 1990. The survival value of dispersal in terrestrial arthropods. *Biol. Conserv.* 54: 175-192
- Dennison, D.F. and I.D. Hodkinson 1983. Structure of the predatory beetle community in a woodland soil ecosystem. I Prey selection. *Pedobiologia* 25: 109-115
- Digweed, S.C. 1993. Selection of terrestrial gastropod prey by Chydrine and Pterostichine ground beetles (Coleoptera: Carabidae). *Can. Entomol.* 125(3): 436-472
- Digweed, S.C., C.R. Currie, H.A. Carcamo, and J. R. Spence 1995. Digging out the "digging-in effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39: 561-576
- Duchesne, L.C. and R.S. McAlpine 1994. Using carabid beetles (Coleoptera: Carabidae) as a means to investigate the effect of forestry practices on soil diversity. Forestry Canada. PNFI Technical Report.
- Elias, S.A. 1991. Insects and climate change. *Bioscience* 41: 552-559
- Freitag, R., L. Hastings, W.R. Mercer, and A. Smith 1973. Ground beetle populations near a kraft mill. *Can. Entomol.* 105: 299-310
- Greenslade, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* 33: 301-310
- Heijerman, T.H. and H. Turin 1994. Towards a method for biological assessment of habitat quality using carabid samples (Coleoptera: Carabidae). p. 305-312 *In* Desender et al. (eds.) *Carabid beetles: Ecology and Evolution*. Kluwer Academic Publishers, Netherlands.
- Hengeveld, R. 1987. Scales of variation: their distinction and ecological importance. *Ann. Zool. Fenn.* 195-202
- Holliday, N.J. 1991a. Species response of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Can. Entomol.* 1369-1389
- Holliday, N.J. 1991b. The carabid fauna (Coleoptera: Carabidae) during post-fire regeneration of boreal forest: properties and dynamics of species assemblages. *Can. J. Zool.*
- Honek, A. 1988. The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera) and Lycosidae (Araneae) in cereal fields. *Pedobiologia* 32: 233-242
- Jennings, D.T., M.W. Houseweart, and G.A. Dunn 1986. Carabid beetles (Coleoptera: Carabidae) associated with strip-clearcut and dense Spruce-Fir forests of Maine. *Coloep. Bull.* 40(3): 251-263

- Kharboutli, M.S. and T.P. Mack 1991. Relative and seasonal abundance of predaceous arthropods in Alabama peanut fields as indexed by pitfall traps. *J. Econ. Entomol.* 84: 1015-1023
- Kolbe, W. 1988. Okotoxikologische Aspekte-aufgezeit als beispiel der coleopteren Fauan von Waldboden. *Mitt. Dtsch. Ges. Allg. Angew. Ent.* 6: 458-463
- Langor, D.W., J. Niemela, and R.J. Spence 1991. Effects of forestry practices on carabid assemblages in lodgepole pine forests in western Alberta. *Proc. Can. Ent. Soc. Meet. Montreal, Que., September 21-23, 1991.*
- Lenski, R.E. 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the Southern Appalachians. *Ecol. Entomol.* 7: 385-390
- Lindroth, C.H. 1961-69. The ground beetles of Canada and Alaska. *Opuscula Entomologica (Suppl.)* 20, 24, 29, 33, & 34. 1192pp.
- Luff, M.L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* 19: 345-457
- Luff, M.L. 1986. Aggregation of some Carabidae in pitfall traps. In *Carabid beetles: their adaptation and dynamics*. P.J. den Boer, M.L. Luff, D. Mossakowski and F. Weber (eds.). Gustav Fischer, Stuttgart. P 385-397
- Mclver, J.D., Parsons, G.L. and Moldenke, A.R. 1993. Litter spider succession after clear cutting in a western coniferous forest. *Can. J. For. Res.* 22: 984-992
- Mitchell, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. *J. Anim. Ecol.* 32: 377-392.
- Niemela, J.D. 1990 Effects of change in the habitat on carabid assemblages in a wooded meadow on the Aland islands. *Notulae Entomologicae* 69: 169-174
- Niemela, J.D., Y. Haila, E. Halme, T. Lahti, T. Pajunen, and P. Puntila 1988. The distribution of carabids in fragments of old coniferous taiga and adjacent managed forest. *Ann. Zool. Fennici* 25: 107-119
- Niemela, J., J.R. Spence and D.H. Spence 1992. Habitat associations and seasonal activity of ground beetles (Coleoptera: Carabidae) in central Alberta. *Can. Entomol.* 124: 521-540
- Niemela, J., J.R. Spence, D.W. Langor, Y. Haila & H. Tukia 1993. Logging and boreal ground beetle assemblages on two continents: implications for conservation. p. 29-50 *In* Gaston, K.J., T.R. New and M.J. Samways (eds.) *Perspectives in Insect Conservation*. Intercept Ltd. Andover.
- Niemela, J. and J.R. Spence 1994. Distribution of forest dwelling carabids: spatial scale

- and the concept of communities. *Ecography* 17: 166-175
- Rykken, J., D.E. Capen, and S.P. Mahabir 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conserv. Biol.* 11(2): 522-530
- Southwood, T.R.E. 1978 *Ecological methods: with special reference to the study of insect populations.* Chapman and Hall, New York.
- Spence, J.R. and J. Niemela 1994. Sampling carabid assemblages with pitfall traps: the method and the madness. *Can. Entomol.* 126: 881-894
- Stubbe, A. and F. Tietze 1982. Okoligsiche Untersuchungen an carabidengesellschaften entlang einer Trasee immissionsgeschadigter Kiefernforste in der Dubener Heide *Arch. Natur. Land Berlin* 22: 27-44
- Sustek, Z. 1981 Influence of clearcutting on ground beetles (Coleoptera: Carabidae) in a pine forest. *Czechoslovanicae* 12: 243-254
- Sustek, Z. 1984 Carabidae and Staphylinidae of two forest reservations and their reactions on surrounding human activity. *Biologia (Bratislava)* 39: 137-162.
- Terrel-Nield, C. 1990. Is it possible to age woodlands on the basis of their carabid beetle diversity? *The Entomologist* 109(3): 136-145
- Thiele, H.U. 1977. *Carabid beetles in their environments.* Springer-Verlag, Berlin.
- Uetz, G.W. 1991 Habitat structure and spider foraging. *In* *Habitat Structure: the physical arrangement of object in space.* Eds. S. Bell, E. McCoy, H. Mushinsky. Chapman and Hall New York.
- Waage, B.E. 1985. Trapping efficiency of carabid beetles in glass and plastic pitfall traps containing different solutions. *Fauna Nor. Ser. B.* 32: 33-36
- Walsh, P.J., K.R. Day, S.R. Leather, and A. Smith 1993. The influence of soil type and pine species on the carabid community of a plantation forest with a history of pine beauty moth infestation. *Forestry* 66(2): 135-145
- Wise, D. (1995) *Spiders in Ecological Webs.* Cambridge University Press, New York.