Memoirs of the Museum of Victoria 56(2):623–630 (1997) 28 February 1997
https://doi.org/10.24199/j.mmv.1997.56.60

ANIMALS ON THE EDGE: THE 'CANCELLING-OUT EFFECT'

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Abstract

Neville, P.J. and Black, D.G., 1997. Animals on the edge: the 'cancelling-out effect'. *Memoirs of the Museum of Victoria* 56(2): 623–630.

An examination of ground-frequenting invertebrates of forest edges in Tarra-Bulga National Park identified a 'cancelling-out effect' of animals at the order level. Some species increased in abundance towards an edge and other species decreased in abundance at the same edge. Such individual species responses are masked by analysis at the order level. This phenomenon stresses the need for documentation of responses at the species level for a more precise understanding of the effects of habitat edges on distribution patterns of invertebrates.

Introduction

Edge effects along a walking track at Tarra-Bulga National Park in Gippsland, Victoria were examined. The greater variety and density of organisms in the boundary zone between ecosystems has been used to recognise edges (Laurence, 1991). It has been documented by Noss (1991) that abiotic factors play an important role within these transitional zones between edges. Edge effects are described here as the responses of each species to the changed abiotic conditions found at edges.

If species do respond to edges these responses are due to changes in individual microhabitats. Matlack (1993) detected significant differences in abiotic factors including light, temperature, humidity, litter moisture and vapour pressure between the edge interface and the interior of forests. Studies by Bradshaw (1992) indicated that leaf drop, shrub cover and the number of disturbance adapted plants increased within the edge zone of forests.

Recent studies of the effects of edges have revealed that there is not a 'typical' edge response of organisms to edge zones. Sisk and Margules (1993) proposed six hypothetical edge responses which can be seen in Figure 1. Figure 1a illustrates a habitat generalist, where there is no significant change in abundance due to the ability of this species to utilize both habitats and the edge zone equally. Figure 1b depicts a habitat specialist. These species can only exploit one habitat and decline rapidly in abundance at the edge zone of the unsuitable habitat. Figure 1c represents a habitat generalist edge exploiter. These species have the ability to exploit both habitats and demonstrate an increase in abundance at the edge zone. Figure 1d illustrates a habitat specialist edge exploiter, being found in one habitat, but increasing in abundance at the edge zone before exhibiting a very rapid decline. Figure 1e represents a habitat generalist edge avoider, where these species occurring in both habitats and demonstrating declines in the edge regions where they are unable to exploit the environment successfully. Lastly, Figure 1f is an example of a habitat specialist edge avoider. These species occur in only one habitat and show a decreased abundance as they approach the edge zone. Sisk (1992) was able to recognise these six edge responses in bird communities in California.

During the study of edge effects at Tarra-Bulga, what we term a 'cancelling-out effect' occurs when analysis is carried out at the order level. This cancelling-out effect can be observed when two co-occurring species show opposite edge responses. Our results suggest that at the order level, abundance does not appear to change at an edge. However, individual species can show dramatic changes in abundance. A number of different edge responses were observed by morphospecies within the four study groups targeted.

Study site and methods

The study was conducted in Tarra-Bulga National Park, 35 km S of Taralgon, approximately 200 km E of Melbourne. The park is on the south-eastern end of the Strzelecki Ranges and is well known for its significant stands of cool temperate rainforest and its prolific populations of ferns (Campbell, 1987). It consists of 1625 hectares with 14 recognised vegetative communities including heavily modified areas (Ashwell, 1991).

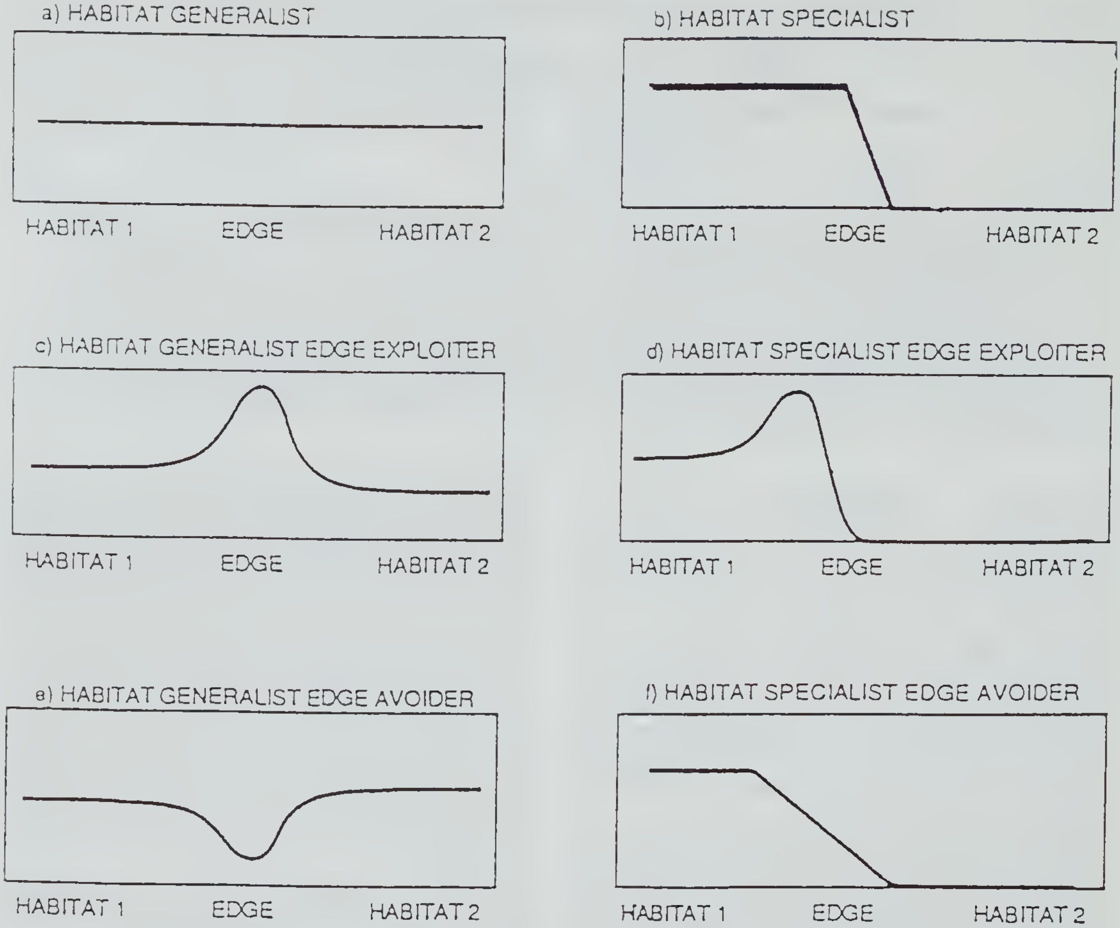

Figure 1. Hypothetical edge responses for species occurring near an abrupt edge between different habitat types (Sisk and Margules, 1993).

Tarra-Bulga National Park in being relatively small could potentially suffer through external forces. A number of roads border and intersect the National Park increasing the edge to interior ratio. A number of walking tracks and fire vehicle access tracks also intersect the park. These areas are in danger of invasion by foreign plant species being carried in by hikers and/or access vehicles. Most roads and walking tracks have the potential to divide habitats and allow altered abiotic factors to modify the composition of edge habitats. The invasion of foreign plant species will enhance this response and may cause dramatic structural differences to these habitats. If edge effects are occurring much of the park may be affected.

Two 88 m transect lines were used as a guide for the sampling of two habitats, wet sclerophyll forest and cool temperate rainforest. Each line straddled a walking track and ran over 40 m into each habitat type. Sampling occurred every 8 m along the transect with five pitfall traps placed to the east of the transect running parallel to the walking track. Soil and litter samples were collected to the west of the transect line at each sampling site. Three sampling techniques were performed in an attempt to reduce the possibility of not sampling all patches within the habitats, and transects were replicated.

All invertebrates were identified to order using Naumann (1991), Harvey and Yen (1993) and Goode (1987). Four detailed studies were carried out on the orders Araneae, Hymenoptera and Coleoptera and on the Class Collembola. The Araneae were identified to family using Davies (1986) and then to morphospecies. The Collembola and Coleoptera were both identified to family using Naumann (1991) and then to individual morphospecies. Lastly, the Formicidae were identified to genus using Andersen (1991) and Holldobler and Wilson (1990) before being split into morphospecies. The voucher collection has been lodged in the School of Zoology at La Trobe University. Preliminary statistical analysis has been carried out using chi-squared analysis in order to identify edge responses. No statistical results are reported here, but some edge responses are signified. Error bars have not been included on graphs for the sake of simplicity.

Results and discussion

In presenting the results, a hypothetical example is first given to illustrate the cancelling-out effect. Figure 2 shows the abundance of hypothetical species A. It can be observed that this species is a habitat A specialist edge avoider, occurring in large numbers within the interior of habitat A and decreasing in abundance towards the edge zone. Hypothetical species B is depicted in Figure 2B. This species is a habitat B specialist edge avoider (occurring in high abundances within habitat B and decreasing towards the edge zone). At the species level, these two responses are clear. However, at the order level (Figure 2C) it can be observed that there appears to be relatively equal level of abundance across all sites along the transect. It seems that there is a single edge response, that of a habitat generalist.

The actual trends observed were not this clear. Figure 3 represents the total abundance of 19 collembolan morphospecies over one of the transects. Sites A to C represent the wet sclerophyll forest with site A being the most interior site and C being the site closest to the edge zone. Sites D to F represent the cool temperate rainforest with D being the site closest to the edge and F being the most internal site. The symbol WT represents the walking track or edge zone over which the transect straddled. It can be observed from this figure that there seems to be little if any edge effect present. The only trend observed is that of the habitat generalist, where the species present are able to exploit both habitats and the edge zone successfully. Values of

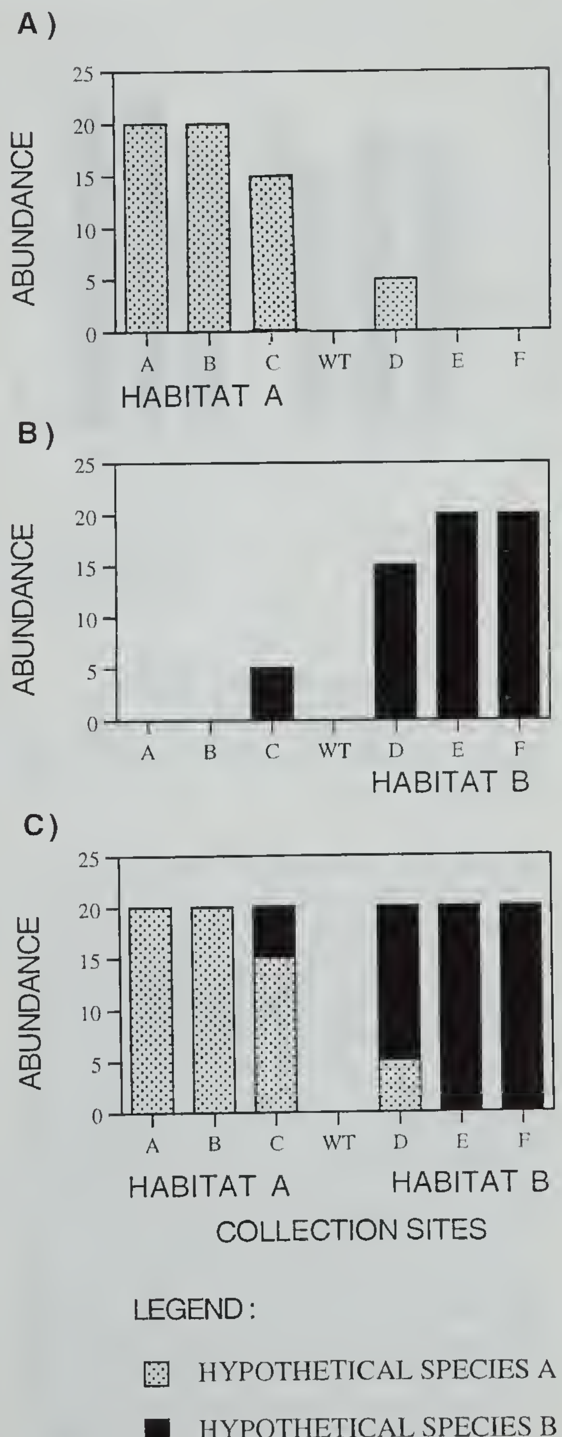

Figure 2. A hypothetical example of the 'cancelling-out' effect where A and B represent hypothetical species and C represents the total abundance of hypothetical species A and B (WT = walking track or edge zone).

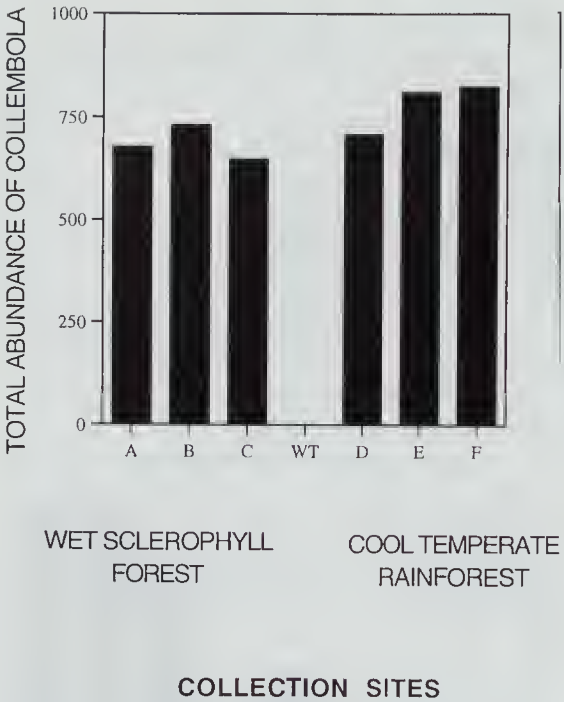

Figure 3. Total abundance of 19 collembolan morphospecies over the transect (WT = walking track or edge zone).

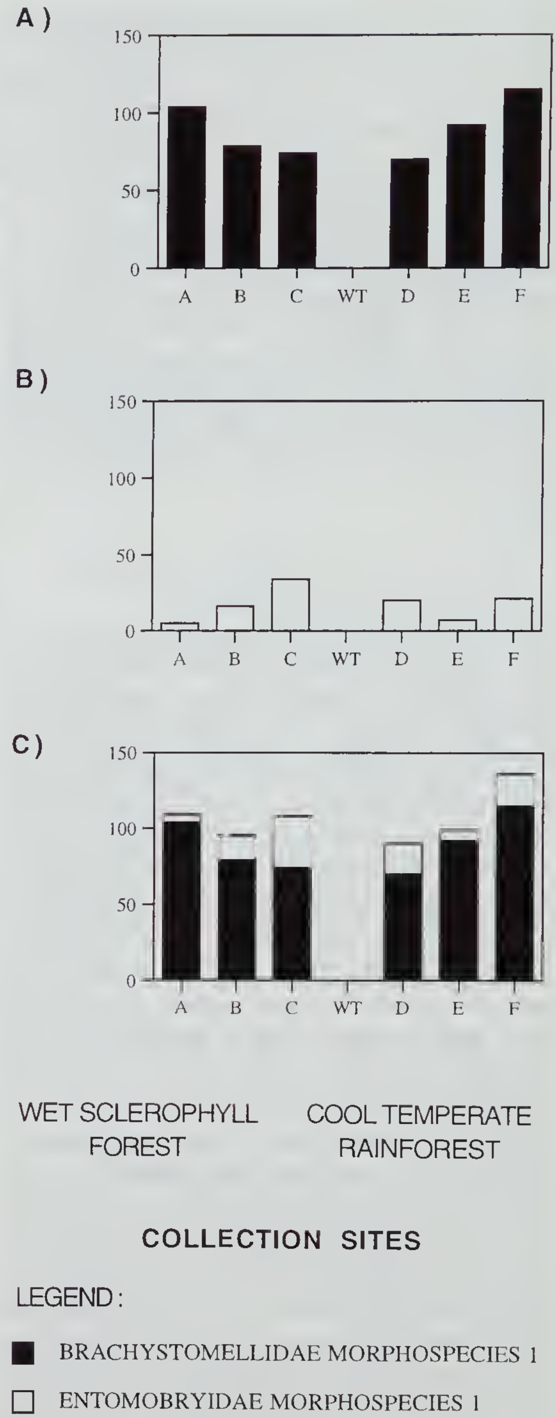

Figure 4. Abundance of Collembola. A, Brachystomellidae morphospecies 1; B, Entomobryidae morphospecies1; and C, Brachystomellidae morphospecies 1 and Entomobryidae morphospecies 1 (WT = walking track or edge zone).

abundance seem to remain relatively constant over the entire transect.

However, when we look at individual species, for example, a species from the family Brachystomellidae and a species of Entomobryidae we can observe two individual trends. Brachystomellidae morphospecies 1 tends to decrease over the transect towards the edge zone suggesting a habitat generalist edge avoider (Figure 4A). Entomobryidae morphospecies 1 (Figure 4B) demonstrates the opposite trend in wet sclerophyll forest, and a mixed response in cool temperate rainforest. When these two species abundances are plotted together (Figure 4C) it can be observed that these two species responses can no longer be distinguished. The trends in the wet sclerophyll forest are lost and it can be assumed that these species are wet sclerophyll forest generalists with no response to the edge zone. This additive response is very similar to that found for the total collembolan abundance histogram (Figure 3).

The cancelling-out effect can also be observed within the order Coleoptera. Figure 5 presents the total abundance data for the 116 coleopteran morphospecies at each site over the entire tran-

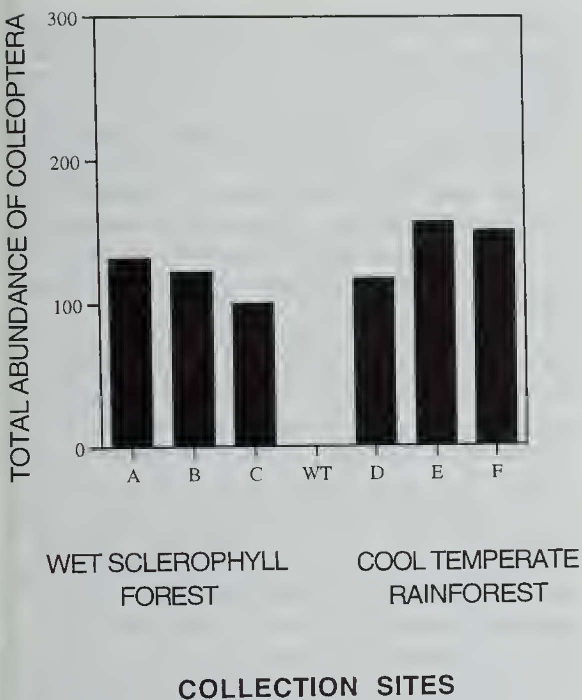

Figure 5. Total abundance of 116 coleopteran morphospecies over a transect (WT = walking track or edge zone).

sect. It appears from this figure that this order is composed of species which are habitat generalists. There seems to be no clear edge effect. However, when these data are examined at the morphospecies level, edge trends can be observed. For example, Curculionidae morphospecies 1 could be classified as a wet sclerophyll habitat specialist edge exploiter (Figure 6A). It can be observed that there are higher abundances of this morphospecies within this habitat and an increase in abundance at the edge zone. However, Curculionidae morphospecies 2 demonstrates a different trend (Figure 6B). It is suggested that this morphospecies is a habitat generalist edge avoider, having decreased abundances at the edge zone. When these two morphospecies from the same family are plotted together, a very different trend can be observed. Abundances become more similar between sites within each habitat. The family level analysis leads to a cancelling-out of species trends, masking how individual species are responding to edges.

Another beetle example shows this cancelling-out effect a little less clearly. Staphylinidae morphospecies 1 is a cool temperate rainforest specialist edge exploiter (Figure 7A). Leiodidae

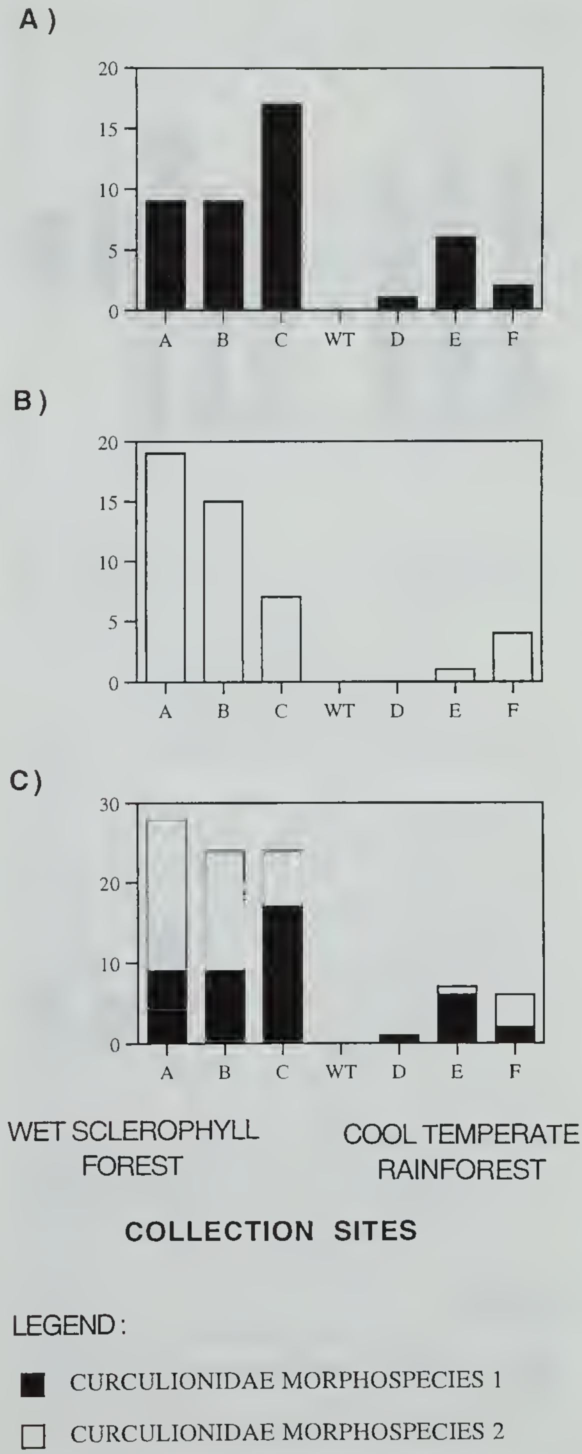

Figure 6. Abundance of Coleoptera. A, Curculionidae morphospecies 1; B, Curculionidae morphospecies 2; and C, both morphospecies of Curculionidae (WT = walking track or edge zone).

morphospecies 1 could be classified as a cool temperate rainforest specialist showing dramatic decreases in wet sclerophyll forest and at the edge of the rainforest (Figure 7B). However, when these two species from different families are plotted together (Figure 7C) it can be observed that the differences in abundance between adjacent sites decreases. Once again, by simply adding the abundances for two species together, the individual trends observed at the species level are slightly cancelled out.

Although this cancelling-out effect has been observed within the Collembola and Coleoptera, the Formicidae remain variable in abundance over the transect (Figure 8). The cancelling-out effect does not seem to apply for ants in this study. A number of factors may explain this. It has been demonstrated by numerous researchers that particular groups of species prefer particular environmental conditions. The most abundant ant at these sites was a species of *Notoncus* which are generally known to prefer wetter sites, being cool-adapted species and are often nocturnal foragers (Andersen, 1986). They are often competing directly against *Iridomyrmex* species and it is believed that this has caused the nocturnal habit to evolve. The second most

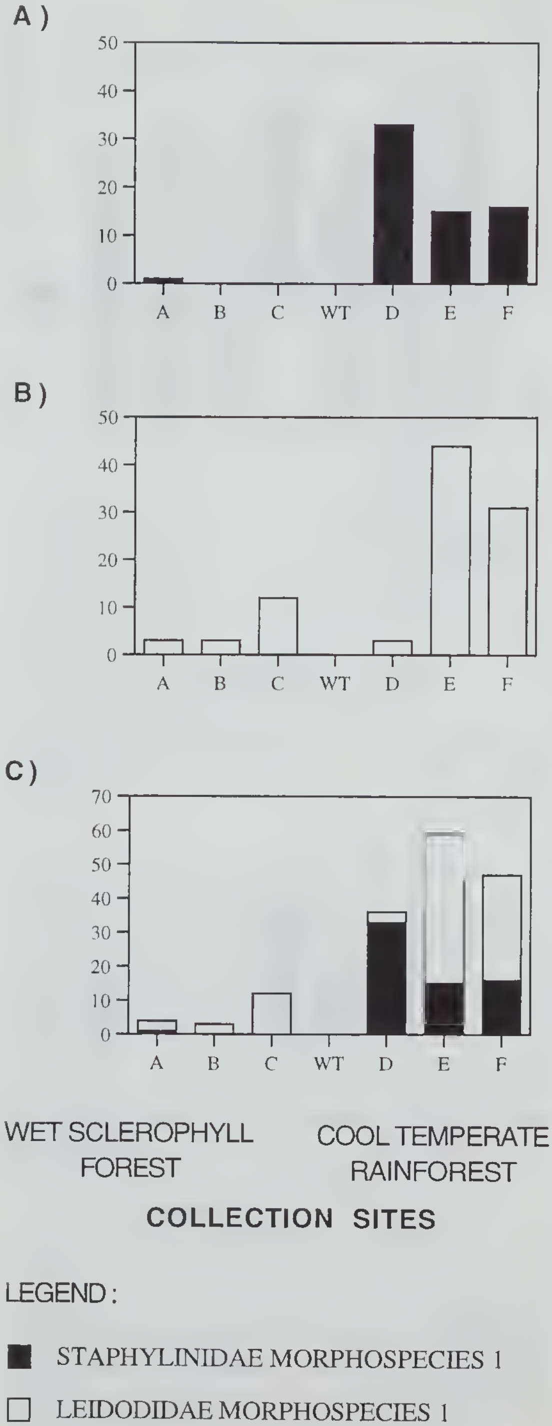

Figure 7. Abundance of Coleoptera. A, Staphylinidae morphospecies 1; B, Leiodidae morphospecies 1; and C, both Staphylinidae morphospecies 1 and Leiodidae morphospecies 1 (WT = walking track or edge zone).

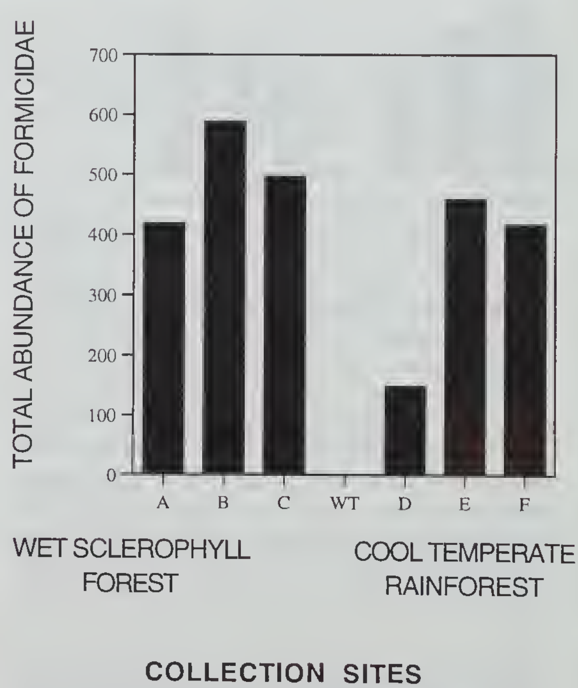

Figure 8. Total abundance of 12 morphospecies of Formicidae (Hymenoptera) over a transect (WT = walking track or edge zone).

common ant species was a species of *Monomorium*, which are known to prefer open habitats. Due to the unspecialised behaviour of many species of *Monomorium* they are very successful opportunists (Andersen, 1984). The third most common species belongs to the genus *Iridomyrmex*, of functional group one, or the dominant group. These species are abundant, aggressive and are known to monopolise resources (Andersen, 1984). They also prefer sunny, open conditions. Competitive interactions between ants has led to the development of tightly structured communities in the arid zone (Greenslade, 1979) and may be partly responsible for the variation observed over the transect. The ability of ants to forage over large distances will also play a role in the variation of abundance over the transect. Due to these high levels of mobility, the association between the organisms and a particular microhabitat will be reduced. Therefore, particular ant species will be found in more sites along the transect due to their ability to forage over large areas. For ants social interactions may also play a large role in the variable distribution observed along the transects.

One other order of arthropods were examined, the Araneae. As for the Collembola and Coleoptera, spiders demonstrate similar abundances across all sites along the transects at the order level (Figure 9). Once again, the only trend observed at the order level is that of the habitat generalist.

However, when examining the spider data at the morphospecies level a number of trends can be observed. Figure 10A depicts the abundance of Cycloctenidae morphospecies 1. This species is declining towards the edge in wet sclerophyll habitat and declining towards the interior of the cool temperate rainforest. The abundance of Cycloctenidae morphospecies 2 can be observed in Figure 10B. This morphospecies represents an increase within the middle sites of the wet sclerophyll habitat and increases towards the interior of the cool temperate rainforest. Figure 10C includes the abundance of both morphospecies of Cycloctenidae. The trend within this family changes to that of the habitat generalist for the cool temperate rainforest.

Other factors play a role in the cancelling-out effect. Sampling bias, and the difficulty in providing a sampling regime that will account for patchiness within the environment is also important. Three sampling techniques were performed during this study in an attempt to reduce the possibility of not sampling all patches within the habitats, and transects were replicated.

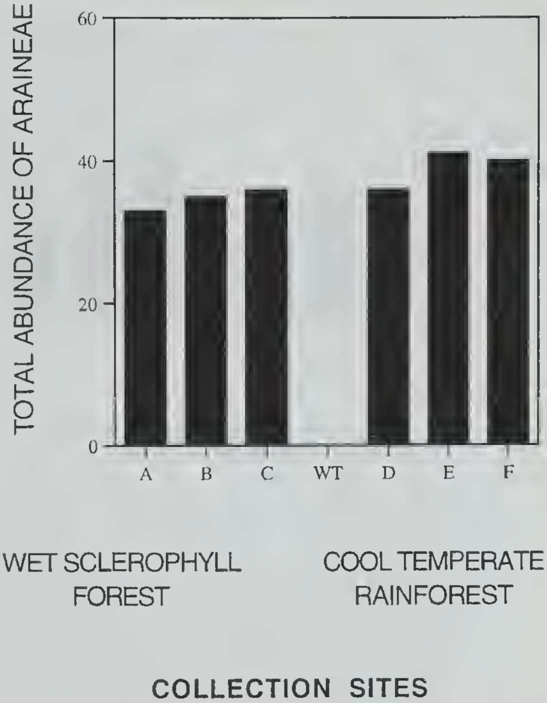

Figure 9. Total abundance of 31 morphospecies of Araneae over a transect (WT = walking track or edge zone).

Generalist trends may appear at the family and order levels through the combination of inadequate sampling procedures, chance variation and real life differences in individual responses. Without statistical analysis it is not possible to say if the edge responses observed are real. However, preliminary tests using chi-squared analysis indicate significant trends for some species. These trends are lost if analysis is carried out above species level.

It has been demonstrated that a cancelling-out effect occurs at both the family and order level of analysis. To observe trends in ecological systems examining such factors as edge effects it is essential that classification of organisms must be completed to the species or morphospecies level. Only when this has been done will real edge responses be identified. The cancelling-out effect discussed here may have wider implications for ecological studies involving analysis of colonisation trends of organisms after more widespread disturbances such as fire.

Acknowledgements

Thanks to the Museum of Victoria for providing partial funding for the project through an honours grant. The authors also thank the

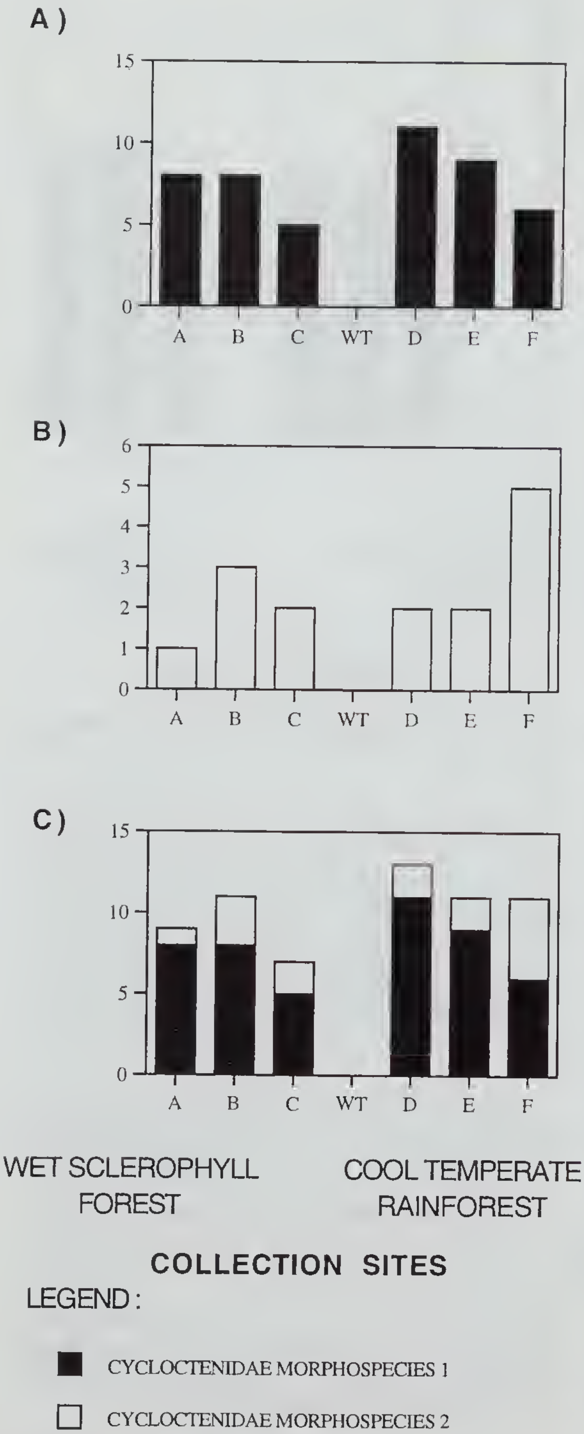

Figure 10. Abundance of Araneae. A, Cycloctenidae morphospecies 1; B, Cycloctenidae morphospecies 2; and C, both Cycloctenidae morphospecies 1 and 2 (WT = walking track or edge zone).

anonymous reviewer for helpful comments on the manuscript.

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