Impacts of invasion on community structure: habitat and invertebrate assemblage responses to *Calluna vulgaris* (L.) Hull invasion, in Tongariro National Park, New Zealand

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ABSTRACT

Invasion ecology, disturbance and successional ecology, and conservation biology are four areas of increasingly realised importance in the maintenance and understanding of the world's remaining 'natural' ecosystems. The impacts of biological invasions and the role of physical disturbance on whole communities is difficult to comprehensively study, but can often be best viewed via invertebrate assemblages and their plant habitats. In this thesis I have taken the opportunity to study these concepts in an area where conservation is of national importance, Tongariro National Park (New Zealand). The Park, for the last 80 years, has and is, suffering from invasion by *Calluna vulgaris* (European heather), which radically changes the plant composition of many of the landscapes in the Park and thus the resource base of the invertebrate communities. This is a community-based study focusing on the structures of invertebrate assemblages, their ability to adapt and be resilient in relation to their changing habitat and resources. It primarily compares features between invaded (disturbed) and 'normal' communities (i.e: their structures, adaptations/impacts caused by the invader, and community cohesiveness before and after invasion).

The vegetation composition was investigated in a range of selected communities of lowland tussock grassland and heathlands in Tongariro National Park, Central North Island, New Zealand. These varied in their developmental history and conspicuous native species. Sites were partnered with adjacent communities of comparable composition, but invaded by *Calluna vulgaris*. Ecosystem resources were measured through attributes of the invader such as biomass, mineral content, and architectural complexity, and were compared with conspicuous indigenous shrubs. Pair-wise comparisons of uninvaded and invaded communities showed that species richness changed very little with invasion, although the percent cover of the conspicuous indigenous component declined from 90% to 40%. *Calluna* was found to add architectural complexity to the indigenous plant communities, many features of which may provide novel invertebrate living space. I conclude that *Calluna* has modified the indigenous communities, lowering the obviousness of indigenous plants, and providing a structural form that occupies a greater volume of space with stem and foliage than the indigenous shrubs.

To ascertain if invasion and dominance by *Calluna* caused local extinctions, reductions, or other modifications to indigenous invertebrate fauna, the impact on the invertebrate assemblages in the invaded indigenous vegetation habitats was explored and compared to similar, uninvaded, habitats. Basic descriptive statistics are presented for each assemblage and compared, as are diversity measures, abundance distributions, and feeding guilds. Cluster analysis and ordinations are used to illustrate the assemblage groupings. Seasonal variation is briefly examined, as are relationships with plant architecture, nitrogen levels, and successional rank of the habitats (vegetation resource). The tussock grasslands and flax wetland assemblages in particular appeared to lose their original 'character' after invasion. The phytophagous group, Homoptera, had noticeably greater abundance in summer and spring in tussock and manuka habitats than their partnered invaded habitats. There are positive correlations of abundance with plant architecture and successional rank. None of the taxa caught were recognised as exotic, implying *Calluna* has not provided a resource for exotic invertebrate species. Tongariro's *Calluna* fauna has not nearly the number of herbivores and associated invertebrates as seen in Europe, implying 'free niche space'. The changes found in this study appear subtle, and in line with successional changes that one might expect normally from an indigenous successional progression.

Feeding on *Calluna* by some native invertebrates was seen to be possible, and does impact on *Calluna* performance, but this is unlikely to cause interference to the proposed biological control agent. Laboratory trials were done involving two prominent herbivores (alpine grasshopper (*Sigaus piliferus*) and manuka beetle (*Pyronota festiva*)). Their performance (weight change), preference for, consumption of, and damage to, *Calluna* was measured and compared to that of indigenous food plants, *Hebe stricta* and two varieties of manuka (*Leptospermum scoparum*). It was obvious that there are some native fauna able to incorporate new hosts, but there is still a large food resource (ie.*Calluna*) under-utilised. The two herbivores are estimated to consume ~ 0.6 to 3 % of a year's *Calluna* shoot crop. Addition of the biological control agent (a Chrysomelid beetle: *Lo~~a~~chmaea suturalis*) is predicted to increase this figure to around 20 % and though this figure is below suggested herbivory levels that cause serious damage to *Calluna*, prolonged damage at this level in combination with the climate at the Park may result in control of *Calluna*.

Browse impacts were manipulated in field experiments where areas of *Calluna* had either their roots protected from insect attack (using insecticide granules) or the entire plant protected (through the use of a systemic insecticide). An additional treatment simulated the damage level expected by a large population of the prospective biological control agent. These exclusion trials showed that shoots in the protected treatment grew more than the control shoots, though the difference was not statistically significant (C.I. 95%). Defoliating *Calluna*, to simulate the potential biocontrol agent's damage, resulted in a positive growth response.

Measuring the effects of physical disturbance, not the ability to resist (withstand) a disturbance, but the ability to recover from a disturbance, and thus the ability of a community to persist, either as the original or as a new entity, informs us of the 'character' of a community and its likely responses to future disturbances. Two communities were chosen as being the most important in the Park: one, the most vulnerable, tussock grassland, and the other, the problem, *Calluna* heathland. Measures of community complexity, resilience, persistence, and consistency (i.e. fidelity) in these two assemblages allowed insight into assemblage stability of invaded and indigenous invertebrate assemblages. The measures involved assessments of the rate of return and the composition of returning fauna after an applied disturbance. Complexity based on number of species, connectence (food web links), and evenness of abundance in feeding guilds was greatest in *Calluna* heathland invertebrate assemblages. Resilience, the time taken for the return to a similar 'functional' state, was fastest in *Calluna* heathlands. Consistency,

the adherence of the returning taxa to the original composition, was best in tussock grasslands. The evidence suggests that the strategy of 'survival' of the tussock grassland's invertebrate assemblage leans more towards resistance than resilience, though resistance was not tested. The community found on *Calluna* appears more ‘plastic’ (capable of rapid restructuring) than the tussock grassland.

No local extinctions were recognised in this study; the bio-diversity remained relatively constant. The 'new' assemblages were still indigenous and may be viewed as assemblages that represent a successional stage similar to native heathlands (*Dracophyllum* and manuka serial stages), indicating that the natural processes continue. Differences were found, but it is my belief that the differences are not, for conservation (in an ecosystem sense), significant. The key features are, that the indigenous 'integrity' is still intact, and that stability (i.e. maintenance of an ecologically functioning community) and persistence is, if anything, better. However, if *Calluna* continues to spread, the mosaic of habitats that now exist may disappear; then so too will elements of the invertebrate fauna, resulting in a decline in species diversity with flow-on effects to the ecosystem. Conservation of biological diversity, *per se*, is less successful in the long term than protection of native ecosystems, indigenous processes, and natural landscapes. By protecting these structures (habitat diversity) the components, and processes within, will also continue to exist.

Chapter 1

Invasion: a continual process challenging 'Communities'

Introduction

As the necessity to predict the impacts of invaders becomes more important to the continuity of reserves, there grows a need for a general theory of invasion ecology (Townsend 1991). Such theory must be able to predict the costs and benefits of invasive species, and be able to supply management strategies that are most effective and efficient.

For any land manager measures of an exotic invader's impacts on (a) the habitats within the resource base, (b) the assemblage structure, and (c) the illustration of 'open resource' created by invasions for the further invasion of beneficial organisms e.g. biological control agents, gives better understanding of the invasion process, and thus must aid management decisions. The management of invaders in conservation areas such as *Calluna vulgaris* in Tongariro National Park is a front-line issue for the wardens of this reserve (the Department of Conservation) (Harry Keys pers. comm.). This first Chapter outlines the present state of invasion ecology theory. This thesis tries to provide useful information about some of the effects of *Calluna* invasion into the Park.

Communities

The study of communities is perhaps only 100 years old since Forbes, Clements and Shelford opened the way (Southwood 1987), while subsequent researchers like Elton, Odum, and MacArthur were to lay the modern foundations of community ecology in the early 1920s, 30s and 50s. The term 'community' is used to describe some unit of the natural world. Areas of land and volumes of water and air contain assemblages of different species, in different proportions, doing different things (Begon *et al. 1986*). Human investigators use the label 'community' to categorise areas and their components. The scale and relevance of the unit, i.e. biological relevance, is thoroughly anthropomorphic, and usually without relevance to individuals within a community. Yet communities have emergent properties not possessed by the individual populations that comprise them (Begon *et al.* 1986). “Community” describes associations, interactions and other properties that are more than the sum of the properties of individuals, e.g. stability, diversity, structure of food webs, productivity etc. The study of communities requires a great deal of time and a multi-disciplinary approach. For this reason many researchers study only compartments of communities, such as assemblages, or some aspect of an assemblage, and though largely descriptive, these measures imply much about the 'community' the assemblage belongs to.

The belief that certain habitats contain characteristic communities (Elton 1966) is still attractive today. It seems intuitively correct that a habitat has a type of resource base that geology and climatic history have determined. These resources (rock, soil, rain, sun, and temperature) provide the basis for formation of habitats. Thus there will be a range of types of habitats with a particular type of resource available to occupying species. This connection between biotic and abiotic elements is usually described as the ecosystem (Begon *et al*. 1986). The definition of where one habitat ends and another starts is often unclear. Normally there is a gradient of change from one discernible habitat to the next.

Community structure and processes as a whole evolve, given the above templates. Over time some form 'stable' systems, apparently non-dynamic; some, more dynamic, fluctuate with cyclic or frequent disturbances, yet are often still 'stable' depending on the time frame of consideration; some are only ever transitory, and specialised species have developed for these systems. When a community forms there is often a pattern of accumulation of organisms. First to participate in the formation (colonisation) of a 'new' community are:

* the most mobile;
* the closest;
* the physically tolerant;
* the adapted;
* resource generalists.

Most often these species (plant or animal) are '*r*' strategists (rapid reproducing, small short lived) and make exhaustive use of particular resources available in 'new' (un-inhabited) habitat. Over time other organisms arrive; they are:

* slower;
*more distant;
* ones needing improvement of conditions (amelioration of the environment);
* those needing more complex food webs than initially present.

'Niche' spaces become occupied and early species often get replaced as conditions change. Simply, there are community assembly 'rules' which are more obvious closer to the start of the process but become more unclear as the community develops, and these roughly set dynamic limits on residency space and resources.

A maturing community develops 'abilities' to capture and partition energy, to recycle material, to change the physical parameters (eg. temperature, humidity etc.), to evolve associations between components, to resist change, to be resilient to change, and to persist, either as any functioning form or as a 'set' form developed over long periods of evolution and limited variation in the resources and conditions present. In either system invasion of organisms is constant, and successful until niche space (available resources) are exhausted; this is the point where the community appears complete (stable). Invaders continue to attempt to invade but are more often 'repelled'; the system begins to demonstrate resistance and consistency.

The invasion syndrome

Species move between habitats and between communities; this movement is usually termed dispersal. Dispersal is the movement of one or many individuals, at once or spread over time, to new locations. Dispersal results in one of three events:

a) enlargement of the existing population through individuals travelling to, and establishing at, the bounds of the population range;
b) the establishment of new populations in new areas (Safriel and Riffe 1983);
c) 'death on the road'.

The establishment of new populations is a result of ingression and is either through additional ground being occupied at the front of a population, or through occupation of new areas, separate from existing populations. Both are range extensions.

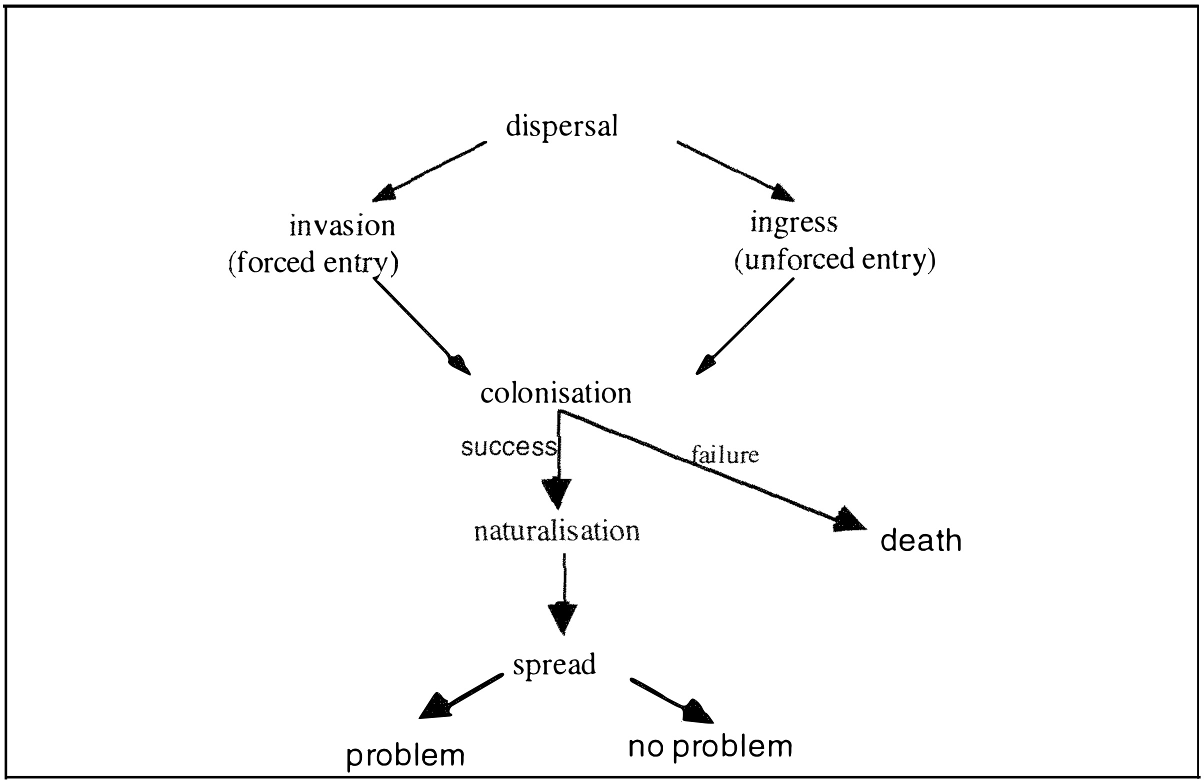
Ingression and invasion

Invasion was once used to describe the process of initial contact (Auld and Tisdell 1986), but is now used in a much broader sense. It is a continual 'natural' process that has become synonymous with human habitation. It differs from ingress (defined here as an unforced entry) in that the species invading tend to be:

1. exogenous (not from the same system);
2. human associated and often assisted, which greatly enhances the distances involved (Sykora 1990);
3. aggressive (disruptive and displacing of other species).

Colonisation is the establishment phase following ingress or invasion (Fig. 1.1), though it is often used to describe the successful dispersal to a new area, and the occupation of that area, which may be bare of existing communities or through non-disruptive establishment into existing communities (Safriel and Riffe 1983).

Fig 1.1 *The process of dispersal through two modes, disruptive (invasion) and non-disruptive (ingression) entry leading to population establishment, colonisation and incorporation into existing communities.*



Invasion now tends to be used to describe the complete process (introduction, colonisation, naturalisation and spread) (Groves 1986, di Castri 1990). Invasions, then, are natural, normal events, that have become more frequent due to human activity. After naturalisation (when the species is breeding successfully in its new surroundings, R. Thomas pers. comm.), the invader can either be a 'problem' or no problem. If it is not a problem it implies the invader has become non-apparent (visually) in the system and the rate of impact has declined. A 'problem' is, for the most part, viewed from the human perspective, and is addressed in relation to human values. A major concern, with gathering appreciation and urgency, is the conservation of pristine native habitats. The impact of invasive species on these special (intrinsically valuable) areas, and on resources important to the human system is a pressing problem (Usher 1986).

What makes a species invasive ?

Consideration of the features that make a successful invader, and whether they are definable and common to all invaders, has been a topic of invasion ecologists' thinking since Elton (1958), who proposed a condition of communities that should determine the successfulness of invaders. He proposed that a community should exhibit strong resistance to disturbances because of interactions (such as competition) developed between species in a way that forms a food web. The ability to overcome the resistance of existing interactions, to cause restructuring of the community, and to become part of the food chain, is a necessity to successful establishment after invasion.

Today many authors attempt to pinpoint a particular suite of traits - genetic (Barrett and Richardson 1986), morphological (Newsome and Noble 1986), behavioural or demographic (Crawley 1986) that describe an invader and why it succeeds in certain habitats. The classic invader is of small size with high mobility, having a high fecundity and short longevity; it may be a 'poor 'competitor but through overwhelming numbers and because of a wide niche it gains adequate resources. The classic invader also exhibits a simplistic, low energy mating scenario, ensuring high fertilisation success. Apparently these are features that describe the classic *r*-strategist (Southwood 1977). Emphasis is placed on speed and plasticity, but this model was designed for invasions of ephemeral habitats, and is most often applied to types of habitat that are very early in the successional chain or so degraded or unpredictable as to be inaccessible to most *K* strategists. Of course many invaders do fit the *r*-strategist profile well (e.g. mice, rice weevil, sparrows, (see Kitching 1986, Laycok 1966 for examples), Chironomids, Muscidae, wasps), and fill the same niche as in their original range, but now in a totally new geographical area (cf. di Castri 1990 for an excellent review).

The invaders

The organisms that successfully invade new ranges all have two attributes in common:

a) they thrive in a country in which they were previously not present (Roy 1990), and:
b) they upset the existing ecological equilibrium (Gouyon, 1990).

Table 1.1 is an attempt to draw plants and animals, invertebrate and vertebrate, together to examine their participation in a set of characteristics related to invasion success. The scores (*) are hypothesised from the literature and pure speculation; the total scores are the sum of the number of asterisks.

As to a common suite of attributes, Roy (1990) concluded that for plants, invaders are from a large array of plant taxa. He felt that no attributes were common to all invaders, but that, since invasion is not merely a stochastic event, the invaders often do have many of the features predicted (Table 1). He constructed a list of physiological and demographic attributes based on Baker's (1965) and Bazzaz's (1975), ideal weed species characteristics, and Barrett and Richardson (1986) review of genetic traits. Newsome and Noble (1986), also working on Baker's list of 14 invader attributes, concluded that no one

plant contains all features and that possessing only a few attributes of the list does not imply a successful invader. Their analysis of data from 86 weed invaders induced them to propose four different eco-physiological styles of life, rather than specific attributes, that indicated an invader. They were 'gap grabbers' (early germinators or fast vegetative growers able to occupy space,
quickly, e.g. thistles), 'competitors' (those with growth forms that exclude resources from others, e.g. vegetative structures that shade others, or deeper roots), 'survivors' (long-lived species that are resistant to harsh conditions and predation), and 'swampers' (mass germinators, or emergers that enter a system *en masse*, so long as mortality is not density dependent). A successful invader has its attributes 'tuned' for one or more of the above life strategies enabling it to move into existing communities.

Invertebrate invaders, like weeds, have been largely studied with respect to agriculture and horticultural systems, and can also be scrutinised for a suite of common attributes. Many invasions of insects are attributed to genetic modification, often of a phenotypic feature that relates to the plant species they reproduce, oviposit, or feed, on, resulting in new host selections (Rausher 1983), though some maintain that, in fact, insects are not so adaptable (Futuyma *et al.* 1993). This adaptability may allow them to invade areas with resources previously barred to them. Natural 'invasions' of invertebrates tend to be of limited distance, excepting those which are borne long distance on wind and water, or are good fliers. Invasion into the variety and over the distances of habitats that invertebrates have managed has only been achieved through a close association with humans. The traits of these invaders (be it the ability to invade systems adjacent or far) tend to follow a similar pattern to those of plants (Table 1.1).

Vertebrate invaders, particularly mammals, tend to be strongly associated with humans. Rats, mice, rabbits, cats, mustelids, dogs, deer, and goat, have achieved invader status in many places of the world because of humans. They are all different types of organisms, varying in size, trophic level, and habitat type. To pick a suite of attributes, then, for mammals is even more difficult than for invertebrates and plants.

For birds, Mayr (1965) has listed six features he thought diagnostic of successful invaders (though he used the term colonisers). These were:

social and travelled in flocks;
commensal with humans;
granivores;
habitats associated with fresh water;
good dispersers;
able to shift habitat preferences.

Newsome and Noble (1986) picked up Mayr's diagnostic features as a base and, using data sets from colleagues in Australia, compared behavioural, ecological and physiological attributes necessary for success of 65 foreign and 34 native bird invader species. Newsome and Noble concluded that 'no single eco-physiological quality or simple selection typified a successful bird invader'. The chief factor contributing to success among foreign birds was being a human commensal (see also Wodzicki 1965) (Table 1.1).

What has not been stated as a crucial determinant is how many times introductions (invasions) occur (C. Veltman pers. comm.); obviously the more times a potential invader gets the opportunity to enter a system the more chance that conditions will be right for it to establish.

For just about every feature of successful invaders, a good example can be thought of for each invader group. King (1990), for example, illustrates the mammal invaders into New Zealand and shows that the chamois (*Rupicarpa rupicarpa*), reaches reproductive maturation very early, earlier than in its home range, and grows faster, but to a smaller size. Plants appear to have the greatest range of features available to them (of course research has been biased towards plant attribute consideration). It may be though, that plants are, and need to be, the first and better invaders, being at the base of the food chain.

A trend can be seen in Table 1.1 moving from plant to invertebrate to mammal to bird of increasing variation (uncertainty) in attributes that pertain to invaders. This trend runs parallel to one of increasing mobility (sessile -> flight). In general the successful seem to be the hardy, unspecific, "tough", the broadly ecologically tolerant (Roy 1990), and, perhaps of greatest importance, those commensal with humans.

Adding an extra dimension, Kitching (1986) suggest that an organism's attributes determine success depending on the habitat type to be invaded (see also Greenslade 1983). It seems then that a match between habitat type (heterogeneity in space and time), existing community structure, and resources must coincide with the attributes of the invading organism and some habitat condition (usually disturbance), enabling them to get resources. The current progress in research has recognised this fact and has shifted focus to interactions between invaders and target communities (Lodge 1993).

Table 1.1 Features considered advantageous for an invasive species; compare the relative level of these features between plant, invertebrate, mammal and birds , *** means highly advantageous.

Feature of invaders	plant	invertebrate	mammal	bird
Demographic:				
high population growth rate	**	***	*	
early reproductive maturity	*	***	**	
high reproductive energy allocation	***	**	*	*
gamete production in a wide range of environmental conditions	*		**	*
high fecundity	***	**	*	
long reproductive period	***		**	*
high mobility of offspring		*	**	***
Physiological:				
high acclimatisation ability	*		***	**
physiological tolerance	*		***	**
fast growing	*	**	*	
small size	**	*	**	*
special competitive features	**	*	*	
behaviour that avoids predation		*	***	**
ability to use a wide range of resources		*	***	**
aggressive	*	**	***	**
simple mating system	**	*	***	
Genetic:				
self compatible or parthenogenetic	***	**		*
high rates of recombination	***	**		
high genetic variability	**	***	*	
polyploidy	***			
Life strategies:				
human commensal	**	**	***	**
no need of disturbance	*	*	***	**
Eco-physiological strategy:				
'gap grabber'	***	***	*	*
'competitor'	**		***	*
'survivor'			**	***
'swamper"	***	***	**	*
Total score (number of *'s)	45	36	48	28

System susceptibility to invasion, and the role of disturbance

Communities are becoming more and more exposed and vulnerable to potential invasions through the actions of humans. By contrast there is growing and urgent concern for the conservation values of native systems. Hence there is a mounting need for the information that allows predictions as to an ecosystem's vulnerability. In this endeavour community stability measures, resilience, consistency etc. are often the only tools.

A community's stability, maturity, resistance, resilience and usual rate and scale of disturbance should influence its susceptibility to invaders (see Chapters 5&6). Maturity and stability imply complex interactions on many levels for all the existing species, developed over time to a condition of balance ensuring continuity and fidelity. Resistance and resilience are terms used to describe how difficult it is to change the order of interactions, and how quickly the system can return to what it was.

Fundamental, then, to the interactions of a community's species is the resource base; 'spare' resource (vacant niche ?) implies the potential for a new user, an invader, to enter, or for the explosion of an existing species population. Assemblages co-evolve forming communities that utilise their resources maximally (a maximum benefit - minimum cost process), i.e. succession. It is reasonable to expect some, if not all, the indigenous invertebrate communities in Tongariro National Park that have been there for some time (100's of years ?) will have achieved this state; while the newer communities of the *Calluna* invaded areas will be in a state of disorganisation (ie. have free resource).

The entry of an invader is a probabilistic event; since species are continually 'knocking on the door', sooner or later the opportunity will arise for them to 'enter'. What often determines success is how often they 'knock', i.e. how often they attempt to enter a system, and in what number. This being so, what features of a community withstand the invaders? Fox and Fox (1986) raised 4 null-hypotheses which relate to conditions of an ecosystem at the time of invasion and, using data from the literature, tested them:

Hypotheses:

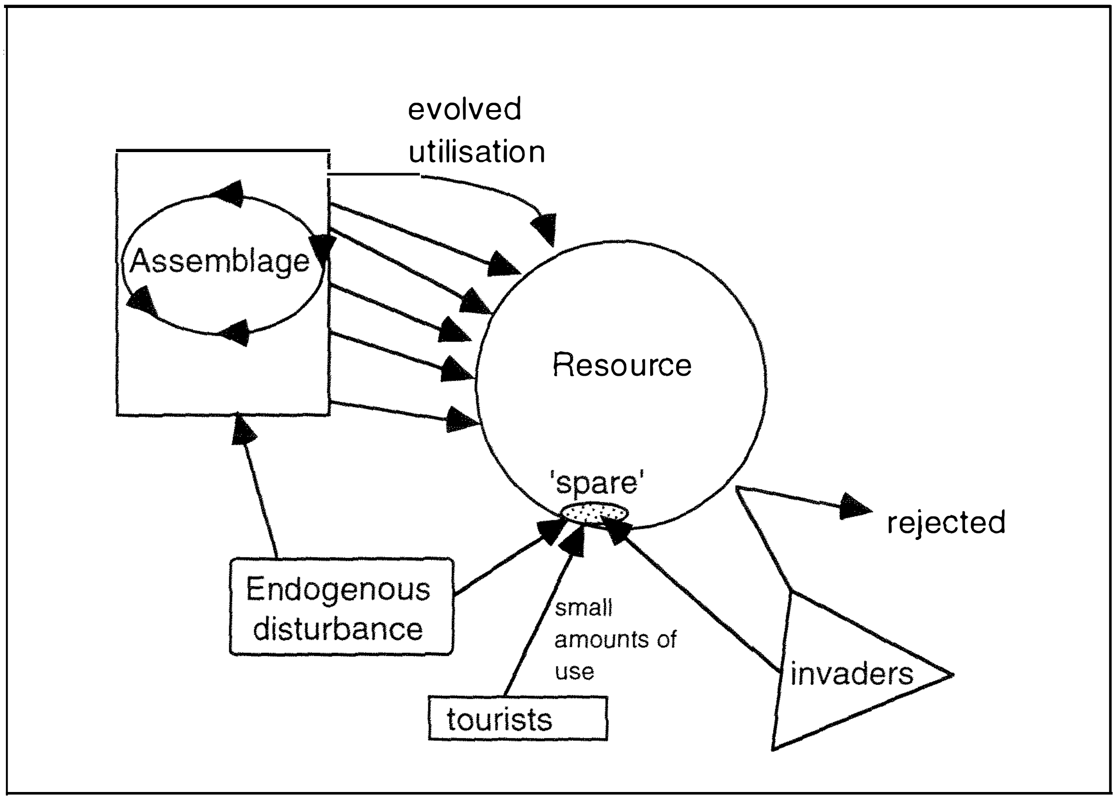
1. Invasion occurs independently of disturbance; but if not, then there is no relationship between the magnitude of disturbance and the degree of invasion;
2. There is no connection between community richness (i.e. number of species) and invasion.
3. All structural (plant) formations are equally susceptible to disturbance, and thus invasion;
4. Communities will be equally susceptible to invasion across an environmental gradient.

Their analysis caused them to reject hypotheses 1,2 and 4 but accept the third. Thus they accepted that invasion was not independent of disturbance and there existed a relationship between extent of disturbance and degree of invasion. The greatest determinants of invasibility were disturbance events and their magnitude. The effect of species richness on resistance is controversial (Fox and Fox 1986). Simpler systems are thought to be more resistant to physical disturbances than complex systems, while complex systems are considered more resistant to biotic disturbances such as invasions (cf.

Chapter 5). While they found that plant structure (hypothesis 3), did not directly affect the chance of invasion, it did affect the likelihood and magnitude of disturbance events, and therefore it had an indirect effect on invasibility; i.e. the more biomass, the more structurally complex, the more resistant to disturbance.

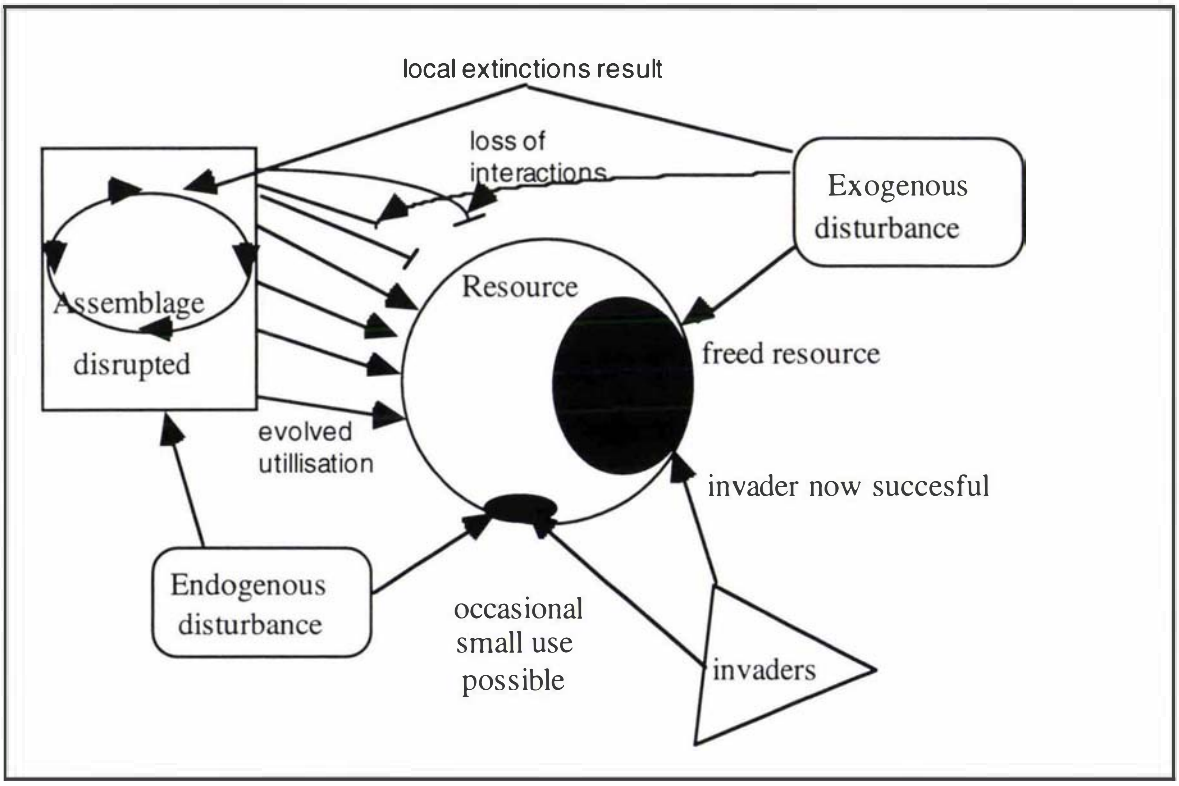
Disturbances generally affect the resource base of a system. There are two sorts of disturbance, endogenous and exogenous. Endogenous disturbances in a system are 'naturally' occurring perturbations repeatedly experienced through evolutionary time; e.g: periodic flooding, wild fires, herbivore irruptions. They tend not to be catastrophic to the system as evolution has resulted in methods of coping and re-establishing the community. Figure 1.2 illustrates the normal condition of a simplified system in relation to endogenous disturbance, resources (plants and substrate), animal assemblages, and invader access (presence of invader) . The two major components, animal assemblage and plant resource, interact; these interactions usually form a stable, if also dynamic, association. Though much of the resource is utilised there will always be some that is not, or some that is not predictable in its availability, represented by the hatched oval in figure 1.2. This 'spare' resource may provide short term access for transient species, 'tourists' to the system; it does not usually permit their establishment. Invasive species are usually 'denied' access to the system because there is no free resource and there is a fully functional animal assemblage (with respect to animal invaders), ie. no vacant niche space.

Fig. 1.2 *A community with a 'full' complement of resource users (large, left, oblong) that utilise the bulk of the existing plant resource (central circle). This generally does not allow invasions of species into the system. Endogenous disturbances may be responsible for the creation of 'spare' resource (stippled oval in resource circle).*



Unusual disturbances, either novel or unusually extreme, may have major impacts. These disturbances, outside of the evolutionary history of the system, are exogenous disturbances (eg. volcanic eruptions, large fires). Since the 'rise' of human kind, most exogenous disturbance is human related and often on a major scale. Exogenous disturbances cause breaks in the complete utilisation of resources, resulting in spare or new resources, through local extinctions and abiotic structural changes. Figure 1.3 illustrates the action of exogenous and endogenous disturbance on a system and how this affects a possible invader. Exogenous disturbances usually create conditions that are not inside the system's evolutionary history. As a result they can cause large 'pools' of 'spare' and new resources because they can remove most, or even all, individuals of one, or several species (local extinctions) from that area and so break the interactions within the food web (Power and Marks 1992). It is these gaps that allow invaders the time, space, and resources to establish (Fig. 1.3).

Fig. 1.3 *A diagrammatic presentation of a community's response (the left block and arrows) to exogenous disturbance; and the effect of this lack of 'repair' on the utilisation of its resource base, and so the availability of resources for invasive species. Endogenous disturbances have no effect on the functioning of the normal community unit.*
The potential invader (triangle) takes advantage of deletions in the resource-community bonding (freed resource) and often successfully invades the existing community.

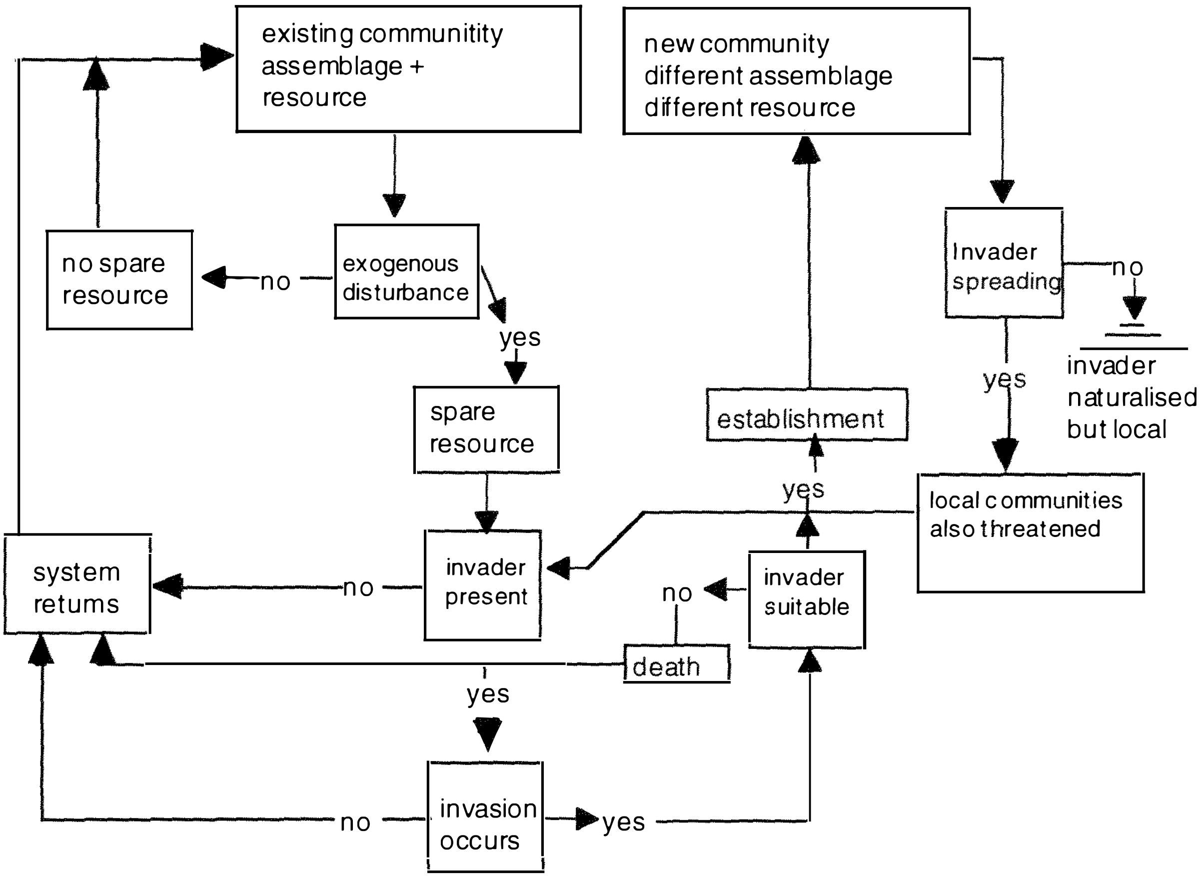


In summary there is generally no invasion into established plant and insect communities without disturbance, usually exogenous, and a community's resistance and resilience depend largely on species richness and the length of time of co-evolution. This is a very cosmopolitan ecosystem view. New Zealand systems may have 'niche' opportunities without disturbance for exotics. Mammal species which invade New Zealand do not always appear to need exogenous disturbances, rather just the opportunity to be there: the Australian possum (*Trichosurus vulpecula*) has more than adequately established in the New Zealand bush without disturbance; the Brown hare and chamois in alpine habitats (King 1990), a range of mustelids, and even the ship rat have established in the New Zealand bush (King 1990) without being aided by disturbance.

Summary of the invasion process

A flow diagram of the process of invasion simplifies the conditions required but still gives a good overview (Fig. 1.4). If the invader is spreading after establishment then it is easy to imagine Figure 4 being a loop as establishment in a new community increases the probability of the invader being present at disturbance of other local communities.

Fig. 1.4 *A simplified flow chart of the invasion process determined by resources being freed by disturbance and the presence of the invader species to make use of them.*



The impact of invaders in New Zealand

In New Zealand's natural reserves, records of invasion could have served to illuminate impacts, and supplied much needed information for future predicability of new impacts, had work in such areas been deemed important in the late 1800s and early to mid 1900s, when impacts of introduced species were prominent (e.g. trout, deer, mustelids, wasps, *Calluna*, broom; see King (1990) and Laycock (1966) for summaries of mammal and bird introductions). Certainly the agricultural and horticultural systems have received much more research into introduction and invasion problems, mostly with respect to the impact of introduced biological control agents, and cost-benefit analysis of pests (Auld and Tisdell 1986). Knowledge on a 'community' level, about communities and assemblages is poor, though many authors acknowledge that invasions are 'unacceptable' and cause significant change (Herbold and Moyle 1986, Hengeveld 1988, Townsend 1991). Generally the impact of an invader can not be fully appreciated until its establishment and spreading phases. The impact of deliberately introduced invaders, i.e. biocontrol agents, is starting to supply information that may be useful in predicting accidental invasion impacts (though the information is limited due to the specificity of introduced species for target species). Impact is most often due to resource 'stealing' i.e. competitiveness, resource modification (especially considering plant invaders), predation, parasitism, and space occupation. It is generally dependent on the invader's ability to spread and to control the resources of a system.

A plant invader in Tongariro National Park

The invasion by *Calluna vulgaris* at Tongariro National Park, Volcanic Plateau, North Island, New Zealand, offers a unique opportunity to monitor impacts of a major weed on native ecosystems (though eighty years after its introduction). The invader exhibits many of the attributes considered advantageous to a plant invader (Watt 1955; Gimingham 1960; Barclay-Estrup 1970; Gimingham *et al.* 1979; Miller 1979; Helsper *et al.* 1983; Jalal and Read 1983; Helsper and Klerken 1984; Chapman 1984; Hobbs & Gimingham 1987; Aerts 1989; Welch *et al.* 1990; Grant and Armstrong 1993; MacDonald *et al.* 1995). They are:

germination under many conditions;
rapid seedling growth;
fast vegetative growth;
abundant vegetative growth = high standing crop;
layering (vegetative reproduction);
self compatible, but not obligatory self pollinated;
pollinated by non-specific pollinators and/or by wind (simple mating system);
seed produced early in life;
production of seed in a wide range of environments;
high seed output;
great longevity of seed (ca. 12 years);
long dispersal of seed in time;
competitive features, allelopathy and 'choking' vegetative structure;
human distributed and aided.

Calluna also has three of the four life strategies previously mentioned; it is a 'gap grabber', a 'competitor', and a 'swamper'. Combine all these traits with human created, hence exogenous, disturbance to the grass and shrub communities of Tongariro National Park, and it is a formula for successful invasion.

Thesis outline

Tongariro National Park is situated on the Volcanic Plateau in the central region of the North Island of New Zealand. It has a sub-alpine environment with the central mountains determining rainfall pattern, and its volcanic origin determining the soil depth and types. The boundaries are set by altitude and the surrounding exotic agriculture and silviculture to the west, north and south. These regions are also sources of invasive weeds. To the east are the Kaimanawa and Ruahine Ranges. In the Park a mosaic of vegetation types exist, clearly divisible into different communities (Atkinson 1981).

In the following chapters I plan to:

1. Outline the concept of a community, to introduce what is now often refereed to as invasion ecology and its role, in conjunction with disturbance, in affecting existing communities. This is the scenario in Tongariro National Park, and the study of this thesis.
2. Investigate the *Calluna* invasions impact on the invertebrate community's resource base, ie:
    - a) effect on plant species diversity;
    - b) effect on indigenous plant species apparency and hence availability;
    - c) physical structural changes to the vegetational architecture;
    - d) nutritional state of the invader - quantity (biomass, cover) - quality (mineral and nitrogen content), with the nitrogen levels also being compared to those of prominent indigenous plants species;
    - e) brief comparisons of the developed *Calluna* heathlands with that of the normal home range.
3. Ascertain the invertebrate communities' response to *Calluna* domination of many landscapes by comparison of invaded and non-invaded communities (5 types). Through multiple sampling methods I will investigate :
    - a) assemblage structure of the invertebrate communities;
    - b) species diversities;
    - c) abundance patterns;
    - d) feeding guild structures;
    - e) predator ratio differences;
    - f) seasonal patterns of some of the invertebrates;

and compare, briefly, some of my findings with those in the South of England and Northern Spain to illustrate the niche occupancy of *Calluna* here in New Zealand and its 'natural' range.

4. Having discovered the community constituents, then:
    a) Investigate whether the indigenous phytophagous fauna has some members that can adapt and adopt*Calluna* as food, creating some challenge for the invader;
    b) try to measure this challenge through laboratory feeding trials and through field trials involving the exclusion of herbivorous feeding and monitoring the growth response of the *Calluna*.

    This information could be useful when considering bio-control agents (competition, additive effects, niche space etc.).
5. To show, through measures of stability (resilience, rate of return, and consistency), the capacity of an indigenous community (tussock grasslands) to recover from a disturbance as compared to the ability of the 'new' invertebrate community in *Calluna* heathland. The estimation of community complexity coupled with the speed of return of fauna after a disturbance and the fidelity of the returning fauna to the previous assemblage structure could help in predicting each community's future responses to disturbances (continued *Calluna* spread), natural disasters (volcanic fires), or control of *Calluna*, resulting in more abundant tussock grassland habitat. If the Park regains its characteristic tussock grasslands will it regain the characteristic fauna ?
6. The final chapter revisits the invasion process and relates it to the situation discovered in the Park. I make an attempt to model the process and effects, using thata gained; this supplies a useful over-view. Here I also briefly examine the proposed bio-control agent as a new invader. Finally I present my opinion as to the impact *Calluna* has had on the invertebrate communities in Tongariro National Park.

Chapter 2

impact of *Calluna* on vegetation structure and as resource for invertebrates

ABSTRACT

New Zealand's indigenous vegetation may be susceptible to invasion because it has habitats that are generally species depauperate. Successional status and disturbance history further determine this susceptibility to invasion. Following invasion by introduced exotic shrubs, there are changes in species composition and resources, and follow-on effects for the faunal component of the ecosystem.

Vegetation composition was investigated in a range of selected communities of lowland tussock grassland and heathlands in Tongariro National Park, Central North Island, New Zealand. These varied in their developmental history and conspicuous native species. Sites were partnered with adjacent communities of comparable composition, but invaded by *Calluna vulgaris*, an exotic heath from northern Europe. Ecosystem resources were measured through attributes of the invader (ground cover, biomass, mineral content, foliage nitrogen levels, and architectural complexity). These measures, except mineral content and biomass, were compared with those of conspicuous native shrubs, and with *Calluna* in its native habitat (ie. United Kingdom).

Uninvaded native communities ranged in species richness from 11 to 30 species, while a fully established *Calluna* community held 14 species. Pair-wise comparisons of uninvaded and invaded communities showed that species richness changed very little with invasion, although the percent cover of the conspicuous indigenous component declined from 90% to 40%. Communities containing *Calluna* had between 40 and 95 percent *Calluna* cover with *Calluna's* biomass values ranging from 0.4 to 4.8 kgm^{-2}. Unlike most natives (eg. tussock: ~4 mgg^{-1} in 2.5 mgg^{-1} soil), *Calluna* appears to be a good nitrogen accumulator, having relatively constant nitrogen levels (~8 mgg^{-1} dry material) irrespective of soil nitrogen (range 2.5 mgg^{-1} to 5 mgg^{-1}). There was observed a seasonal variation in nitrogen levels in *Calluna*; often statistically significantly (95% C.I.) greater levels were recorded in summer than in winter, but even if the values were not statistically different, summer ones were never less. Tall *Calluna* adds architectural complexity to the indigenous communities, it has an abundance of leaves and a complex stem branching pattern, and it occupies a large volume of space with densely packed material. Using an index to rank plant architecture, tall *Calluna* ranked as almost twice as complex as any other plant tested. Many of the features of *Calluna* structure discovered may provide novel invertebrate living space. Pyramid diagrams depicting resource spatial stratification show that *Calluna* has modified the indigenous communities; conspicuous is the development of a structural form that occupies a greater volume of space with stem and foliage than for the indigenous shrubs, which exhibit a dominance of structure lower down the plant.

Key words: *Calluna vulgaris*, community structure, invasion, indigenous vegetation, invertebrate resource.

INTRODUCTION

Most invertebrates depend on plants for resources. This dependence is on the physical structure of the plant, as a habitat, providing accommodation and transport 'arteries', and on its nutritional properties. Thus the plant species diversity and the structural complexity affect the potential invertebrate users. The impact of a plant invader on these parameters is unknown. The invasion of the exotic heathland plant, European heather (*Calluna vulgaris*) into the tussock grasslands and other non-forested habitats of Tongariro National Park, gives an opportunity to investigate this.

Plants as resources for invertebrates

The physical structure of the plant community has great relevance to the micro-climate of invertebrates (temperature, light, air movement, atmospheric moisture and fall through precipitation) and to the surfaces available on which invertebrates perform living activities (e.g. nutrition, breeding and ovipositing sites). Plant architecture, then, is an important vegetation parameter describing a resource feature. Lawton (1978) suggested that plant architecture plays a key role in determining insect diversity. He described the dependence of invertebrate species on plant architecture as the "Architecture hypothesis" and couples it to the "Chemical hypothesis" - the seasonal change in plant chemistry which results in changing invertebrate species diversity (Lawton 1976). Lawton found the architecture hypothesis best explained the total number of insect species which evolved to exploit a plant, in conjunction with geographical range (Lawton 1978), though seasonal changes in plant chemistry (chemical hypothesis) had profound effects on which species of insect exploit plants, and on the season of exploitation. Measures of architectural complexity can therefore be used to rank a plant or a community's resource value to insect herbivores.

The quantity of material available (abundance of food) and itsquality are other basic parameters. Quantity is generally measured by biomass. Biomass is the amount of the entire plant material, root, stem, shoot, and leaf available; often only the biomass of the above ground, or even just the non-woody tissue above ground, is important. Its measure states what may be available (i.e. present), but not what is actually utilisable (physically attainable) by a consumer (Schultz 1992). Quality can be assessed based on nitrogen levels, and on non-combustible mineral content of the vegetation.

Nitrogen availability controls growth rates, body size, fecundity, productivity and hence population size of herbivorous invertebrates (McNeill and Southwood 1978, Brunsting and Heil 1985, Crawley 1985). Correlations between insect abundance or diversity and food plant nitrogen levels have been found (Prestidge and McNeil 1981, McNeil and Prestidge 1982, Van der Meijden *et al*. 1984). Measures of nitrogen levels in some native plants, and in the adventive, *Calluna vulgaris*, in areas with different history of invasion, will highlight how this resource is distributed. It will also show how efficient the invader has been at capturing this resource. Where *Calluna* has invaded extensive areas of native vegetation (e.g. tussock/herb fields in the north western region) the ecosystem may still contain much nitrogen, but little of this may be available to native invertebrates because it is trapped by *Calluna* .

The non-combustible mineral content of plants, ie. trace minerals, illustrates the quality of the invertebrate resource. Detailed descriptions of the important mineral components in European *Calluna* can be found in Chapman (1967), Tyler *et al*. (1973), Gimingham *et al*. (1979), Miller (1979), and Bannister (1981).

History of the invasion of *Calluna vulgaris* in New Zealand

New Zealand has around 2300 indigenous vascular plant species, 85% being endemic (Wardle 1991), and a relatively large exotic flora, with around 1860 naturalised species (Wardle 1991). The core source of supply of exotic plants was Northern European. Great Britain, for example hosts 1443-1750 species of vascular plants, though only 1.2-1.3 % are endemic (Major 1988). Though New Zealand appears, relative to Great Britain, species rich, individual habitats tend to be species depauperate, i.e. many species are common only to a small localised area, whereas in Great Britain more species are generalists. This habitat depauperate condition may be the reason for the high number of successful invasions. Because New Zealand lacks strong representation in some of the more successful families world-wide (Fabaceae, Brassicaceae, Solanaceae), and has no Lamiaceae, the available resources for plants may not be as fully used as in, say, Europe (Wardle 1991). Thus exotic plant invaders, more adept at competing for, and utilising resources, are often able to successfully invade indigenous communities (Wardle 1991).

The rate and extent of successful invasions, and the susceptibility of a community to these, are also related to the successional status of the invaded community, early successional communities being generally more invasible than later when resources are more tightly allocated (Brown 1982, Brown *et al*. 1988).

In Europe, successful invasions generally do not occur without disturbance (cf. Harte and Levy 1974, Levin and Paine 1974a, b, Hengeveld 1989, di Castri 1990). The presence of disturbance is also an important feature in establishment of invaders in New Zealand. Disturbances release resources that were previously utilised, and it is at these sites of disturbance with unused resource that invasions more readily and successfully occur.

In Tongariro National Park, a World Heritage Park, there have been major endogenous disturbances (volcanic activity) that have reset the climax communities of Beech forest (*Nothofagus* spp.), and *Phyllocladus-Halocarpus* complexes (Wardle 1991) to herb fields and tussock grasslands. These areas are New Zealand's equivalent of European higher altitude moor-heathlands. They commonly contain tussock (*Chionochloa rubra*), manuka (*Leptospermum scoparium*), *Gleichenia*, ferns (Bracken), ericads, *Dracophyllum spp*., and epacrids (e.g. *Gaultheria*). Continued exogenous disturbances, i.e. human burning and clearing since AD 900, probably helped maintain this state of the vegetation (Wardle 1991), especially on the north-western side of the Park. This has created a mosaic of communities of different successional status.

Tongariro National Park's disturbance history proved ideal for the successful invasion of *Calluna vulgaris* in conjunction with orchestrated anthropic disturbance. The original introduction of *Calluna* to New Zealand from northern Europe is poorly documented, but occurred ca. 1860 at Opeope Bush near Taupo (Chapman 1984). Planting in, and adjacent to, Tongariro National Park began in 1912-1913, chiefly by police commissioner and honorary park warden John Cullen (Bagnall 1982; see Table 2.1 for a chronology of *Calluna* in Tongariro National Park). He believed that he was beautifying the tussock lands and, importantly, establishing a habitat for grouse (*Lagopus lagopus*), black-cock (*Tetrao tetrix*), and ptarmigan (*Lagopus mutus*), specifically for game shooters. The invasion was initiated, consolidated, and extended, through human disturbances (i.e. controlled burnings of native vegetation before sowing of *Calluna* seed, and planting of *Calluna* seedlings) to the indigenous communities.

Though *Calluna* appears relatively slow spreading, anecdotal evidence (B.Jefferies, once Head Park Ranger pers. comm.) tells of once native habitats that are now "seas of *Calluna* ". Ian Atkinson, when surveying the Park's flora, described and photographed (Ogle pers. comm.) a view from Mangatepopo road looking south-east (Photos 1, 2) clearly showing the transformation from the 1960s to 1993. *Calluna* now occupies (with some *Erica cinerea*) about one third of the surface area of the Park (Keys 1991).

Calluna has not contained itself to the Park; it can now be found in about 500,000 hectares from Taupo east to Napier and east of the Park into the Kaimanawa ranges. It is in some head waters of the Wanganui river and from west Taupo south to north-western Taranaki (Fig. 2.1). The rate of spread will increase as the size of the invasion front grows. The invasion continues to threaten other native ecosystems, for example the Moawhango ecological region (Fig. 2.1).

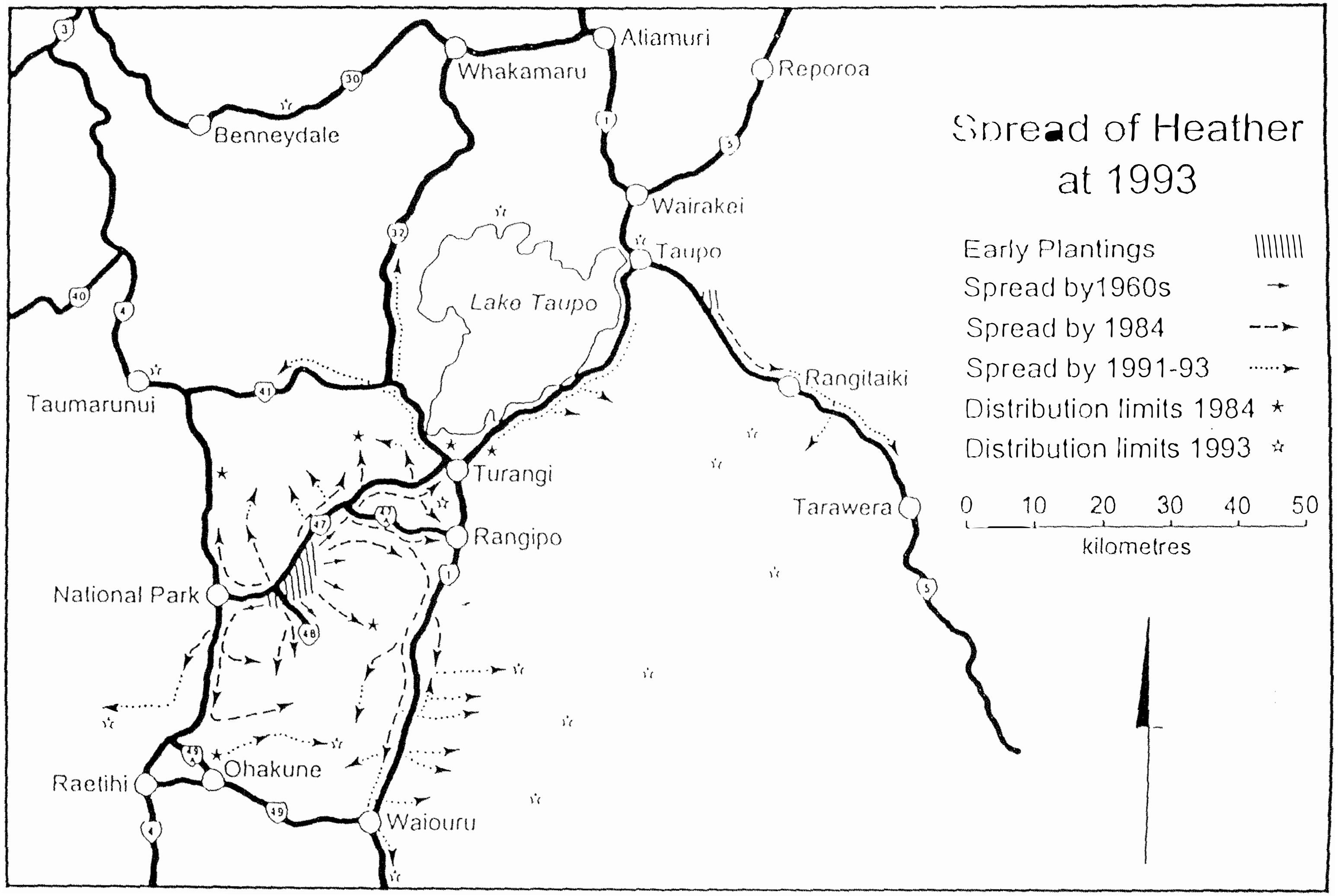


Fig 2.1

The spread of *Calluna vulgaris* (European heather) from Tongariro National Park as of 1993.
(from Willams & Keys, Heather workshop 1993)

Photos 1 and 2 At Mangatepopo road near the base of Pukeonake. a) **A** 1960s view of tussock-shrubland, and b) 30 years on, the result of *Calluna* invasion on the land scape

a)

b)

Table 2.1. History of *Calluna* introduction into Tongariro National Park

1860s	Inspector Scannel, and/or Captain Mair, and/or Major Roberts spread *Calluna* at Opeope bush.
	A small area at the summit of the Pouakai Range (Taranaki) is planted by James Henry (Rogers 1994).
1890s	The Tourist Department gains responsibility for the Tongariro National Park.
1910	Inspector Cullen outlines the income game shooters would bring if there were game to shoot. He proposes a grouse heathmoor; his arguments enable him to start planting *Calluna.*
1912	Cullen begins his *Calluna* planting campaign (Fig. 2.1).
1914	Prof. H.B. Kirk protests to Prime minister W. Massey about the planting of *Calluna* in a reserve.
May 1914	Cullen accelerates his planting of *Calluna*; he imports *Calluna* seed from Great Britain.
mid 1914	Constables in the area begin assisting Cullen in his planting. Rangipo prisoners are also used to plant seedlings. *Calluna* seed is gathered from a patch of *Calluna* at Opeope Bush. World War One puts a halt on the importation of overseas seed. In response, local nurseries step up their supply of *Calluna* seedlings. *Calluna* is now sown in an area 4.5 kms (east-west) by 7.5 kms (north-south), between highway 42 and the base of Ngauruhoe and Ruapehu. Many 'accidental' fires occur, which help establish *Calluna* over native vegetation.
late 1914	One and one half tons of seed in all, at this time, have now been sown in the Park.
Autumn of 1915	An estimated 4000 plants of *Erica vulgaris* (*Calluna*), and *Erica cinerea* (Bell heather) have been planted between the Whakapapaiti and Whakapapanui streams (Fig. 2.1).
1916	A further 3000 *Calluna* plants are planted on Pukeonake (Fig. 2.1).
1916-1920	The planting and spread continues, with 3000 hectares, to this date, planted.
1920	The acting general manager of the Tourist Department tells Cullen of a complaint about the sowing of *Calluna.* Cullen replys "Heather is not detrimental to any native vegetation or wildlife'. Nothing is done.
1921	Protests are made by H.F. Van Haast, W.H. Field, M.B. & F.W. Vosseer against Cullen's work.
1922	Cullen arranges the importation of grouse and blackcock to be liberated into the heathlands.
1923	Lands and Survey Deptartment assumes control of the park and stops the planting of *Calluna.*
1924	Cullen releases six grouse; this was Cullen's last major act, but the grouse do not establish. The Lands and Survey Department do nothing more than occasionally monitor *Calluna*.
1960-1966	Ian Atkinson's Park vegetation survey (the first mapping of the extent of *Calluna*) is done (Atkinson 1981).
1961	The Pouakai range population stuggles to survive (Scanlan 1961).
1979	Initiation of a control programme in a single two hectare area at Wilderness Reserve near Mossman, South Island. Control is never achieved.
1984	Hazel Chapman's thesis on the phenology of *Calluna* in the Park is completed (Chapman 1984). The presence of *Calluna* is now being monitored (Harry Keys pers comm.) at the zones of spread and increases of 30% are seen in nearly 10 years.
1986	The first heather workshop is held discussing the extent of the problem; solutions are outlined
1993	Heather workshop (Williams and Keys 1993) is held to share information and discuss control options.
1994	The Pouakai range population falters; conditions are not as ideal as in the Park, and weeding by concerned people has removed much of it.

Aims

This chapter assess the changes wrought on the native plant communities' composition by invasion of *Calluna*. Estimations were made of the type of plant communities that were present in Tongariro National Park, the percent cover of prominent plants, and how their compositions changed with the introduction of *Calluna* (Fig. 1.3, Chapter 1). As indicators of resource value for invertebrates, nitrogen and other mineral contents of some native plants and *Calluna*, *Calluna* biomass, and the change in structural complexity of the vegetation assemblages were measured. These measures are also useful as a prelude to assessing the suitability of the invader to invasion itself, ie. by the native invertebrates, and by the biocontrol agent.

METHODS

Site selections

Study sites were chosen within, or near, Tongariro National Park to observe changes in community resources brought about through invasion by *Calluna vulgaris*. Resource constraints decreed that only a limited number of sites could be studied. Two approaches to site selection were possible: (a) use of at most two or three habitats, with replication of at least three sites per habitat type; or (b) use of more habitat types but without replication. The first approach has the advantage of generating data in which high confidence can be placed, while the second gives data of much less reliability, but of much better coverage of the situation over the whole Park. The second was selected. Thus, differences between habitats can still be (albeit cursorily) examined but, more general trends across habitat types can be derived, and extrapolated to all lowland vegetation of the Park, increasing the explanatory power. Consultation of Atkinson's vegetation survey (Atkinson 1981), Department of Conservation (DOC) advice (H. Keys pers. comm.), and reconnaissance trips, led to selection of five indigenous vegetation types:

tussock grassland; *Dracophyllum* shrubland; *Gleichenia* wetland; flax swampland; manuka scrubland.

The choice of site was based on the following criteria:

1. A dominant vegetation type, prominent in the Park;
2. Some part of that habitat had to be undergoing invasion by *Calluna* during the study to form a comparison;
3. Large uninvaded areas of each habitat type still existed;
4. The site had to be accessible on foot.

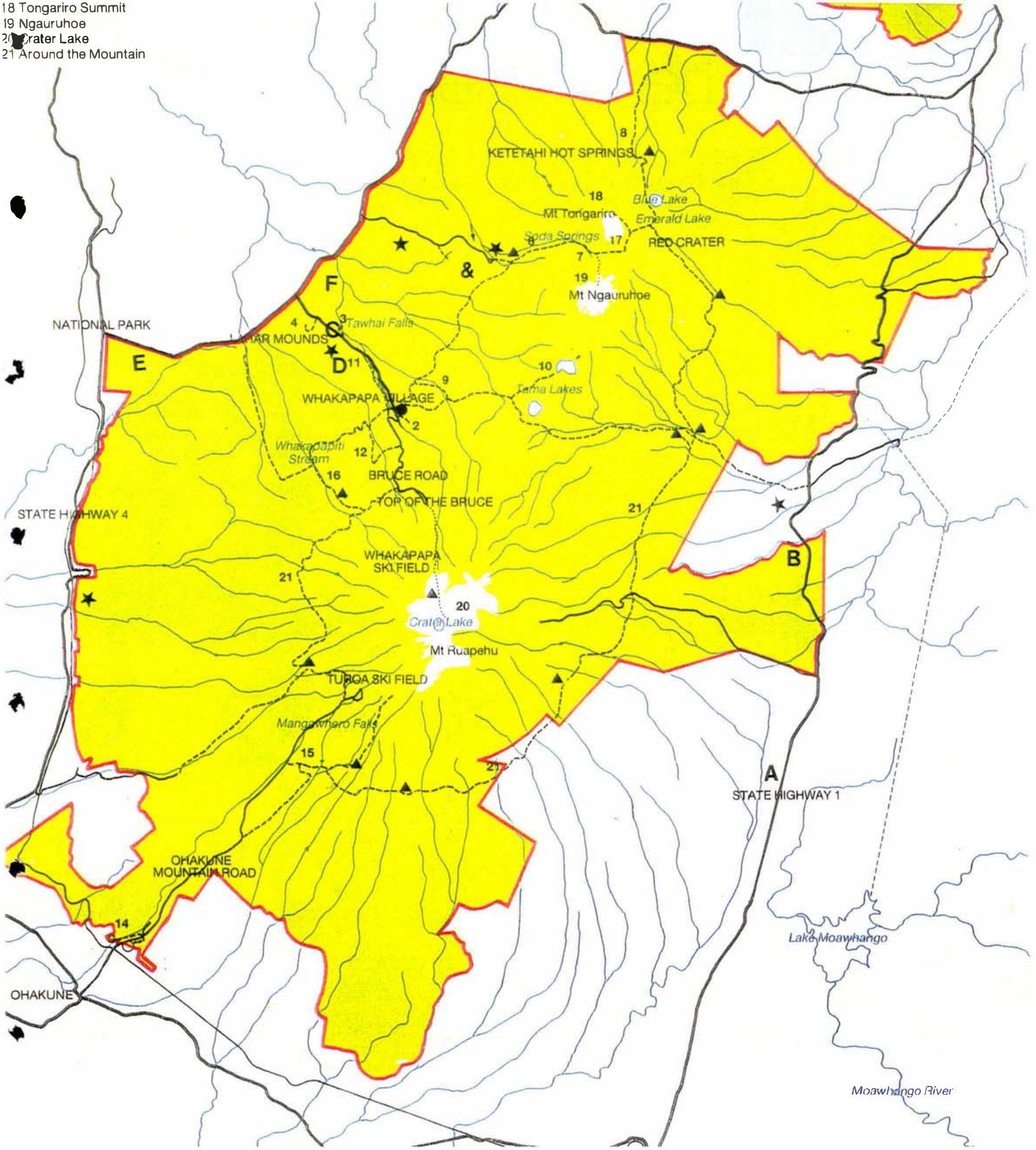
Thus for each vegetation type, a site was chosen haphazardly but approximately 200m from a partner site of what appeared to be the same native vegetation but which was invaded by *Calluna*. An eleventh site of *Calluna* only (in the earliest established area of *Calluna* in the Park) was also chosen for comparative purposes. Site locations are given in table 2.2 and illustrated in figure 2.2, Photos 3 to 13.

Table 2.2 Location of sample sites in Tongariro National Park chosen for habitat survey. Those sites with *Calluna* represent the invaded member of each pair

Site no.	Prominent veg. type	place	Grid ref.
1	tussock/*Calluna*	Moawhango Ecol. area	6205000N 2745000E
2	tussock	Moawhango Ecol. area	6205000N 2745000E
3	*Dracophyllum/Calluna*	Desert Road	6213500N 2746000E
4	*Dracophyllum*	Desert Road	6213500N 2746000E
5	*Gleichenia*	Bruce Road	6222000N 2727000E
6	*Gleichenia/Calluna*	Bruce Road	6222000N 2727000E
7	manuka	Bruce Road	6222000N 2727000E
8	manuka/*Calluna*	Bruce Road	6222000N 2727000E
9	flax/*Calluna*	National Park township	6222000N 2718500E
10	flax	National Park township	6222000N 2718500E
11	*Calluna*	Highway 42, near Pukeonake	6224000N 2726000E

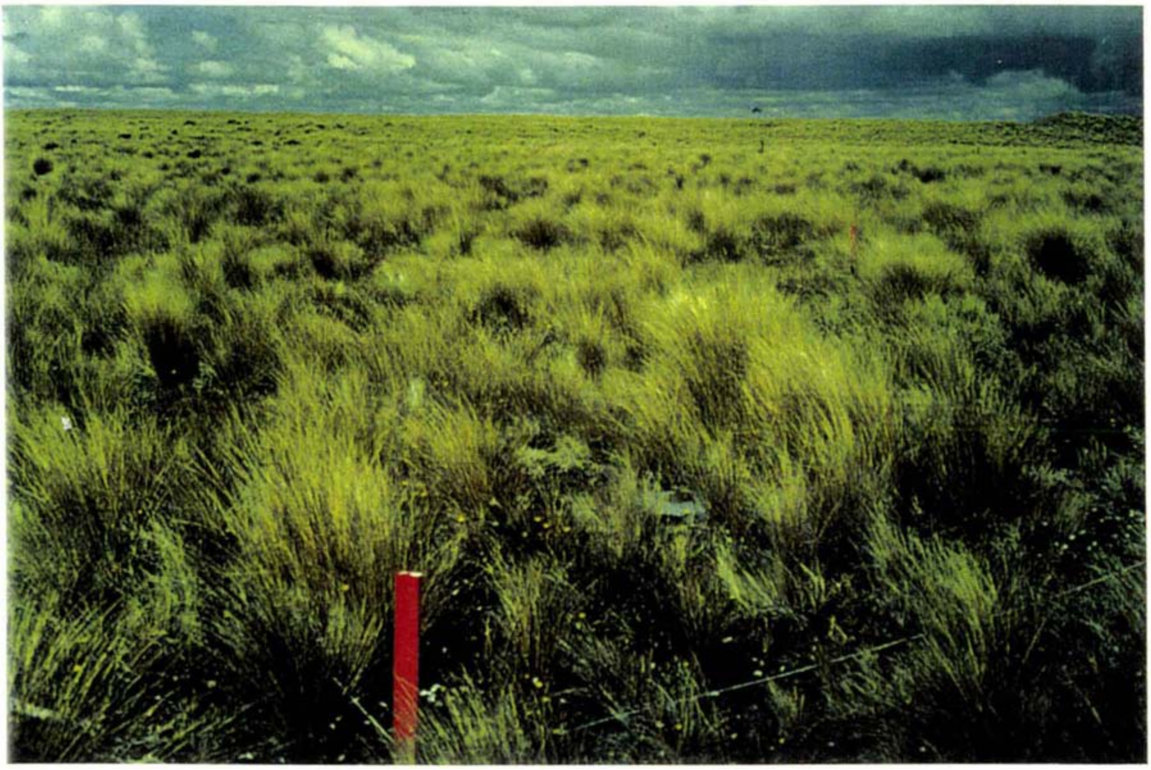
● Park Headquarters
Ranger Stations
▲ Huts
1 Alpine Gardens
2 Ridge Track
3 Tawhai Falls
4 Lahar Mounds
5 Hinemihi's Track
6 Mangatepopo Valley
7 The Saddle
8 Ketetahi Springs
9 Taranaki Falls
10 Tama Lakes
11 Whakapapanui Track
12 Silica Rapids
13 Lake Rotopounamu
14 Mangawhero Forest Walk
15 Waitonga Falls
16 Whakapapaiti Valley
17 Tongariro Craters
18 Tongariro Summit
19 Ngauruhoe
20 Crater Lake
21 Around the Mountain

Fig 2.2 Location of sampling sites in Tongariro National Park.
Plant/Invertebrate sampling sites:
A = sites 1&2; **B** = 3&4; **C** = 5&6; **D** = 7&8; **E** = 9&10; **F** = 11.
★ = sites at which plant architecture was measured.
↘ = where chapter 5's disturbance experiment was conducted.
& = where chapter 4's exclusion experiment was conducted.



Photos 3 & 4

Photo 3 shows the tussock grasslands site used for plant and animal sampling. Photo 4 shows the tussock partnered site after perhaps 5 years of *Calluna vulgaris* presence. Both these sites are located just west of the Desert Road (state highway 1).



Photos 5 & 6

Photo 5 shows the *Dracophyllum* shrubland site used for plant and animal sampling. While Photo 6 shows the partnered site after perhaps 10 years of *Calluna vulgaris* presence. These sites are also located just west of the Desert Road (state highway 1).

Photos 7 & 8

Photo 7 shows the *Gleichenia* wetland site used for plant and animal sampling. And Photo 8 shows the partnered site after perhaps 5 years of *Calluna vulgaris* presence. Both these sites are also located on the western side of the Park on the Bruce Road.

Photos 9 & 10

Photo 9 shows the manuka shrubland site used for plant and animal sampling. Photo 10 shows the manuka partnered site after perhaps 20 years of *Calluna vulgaris* presence. Both these sites are also located on the western side of the Park on the Bruce Road.

Photo 11 & 12

Photo 11 shows the flax swampland site used for plant and animal sampling. And Photo 12 shows the partnered site after perhaps 20 years of *Calluna vulgaris* presence. Both these sites are also located on the western side of the Park near the National Park service station.

Photo 13

Photo 13 shows the *Calluna* only site. The oldest area of *Calluna* in the Park, planted up to 80 years ago. *Calluna* is the dominant plant present.

In the uninvaded areas the sites were haphazardly chosen. For the invaded sites, an arbitrary minimum of 40% *Calluna* cover formed the major choice criterion. At each site a 10 metre by 10 metre area was chosen and pegged. The species present, within the pegged areas, at each site were listed, and the percentage cover of the 3 or 4 most prominent cover species was estimated by averaging values of three independent observers.

Exploratory data analysis was with 'Minitab' and comparative analysis with Systat (Systat, inc. 1989). The data were used to form a presence/absence matrix on which ordinations, and cluster analysis were performed. A cluster analysis (average linkage, Euclidean distance) shows the level of similarity between paired sites to confirm the pairing of sites initially made by eye in the field. Principal component analysis (PCA) was applied to a reduced matrix involving just the uninvaded and *Calluna* only sites to better represent the distinctive characters of each native vegetation type (such as successional state). The ordination displays the sites onto which a vector plot of the component loadings is super-imposed. A table (Table 2.4) is supplied listing species that comprise each vector.

Resource modifications

Biomass

Biomass samples were collected from the five *Calluna* invaded sites, the *Calluna* only site, and three other areas called: 'Pukeonake' (the base of Pukeonake on the south side of the road, Fig. 2.2), 'Mangatepopo-a', and 'Mangatepopo-b' (approximately 100 metres south of the Pukeonake site, and themselves separated by 50 metres in a southerly direction). All these sites are within the original planting area of *Calluna* and should represent the biomass of *Calluna* in its dominant state. Sampling was done in August (1993) at the end of winter when the standing crop was most likely at its annual minimum. All *Calluna* material above ground was removed from a 50 cm by 50 cm square with projected vertical sides. Four samples were taken haphazardly from each site. The percentage cover of *Calluna* in a 10x10 m area at each site was noted. The samples were dried in a Cuddon vacuum oven (~ 60^{O}C, -15 atm) at HortResearch, Palmerston North for 14 days with test samples being removed on days 8, 10 and 13 to determine if weights were stable.

The data were log transformed and analysed using ANOVA testing for differences between sites, on which a Bonferroni means comparison was done, this being a robust multiple range test (Systat manual). The Bonferroni results are presented as line diagrams joining means which are not statistically different (at a 5% confidence level).

Mineral content

To assess the mineral content of above ground parts of a *Calluna* plant, three individual plants from the Mangatepopo area were removed, again from the area of oldest and most mature *Calluna*. The plants were separated into new foliage (this year's growth), old foliage (> 1 year), and woody tissue, and then freeze dried. Six haphazardly chosen samples of ~3 g of each of the three categories were placed into crucibles and weighed. The samples were then incinerated at 500 °C for 12 hours, and reweighed. The ash remaining was considered the mineral portion, the burnt off portion the carbon and nitrogen compounds.

Nitrogen

Soils and plant material were taken for analysis of nitrogen content in winter (17/8/1992) from the tussock/*Calluna, Dracophyllum* /*Calluna* , manuka/*Calluna* , flax/*Calluna* , and *Calluna* only sites (Table 2.2). *Calluna* samples were also collected from the same sites once in summer (6/1/1993) in order to establish seasonal differences between nitrogen levels in *Calluna*. From each site the top 10 cm of foliage (ca. 10 grams wet weight) of five *Calluna* , or five native plants were taken, i.e. five replicates per site per plant type. The samples were freeze dried (72 hours), ground to powder ('Glen Creston' seed mill), and analysed by the Kjeldhal method (an acid extraction method) by the Soil Science Department, Massey University. Soil samples were collected, oven dried at 60°C for four days, ground, and analysed for nitrogen by the above method.

Plant architecture

The measurement of plant architecture is very new, and there is, as yet, I believe, no comprehensive method. Commonly used is the point-intersection method, or some derivation (Brown, 1991) but this best works in grasslands (but see Dickinson and Mark 1992). I have surveyed features of bushes considered relevant to insect use, and then constructed an index of architectural complexity.

The survey was on ten haphazardly chosen plants of each of eight plant types in November 1994. Tussock plants (*Chionochloa rubra*), the colonising form of manuka (< 1 metre tall), and the isolated bush, dwarf type *Calluna* (short *Calluna* < 50 cm) common on the eastern side of the Park were measured on the Desert Road approximately 2 km south of the Waihohonu track. *Dracophyllum*, *Celmisia*, the dense tall (> 1metre) form of manuka, and the tall rangy, dense, interlinked form of *Calluna* (tall *Calluna*), found predominantly north of Hauhaungatahi towards the northern Park boundary and west of the mountain axis were measured from the end of the Mangatepopo road. Flax (*Phormium tenax*) was measured from around Erua (Fig. 2.2).

In the field, 10 plants of the type required were haphazardly chosen and surveyed. The measurement of features was divided into 2 sections: 'objective' measures; and 'subjective' measures, as described below. The 'objective' measures consisted of 14 measures grouped into 4 categories: plant structure, stem and branch attributes, leaf attributes, and bush dimensions (height plus bush radius). The 'subjective' measures had two categories, base complexity, and lichen cover. My own 'Fiddler' score is based on the premise that the measures of the survey miss nuances an observer may notice about plant structure in relation to invertebrate use.

Architectural index

Objective measures (cf. appendix 1a for an example score sheet):

1. Structure, a whole plant aspect.

From observation it was determined if a plant was separate, touching, or interlinked with neighbours of the same species, and, if touching, the number of individuals it was touching was recorded. A plant's own branch inter-linkage, i.e. branches crossing within an individual plant, was scored through estimation by eye and consisted of the categories - no branches crossed, 1-10%, 10-50%, 50-75%, 75%+ crossed (scored as 0-4). General branch orientation, mostly vertical, mostly horizontal, or some of both was recorded (1-3).

2. Stem.

The number of main stems was counted. Then the number of branches from a haphazardly selected main stem in the categories 1^0, 2^0, 3^0, 4^0, as divisions of branching order, were counted, and the angles of the branches from their immediate superior recorded.

3. Height and radius.

Height to highest point, and radius at the roundest point were measured and recorded for each bush.

4. Leaf.

Leaf attributes involved where they were found, i.e. on ultimate, penultimate or on many branches (1-3); their spacing in relation to each other, i.e. single or packed as a unit (1-2); and then the spacing relationship of these units on the branch, e.g. a few units spaced, to lots of units spaced, to lots clustered (1-6).

Subjective measures:

1. Litter.

Litter and debris, live or dead, at the base of a plant was scored from 1 (meaning no litter) to 10 and described the amount of litter.

2. Lichen.

The amount of lichen hanging in the foliage and between stems was scored from 1 to 10.

To form the index the raw values of a category were transformed to a percentage of the largest score for that category. This reduced the weightings of larger categories, given the different scales used. Then all the category scores for each plant were summed to give a pre-index value and the mean value for each plant type attained. These values were again divided by the highest mean-index score, giving a range of 0 to 1 for the index.

'Fiddler' score

My own score (1-10) was purely subjective, but imagines that the survey method does not account for the **intuitive** measure that an observer has. For example *Dracophyllum* has many thin leaves arranged horizontally and packed densely. It looks complex and sheltering; however the landing sites are minimal (due to its horizontal nature) and the foliage is 'harsh'. Thus it is only 'useful' for crawling insects such as beetles, spiders, and wood scale. The score ranks the plant species based upon knowledge of the invertebrates likely to use each plant and their probable requirements (see Appendix 1a for more detail).

Analysis

Both indices allowed a ranking of the plants, in terms of structure, from most 'useful' to invertebrates to least. A PCA ordination analysis was used to separate the plant species by their indices, and groupings circled and identified by eye with shading. A table of components illustrates what features are prominent in which plant, while multifactorial ANOVA analysis and Bonferroni range tests were used to determine statistically significant differences between plants index components. Resource arrangement was illustrated for all the plant community types explored through pyramid diagrams of base, stem, structure, and leaf, depicted by size of bar. The size of a bar of a pyramid was calculated by multiplying the index component score by the percent cover of the plant species involved in that community.

RESULTS

Community diversity assessment

A total of 103 plant species was found in the eleven sampled vegetation sites (Appendix 1). The number of species per site ranged from 11 to 30. Tussock grasslands with *Calluna* (tussock/*Calluna*) held the most (30 species), and *Gleichenia* with *Calluna* the least (11 species). The *Calluna* only site had a distinctly low number of species (14) (Table 2.3). The total number of species between paired sites (native and native invaded by *Calluna*) are similar, but there are consistently fewer species at the invaded sites.

The percentage cover of the dominant native species decreased with invasion of *Calluna*: when partnered sites were compared, tussock dropped to 40%, *Dracophyllum* to 45%, and flax to 60% cover (Table 2.3).

Ordination of the indigenous sites separated them, roughly from east (left) to west (right) on the first axis, explaining 28% of the variation, and perhaps representing a successional transition (Fig 2.3). The separation on the second axis accounts for a further 22.3 % of the variation in the data, and may be a wet (positive score) to dry (negative score) transition.

Each vector of the component vector plot has several species comprising that vector. Vector F, for example, represents 17 species, nearly all of which are exclusive to the manuka site (Table 2. 4), re-inforcing site differences in terms of species present.

The cluster analysis of the species presence/absence matrix (Fig. 2.4) confirmed the field pairings of sites, except with the manuka and *Calluna* /manuka sites. The cluster paired the manuka site with the *Calluna* only site (site 11), and then left the *Calluna*/manuka site as being unique. The *Dracophyllum* and *Dracophyllum* /*Calluna* sites clustered most tightly, followed by tussock and its partner, then *Gleichenia* and its partner and finally flax and flax/*Calluna* (Fig. 2.4).

Resource assessment

Biomass

Invaded tussock grassland, represented by the Desert Road site, has the lowest *Calluna* biomass per unit area, followed by the more northerly Desert Road site containing *Dracophyllum*. The western side of the Park has 200-300% more biomass of *Calluna* than the eastern side (Fig. 2.4). Manuka/*Calluna*, the most sheltered site and the site with the tallest neighbouring foliage, had the greatest biomass, and also the tallest *Calluna* . The tussock invaded *Calluna* site has a lower biomass than the western park samples. The site differences observed are significant (ANOVA, $R^2 = 0.901$, F = 18.125, Df = 7, P = 0.000). The data suggest a "cline" effect (Fig. 2.5) where change is continuous.

Table 2.3

Number of species (top line) and % cover of prominent vegetation at sampling sites. Species with less than 5% cover are included in the moss & bare ground and other category. Numbers in bold are the % covers of the characteristic vegetation types of the sites, before and after invasion

	tussock	tussock-*Calluna*	*Dracophyllum*	*Dracophyllum-Calluna*	*Gleichenia*	*Gleichenia-Calluna*	manuka	manuka-*Calluna*	flax	flax-*Calluna*	*Calluna*
Number of species	30	26	20	25	12	11	29	26	23	21	14
% cover											
tussock	**60%**	**20%**	10%	10%	.	.	.	.	.	.	.
Calluna	.	65%	.	40%	.	65%	.	90%	.	55%	95%
Dracophyllum	.	.	**75%**	**30%**	.	.	.	.	.	5%	.
Gleichenia	.	.	.	.	**85%**	**10%**	.	.	.	.	.
manuka	.	.	.	.	.	.	**95%**	**5%**	.	5%	5%
flax	.	.	.	.	.	.	.	.	**95%**	**30%**	.
moss & bare ground	25%	15%	15%	20%	.	25%	.	3%	5%	5%	.
herbs	15%	.	.	.	.	.	.	.	.	.	.
other woody spp	.	.	.	.	15%	.	5%	5%	.	.	.

Fig. 2.3

Biplot ordination of indigenous and 'pure' *Calluna* sites by species. Component loadings, plotted as the vector lines, are grouped into broader catagories labeled in bold upper case (see table 4)

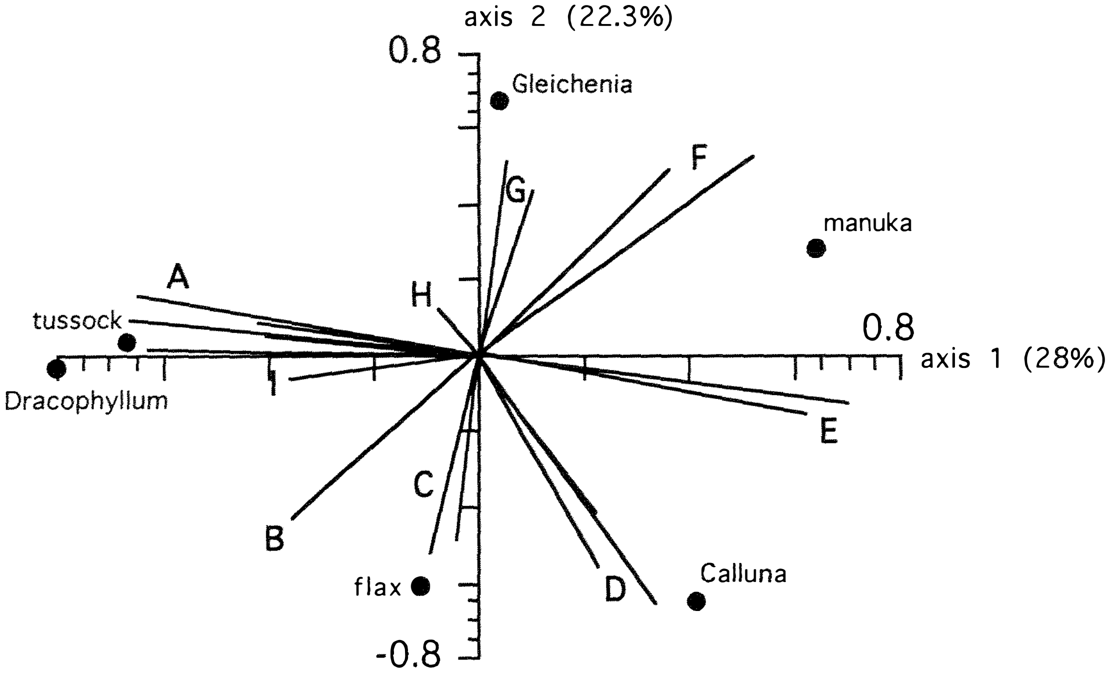


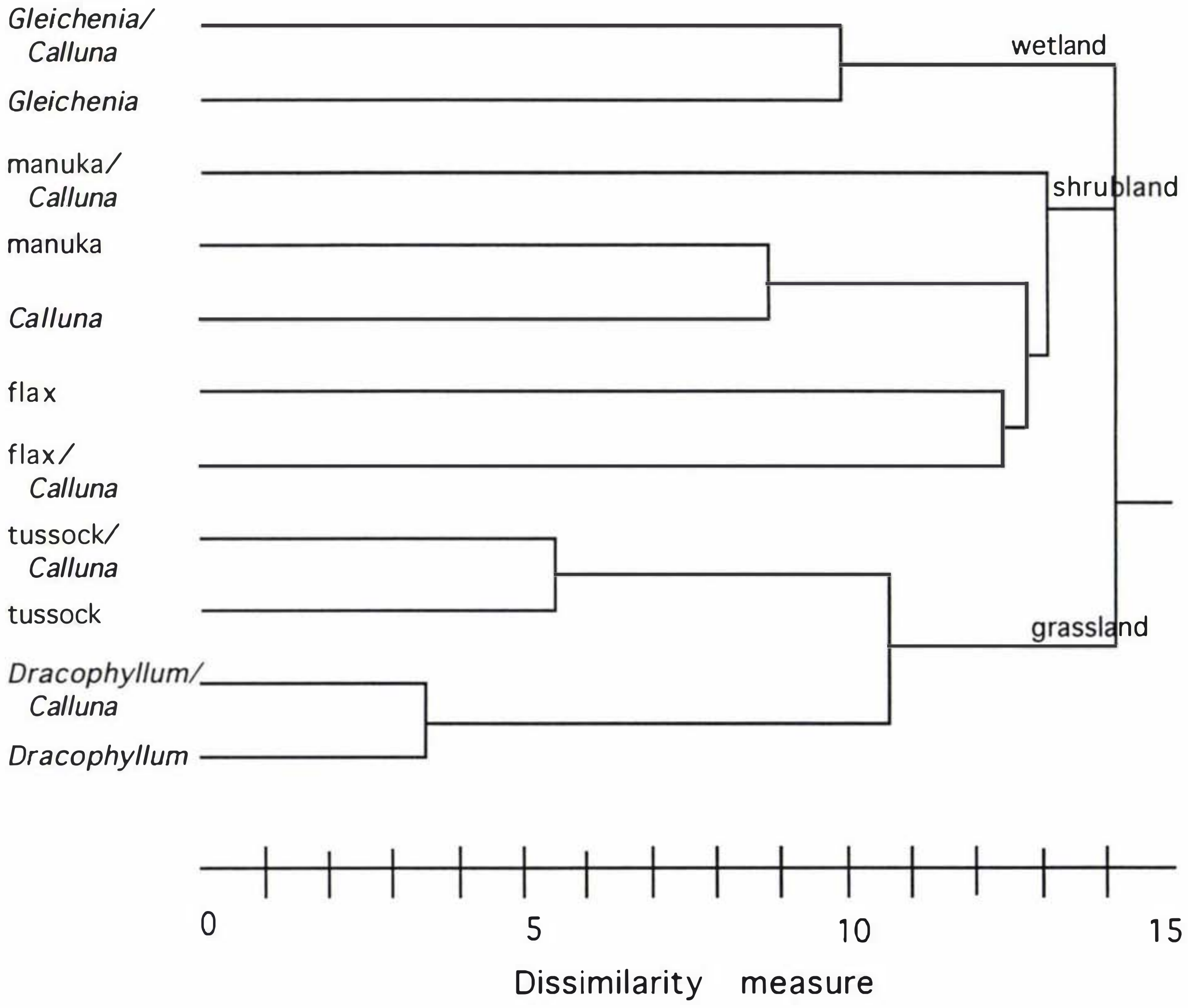
Table 2.4

The species presented comprise the component vectors (bold letters) for the ordination plot (Fig 2.3). The site which certain vectors typify is noted in bold

H	A	I	E	D	F
***Gleichenia* site specfic**	***Dracophyllum* site specifics**	**tussock site**	***Leptospermum or Calluna***	**flax and *Calluna* sites**	**manuka site specific**
Carpha alpina	*Cassina fulvida*	*Elymus rectisetus*	*Phormium tenax*	*Blechnum capense*	*Aristotelia fruticosa*
Carex echinata	*Celmisia glandulosa*	*Epilobium* sp.	*Hebe stricta*	*Blechnum fluviatile*	*Aristotelia serrata*
Carex geminata	*Celmisia spectabilis*	*Coprosma cheesemanii*	*Viola cunninghamii*	*Blechnum pennamarina*	*Astelia* sp.
Empodisma minus	*Coprosma microcarpa*	*Coprosma perpusilla*		*Centaurea erythroea*	*Cladonia* sp.
Gleichenia dicarpa	*Dracophyllum recurvum*	*Leucopogon fraseri*		*Chrysanthemum leucanthemum*	*Coprosma australis*
Schoenus sp.	*Hebe* sp.	*Luzula* sp.		*Cirsium vulgare*	*Coprosma foetidissima*
	Pimelia prostrata	*Ourisia vulcanica*		*Crepis capillaris*	*Coprosma robusta*
G	*Poa colensoi*	*Pinus contorta*	**B**	*Lotus pedunculatus*	*Corokia cotoneaster*
Rhytidosperma setifolium	*Chionochloa rubra*	*Thelymitra* sp.	***flax sites***	*Mycelis muralis*	*Dracophyllum longifolium*
Lachnagrostis filiforme	*Aciphylla squarrosa*	*Agrostyis capillaris*	*Hypochaeris radicata*	*Polysticum sylvaticum*	*Gaultheria depressa*
	Dracophyllum subulatum	*Hierachloe redolens*	*Calluna vulgaris*	*Prunella vulgaris*	*Libocedrus bidwillii*
	Celmisia gracilenta			*Pseudopanax arborea*	*Melicope simplex*
	Euphrasia cuneata		**C**	*Pterdium esculentum*	*Myrsine divaricata*
	Lycopodium fastigiatum		*Anthoxanthum odoratum*	*Ranunculus acris*	*Pseudopanax simplex*
	Pentachondra pumila		*Poa cita*	*Ranunculus repens*	*Podocarpus hallii*
	Racomitrium lanuginosum		*Holcus lanatus*	*Sarothamnus scoparius*	*Pseudowintera colorata*
	Wahlenbergia pygmaea			*Lepidosperma australe*	*Rubus schmidelioides*

Fig. 2.4

Cluster diagram of sites based on presence/absence of plant species (Euclidean distance; average linkage method)



Mineral content

There was a significant difference in mineral content between the tissue types (ANOVA, R^2=0.964, F=202.07, Df=2, P=0.000). Old foliage (older than one year) had the highest mineral content, new foliage the next, while wood tissue contained the least (Fig. 2.6).

Nitrogen

Mean nitrogen levels in *Calluna* are higher in summer (9.23 mg per g (dry weight) sample) than in winter (7.92 mg per g sample). The difference between summer and winter is significant (ANOVA, R^2=0.812, F=8.516, Df=4, P=0.043). The difference between sites was not statistically significant (ANOVA, R^2=0.812, F=2.188, Df=4, P=0.233; Fig. 2.7), though there were observable differences at the manuka/*Calluna* and flax/*Calluna* site.

Results of plant nitrogen analysis show that flax has the highest nitrogen content, with *Calluna* and *Gaultheria* having similar but lower values, and *Dracophyllum* and tussock the lowest shoot nitrogen values. The differences are statistical significant (ANOVA, R^2=0.878, F=58.5, Df=4, P=0.000; Fig. 2.8). Site, a covariate in the ANOVA, was also a significant factor (F=8.4, P=0.006).

Soil analysis (Table 2.5) shows that the *Calluna* invaded manuka swamp (*Calluna*/manuka), with a deep organic layer, to be the richest in nitrogen; the *Calluna* only site, about 2 km west, is the next richest, followed by the eastern sites, tussock grasslands and *Dracophyllum* (refer to map, Fig. 2.2).

Table 2.5 Soil nitrogen level (mg per g sample (dry weight)) at each paired site. Letters correspond to statistically similar values (T test). n = 5

site	tussock	tussock/ *Calluna*	*Dracophyllum*/ *Calluna*	manuka/ *Calluna*	flax/ *Calluna*	*Calluna*
Soil nitrogen	2.52 a	2.78 ab	1.93 abc	5.2	2.94 ac	3.3 a

Soil nitrogen levels are not correlated with *Calluna* nitrogen levels in winter-collected shoots (r=0.195, P >0.05 from Pearson Correlation Coefficient), while summer-collected *Calluna* shoot levels are more strongly, and negatively though still not significantly correlated (r=-0.796, P>0.05). Nitrogen values of tussock are similar to the soil levels at sites 1&2, tussock-tussock/*Calluna*, while flax has five times as much nitrogen as the soils at the flax site (sites 9&10) . *Calluna* appears to maintain a constant level of nitrogen independent of the soil level, or site (Fig. 2.7).

Fig. 2.5. Biomass (dry weight) of *Calluna* from 50cm X 50cm plots (n = 4)

The horrizontal lines below the plots represent the Bonferroni range tests comparing means (separation at 95% C.I.)

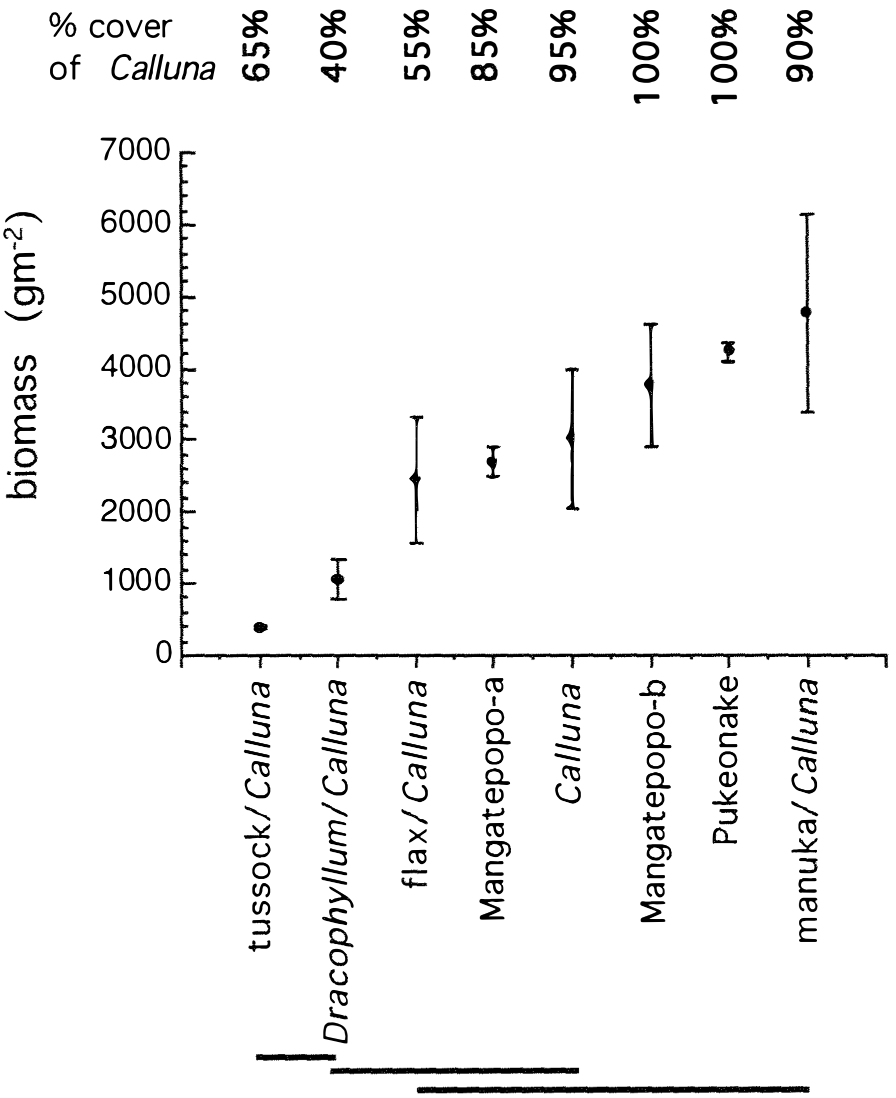


Fig. 2.6

Mineral content of *Calluna* as
mean percent of initial dry weight after incinerating.
Bars represent S.E.M.

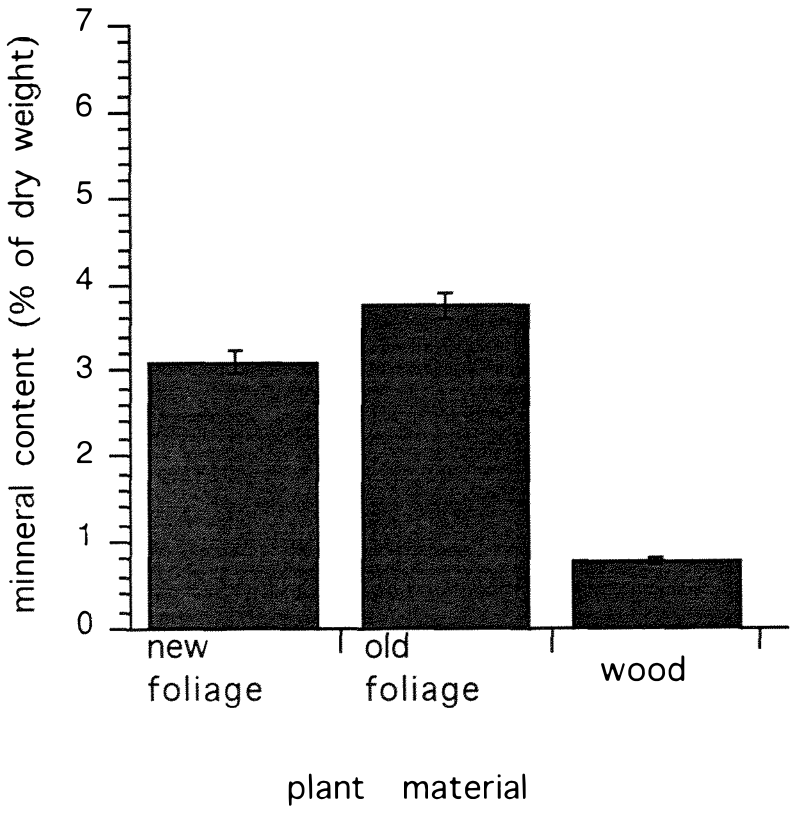


Fig. 2.7

Nitrogen levels in soils and in *Calluna* foliage during summer and winter at each invaded site and the tussock site

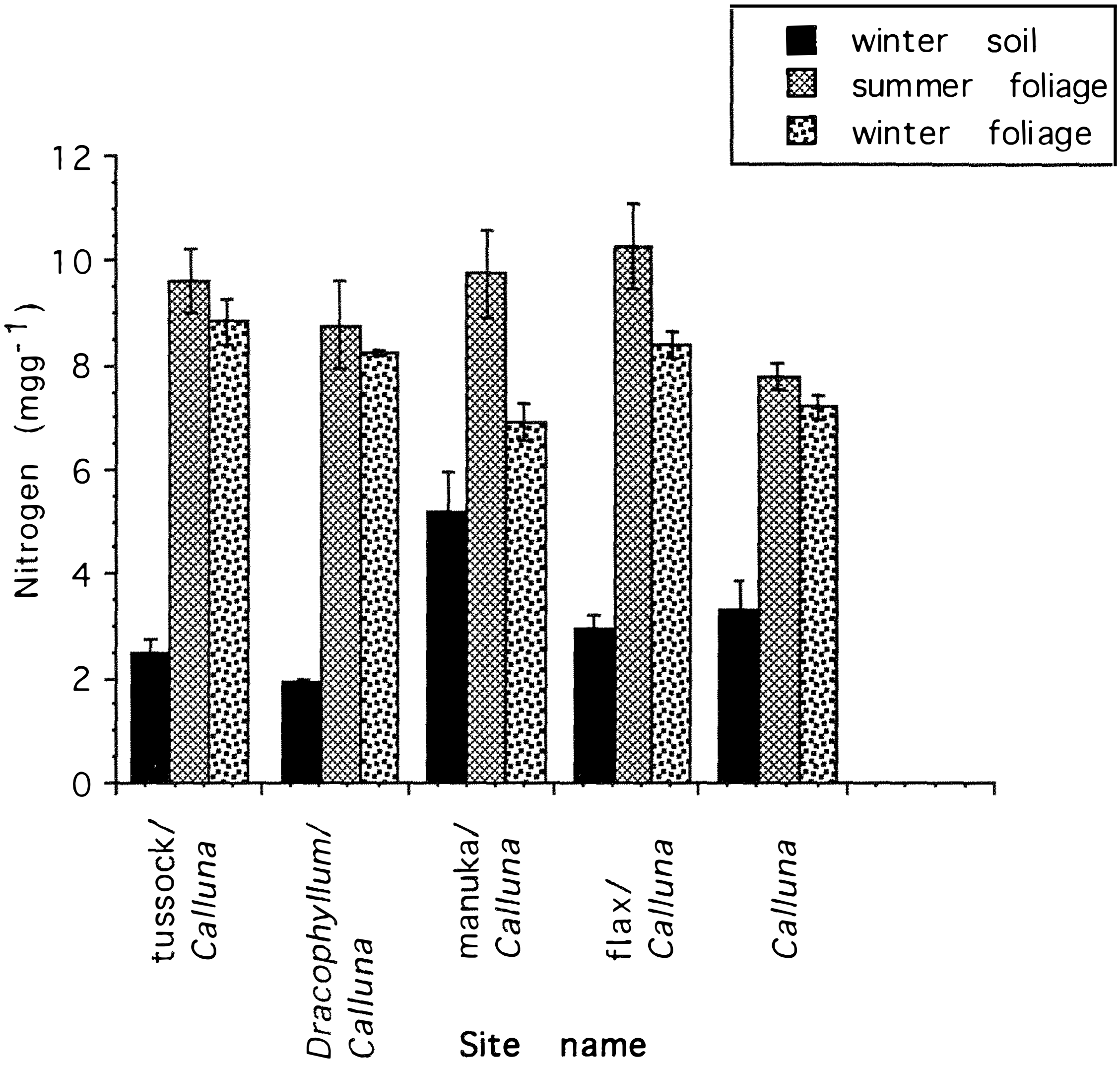
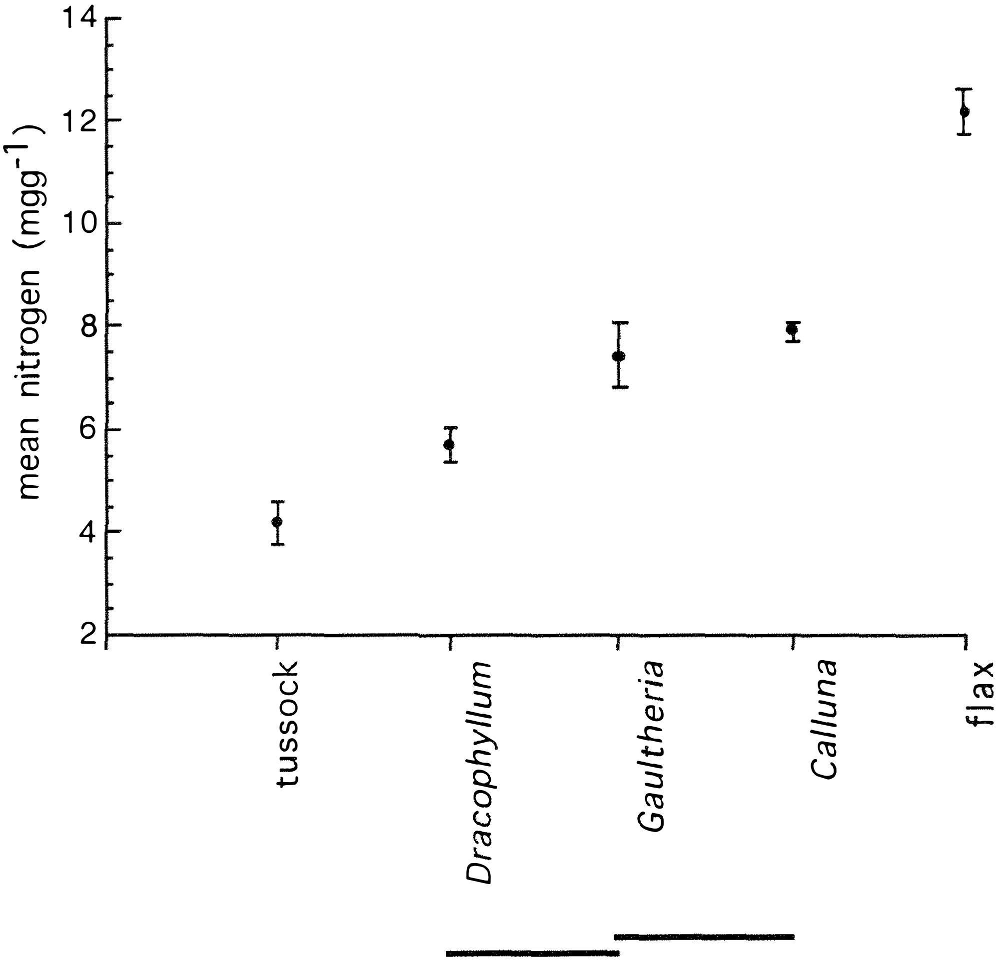


Fig. 2.8

Average plant foliage nitrogen levels from winter samples

Bonferroni range test, lines join sites which are not statistically different (95% C.I.)



Plant architecture

Species architectural complexity was ranked: tall *Calluna* > flax > *Dracophyllum* > tussock > *Celmisia* > short *Calluna* = tall manuka > short manuka (Fig. 2.9). Tall *Calluna* and *Celmisia* had the most 'complex structure' (Table 2.6), while *Dracophyllum* had the best (i.e. most complex) stem score, flax the most complex base, and manuka the greatest height. Tall *Calluna* dominated in four of the seven measures of architectural complexity. Significant differences were found in all categories between the plants (Table 2.6), though their nature depended on the category in question; however there was no clear trend. An ANOVA of the architecture index was also significant (R^2=0.814, F=45.11, Df=7, P<0.000), and the Bonferroni range test (Fig. 2.10) demonstrated significant differences between short manuka and *Celmisia*, and between flax-tall *Calluna* and all others. The 'Fiddler' score ranked the plants: tall *Calluna* > flax > tall manuka > *Dracophyllum* = short *Calluna* > short manuka > tussock > *Celmisia*. Comparison of the two indices reveals that both agree as to the two most complex plants, tall *Calluna* and flax, but after that the order is much different, the 'Fiddler' score ranking the small, non woody plants as less complex than the architectural index, which promoted these two plants (tussock and *Celmisa*) because of their excellent base and structure components.

The ordination of architectural categories displayed tall *Calluna* clearly apart from the rest on axis one, which explained 29% of the variance, placing it furthermost from *Celmisia* and tussock (Fig. 2.10). Axis two (explaining a further 26%) separated the shrubby *Calluna* and manuka species, from flax, and then *Celmisia* and tussock. *Dracophyllum* mostly grouped between flax and tussock but some plants are scattered throughout the plot (Fig. 2.10). The biplot (component vectors) suggests that *Celmisia* and tussock were distinguished by their low height and complex base scores, and tall *Calluna* on its high leaf, high stem, and high structure scores. A correlation between plant type and architectural components gave very strong positive correlations (P>0.008) suggesting features of the components were strongly associated with particular species.

Resource strata profiles of the vegetation at each of the sites are depicted using cover values for each plant species at the site multiplied by the architectural category value for the appropriate species at that strata level (Fig. 2.11). The profiles of each species illustrate the change in spatial and physical attributes from ground level to plant apex due to the invasion of *Calluna*. The indigenous vegetation sites have better base resources than *Calluna* invaded communities; however leaf and structure properties all increase after *Calluna* establishment. When comparing the tussock and tussock/*Calluna* profiles, the lack of stem component and considerable base complexity is obvious; the addition of *Calluna* to this habitat type has created a better balance of complexity over the strata levels. A similar trend can been seen when comparing the flax and flax/*Calluna* sites. The manuka profile is almost completely inverted after invasion, though both habitats have a small base component. *Calluna* appears to invert the resource partitioning of indigenous vegetation communities, which is best seen when comparing the *Calluna* only site with any, or all, of the indigenous sites (Fig. 2.11).

Fig. 2.9

Architectural index scores (●) for the range of plant types examined from Tongariro National Park, n=10, —●— indicates the mean index value

Bonferroni range test, lines join sites which are not statistically different (95% C.I.)

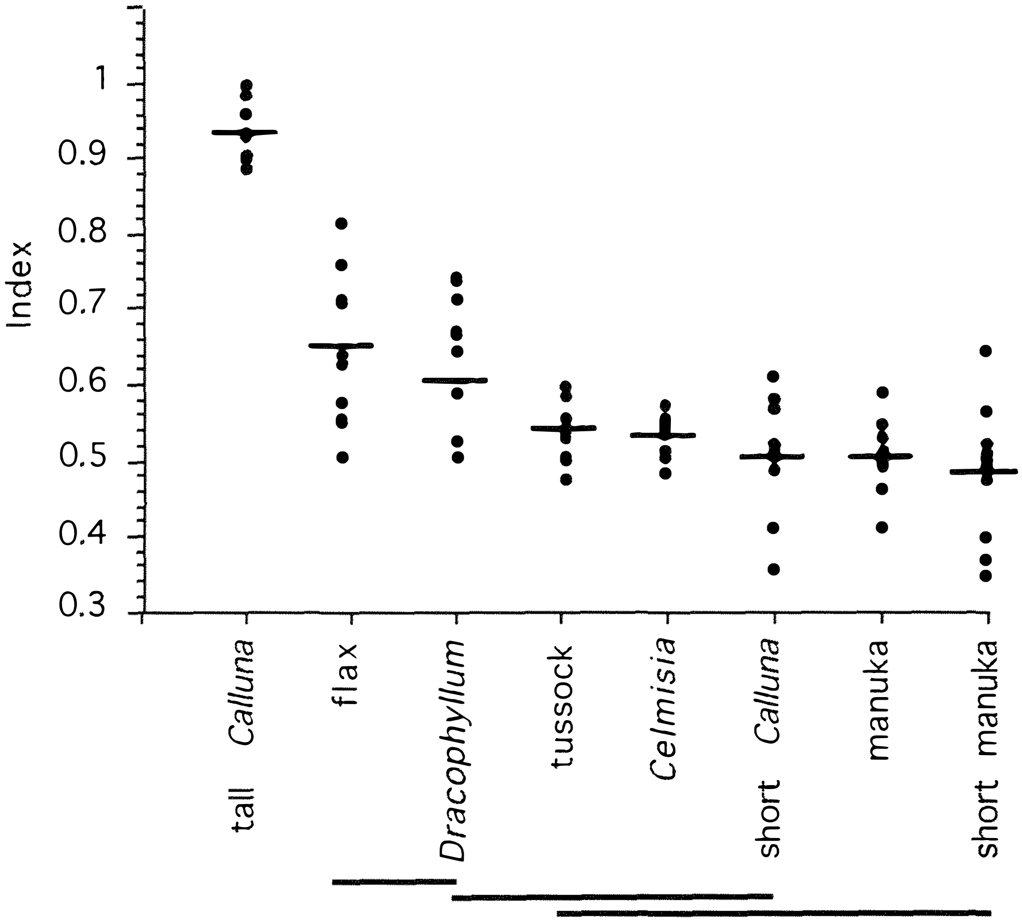


Table 2.6

Plant architecture index divided into its components, presented as the mean values of each of 10 plants. Values followed by the same superscript, within rows, are not significantly different ($P<0.05$, Bonferroni test).
The fiddler score refers to my own subjective score.

Category	*Dracophyllum*	tall manuka	short manuka	tussock	tall *Calluna*	short *Calluna*	*Celmisia*	flax
structure	0.313^{12}	0.413^{23}	0.380^{123}	0.373^{123}	0.993^{4}	0.240^{1}	0.927^{4}	0.480^{3}
stem	0.725^{1}	0.623^{12}	0.528^{23}	0.000^{5}	0.633^{12}	0.456^{3}	0.318^{4}	0.200^{4}
leaf	0.340^{5}	0.200^{1}	0.550^{2}	0.700^{4}	1.000^{3}	0.910^{3}	0.200^{1}	0.500^{2}
base	0.660^{4}	0.160^{1}	0.210^{12}	1.000^{3}	0.140^{1}	0.230^{1}	0.970^{3}	0.500^{2}
lichen	0.220^{2}	0.150^{23}	0.000^{1}	0.010^{1}	0.700^{4}	0.140^{3}	0.000^{1}	0.000^{1}
height	0.565^{1}	0.918^{2}	0.393^{13}	0.388^{34}	0.470^{13}	0.278^{4}	0.079^{5}	0.781^{2}
radius	0.684^{1}	0.535^{1}	0.221^{1}	0.595^{1}	1.000^{2}	0.793^{1}	0.216^{1}	0.594^{2}
INDEX	0.607^{12}	0.506^{3}	0.482^{3}	0.536^{23}	0.934^{4}	0.506^{23}	0.535^{23}	0.645^{1}
Fiddler rank	4	5	3	2	7	4	1	6

Fig. 2.10

Separation by PCA of plant species based on their Architectural differences.

Component loadings are plotted in vector form to illustrate which categories of architecture measured induced the separations

vector key

a = structure
b = lichen
c = radius
d = leaf
e = base
f = height
g = stem

■ = *Dracophyllum*, the only 'scattered' plant type

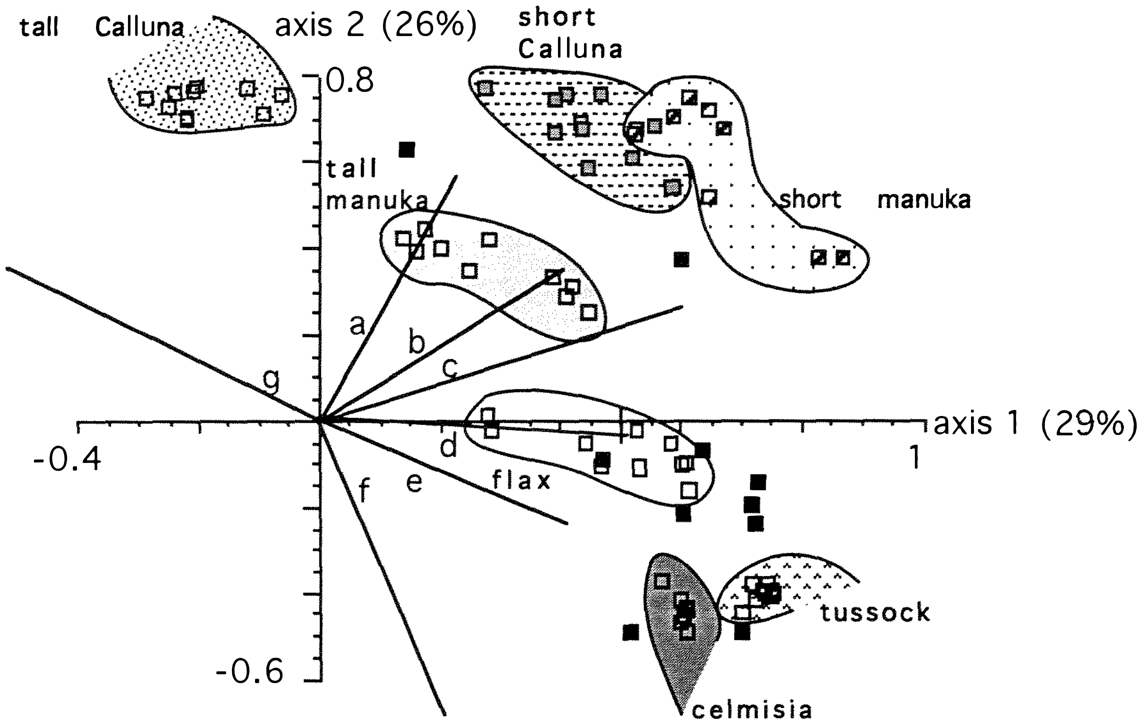
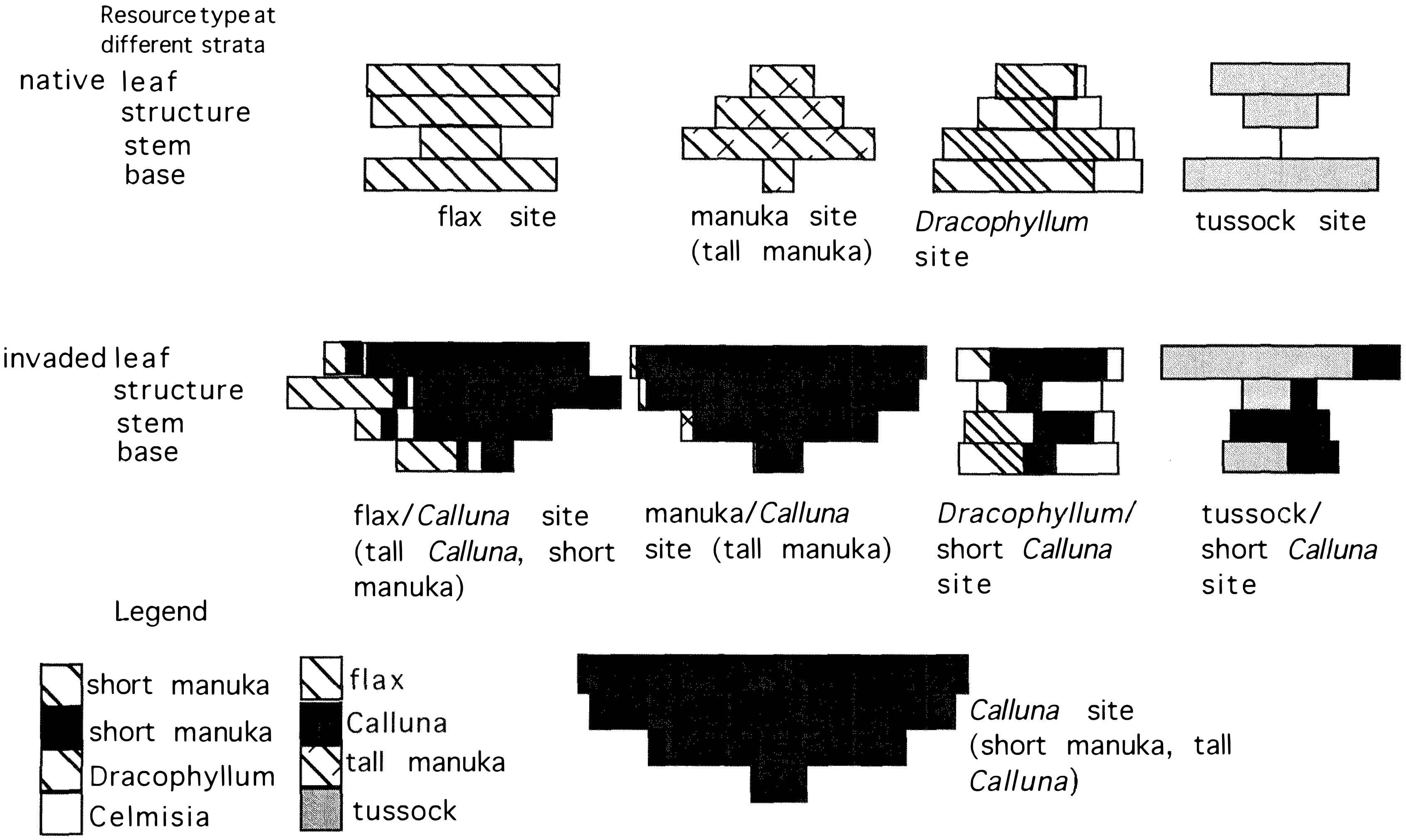


Fig. 2.11 Architectural resource partitioning in space. A profile approximating the physical location of the components of structural architecture. The size of each bar reflects the relative amount of that architectural component in that vegetation community. The patterns on the bar represent the relative contribution of the species listed in the legend



DISCUSSION

Calluna in Tongariro National Park has not had to overcome the usual problems of classic invasion, the initial self introduction, repeated later self introductions, establishment, and spread (Bagnall 1982, Chapman 1984, Chapman and Bannister 1990, Williams and Keys 1993) because it was human introduced, acclimatised, and dispersed. It found conditions in the park perhaps novel but suitable (see Gimingham 1960, Barclay-Estrup 1970, Atkinson 1981, Chapman 1984). In Europe it is an early succession species, usually only establishing on the poorer soils where other species are slow to establish. In England, if unmanaged, heathlands rapidly succeed to birch woodlands (S. Fowler, N Webb pers. comm.). In New Zealand *Calluna* has found richer soils, with slower re-afforestation rates by natives. *Calluna* in the Park has been a successful invader, spreading and flourishing (Chapman and Bannister 1990). The 'new' *Calluna* heathlands that have, and are, establishing, are a different vegetation community for Tongariro National Park, (Fig. 2.3), but less diverse than most of the indigenous vegetation communities they have replaced (Chapman 1984; Table 2.3).

Where *Calluna* has visually come to be a single species stand there is an obvious dissimilarity between the number of indigenous species present and the number expected from when it was tussock grasslands 30 years ago (I. Atkinson pers. comm.). Fourteen species were recorded in the surveyed quadrat at the *Calluna* site compared to 30 species in the tussock grasslands. Indeed, considering all the indigenous sites, there is a mean decline of 8 native species (36%), commonly *Poa* spp., *Celmisia* spp., prostrate *Coprosma* spp., and small flowering herbs, e.g. *Wahlenbergia* spp. The *Calluna* community's species richness in Tongariro National Park is not comparable to that in its normal indigenous range e. g. Britian with a mean of 32.5 species (Gimingham *et al*. 1979). In all the indigenous sites studied there was a noticeable decrease in the percent cover of the most prominent indigenous vegetation (50%) as illustrated in the time series photographs (photos 1 and 2). In just 30 years *Calluna* has changed the vegetative landscape: its colour, texture, height and form.

The sites with *Calluna* invading were chosen to be representative of their indigenous partners. The *Calluna* only site, however, does represent the new community form. The ordination analysis of habitat types (Fig. 2.3) placed *Calluna* as being very different from all the indigenous community types except manuka on axis one, and then splits these two sites substantially on axis two. Axis one appears to represent a successional transition of native plant assemblages, at least in as far as physical characteristics, if not the actual 'maturity' (i.e. age of evolutionary co-existence) of the systems. That is, those sites on the far right of figure 2.3 are tall, have high biomass, lower productivity, more developed soils, and a high shoot to root ratio. It may be that those sites further left on axis one (tussock and *Dracophyllum*) are more susceptible to *Calluna* invasion simply because they are communities of herbaceous, leafy, species rather than woody, taller species as in the manuka community. Indeed invasion has, and is, occurring fast in the tussock grasslands of the Moawhango ecological region (Rogers 1991, Rogers and Leathwick 1994, Dickinson, Mark & Lee 1992). *Gleichenia* and flax communities may be harder to invade because they exist in very wet soils, probably outside the normal European heathland's range. *Calluna* at once accelerates the successional trajectory of the communities it invades, but also inhibits them from continuing into forest, though this is a debated matter (see esp. comments by Rogers, Rapson, Dickinson, Mark reported in Williams and Keys 1993).

Alteration of Resources

Because the *Calluna* in the Tongariro National Park has had no management of the type practised in Europe, where it is mown, fertilised, rotationally burned, and grazed (Gimingham *et al.* 1979, Moore 1962), it has developed a 'natural' growth form. The result has been (on the western side of the park) tall, or long, lush stands of *Calluna* similar to many Scottish heather moors (Barclay-Estrup 1970, Miller and Watson 1978, Miller 1979). Any gaps caused, perhaps, by senescence are colonised by decumbent branches, circumventing the traditionally conceived pioneer-degenerate cyclic pattern (Chapman and Bannister 1994, Gimingham 1988).

The eastern side of the Park, lower in rainfall and with poorer soils, has less *Calluna* (ca. 400-1000 g m^{-2}). The western side of the Park appears to offer food resources, in the form of *Calluna* (ca. 3000 g m^{-2}), for any herbivore capable of utilising it. With increasing *Calluna* biomass and ground cover indigenous plants become less abundant and so harder to find; the native food resource of invertebrates is effectively reduced.

The vegetative resource of *Calluna*, in dense stands that are mature to old in stature, exhibits a difference of up to three times more biomass in the Park as compared to the levels in Europe (Table 2.7). Mature western Park *Calluna* biomass is 1000 gm^{-2} more than those recorded in Europe. As Chapman and Bannister (1994) point out, this is probably due to *Calluna* having developed a high proportion of wood in New Zealand, possibly through lack of grazing and burn management, but also through woody tissue persisting and production of new stems from root stocks (C. Lake pers. comm.).

The measure of nitrogen and mineral content in *Calluna* and indigenous plants illustrates the possible change in the ecosystem's resources, implying what levels of resource are now available to the invertebrates capable of using it, or 'lost' to the bulk of the ecosystem. There is good evidence that plants rich in nitrogen make better food for insects; insects grow faster, bigger, and produce more offspring on richer nitrogen diets (S.Uren pers. comm., Prestidge and McNeill 1981, McNeill and Southwood 1978). The nitrogen content of the indigenous plants measured, except flax, was below that of *Calluna*, though the level in *Gaultheria* was not statistically different. From a resource perspective, though, *Gaultheria* is neither abundant or wide spread. Surprisingly, the nitrogen levels found in *Calluna* from all over the park were similar (between ~ 8 and 10 mg g^{-1} (winter values)) even though the plants were growing in soils that contained statistically significantly different levels of nitrogen (1.93 - 5.2 mg g^{-1} sample dry weight). It appears that *Calluna* is a nitrogen accumulator, developing a constant internal level of nitrogen. This accumulation has caused a location shift of the ready source of nitrogen in the plant community, sometimes, as in tussock grasslands, enhancing the standing vegetation's total nitrogen, sometimes lowering it, as in flax communities invaded by *Calluna*. However, *Calluna's* accumulation of nitrogen and considerable biomass may mean that there is a considerable reduction in the availability of nitrogen to native invertebrates feeding on indigenous plants in *Calluna* invaded habitats.

Table 2.7 Biomass comparisons of European and Tongariro National Park *Calluna*

Gimingham's life phases	biomass (gm^{-2})	overseas mean	Author	location
building	1508		Barclay-Estrup 1970	Elsick Heath (Scotland)
	573		Chapman *et al.* 1975	Dorset Heathlands (England)
	740		Forrest 1971	moor house
	1180	1000	Miller & Watson 1978	Kerloch Moor (Scotland)
	2500		**This study 1993**	western Park (New Zealand) site 10
mature	2000		Miller & Watson 1978	Kerloch Moor (Scotland)
	1502		Chapman *et al.* 1975	Dorset Heathlands (England)
	741		Tyler *et al.* 1973	Sweden
	2100		Miller 1979	Scotland
	1924	1653	Barclay-Estrup 1970	Elsick Heath (Scotland)
	400		**This study 1993**	eastern Park (New Zealand) site 1, 3
	3000		**This study 1993**	western Park (New Zealand) site 11
old	590		Aerts 1989	Holland
	1043		Barclay-Estrup 1970	Elsick Heath (Scotland)
	2200		Miller & Watson 1978	Kerloch Moor (Scotland)
	1966	1449	Chapman *et al.* 1975	Dorset Heathlands (England)
	5000		**This study 1993**	western Park (New Zealand) site 7

Comparison of nitrogen levels here and in its native home, northern Europe, (Table 2.8) reveals that the *Calluna* in Tongariro National Park has similar contents as in Sth England, at a single bush level. On the ecosystem level, due to its larger biomass and extensive cover, the New Zealand grown *Calluna* offers twice the nitrogen resource of English, and Scottish heath.

Table 2.8

Comparisons of *Calluna* nitrogen levels between those reported in Europe and in Tongariro National Park. (Units are mg100g^{-1} dry wt for single bush, and kgha^{-1} for ecosystem values.)

	Author	summer	winter	place
single bush				
	these data 1993	923	791	Tongariro National Park
	McNeil & Prestidge 1982	1060	670	Sth. England
	Brunsting & Heil 1985	220	160	Netherlands
Ecosystem				
	these data 1993	258*		Tongariro National Park
	Chapman 1967	107.7		Sth. England
	Robertson & Davies 1965	102		Scotland

* *This figure was calculated using the mean nitrogen level between summer and winter, multiplying this figure by the percent cover of Calluna at site 11 (Calluna only in a 10m by 10m plot), and then multiplying this figure to get a measure for one hectare.*

The new *Calluna* resource has a large contingent of specific secondary compounds and metabolites (Robertson and Davies 1965). This would generally deter any rapid host plant shifts to *Calluna* by insects (Bernays 1981, Lundberg and Åström 1990), making a mineral and nutrient 'pool' of un-utilisable material.

Minerals other than nitrogen and carbon compounds, left after incineration, were in greatest abundance in older *Calluna* foliage. It is this tissue that has had time to accumulate secondary metabolites and other non-carbon based substances. With no active management (fire, mowing) and very little herbivory (see Chapter 3) there is little removal of older foliage, unlike in Europe. This, like the biomass, implies a large resource of generally unusable material for herbivores in Tongariro National Park. Like nitrogen, the ecosystem implication is that much of the mineral substances that were once cycling through the native system before *Calluna,* are now delayed, trapped in *Calluna* foliage. This, surely, has repercussions on the invertebrate assemblage's abundances and diversity.

Plant architecture

The measures pioneered here of architectural complexity, suitable to invertebrates, of the species and vegetation at Tongariro National Park demonstrated that each plant type tended to have one or two components outstanding as habitat features for invertebrates. Tall manuka has excellent height and stem characteristics, while *Dracophyllum*, on the other hand, has its complexity in its wooden structure (thick stem and branches) and in the lichen in the forks of its branches. Short *Calluna* had high complexity in its leaf and radial component scores, while *Celmisia* had high structural complexity, though little else. Tussock, though having many and densely arranged leaves and a complex base, has no stem and branch structure. Further, tussocks are now often isolated from one another, rarely interlinked, and generally encompass small volumes with their foliage. Tall *Calluna*, the most architecturally complex, had high scores for four of the seven features; it gained this complexity from possession of a myriad of slender branches, close association with other *Calluna* bushes (interlinkage), a large number of leaves, and vast arrays of lichen supported in, and filling the space between, a mass of horizontally and vertically arranged stems. *Cassina vauvilliersii,* though not indexed, if appraised using the 'Fiddler' concept, is perhaps one of the most complex native shrubland plants in the park. It has a compact array of medium sized leaves, with the bush arranged in a hemisphere and the leaves on the outside, packed closely on the branches and extending down into the interior of the bush. The leaves are thus presented in a variety of angles, with a variety of shelter associated with them. The inside of a *Cassina* bush is dense with branches, very sheltered and three dimensionally complex. There are, however, not many *Cassina* plants (relative to *Calluna* or *Dracophyllum*, or tussock) present in the Park, and no study to sugest the abundance and variety of invertebrates on it.

The architectural features of plants, coupled with the immense spread of *Calluna* and the reduction of the indigenous plants, may be responsible for large changes in the invertebrate life in the Park. *Calluna* differs from native plant structures; it creates a more uniform expansive micro-climate in and under *Calluna* compared with tussocks and *Dracophyllum*. The presence of *Calluna* has created a larger volume of plant material in three dimensions than previously existed. Dickinson, Mark & Lee (1992) illustrate this point clearly using height profile images which show how *Calluna* occupies more space than any other companion plant (Fig. 2.11). It has packed this volume with complex patterns of stem and leaf, creating novel food for herbivores at the expense of their normal sources. A habitat now exists which is ideal for web spinning spiders (Foelix 1982) and flying 'tourist' (Moran and Southwood, 1982) insects. This change, likely to favour predator organisms, generates an increased risk of predation for herbivores.

Conclusion

This study has shown that the indigenous plant community has decreased in abundance, frequency, appearance, and complexity. Invasion by *Calluna* has led to changes in the location and availability of minerals, nitrogen and plant matter, perhaps trapping, or at least delaying the cycling of these elements through the indigenous invertebrate-soil-plant ecosystems, as well as generating new invertebrate habitat with implications for the balance of the invertebrate communities. This means a large resource (realising that the notion of what actually constitutes a resource, and its real availability, is often guess work, Schultz 1992) is freed for herbivorous invertebrates capable of making a host shift. For herbivores not able to use *Calluna*, there is pressure to better utilise dwindling indigenous resources or find new ones. The architectural change could result, in combination with the above, in a predominance of the predator guild, adding even greater risk to the normal herbivorous component of the system, and perhaps decreasing the apparent suitability of the new *Calluna* component to the potential native invertebrate invaders, as well as to bio-control agents.

Chapter 3

Impact on native invertebrate assemblages of invasion by exotic heath, *Calluna vulgaris*

ABSTRACT

In Tongariro National Park, the invertebrate assemblages of five indigenous vegetation habitats were explored via pitfall traps, sweep netting and bush beating and compared to similar habitats that had been invaded by European heather (*Calluna vulgaris*). This was done to ascertain if invasion and dominance of *Calluna* has caused local extinctions, reductions, or other modifications to indigenous fauna.

Basic descriptive statistics are presented for each assemblage and compared, as are diversity measures, abundance distributions, and feeding guilds. Cluster analysis and ordinations are used to illustrate the assemblage groupings. Seasonal variation is examined, as are relationships with plant architecture and nitrogen levels, and successional rank of the habitats (vegetation resource).

The number of invertebrate taxa found in any habitat studied was not statistically significantly different, nor was the average abundance of animals caught. An apparent trend is that the habitats further along the successional trajectory have greater numbers of taxa and greater abundances of individuals; eg. *Gleichenia* supports 34 taxa, and had a mean abundance of 5.8 individuals per sample, manuka had 81 taxa and a mean abundance of 9, while flax/*Calluna* had 88 taxa and a mean abundance of 11.5. Since *Calluna* often 'pushes' the habitat it invades further along this trajectory, the structural vegetation resource increases. This has had repercussions on the diversity of invertebrate assemblages. The tussock grasslands and flax wetland assemblages in particular appear to lose their 'character' after invasion. Eg. the numbers of taxa falls from 101 to 85 when *Calluna* invades tussock grassland, and from 104 to 88 after invasion of flax wetland. Invaded habitat assemblages best fit log normal distributions, implying stable assemblages. The indigenous assemblages appear to move from a log series abundance distribution (harsh, early successional habitat distributions) to log normal (more 'stable') distributions after invasion. Seasonal changes were minor except when comparing tussock and *Calluna* invaded tussock, in which thrip numbers boomed at *Calluna* flowering in late summer; eg. a total of 35 specimens compared to 554 specimens in the tussock/*Calluna* (thrips were extensive in number wherever *Calluna* was found). Spider abundance blossomed in summer in the *Calluna* habitat (up to 300/sample), but was highest over winter in tussock grasslands (~ 130/sample). The phytophagous group Homoptera had noticeably greater abundance in summer and spring in tussock and manuka habitats than their partnered invaded habitats. The only general statement about feeding guilds is that invasion of *Calluna* usually results in a decrease in plant eaters, an increase in abundance of the pollen eaters (thrips), and an increase in both frequency and abundance of the predator guild, exceptions being in tussock grasslands

and flax. There are positive correlations of invertebrate abundance with plant architecture and successional rank, (r = 0.668 & 0.633 respectively).

Tongariro's *Calluna* fauna has not nearly the 'depth' (number of herbivores and associated invertebrates) seen in Europe. The changes found in this study appear subtle, and in line with successional changes that one might expect normally from an indigenous successional progression. Only the reduced phytophagous fauna does not correspond with this trend. Interestingly the rare invertebrates are not as affected as the common by *Calluna* invasion. Some groups 'suffer' more than others (herbivores), some thrive (web spiders). From a conservational point of view, of importance is that the assemblages are still all indigenous, and communities still probable function well.

INTRODUCTION

Indigenous invertebrate assemblages of New Zealand are often portrayed as depauperate, lacking some of the more 'advanced' groups of insects like many species of Apididae and Lepidoptera (angiosperm pollinators) (Howarth and Ramsey 1991), while containing an unusually high proportion of Diptera and many other unusual and unique invertebrates. The invertebrate fauna is often portrayed as having many large, slow breeding, poor flying, habitat specific members (Meads 1990), e.g. giant weta, giant land snails, giant earth worms, giant moths, and weevils (Meads 1990). They are described, primarily because of New Zealand's 'long' isolation and variety of climatic changes, as lacking the ability to respond rapidly and effectively to change.

A community's structure, attributes, and functions often change when challenged with disturbances. Disturbances such as invasion, climatic catastrophe and sudden successional development (e.g. invasion of woody spp.) are generally large scale modifiers, and often act together. The magnitude of response of a community depends upon its resistance and resilience. A community with both these features is deemed very stable. New Zealand's invertebrate assemblages are generally considered to have low resilience and a modicum of resistance - leaving them prone to large changes (Howarth and Ramsey 1991).

The special habitats in Tongariro National Park were solely indigenous plant-insect communities, existing in a dynamic mosaic until the 1830s. Over the last 150 years these have been increasingly challenged by modifications (Chapman and Bannister 1990, Atkinson 1981) created by European settlement and land use. Natural habitat changes, due to fires (volcanic), ash deposits, erosion, and succession, have been compounded or superseded by human action. Natural successional stages have been altered by introduced exotic species, e.g. broom, *Ulex*, pasture grasses, *Calluna*, flat weeds, *Pinus contorta*, and human action, e.g. fire, herbicides, grazing, and planting. The increased rate and novelty of these changes is, I believe, changing the normal composition and progression of the invertebrate fauna.

Two issues are prevalent: the effect on invertebrate assemblages of invasion by a dominant, novel, persistent plant; and, within this, the result of accelerated succession brought on by the *Calluna* invasion.

Predicting what changes may occur due to this invasion is complex and dependent on the extent and speed of the invasion. In Tongariro National Park, the transformation has been extensive and relatively fast (20-40 years). This modification has been in the form of: loss in the visually apparency of native plants; mass change in the dominant plant biomass; alteration in herbivore food resource type; and, in many indigenous plant communities, a dramatic change in the architectural structure of the vegetation (cf. Chapter 2). These changes would initially, in theory, result in a decrease in invertebrate diversity, either through loss of taxa, or large scale alterations in the abundances of different taxa (Southwood, Brown and Reader 1979, Lawton 1978, Stinson and Brown 1983). Current wisdom (White 1987) predicts that the taxa exhibiting the greatest change will be the common taxa and not the rare, as was once popularly believed (old wisdom). Further, the common phytophagous taxa will be the most affected because of their close association with, i.e. reliance on, the plant species present. In contrast, as the structural diversity (architecture) of the plant community increases, the invertebrate diversity should like-wise increase (Southwood, Brown and Reader 1979) though, often it is a new set of organisms replacing theold that re-establishes the diversity of a community. This, I believe, will be the case in Tongariro National Park.

As a result of the discussion above I make the following predictions of the effects of *Calluna* invasion on the indigenous invertebrate communities living in native plant communities:

1. Decrease in diversity as measured by number of species;
2. Decrease in the evenness of abundance of species;
3. Abundance of herbivores will be most negatively affected;
4. Change in insect types from resident to tourist (highly mobile) types;
5. Change in the feeding guild structures of assemblages, i.e. increase in proportions of scavengers, detritivores, and predators;
6. Increase in abundance of species utilising complex plant architecture, i.e. spiders.

The predictions are based on the expectation that *Calluna* is a novel food source, too different to allow host range expansion by most invertebrate herbivores, only a few of the most polyphagous herbivores being able to exploit it; and that it becomes the dominant plant biomass in invaded landscapes, reducing the apparency and thus availability of native plant material to invertebrates.

The study of invertebrate assemblages tends to involve large amounts of data. There are, then, many observation portals from which to gain a view of the structure and functioning of those assemblages and the way they are moving in response to change. In this chapter I show differences that may be due to the invasion of *Calluna*.

I have used basic descriptive techniques, correlation techniques (cluster analysis, ordinations), analysis of variance, seasonal comparisons, and measures of diversity and abundance distribution models to examine patterns at the community level. Feeding guild comparisons give a functional view of the assemblages of different habitats. Correlations in assemblage abundance with the changing plant resource base (architecture, successional rank, and nitrogen levels) are presented. Comparison with the herbivorous fauna of *Calluna* overseas illustrates the lack of resource use and the available 'niches' here in New Zealand *Calluna* heath.

METHODS

Invertebrate surveys were conducted to reflect community composition in five prominent vegetation types in Tongariro National Park currently being invaded by *Calluna vulgaris.* The study was conducted on the eastern and western slopes of Mounts Ruapehu and Tongariro. The sampling sites were located along the Desert Road (State Highway 1), and along the National Park-Turangi road (State Highway 47), (Fig. 2.1 Chapter 2). For vegetation and site descriptions refer to Chapter 2. Though the presence of *Calluna* is not the only variable between sites, an effort was made to reduce as many location variables between paired sites as possible.

A range of invertebrate sampling techniques were used, in an effort to cover the usual shortcomings of any one method (Southwood 1978), though limitations in the taxa caught and abundances are acknowledged, as is the lack of description of the Lepidopteran fauna. Late spring to early autumn were the most productive seasons sampled. Winter was very cold, with snow, and sampling with net and bush beating was not productive. Emphasis has been placed on the pit-fall trap and sweep-net records, as their trapping efforts are the most consistent. Pit-fall traps can give satisfactory relationships between taxa type caught and mean density of populations in different habitats and are recognised as the most effective method of sampling ground fauna (Thiele 1977) and demonstrating presence or absence of taxa in various habitats (Watt 1980). Sweep-netting catches the majority of above ground, foliage, and 'on the wing' invertebrates. Thus with the two main methods and the employment of others from time to time, a respectable representation of the types of taxa present and a proportionate measure of their abundances can be achieved and compared; (note: because of temporal sorting difficulties (time) mites and Collembola were omitted). Sampling began in April 1990 and continued until December 1992 in and around the 10 metre by 10 metre plots described in Chapter 2.

Pit-fall traps

Three plastic pails (open surface area 256 square cm, and capacity 6.4 litres) were placed haphazardly in each plot, so their rims sat flush to the soil surface with minimal disturbance to the area around the rim. The soils were compact enough to allow removal and replacement of traps at servicing.

Undiluted Ethylene glycol (90% v/v anti-freeze, BP automotive products; ~200 ml/trap) was used as the killing and preserving agent; its non freezing, non-evaporative and lasting preservative action made it ideal. Tin rooves were installed to prevent snow and rain entering directly. The rooves also provided shelter and warmer areas, possibly leading to congregation of invertebrates. Carrion smells from dead specimens may have created a bias for collecting carrion feeding and carnivorous taxa (Luff 1975); no effort was made to counter this. Run off of surface water was sometimes a problem in winter, leading to traps flooding and lifting. Samples were removed through sieving in the field, then stored in 70 % ethanol; the anti-freeze was reused. Traps were in operation from May 1990 to December 1992. The pit-fall traps were cleared monthly in spring and summer and 2-monthly for the rest of the year.

Sweep-netting

Sweep-netting is a method which catches low-flying invertebrates and those sitting in the top of foliage. Sweep-netting has the restriction that only fine days with low wind result in availability of most insects likely to be caught by this method. Rain or wet foliage rendered this method useless.

An initial trial showed that 5 lines of sweeping with 6 sweeps (one per stride) per line resulted in no new taxa caught by the fifth or sixth line. Thus four lines were swept along each border of the plot, and one perpendicular out from a plot boundary every sampling trip (monthly in summer or bi-monthly in winter. Aerosol insecticide was used to subdue the sample prior to removal from the net.

Bush-beating

Bush-beating was used to catch larger insects, especially beetles and bugs that can be shaken into falling. This method tends to be more specific to phytophagous insects. It is again reliant on good weather and dry conditions. A tray containing alcohol (90% EtOH) was carefully placed under chosen foliage to capture falling invertebrates - 4 beats were delivered per plant. Eight plants were beaten per sampling trip outside the plot and not in any sweep path.

Litter scrapes

A single 20 cm by 30 cm area (10 cm deep) of soil, litter, and prostrate plants was removed intact by spade at each site. Extraction of invertebrates was performed using a Burlies Funnel (40 Watt bulb for 24 hours, stirred once after 12 hours). The invertebrates dropped into water (so there were no rising fumes). This method was done on only the first four sampling events as catches did not differ from pit-fall trap catches.

Sampling regime

The timing of sampling is important and determines the likelihood of a successful catch for sweeping and beating. Invertebrates are active at different times of the day in different weather conditions in different seasons. Most depend upon minium temperature and wind conditions, so that early mornings (cold) are unproductive sampling times, as are late evenings (dark and also cold); mid morning through to mid afternoon is peak time. Because many sites needed visiting between these hours (10 am - 3 pm) a sampling pattern was established. The Desert Road sites were sampled first between 10 am -12 am, then Mangetepopo between 12 am- 2 pm. In the following month's trip the order was reversed.

Analysis

Identification and nomenclature of insect taxa follows "C.S.I.R.O. insects of Australia " (C.S.I.R.O. 1991) and Forster and Forster (1973) for spiders.

The data set is large. To explore the features of the data a spiralling approach from low resolution to higher resolution examination was used. To compare the basic characteristics of the assemblages the total number of taxa and the average number of individuals (abundance) found over the entire sampling program, were extracted; these are presented graphically. The total number of taxa are compared using association tests with a Chi square statistic, while the abundances were subjected to ANOVA and Bonferroni range tests.

Principal component analysis (PCA) was used to separate and group sites based on their species composition. An Analysis of variance was done on the full data set looking for site, trap, and sampling trip influences. The data were then broken down into groups: common taxa of Diptera, Coleoptera, Orthoptera, Homoptera, Heteroptera, and Arachnids, and then the rare taxa; and the groups compared with ANOVA and range tests. The data were first log transformed.

Diversity measures are employed. These measures are still popular tools, though require caution and understanding because data sets treated with different diversity indexes can often give conflicting results (Hairston *et al.* 1968). I have used a Shannon diversity index and the Simpson dominance index (Magurran 1988). The Simpson index (or Yule's index) is weighted towards the abundance of the most common species rather than providing a measure of species richness:

$$D = \sum (ni(ni-1)/ N^*(N-1))$$

were N = total abundance, ni = abundance of the ith taxon. The index (D) decreases as diversity increases; thus, 1/D portrays diversity. The Simpson index has moderate discriminant ability, better than the Berger-Parker index (Magurran 1988). The Shannon index (H) is based on species richness and abundance:

$$H = - \sum ni/N * (\log(ni)/N)/ \log N$$

were ni = number of individuals of the ith species, N = total abundance. The indices are presented graphically.

A presence -absence matrix was constructed for taxa at sites. This allowed a set of clusters (Systat cluster analysis, Euclidean distance, average linkage method) of the sites to be compared with those constructed based on the vegetation (Chapter 2). Five clusters are presented in table form, each based on specific portions of the assemblage data. The first cluster uses all the data; the others use the common invertebrates (frequency > 2, abundance > 5), all invertebrates except spiders, spiders only, and beetles only.

Abundance distributions for each site were fitted to theoretical distribution models (Log series, Negative binomial, Broken stick, Log normal, and Geometric). These models indicate how the resource is allocated, the stability of a system, the successional state, and the 'harshness' of a habitat. Changes to patterns of abundance are evidence of habitat change and indicate the effects of invasion, pollution and succession. For example log-normal distributions most often describe a system that is in ‘equilibrium', and/or not experiencing harsh environmental changes; and beyond the earliest stages of succession, where resource use development has meant a few taxa have become very abundant, while many are ‘quite’ abundant. A log-series fit of a communities abundances implies harsh environmental conditions, or /and early successional stage; development of resource use in this system is not as advanced, and most taxa are in low numbers only. Thus to examine were each site ‘lay’ with respect to its abundance distributions, and hence some measure of its developmental state, computer programmes to fit the data were constructed in QBASIC by Dr I. Henderson (Massey University) based on Pielou (1975, 1977), and May (1974). Distributions were plotted using Octaves on the nominal axis (Magurran 1988), which is a method for lumping successively bigger groups of numbers of individuals into a single number category, e.g. octave 1 = 2 or fewer individuals, 2 = 3-4, 4 = 5-8, ...6 = 17 to 32 etc. The ecological implications of adherence to many abundance models, however, has become increasingly unclear (Gray 1987). May (1975) suggested that 'equilibrium' communities usually fit the log normal. However, it has been argued that log series model fits data from undisturbed ('equilibrium') communities and the lognormal model fits disturbed communities (Kempton and Taylor 1974). Thus assemblages of opportunists or an equilibrium community fit log normal distributions, and log series and geometric fit disturbed communities (Stenseth 1979, Whittaker 1975), though in all cases uncertainty reigns (Gray 1987) (cf. discussion).

Seasonal changes in taxa present and their abundances are graphically illustrated to show *Calluna's* effect on selected groups, particularly Homoptera, Heteroptera, Arachnida and Thysanoptera.

To achieve greater resolution the data have been worked to incorporate feeding guild information (Southwood *et al.* 1982), based on descriptions in C.S.I.R.O. of the families' feeding preferences. Separation into feeding guilds, and examination of the proportions of abundances and taxa in those guilds, gives a functional working view of the systems. The frequency of occurrence and abundance of feeding guilds are presented graphically, and a Chi square contingency table is used to compare the frequency of occurrence of feeding guilds and sites, while a General linear model explains the variability in feeding guild abundances by site. A brief comparison of the herbivorous guild found on

Calluna here in New Zealand, with those of southern England, is presented for comment on utilisation of *Calluna* in the Park.

The last section of analysis involves correlations with plant characteristics measured in Chapter 2. Nitrogen levels, plant architecture, and successional rank (based on vegetation type and height: axis one Fig. 3.4c) are used in the correlations.

RESULTS

Assemblage compositions

In total, seven orders were extracted from the samples: Diptera, Coleoptera, Homoptera, Heteroptera, Orthoptera, Blattodea, and Thysanoptera. Representing the Hymenoptera sampled is the family Formicidae. The Lepidopteran fauna was not successfully sampled. Annelids, through present sometimes in large numbers, are not considered. Within these larger groups a total of 106 families were identified: (see Appendix 3 for a more detailed inventory by site).

Diptera	38 families	5199 individuals
Coleoptera	39 families	2757 individuals
Homoptera	11 families	2776 individuals
Heteroptera	10 families	270 individuals
Orthoptera	5 families	469 individuals
Blattodea	1 taxon level	83 individuals
Thysanoptera	1 taxon level	3117 individuals
Formicidae	several sp.	1824 individuals

The spider fauna (poorly identified) held a total of 56 morpho-species, two of which were Opiliones (Triaenonychidae, Phalangiidae), with a total abundance of 3321 individuals. The most common families were Araneidae, Lycosidae, Tomissidae, Ctenizidae, and Agelenidae.

The most common beetles (Coleoptera) were Carabidae (of which there were at least 7 species, G. Lovei pers. comm.), Staphylinidae, Curculionidae, Lathridiidae, Scarabaeidae, Chysomelidae and Pselaphidae. The most common Diptera belonged to the families Sciaridae, Phoridae, Mycetophilidae, Chironomidae, Tipulidae, Cecidomyidae, Tephritidae, Muscidae and Empididae. Each of the Dipteran families had several species, e.g.: the family Sciaridae was represented by *Sciara rufulenta* and S. *harrisa;* Mycetophilidae by *Rypatula brevis*, *Tetagoneura obsura* , *Mycetophila subtenebroia* and *Mycomyra sp.* (Dr I. Andrews, Department of Biochemistry, Massey University). There were also new species found, e.g. a new *Sciara* species, a new Chloropidae *Tricimba* sp. and a new genus of Margarodidae (scale insect). Further taxonomic work on the collection is sure to reveal other new species. Common Homoptera and Heteroptera were Aphididae, Cicadellidae, Delphacidae, Psyllidae and Coccoidea, Lygaeidae and Miridae. Common Orthoptera were Stenopelmatidae, Rhaphidophoridae and Acrididae. Table 3.1 illustrates the 'most important' taxa at each site; those with the highest abundances, or most frequently encountered in samples.

The number of different taxa caught over the sampling period was higher in the *Calluna* invaded partner sites than in the indigenous sites except for tussock/*Calluna* and flax/*Calluna* (Table 3.2). Total abundances were also higher in the *Calluna* invaded pair of all sites except in the tussock site. Average abundance, the mean number caught per sampling trip, tended to be greater in the *Calluna* invaded habitats (Fig. 3.1), except in flax/*Calluna*. The average abundances between habitats, however, were not statistically significantly different (P = 0.488).

Variation between habitats

Abundance variations

Table 3.2 shows the number of taxa in each major group found and their abundances; the analysis by ANOVA tests the differences between sites for these groups. There were significant differences in all the common taxonomic groups between sites and sampling trips (Table 3.3), but only the 'rare' Coleoptera of the 'rare' invertebrates exhibited any statistically significant difference, site 9 (flax) standing out as unique. The range tests of 'rare' invertebrates (Table 3.4) show that there are generally two very overlapping groups of habitats with generally only one or two sites being different from the rest, e.g. for rare spiders only sites 2 (tussock/*Calluna*) and 8 (manuka/*Calluna*) are different; site 9 (flax) exhibits itself as special containing unusual numbers of both rare and common beetles. The common invertebrates have more complicated patterns of similarity and dissimilarity (Table 3.4); no general trends can be determined, except to state that the sites of mid succession (3 to 7) appear often closer together.

Trap type was also significant for the type of invertebrate caught ($P<0.001$), except for common Hemiptera ($P = 0.527$) and 'rare' Homoptera ($p = 0.289$), where pit-fall, sweep-net, or bush-beating were equally likely to catch these organisms. In general, pit-fall traps specifically caught Orthoptera, Lycosidae, Opiliones, Ctenizidae, Carabidae, Staphylinidae, Annelids, and Collembola, while sweep-netting catches were dominated by Diptera and web spinning spiders. Cicadidae (Homoptera: Cicadidae) though present in numbers, were rarely caught, and their larvae, hidden in the root systems, were not caught at all. Chapter 4 describes a survey method that gives a good estimation of Cicadidae larvae numbers per type of plant. Lepidoptera were also not caught by the methods used. Light trapping was attempted on several occasions, some even seemingly ideal, but, excepting one night, catches amounted to one or two individuals only.

Variation in diversity between habitats

The Shannon index suggests that diversity is greatest in the invaded habitats. In descending order the habitats are arranged thus: tussock/*Calluna* > tussock > manuka/*Calluna* > flax > *Dracophyllum*/*Calluna* > *Calluna* > *Dracophyllum* > flax/*Calluna* > *Gleichenia* > *Gleichenia*/*Calluna* > manuka (Fig 2a). Only *Gleichenia* and flax habitats held more 'diverse' invertebrate assemblages than their invaded partners. The only pair of sites not exhibiting a significant difference in diversity were the *Dracophyllum* and *Dracophyllum*/*Calluna* sites.

The Simpson index (Fig. 3.2b), measuring dominance, shows that the manuka assemblage has the least even distribution of individuals amongst its taxa (dominated by Psyllids). The *Dracophyllum*/*Calluna* exhibited the most even spread of individuals amongst its taxa. Generally the more 'stable' sites, those not recently disturbed, i.e. the indigenous and *Calluna* only sites, exhibit the most evenness (higher Simpson index).

Fig. 3.1

Average abundance per trapping event of invertebrates from sites in Tongariro National Park (error bars are standard error of the means (n = 10))

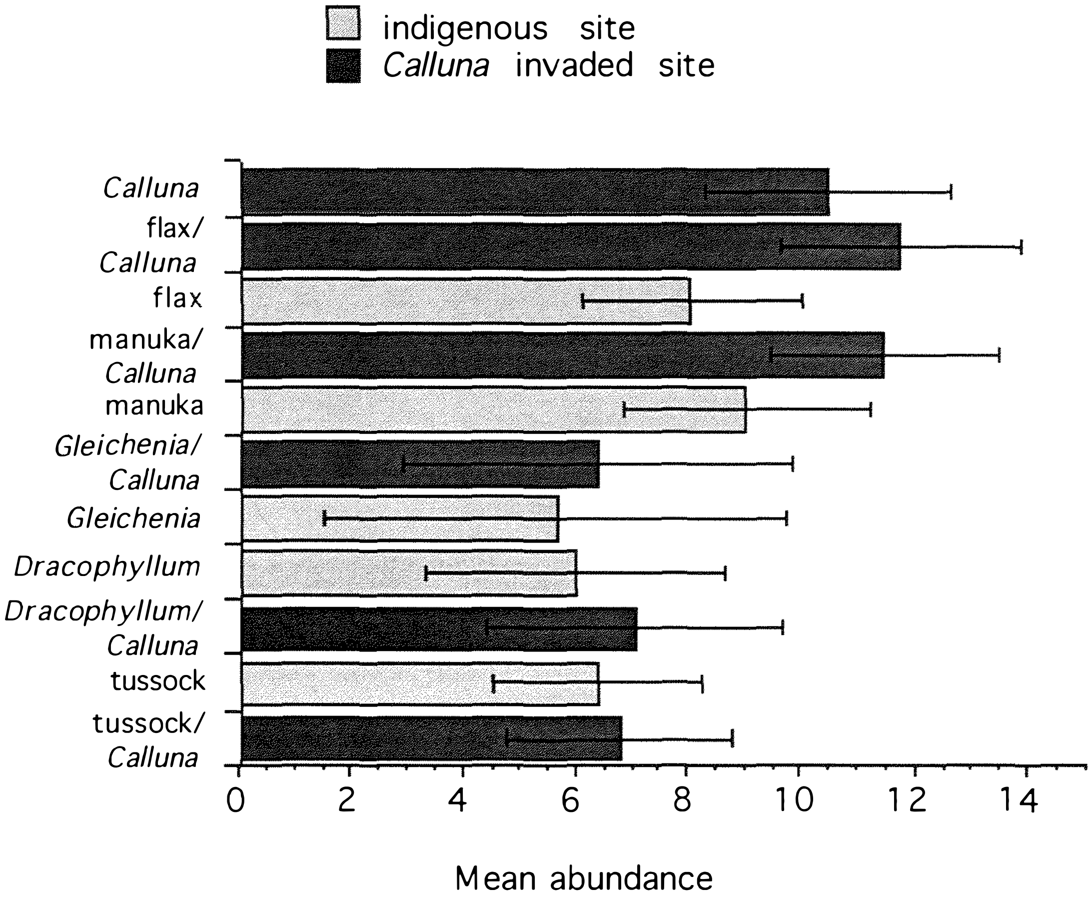


Table 3.1 The most common taxa with the greatest abundances from each site; in bold are those taxa that are a special feature of that habitat. Taxa in the abundance columns not in the frequency column are those whose frequency is less than 5 but whose abundance are large.

site	most frequent species	Abundance	site	most frequent	Abundanace
tussock/*Calluna*	frequency >10		**tussock**	frequency >11	
	Thysanoptera	**554**		**Formicidae**	**494**
	Formicidae	239		**Stenopalmatidae**	**214**
	Lycosidae	130		**Lycosidae**	**207**
	Chironomidae	72		Sciaridae	111
	Sciaridae	65		Mycetophilidae	41
	Araneidae	35		Thysanoptera	35
	Mycetophilidae	35			Agelenidae 76
		Scarabaeidae 53			Scarabaeidae 61
		Pisauridae 44			
Dracophyllum/Calluna Carabidae ? Chloropidae ?	frequency ≥ 5		***Dracophyllum*** ? Stenopelmatidae Phoridae Mycetophilidae	frequency ≥ 5	
	Thysanoptera	283		Formicidae	357
	Formicidae	262		Lycosidae	85
	Phoridae	26		Carabidae	41
	Lycosidae	45		Chironomidae	60
	Sciaridae	64		Sciaridae	68
	Chironomidae	52		Curculionidae	27
	Mycetophilidae	30			Psyllidae 36
		Agelenidae 88			
		Rhapidiphoridae 25			
		Coccoidea 28			
		Salticidae 63			
Gleichenia/*Calluna*	frequency ≥ 5		**Gleichenia**	frequency ≥ 5	
	Psyllidae	242		Araneidae	94
	Lycosidae	91		Chironomidae	75
	Chironomidae	61		Psyllidae	64
				Cicadellidae	20
		Thysanoptera 42			Tephritidae 29
manuka/*Calluna*	frequency ≥ 9		**manuka**	frequency ≥ 9	
	Thysanoptera	**1432**		**Psyllidae**	**1277**
	Psyllidae	317		Chironomidae	145
	Chironomidae	166		Araneidae	66
	Araneidae	79		Coccoidea	37
	Sciaridae	45		Ceratopongonidae	48
	Lycosidae	35		Curculionidae	16
					Sciaridae 37
		Phoridae 320			Carabidae 58
		Formicidae 123			Coccoidea 39
		Carabidae 88			Lathridiidae 43
		Cicadellidae 63			
flax/*Calluna*	frequency ≥ 10		**flax**	frequency ≥ 10	
	Mtcetophilidae	**974**		**Staphylinidae**	**361**
	Thysanoptera	**402**		Sciaridae	153
	Opilione	100		Chironomidae	113
	Chironomidae	252		Araneidae	81
	Psyllidae	88		Mycetophilidae	72
	Lycosidae	73		Opilione	49
	Araneidae	51		Coccoidea	46
		Formicidae 233			**Carabidae 650**
		Phoridae 144			**Lathridiidae 241**
		Lathridiidae 60			Coccinellidae 64
					Phoridae 57
Calluna	frequency ≥ 7				
	Araneidae	**447**			
	Phoridae	**371**			
	Psyllidae	229			
	Chironomidae	199			
	Lycosidae	67			
	Muscidae	60			
	Sciaridae	42			
		Thysanoptera 313			
		Scarabaeidae 254			

Table 3.2 Summary of numerical invertebrate data of each habitat for each of the major taxonomic groups from Tongariro National Park (abun = total abundance, taxa = number of taxa). Total taxa includes other taxa not mentioned here, eg. Blattodea.

Habitat	Coleoptera		Diptera		Homoptera		Heteroptera		Orthoptera		Spiders		Ants	Thrips	total
	taxa	abun	taxa	abun	taxa	abun	taxa	abun	taxa	abun	taxa	abun	abun	abun	taxa
tussock	15	152	25	420	8	107	4	77	5	252	21	449	494	35	101
tussock/*Calluna*	9	129	23	365	5	27	3	42	4	89	20	342	239	554	85
Dracophyllum	10	114	19	122	7	76	2	5	2	29	19	190	357	5	80
Dracophyllum/Calluna	9	65	17	161	7	56	4	8	3	34	20	291	262	283	65
Gleichenia	4	5	13	145	4	89	1	1	0	0	12	134	2	0	34
Gleichenia/Calluna	9	19	21	126	3	248	2	2	1	1	11	152	7	42	60
manuka	22	207	21	297	5	1326	7	17	1	6	22	212	11	023	81
manuka/*Calluna*	22	202	28	649	8	395	8	65	1	18	17	219	123	1432	103
flax	17	1413	25	551	6	92	3	10	3	6	24	274	15	28	104
flax/*Calluna*	14	113	21	1633	6	114	3	23	2	32	20	354	233	420	88
Calluna	15	331	28	878	6	251	2	15	1	4	21	689	37	313	96

Table 3.3. Anaylsis of variance significance levels comparing selected taxonomic groups between sites, trips, traps, and site interactions (- = no significant difference ($P > 0.05$), *= $P < 0.05$,**= $P < 0.001$, ***= $P < 0.0001$).

See Appendix 2 for details as to the mean number of the groups per site and the families of taxa that represent each group.

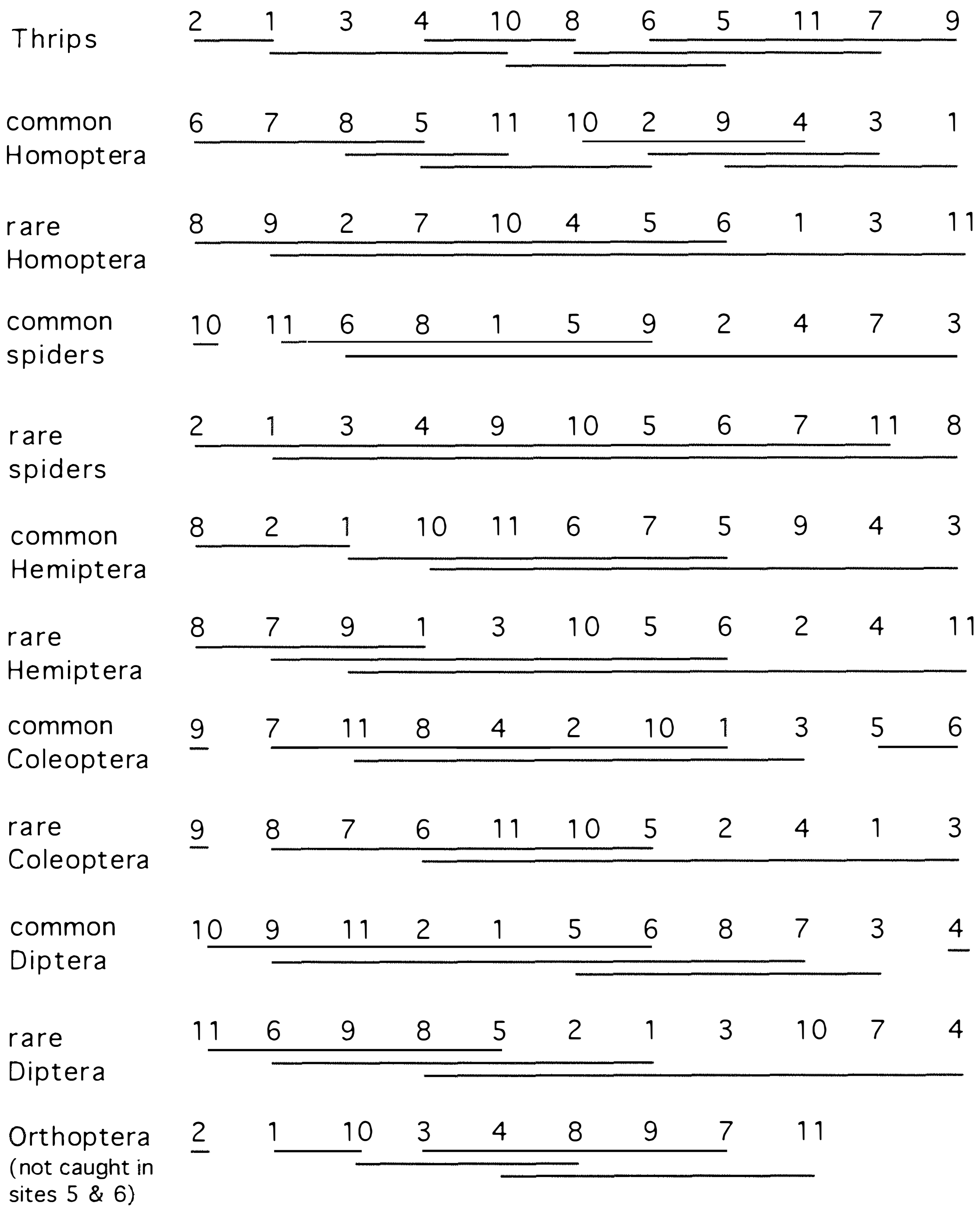
dependent variable	abundance	site	trap	trip	site*trap	site*trip
common Diptera	**5065**	***	***	***	**	-
common Coleoptera	**2116**	***	***	***	*	*
common Homoptera	**2760**	***	*	***	***	***
common Hemiptera	**231**	***	-	***	*	-
common Orthoptera	**462**	***	***	***	***	-
common spiders	**2757**	***	***	***	***	-
rare Diptera	**252**	**	***	***	-	-
rare Coleoptera	**284**	***	***	***	***	-
rare Homoptera	**23**	-	-	***	-	-
rare Hemiptera	**34**	-	***	**	-	-
rare spiders	**883**	-	***	***	-	-
Thrips	**3117**	***	***	***	-	***

Table 3.4

Range test summary comparing sites by distribution of abundances of common and 'rare' taxa

1 = tussock
2 = tussock/*Calluna*
3 = *Dracophyllum*
4 = *Dracophyllum/Calluna*
5 = *Gleichenia*

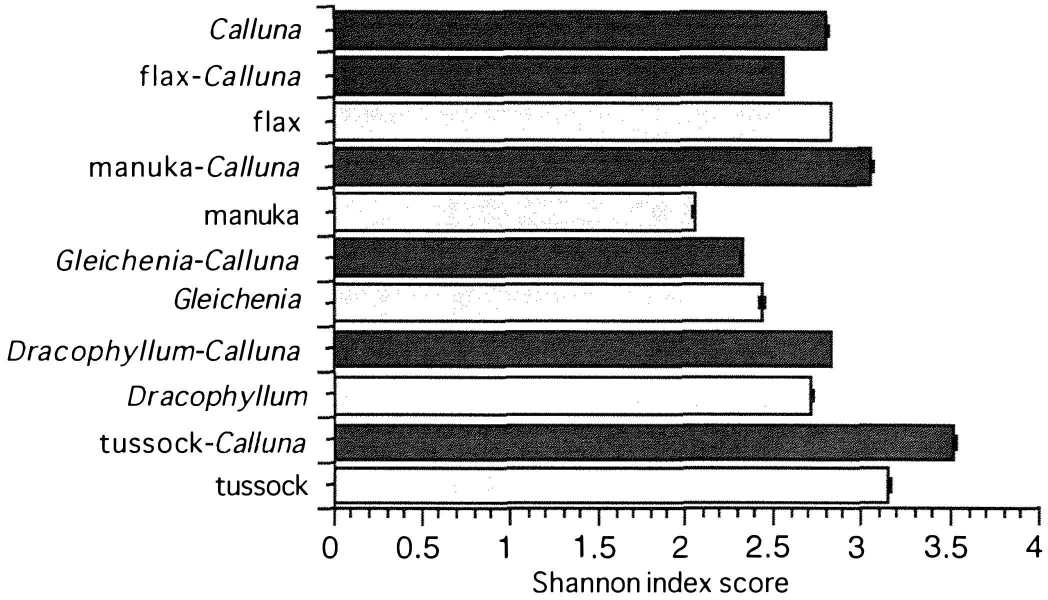
6 = *Gleichenia/Calluna*
7 = manuka
8 = manuka/*Calluna*
9 = flax
10 = flax/*Calluna*
11 = *Calluna*



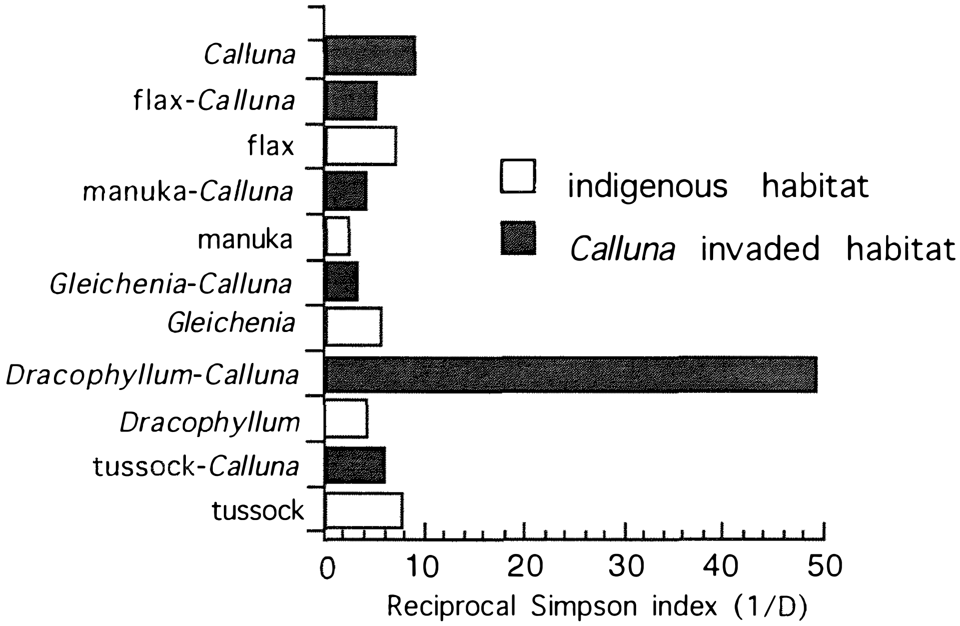
Thrips	2	1	3	4	10	8	6	5	11	7	9
common Homoptera	6	7	8	5	11	10	2	9	4	3	1
rare Homoptera	8	9	2	7	10	4	5	6	1	3	11
common spiders	10	11	6	8	1	5	9	2	4	7	3
rare spiders	2	1	3	4	9	10	5	6	7	11	8
common Hemiptera	8	2	1	10	11	6	7	5	9	4	3
rare Hemiptera	8	7	9	1	3	10	5	6	2	4	11
common Coleoptera	9	7	11	8	4	2	10	1	3	5	6
rare Coleoptera	9	8	7	6	11	10	5	2	4	1	3
common Diptera	10	9	11	2	1	5	6	8	7	3	4
rare Diptera	11	6	9	8	5	2	1	3	10	7	4
Orthoptera (not caught in sites 5 & 6)	2	1	10	3	4	8	9	7	11		

Fig. 3.2 Shannon & Simpson indices calculated for each site using abundance values and number of taxa.
(Standard error of the index, as calculated by the software (Dr. Henderson pers comm.), is shown for the Shannon index)

a. Shannon index



b. Simpson index



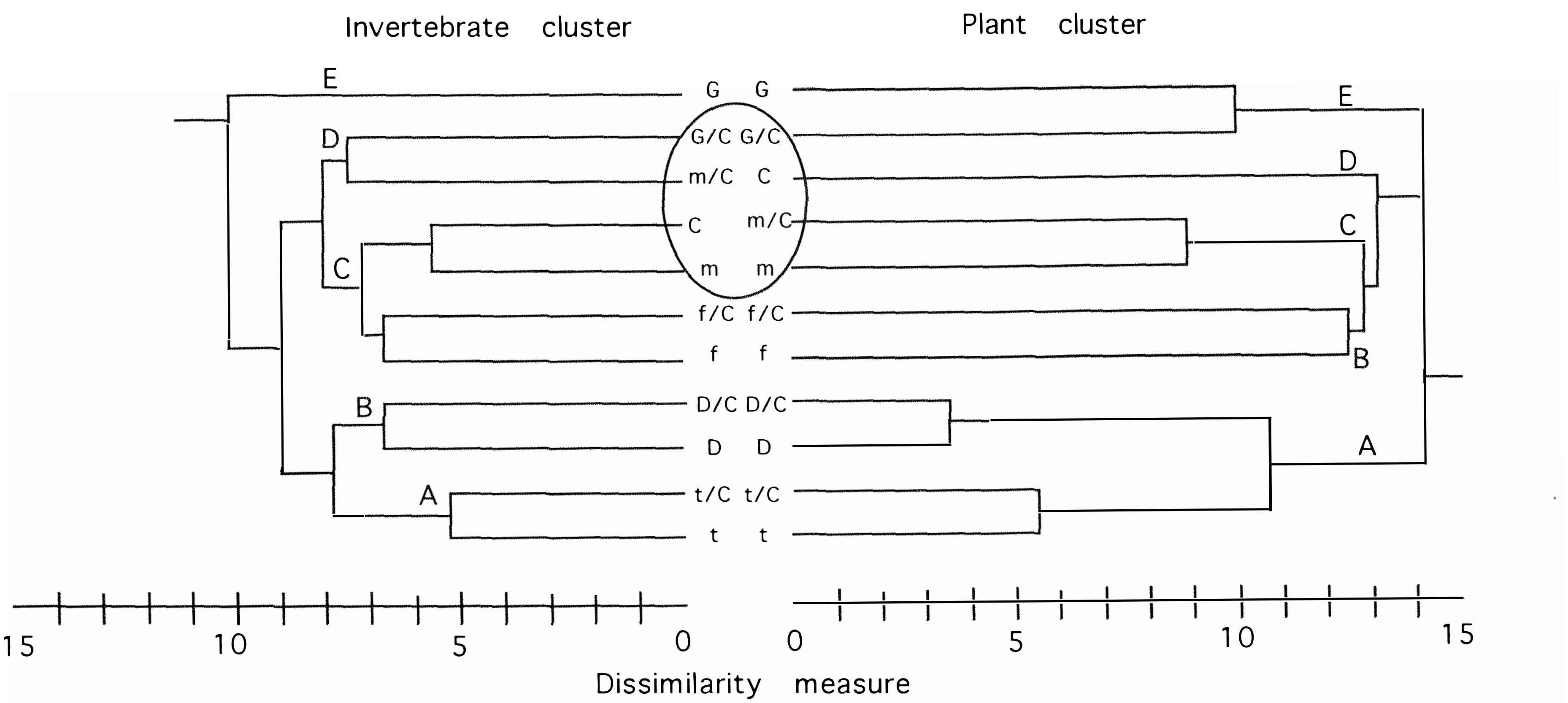
Assemblage associations

Figure 3.3 shows a coupling of the dendrograms produced from cluster analysis of all the invertebrate data and the plant data of Chapter 2. Dendrograms are organised so as to highlight the areas of non-overlap between them. Each dendrogram (Fig. 3.3) showed accurate pairing of the indigenous sites with their respective *Calluna* invaded partner, except *Gleichenia* which stood out as most different. The *Gleichenia/Calluna* site paired with the *Calluna* alone site. The eastern Park sites cluster together separate from the western sites. Aside from *Gleichenia*, the invertebrate pairings are very similar, if not better, than those attained from cluster analysis of the vegetation species (Fig. 3.3). Table 3.5 summarises the outcome of cluster analysis on the special groups, the letters showing groupings at the fourth level of branching. The cluster analysis of common invertebrates only (those with frequency of occurrence > 2 and abundances ≥ 5) gave even tighter groupings (less distance before joining) than that of the whole data set. In this dendrogram *Gleichenia* pairs with its vegetative partner *Gleichenia/Calluna*, but remains separate from the other habitats (Table 3.5). Flax now pairs with manuka and manuka/*Calluna*, and flax/*Calluna* with the *Dracophyllum-Dracophyllum/Calluna* complex. The *Calluna* only site is very dissimilar. The removal of spiders and beetles from the full data set resulted in separation of the *Gleichenia* habitat again, and grouped the *Calluna* alone with the tussock complex, while placing the *Gleichenia/Calluna* closest to the flax and manuka complexes. Further reducing the data to spiders only or beetles only (Table 3.5) caused changes in relationships to the flax-flax/*Calluna* complex, associating the flax with none or with the manuka complex respectively, and the flax/*Calluna* with *Calluna* only or *Gleichenia/Calluna* respectively. In general tussock-tussock/*Calluna*, *Dracophyllum-Dracophyllum/Calluna* and manuka-manuka/*Calluna* habitats always cluster out as first pairings, while *Gleichenia* was most dissimilar. The flax habitat is most variable, though often associated with manuka-manuka/*Calluna*. The *Gleichenia/Calluna* often forms a triplet with *Calluna* alone and flax/*Calluna* instead of pairing with the *Gleichenia* site. The *Calluna* invaded habitats are still very much more like their indigenous partners than like the *Calluna* 'monoculture' assemblage, which is relatively distinctive regardless of the taxonomic group analysed.

Comparison by ordination techniques

The ordination based on abundance and frequency values from the entire data set (Fig. 3. 4 a,b) clearly separate the eastern sites from the west on axis 2, and the tussock grasslands from the *Dracophyllum* shrublands on axis 1. It is, perhaps, more clearly a successional cline than seen in the vegetation ordination (Fig. 3.4c), but also represents a cline from a dry, sandy soil, flat terrain, with high wind to wet, peaty soil, on rolling hills, with more shelter. In both ordinations flax and flax/*Calluna* are at the extreme ends of the plot on axis one, and separate from the other groupings. The western *Calluna* invaded sites share similar abundances, leaving *Gleichenia* and flax on their own, while the frequency

Fig. 3.3 Cluster diagram of sites based on presence/absence of plant species (Chapter 2), and invertebrates (Euclidean distance; average linkage method). highlights where differences occur



key

t	tussock	m	manuka
t/C	tussock/*Calluna*	m/C	manuka/*Calluna*
D	*Dracophyllum*	f	flax
D/C	*Dracophyllum*/*Calluna*	f/C	flax/*Calluna*
G	*Gleichenia*	C	*Calluna*
G/C	*Gleichenia/Calluna*		

Table 3.5 Cluster analysis summary from varied portions of the invertebrate data and plant data of Chapter 2, showing the extent to which cluster analysis of the vegetation and the various invertebrate taxa are comparable.

Common invertebrates had frequency > 2 and abundance > 5 individuals.
Groups (clusters) were assigned a letter label at the fourth level of branching of the cluster dendrogram. Those with the same letter across a row fall into the same cluster. There is usually one main group and a few side groups.

cluster analysis	tussock	tussock/ *Calluna*	*Dracophyllum*	*Dracophyllum*/ *Calluna*	*Gleichenia*	*Gleichenia*/ *Calluna*	manuka	manuka/ *Calluna*	flax	flax/ *Calluna*	*Calluna*
common invertebrates	A	A	A	A	E	D	B	B	B	A	C
plants	A	A	A	A	E	E	C	C	B	B	D
spiders	A	A	B	B	E	D	B	B	F	C	C
beetles	A	A	D	D	E	C	B	B	B	C	C
all but spiders & beetles	A	A	C	C	E	D	B	B	B	B	A
all invertebrates	A	A	B	B	E	D	C	C	C	C	D

Fig. 3.4

Ordination of sites based on (A) abundance, (B) frequency, of invertebrates, other than spiders, and (C) vegetation Groupings are circled by eye.

site names

1 = tussock
2 = tussock/*Calluna*
3 = *Dracophyllum*
4 = *Dracophyllum*/*Calluna*
5 = *Gleichenia*
6 = *Gleichenia*/*Calluna*
7 = manuka
8 = manuka/*Calluna*
9 = flax
10 = flax/*Calluna*
11 = *Calluna*

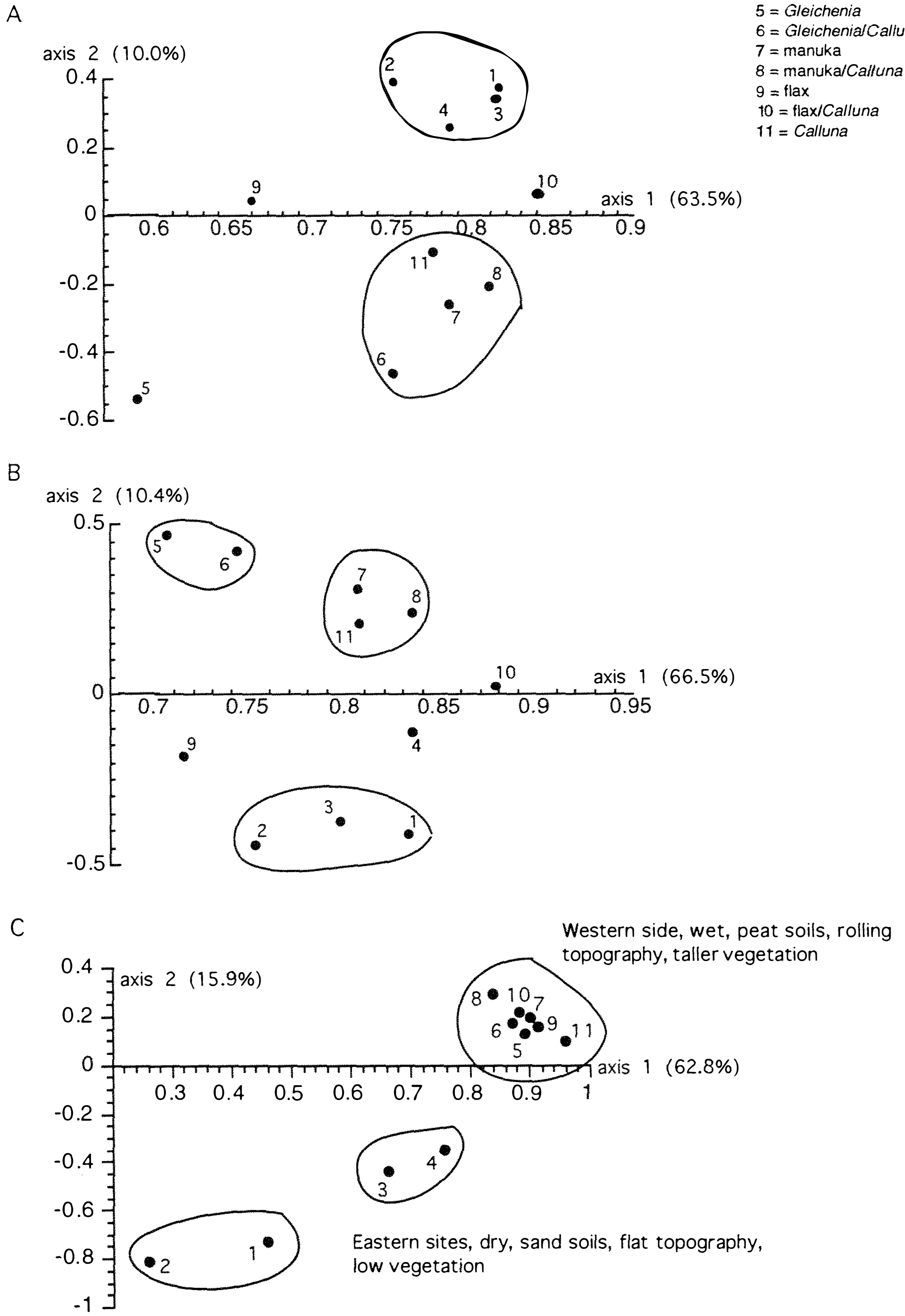
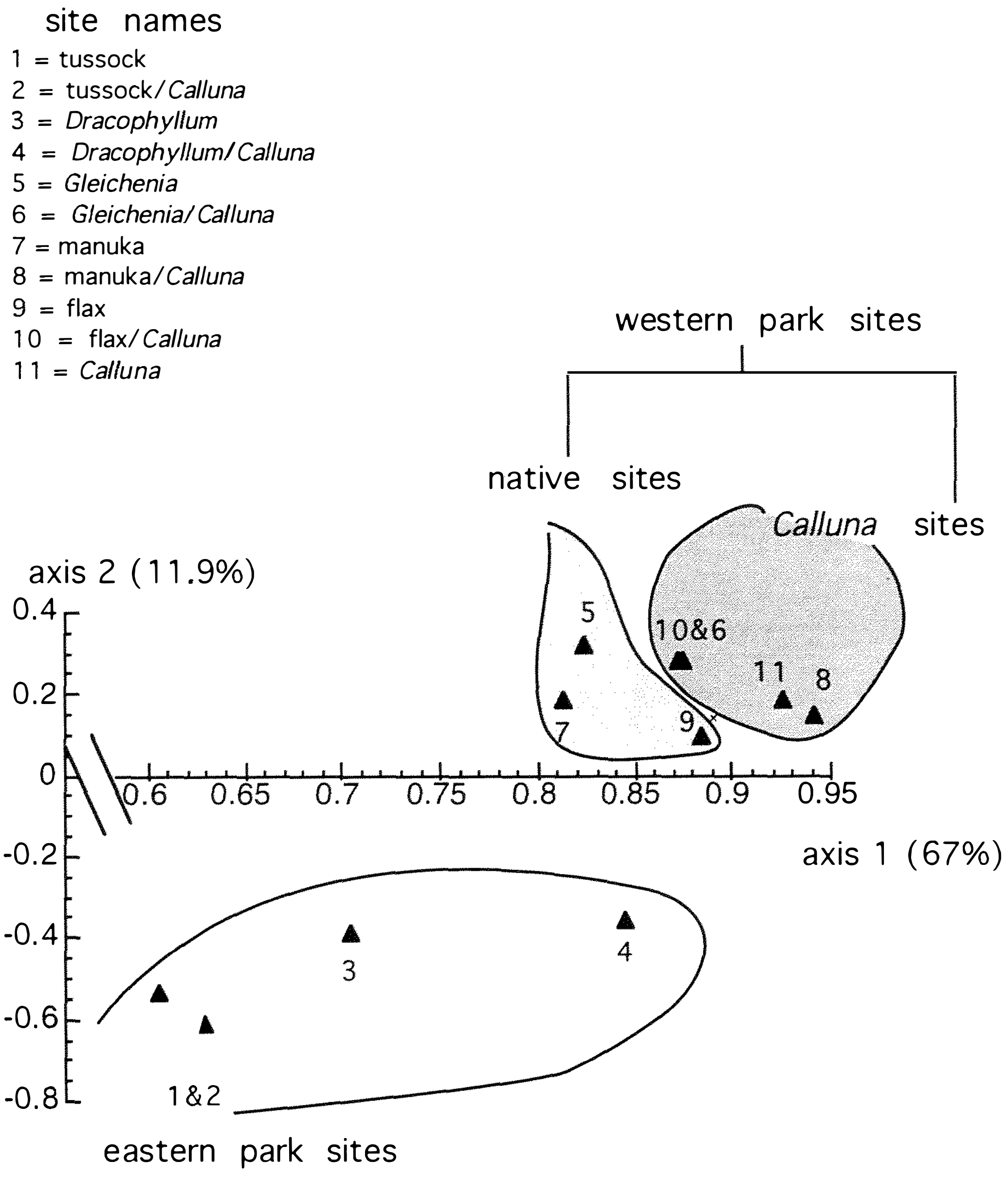


Fig. 3.5

Ordination of sites based on spider abundance and taxon number. Groupings are circled by eye.



plot shows *Calluna* only and the manuka complex as closely associated. The *Gleichenia/Calluna* is most like its partnered site. Figure 3.5, representing the spider data ordination, again shows the east-west divide, but, more interestingly, separates the indigenous habitats from the invaded.

Invertebrate abundance distribution patterns

Table 3.6 demonstrates the fit and maximum-log-likelihood (the smaller the likelihood the better the fit) of each model fitted to the abundance distributions from each habitat. The best fit was always the log normal. The indigenous habitats also fitted the log series. All habitats fitted the Geometric distribution, but no maximum-log-likelihood values were obtained to compare, as these were fitted by regression and not by a more complex program allowing maximum-log-likelihood values to be calculated; the *r*-values for this model did suggest good fits. The plots of number of species per abundance class (Fig. 3.6 a-f) show that after invasion there is a reduction in numbers of individuals representing the lower octave categories (1 or 2 to 3 present) in the tussock (Fig. 3.6 a) and *Dracophyllum* habitats (Fig. 3.6 b), suggesting a transition from log series to log normal. Manuka, flax, and *Gleichenia* habitats (Figs. 3.6 c,d,e, respectively) show an increase, or no change in abundance distributions of taxa. The distribution in the *Calluna* only habitat (Fig. 3.6 f) is most dissimilar to all other habitats, seeming bimodal, having a small, yet clear, peak around the seventh octave. The *Gleichenia* and *Gleichenia/Calluna* have the same distribution but there are more individuals in the invaded site (Fig. 3.6 c).

Seasonal variation

Most of the common families were present throughout the sampling period in relatively constant numbers. The exceptions were Thysanoptera, which had a population explosion when *Calluna* flowered (March-April), most likely because they make use of the pollen and nectar resources. Scarabaeidae and orb spinning spiders all so increased numbers in the *Calluna* heath in January, Psyllids in manuka in December, and Carabid beetles in flax in January.

Trip time was found to be significant, most invertebrates being much more abundant in the summer months than the winter (Table 3.3). Thrips were more abundant at *Calluna* flowering than any other time, represented by a significant difference attained in the site*trip interaction (Table 3.3).

Only two habitats showed any appreciable seasonal difference from their partnered, invaded habitats, in their insect fauna; tussock-tussock/*Calluna* (Fig 7 a,b) and *Gleichenia* -*Gleichenia/Calluna* (Fig. 3.8 a,b). In the tussock complex the number of taxa peaked in January reaching ca. 40 taxa; this midsummer peak was not nearly so high in the tussock/*Calluna*, reaching ca. 30 taxa. The number of individuals followed a similar trend (Fig. 3.7 b) until the flowering of *Calluna* (February-April), when a population explosion of thrips, presumably utilising the pollen and nectar resources of *Calluna*, caused numbers of individuals in the habitat to remain much higher than would be found in tussock grasslands at this time. The *Gleichenia/Calluna* habitat (Fig. 38 a) had maximum numbers of taxa in December-January (ca. 26), approximately 20 taxa more than in the *Gleichenia* at the same time. The number of individuals in

Table 3.6 Abundance model fits (with maxmium log likelihood values) of the invertebrate data (see discussion for details).
Fit of the model was by Chi square, a √ indicating a fit, or a x for no fit.

	log series		negative binomial		broken stick		log normal		Geometric	
site	fit	max. log	fit	max. log	fit	max. log	fit	max. log	r-sq	fit
tussock/*Calluna*	x	-186.8	x	-186.8	x	-210	√	-183.97	.75	√
Dracophyllum/*Calluna*	√	-146.6	√	-146.6	x	-171	√	-144.95	.92	√
Gleichenia/*Calluna*	x	-99.7	x	-99.71	x	-129	√	-95.1	.80	√
manuka/*Calluna*	√	-248.9	x	-248.9	x	-330	√	-241	.87	√
flax/*Calluna*	√	-190.6	√	-188.6	x	-245	√	-186.4	.90	√
Calluna	x	-202.7	√	-202.7	x	-247	√	-202	.92	√
tussock	√	-221	√	-225.9	x	-257	√	-144.9	.96	√
Dracophyllum	√	-135	√	-135.2	x	-159	√	-134	.94	√
Gleichenia	√	-65.8	√	-65.6	x	-76.2	√	-65.8	.90	√
manuka	√	-194.9	x	-194.9	x	-262	√	-186.3	.87	√
flax	√	-215.9	√	-215	x	-262	√	-214.8	.93	√

Fig. 3.6

Graphs of abundance per octave; comparison of abundance distributions between each native site, and its partner dominated by *Calluna*. Where dashed horrizontal lines meet solid lines, then the two lines follow the same course.

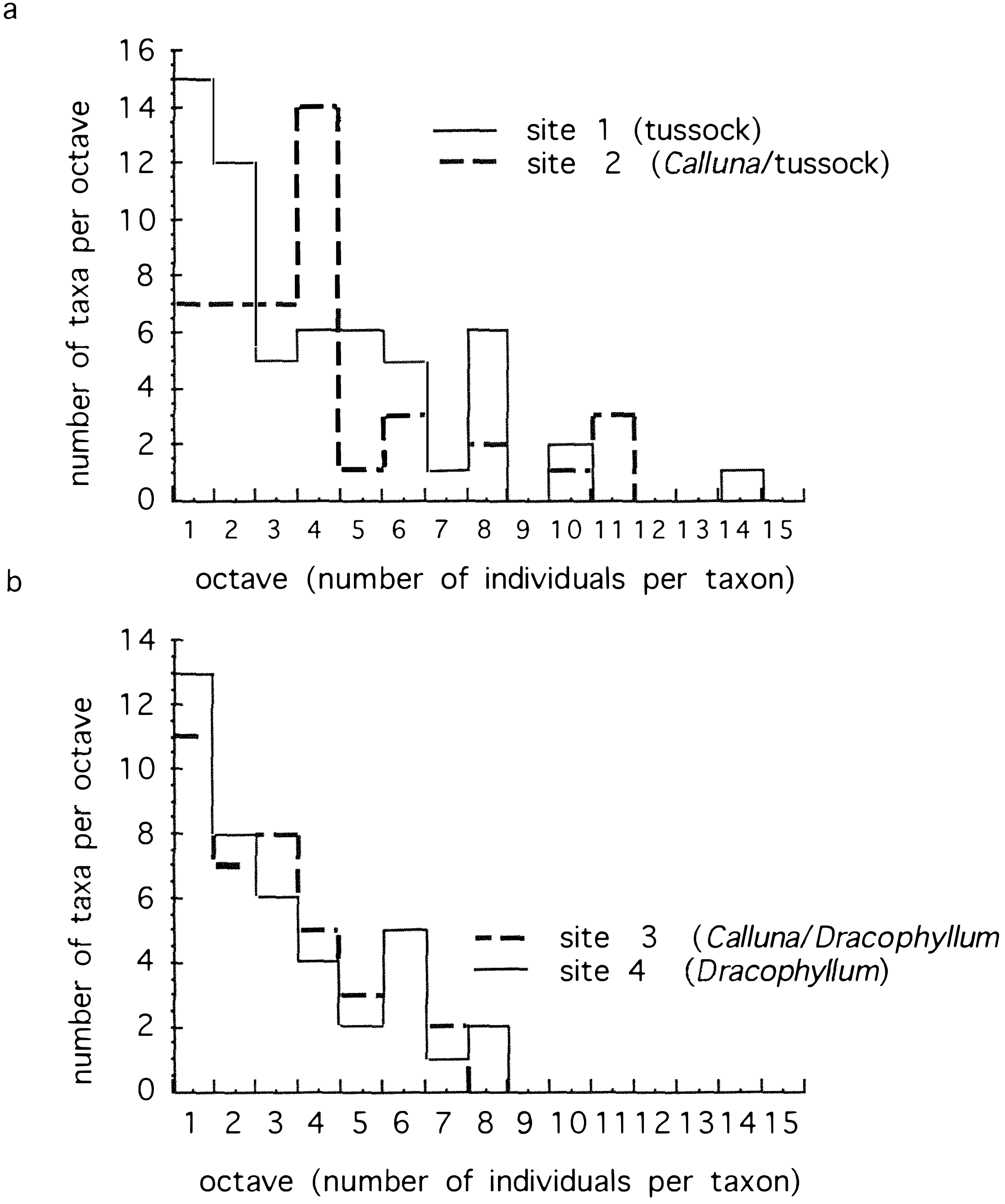
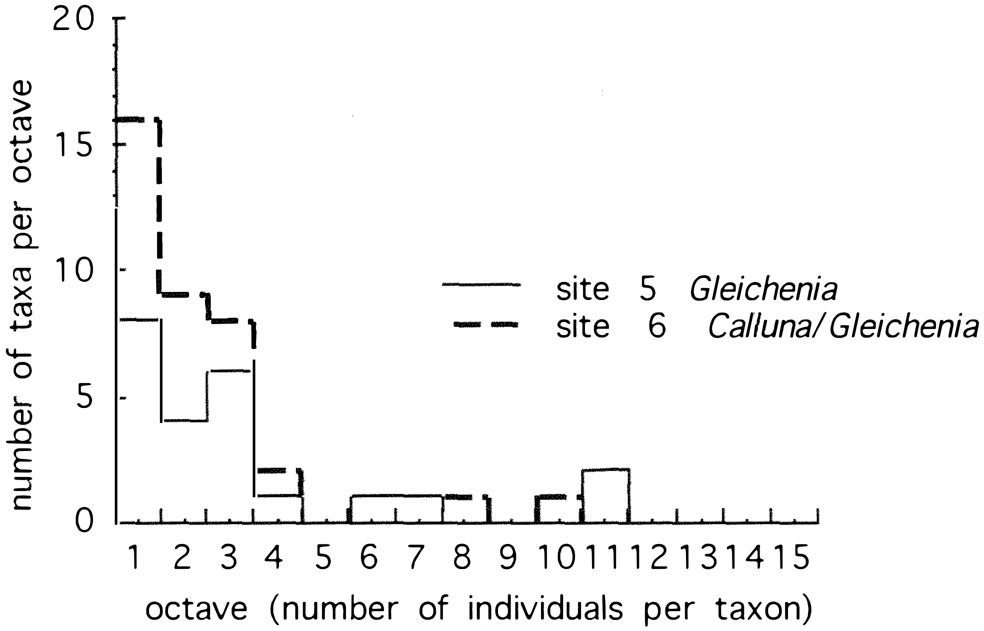


Fig. 3.6

Abundance distributions continued.
(Again, where dashed lines converge with solid, they follow the same course.)

c



d

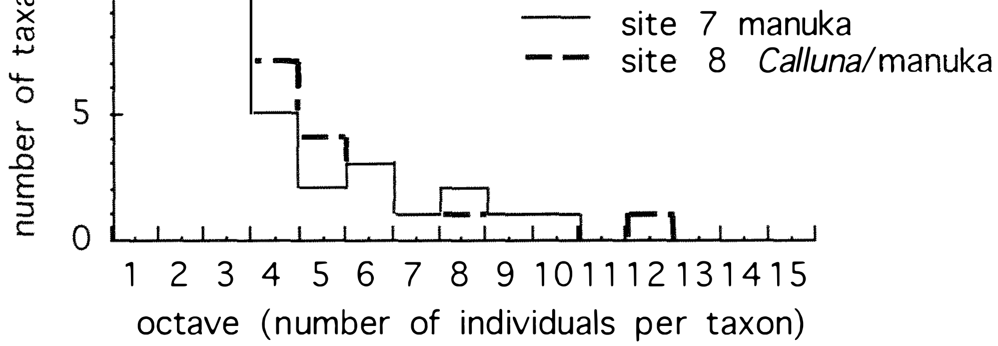


Fig. 3.6

Abundance distributions continued.
(Again, where dashed lines converge with solid, they follow the same course.)

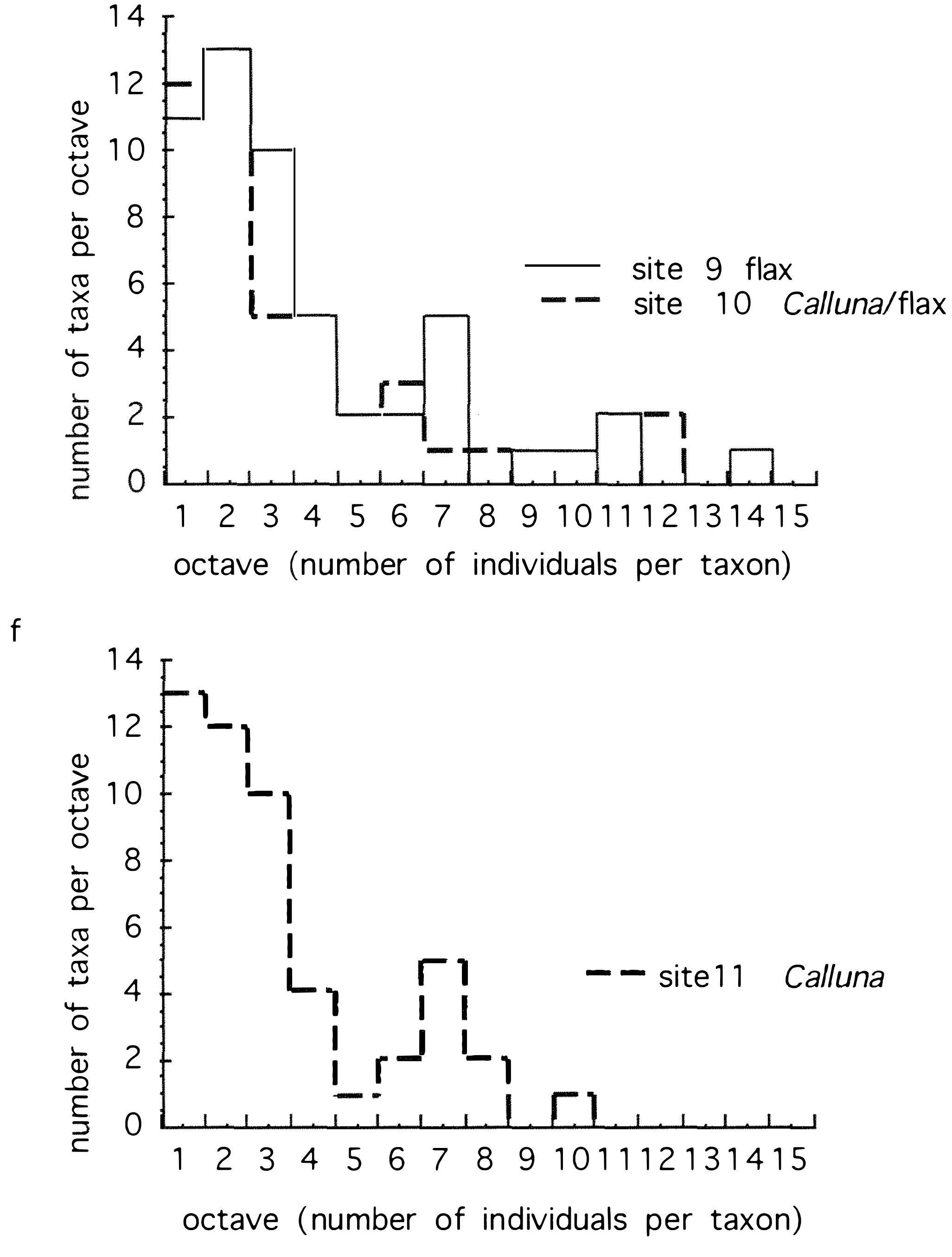


Fig. 3.7

Seasonal variation in the number of taxa & total abundance of those taxa at the tussock and tussock/*Calluna* sites. Data are from one summer period to the next.

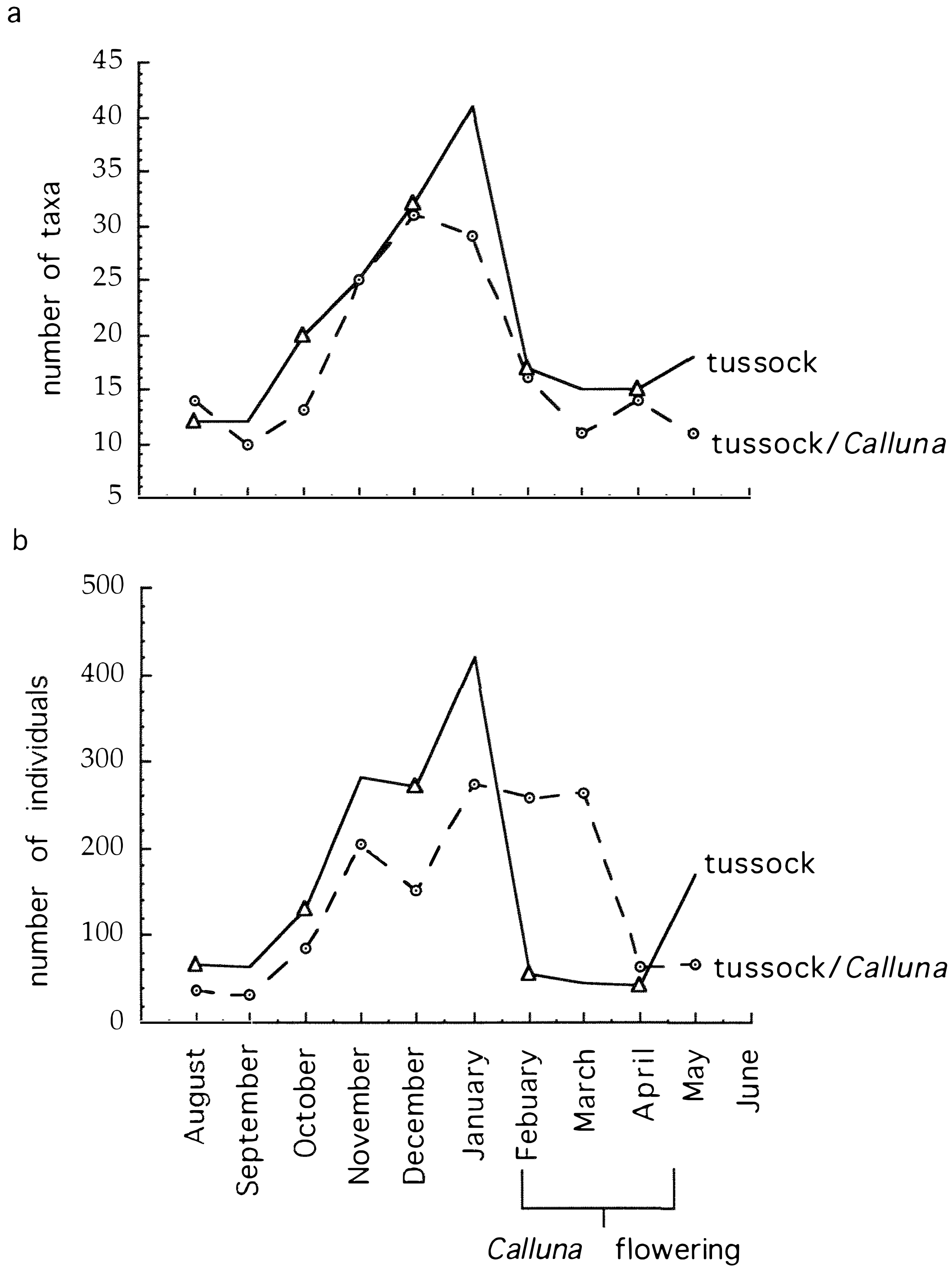


Fig. 3.8

Seasonal variation in the number of taxa & total abundance of those taxa at the *Gleichenia* and *Gleichenia/Calluna* sites. Data are only over two summer periods and one winter.

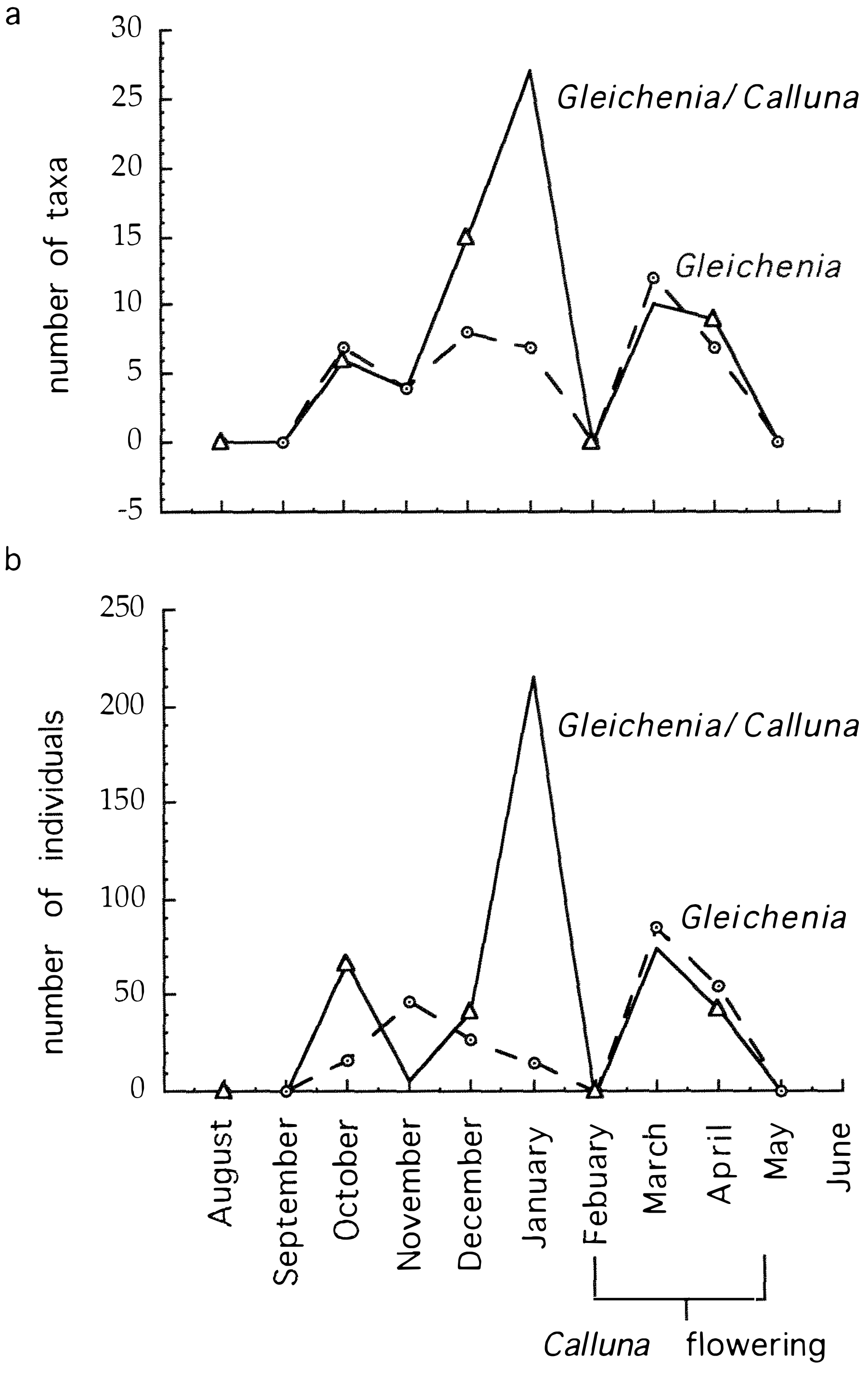
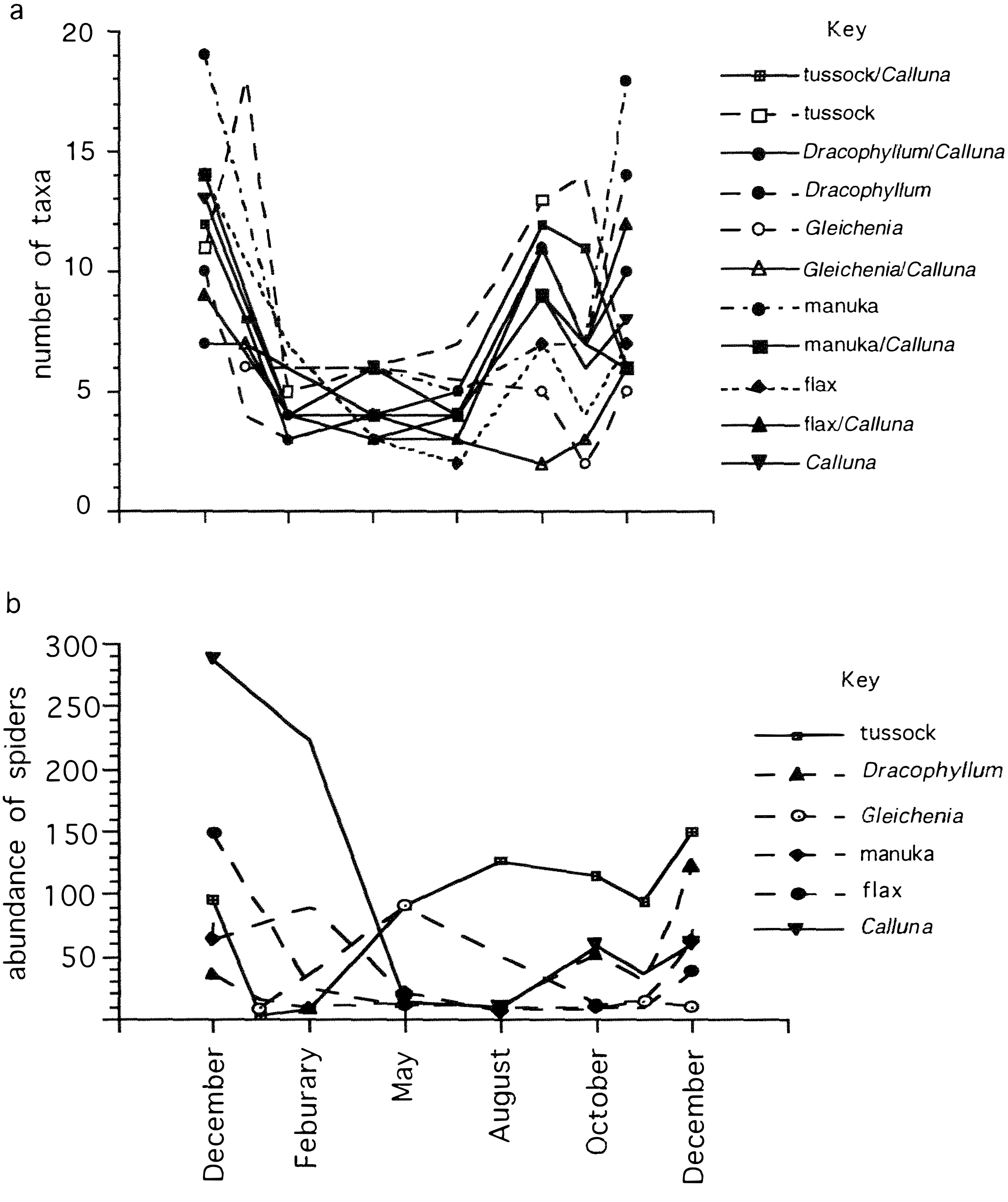


Fig. 3.9

(a) Number of taxa of spiders present in all habitats, and (b) seasonal abundance of spiders in native and *Calluna* only sites. Data spans only from one summer to the next.



Gleichenia/Calluna (Fig. 3.8 b) also peaked at this time due to the presence of increased numbers of Psyllids.

Homoptera and Heteroptera in tussock are higher in numbers in summer than in the invaded tussock/*Calluna*. In the manuka the Homoptera increased in early spring (November) and again, though less so, in late summer, but did not peak at all in the manuka/*Calluna* habitat. The Heteroptera (predators) peak in summer in manuka but are generally higher in numbers throughout spring-autumn in manuka/*Calluna* and attain a greater peak in autumn than the manuka peak in summer. Spider taxa are generally similar in patterns of presence throughout the seasons between habitats (the partners are not plotted, but are virtually the same) (Fig. 3.9 a). The abundance values are more distinct. The *Calluna* habitat clearly has more spiders in summer than any other habitat, and this is due to a large increase in the number of orb web spiders. Over winter, there are appreciably more spiders present in the tussock grasslands (Fig. 3.9 b).

Feeding guild structure

The frequency of occurrence (Figs. 3.10-12) of phytophagous taxa (plant eaters) is consistently higher in indigenous habitats (mean frequency of occurrence in indigenous habitats = 3.33, in invaded habitats = 2.97), except when comparing the manuka-manuka/*Calluna* partners (Fig. 3.11 b). The abundance of the plant eaters also favours the indigenous habitats except in *Gleichenia* (Fig 12 a). This reduction in the plant eater guild on *Gleichenia* is offset by an increase in the occurrence and abundance of the predator guild in all but the tussock and flax comparisons. In the flax complex (Fig. 3.12 a) the large number of predatory beetles creates the disparity seen in the predator guild (summarised in Table 3.1). The pollen eater guild is always more frequently encountered (i.e. found in samples from most sampling trips), and in larger numbers, when *Calluna* is present. Chi square contingency tables suggest that there is no statistically significant difference in the guild frequency for tussock-tussock/*Calluna* (Chi^2 = 14.93, Df = 10, P>0.05), where only the plant eater guild varies greatly; for *Dracophyllum-Dracophyllum/Calluna* (Chi^2 = 13.405, Df = 10, P>0.05); for *Gleichenia-Gleichenia/Calluna* (Chi^2 = 11.47, Df = 9, P>0.05), where only the predator guild exhibits any large difference and for manuka-manuka/*Calluna* (Chi^2 = 6.397, Df = 9, P>0.05). However, in the flax-flax/*Calluna* (Chi^2 = 28.7 Df = 10, P<0.05) there is significant difference noted in the detritivore guild, the predator guild and the scavenger guild, all of which favour the flax habitat. The tussock and flax habitats are the most different and 'complex' habitats that stand to lose the most guild diversity when *Calluna* establishes. Comparison of Figure 3.12 b, *Calluna* only, with tussock (Fig. 3.10 a) and flax (Fig. 3.12 a) illustrates the guilds most affected: scavenger and predator. The abundance of the predator guild in *Calluna* is only ~ 7% of that in flax, and scavengers are only ~ 50 % as abundant as in the tussock grasslands.

Fig. 3.10

Number of occurrences of different taxa and abundance of individuals in each feeding guild in:
a. tussock and tussock/*Calluna* ;
b. *Dracophyllum* and *Dracophyllum*/*Calluna*.
Note the changes in scales on axis

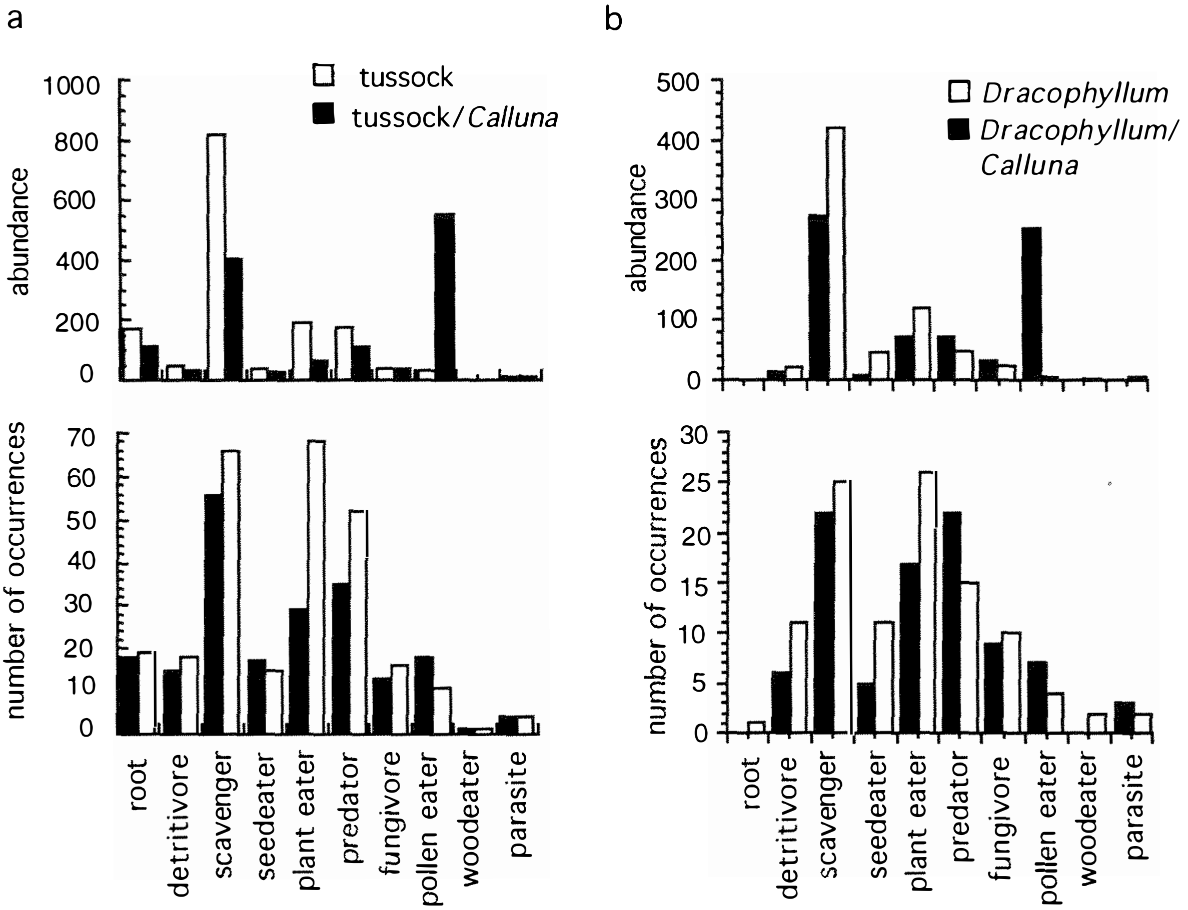


Fig. 3.11

Number of occurrences of different taxa and abundance of individuals in each feeding guild in:
a. *Gleichenia* and *Gleichenia/Calluna* ;
b. manuka and manuka/*Calluna*.
Note the changes in scales on axis

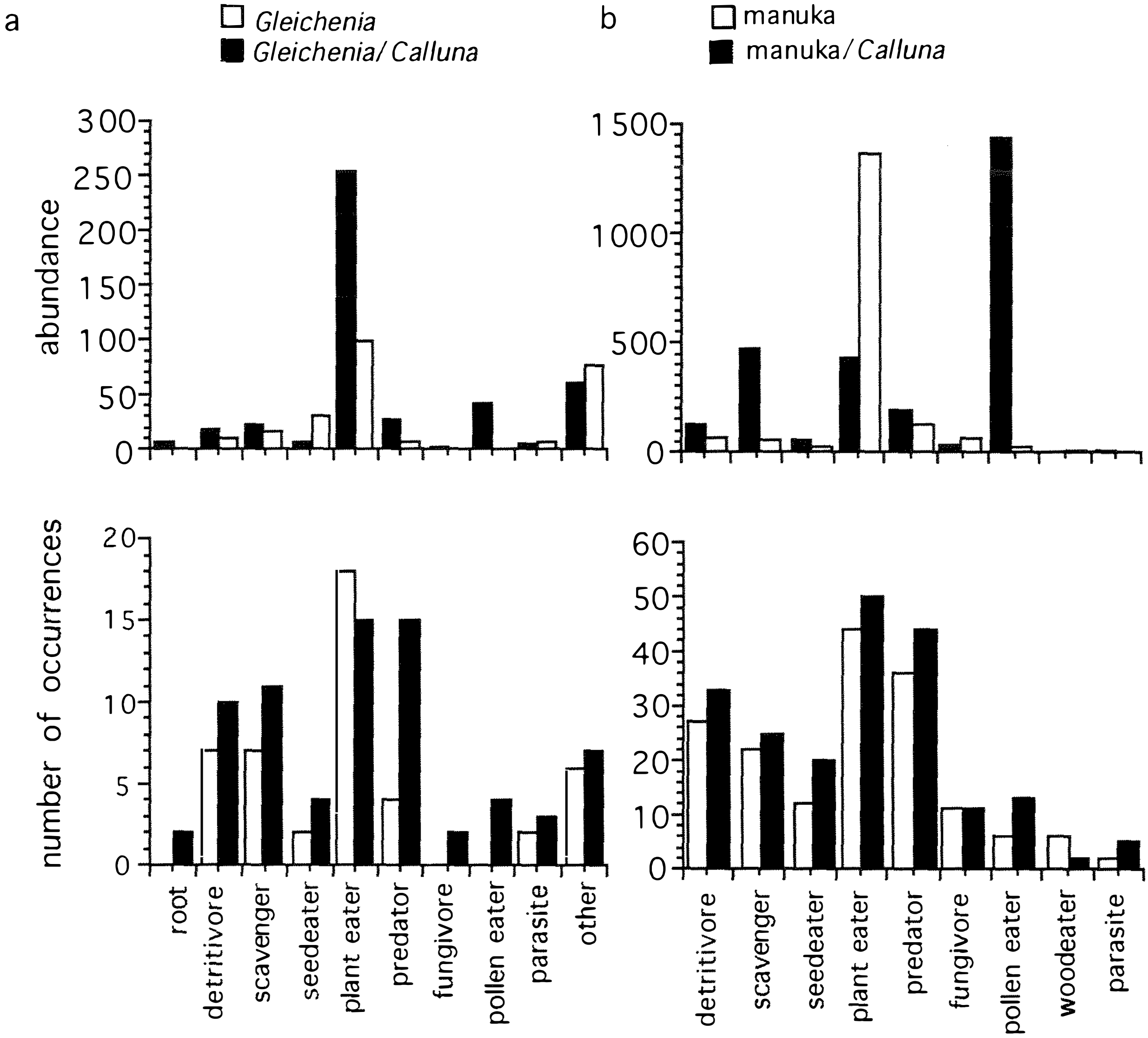
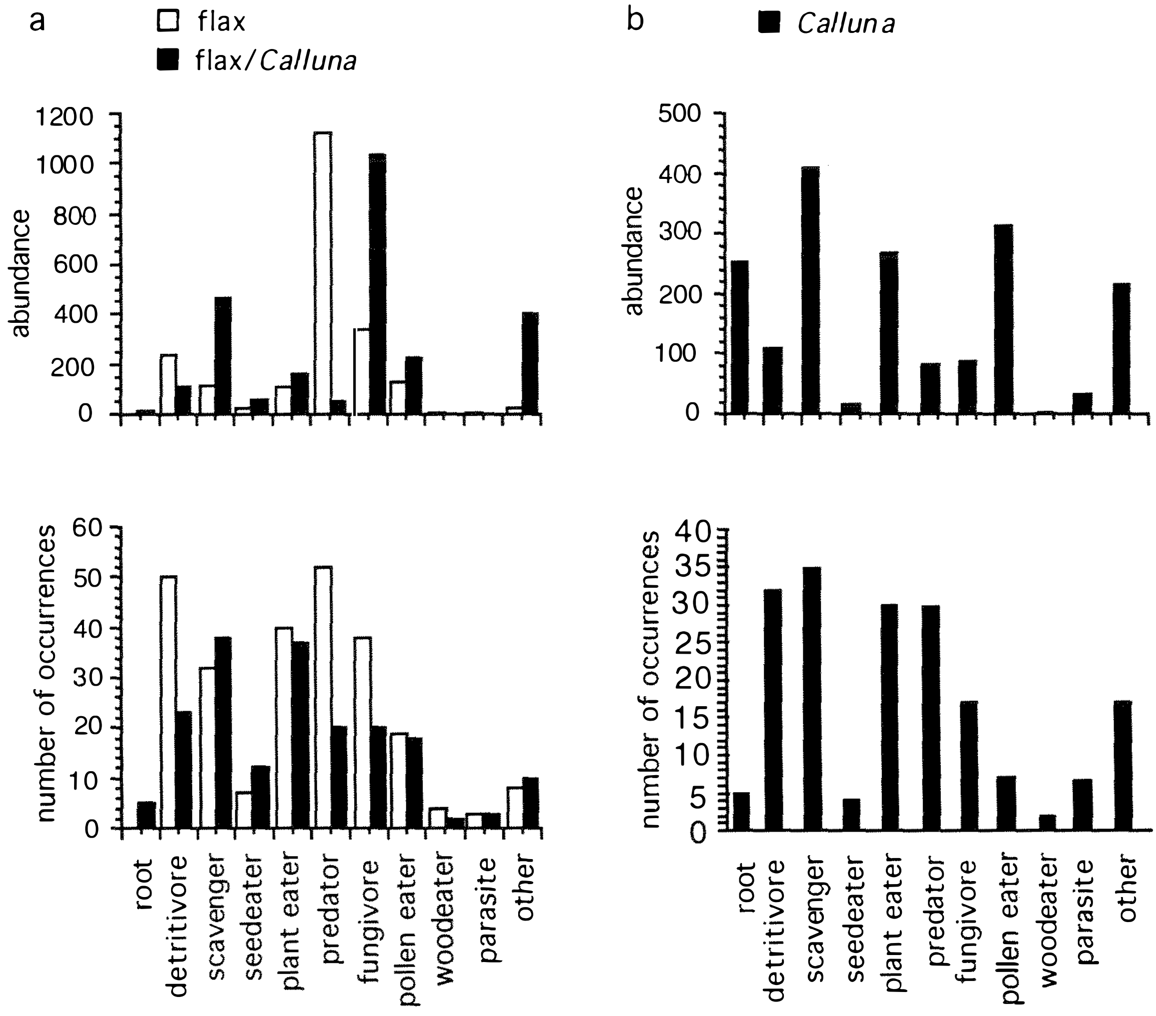


Fig. 3.12

Number of occurrences of different taxa and abundance of individuals in each feeding guild in:
a. flax and flax/*Calluna* ;
b. *Calluna.*
Note the changes in scales on axis



The trophic structure (the proportion of each guild in the food web) changes as the habitats move from indigenous to invaded to *Calluna* heathland (Table 3.7). The plant eater guild is reduced to half its original presence, the scavengers approximately one third their original presence, and predators decrease by nearly two thirds. Pollen eaters (Thysanoptera) and root feeders (manuka beetles (Scarabaeidae) substantially increase in presence (Table 3.7).

Table 3.7 The proportion each guild represents (%) of the entire invertebrate trophic web based on the abundance of individuals found in those guilds

Guild	Indigenous habitat %	Invaded habitat %	*Calluna* dominated habitat %
plant eater	30	18	14
scavenger	24	21	17
predator	16	6	6
detritivore	5	3	6
fungivore	1	9	5
pollen eater	3	3	23
root eater	1	2	14
unknown (other)	20	38	15

Prey-predator ratios are given in Table 8. Numbers are prey relative to one predator, or all guilds that are not predators or herbivores relative to one herbivore. There is no trend relating level of prey to predators, though large differences between indigenous and invaded sites are evident, e.g. a 50-fold difference between flax and flax/*Calluna*. The scavenger, detritivore etc. to herbivore ratios were lowest in the flax, *Dracophyllum*, and tussock sites. This is due to the high number of scavengers in tussock and *Dracophyllum* (Formicidae), and fungivores and detritivores at the flax site. The manuka and manuka/*Calluna* had the closest to 1:1 ratios because of large numbers of herbivores (Psyllids) at these sites. The anticipated higher ratio of herbivores to other non-predator taxa in indigenous sites (Table 3.8) was also masked by the abundant presence of the pollen guild in invaded habitats.

Table 3.8 Prey/predator and Herbivore/non-predator ratios (i.e. scavenger, detritivores etc) for each site based on abundances

ratio	tussock	tussock /*Calluna*	*Dracophyllum*	*Dracophllum/ Calluna*	*Gleichenia*	*Gleichenia/ Calluna*	manuka	manuka/ *Calluna*	flax	flax/ *Calluna*	*Calluna*
Prey/ predator	7.6	10.8	13.9	9.2	33	14.5	12.1	13.5	0.88	47.3	20.4
Herbivore/ non-predator	0.35	0.59	0.27	0.51	0.56	0.75	0.88	0.76	0.19	0.69	0.36

Overseas fauna comparisons

Tongariro National Park's phytophagous fauna in *Calluna* is much less than that of South England (Fig. 3.13). The comparison of the phytophagous fauna in heathland in South England (Hopkins and Webb 1984, Webb and Hopkins 1984, Webb *et al.* 1984, Webb 1989a) with that found in Tongariro National Park (this study), clearly demonstrates the potential *Calluna* heath offers, and the capacity of the New Zealand Volcanic Plateau insects to utilise it, i.e. the herbivorous fauna in *Calluna* heath in Tongariro National Park is 'poor' when compared to the same in England, though the spider fauna is not. Comparison with the invertebrate fauna of upland (altitude ~ 1400 m) Spanish hillside *Calluna* heath, sampled from The Picos De Europa in 1992 by sweep-net, though only once, still shows (Fig. 3.13) that, like south England, this Spanish heathland contains more herbivorous species than a more lush *Calluna* heathland in Tongariro National Park, excepting spiders.

Correlations with plant features

Insect abundance is positively correlated with the architectural measure produced in Chapter 2 (Fig. 3.14 a). Total abundance is also correlated with a habitat successional ranking (Fig. 3.14 b). Successional rank was arrived at using axis 2 of the plant ordination (Fig. 3.4c) and the plant architectural ordination (which was strongly correlated, Fig. 3.14 d) (Fig. 2.9, Chapter 2) and resulted in the following site successional order, sites 2-1-3-4-5-6-11-9-7-10-8. There is no correlation with nitrogen levels, though phytophagous insect abundance, and total abundance are close to significant correlations (Table 3.9). Diversity is negatively (though not significantly) correlated with successional rank, and plant architecture (Table 3.9). The lack of a significant correlation between successional rank and phytophages or spider numbers was surprising. Plant architecture, as expected, does correlate with spider abundance, as does phytophage abundance (Fig. 3.14 c). No plant measure correlated with the number of invertebrate taxa.

Table 3.9 Correlations of invertebrate assemblage features and some plant habitat attributes (* denotes a significant correlation, $P \leq 0.05$). Significant correlations are graphed in Fig. 3.14.

Assemblage attribute	Nitrogen level	Architecture	Successional rank
taxa number	0.342	0.344	0.243
phytophage abundance	0.431	0.633*	0.395
Shannon diversity index	-0.273	-0.582*	-0.565*
spider abundance	-0.012	0.608*	0.242
total abundance	0.462	0.668*	0.671*

Fig. 3.13

Comparison of numbers of plant feeding insect taxa in *Calluna* heath between southern England, northern Spain and New Zealand. Monospecific feeders refer to those that only feed on *Calluna*. Data from England comes from literature, data from Spain are from my own sampling.

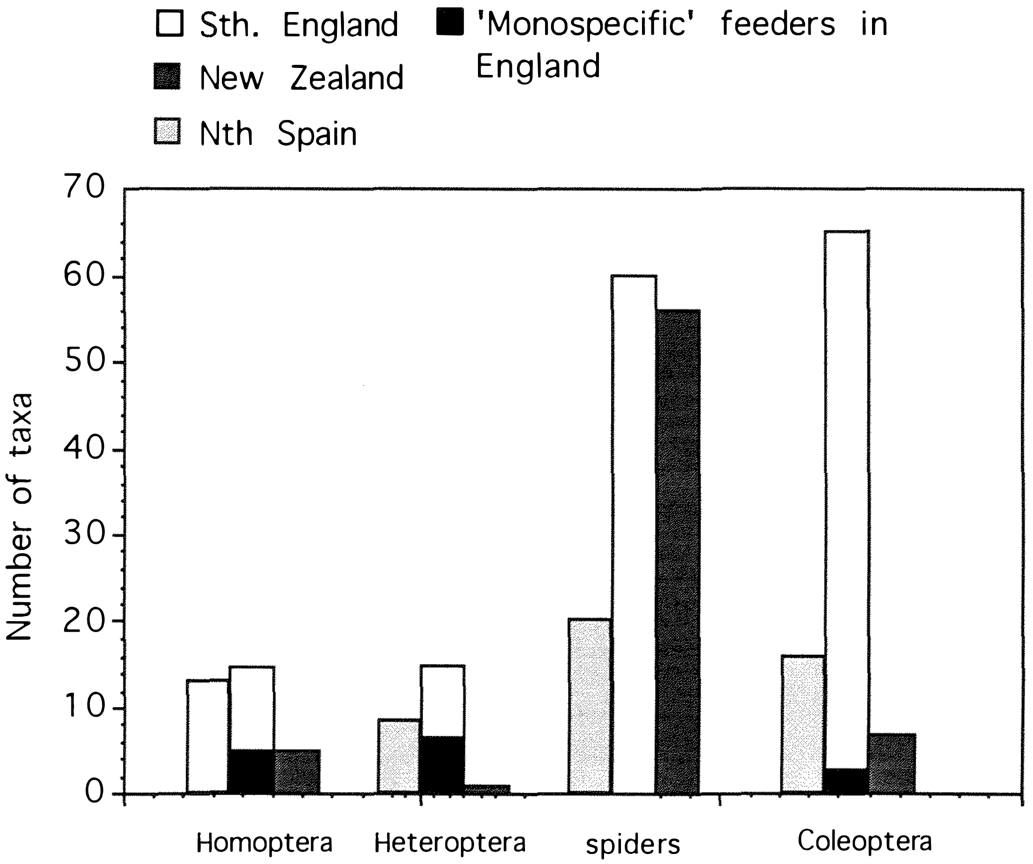
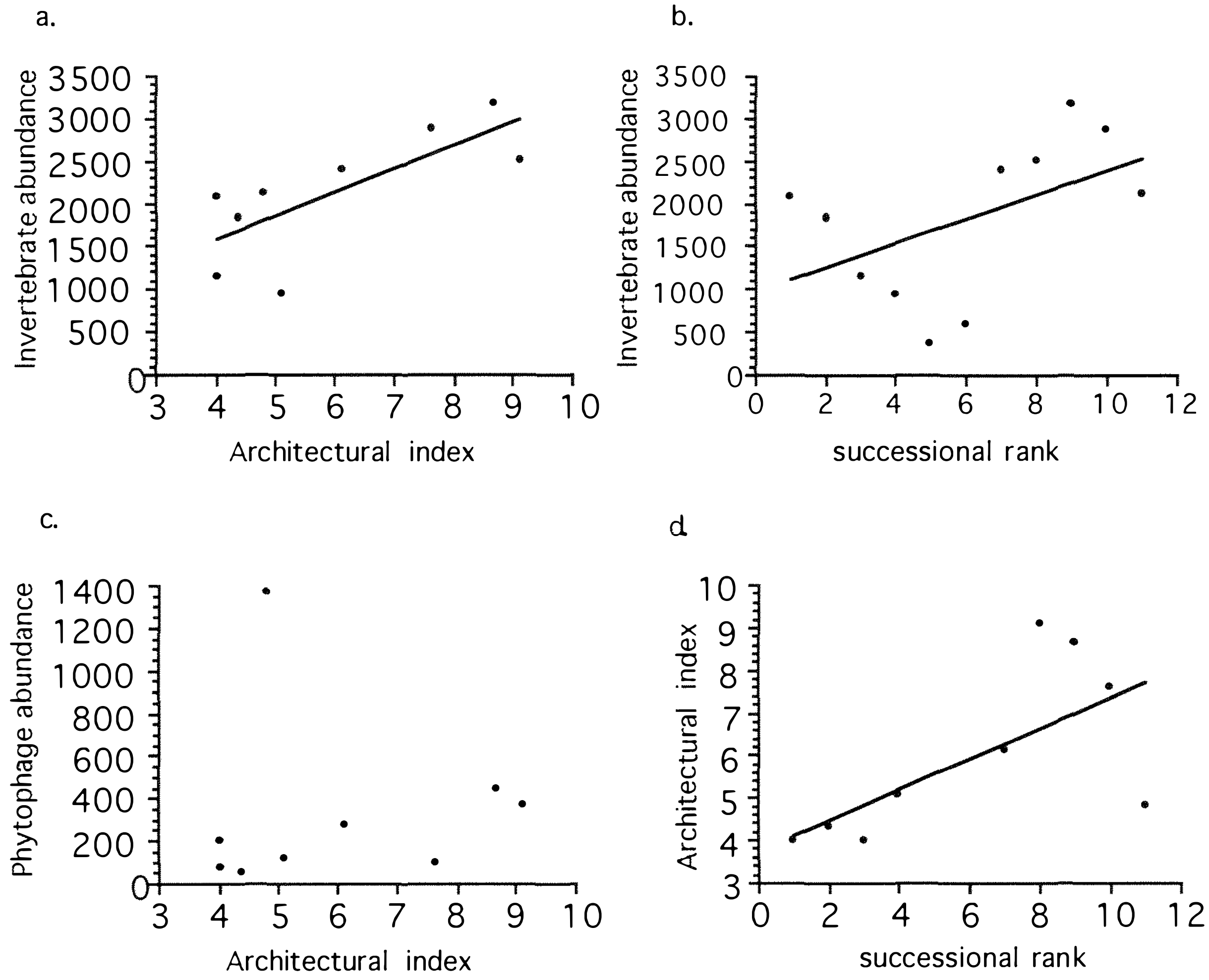


Fig. 3.14

Correlations of Invertebrate abundances and plant community attributes
(a. total abundance and plant architecture (Chapter 2), r= 0.668)
(b. total abundance and successional rank, r= 0.671)
(c. abundance of phytophages and architectural, r= 0.633)
(d. architecture and successional rank, r= 0.894).



DISCUSSION

Conservation of habitat diversity

Habitat structure has three main attributes (Samway 1994): 1. Heterogeneity, the variation due to relative abundance of different structural components; 2. complexity, the variation due to absolute abundance of individual structural components; 3. scale, the variation due to size of the area (or volume). It is recognised that conservation of invertebrate assemblages depends upon the conservation (to the largest extent) of their habitats, i.e. the 3 features listed above (Howarth and Ramsey 1991, Holdgate 1986). Though we know so little about the interactions of insect behaviour and habitat structure (Samway 1994), the significance of structural components, referring mainly to the 'plantscape', has been recognised since the 1960s (Elton 1966), and the identification of the role of plant architecture, (structure rather than taxa) in shaping invertebrate guild composition has been a developing theme (Southwood *et al*. 1979, Strong, Lawton and Southwood 1984).

Habitat diversity, i.e. heterogeneity of plant assemblages in space and time, correlates with, and ensures, invertebrate assemblage diversity and stability (Lawton 1978, Southwood *et al*. 1979, Denno and Roderick 1991, Brown 1991). In Tongariro National Park, the habitat diversity, or mosaic of special plant associations, is under threat from invasion by *Calluna vulgaris*. The native 'pool' of plant structures is dwindling as large areas become inundated with *Calluna* . The repercussions to the invertebrate assemblages should be evident and equivalent to the changes seen in the plant assemblages.

Invertebrate assemblage responses to change

There were few significant differences in the total number of taxa and abundances of invertebrates in either the common, rare or 'special' groups examined between invaded and native habitats. There are trends and species that characterise each habitat type: Formicidae and Stenopelmatidae characterise the tussock grasslands; Chironomidae the *Gleichenia* wetlands; Psyllidae the manuka scrubland; Phoridae the manuka invaded by *Calluna*; and Carabidae, Staphylinidae and Lathridiidae beetles feature in the flax habitat. It is the fungivores, Mycetophilidae, that feature in the flax/*Calluna*; and orb spinning spiders (Araneidae), Phoridae and Scarabaeidae in *Calluna* heathlands. One pervading trend in all habitats invaded by *Calluna* was the significant increase in Thysanoptera abundance at *Calluna* flowering times. Perhaps of greatest importance was the significantly higher numbers of 'rare' Homoptera in invaded sites (i.e. having suffered losses in Homoptera abundance) compared to un-invaded habitats, supporting my conclusion that phytophagous species, in general, have been most adversely affected by the invasion of *Calluna*. It appears that many of the phytophagous taxa have been unable to 'host shift' on to *Calluna*. This is not so unusual, since *Calluna* is a very 'novel' (chemically) food resource, having quite a special secondary chemical repertoire of feeding deterrents (Jalal *et al*. 1982). However, the follow-on effect to predators expected, i.e. the classic slump of predator numbers following prey population decreases (Chesson 1978), was not seen; but then the ingress (or invasion) of 'tourist' taxa from neighbouring habitats (those utilising the new structural resource and decreased competition) may have offered alternative sources of food for predators. Forty to fifty years after establishment of the invader is too long to see many of the initial changes that may have occurred in the Mangatepopo valley region. Even 10 years (Desert Road sites) is probably too long.

Numbers of taxa, with no reference to their 'function', can often mask even obvious changes. Recognition of functional groups, and which taxa occupy them, i.e. the feeding guilds, addresses this problem. It confirms an intuitive suspicion that the phytophagous guild would be the most negatively affected guild by the invasion of *Calluna*. The proportion of herbivores dropped from 30% to 14% after invasion, and their frequency of occurrence became lower in invaded habitats for all but the flax/*Calluna* site; further, their abundance was greater in all the non-invaded habitats except *Gleichenia* and flax (Figs. 3.6 a-e). These changes are most likely the result of native food plants becoming harder to find (isolated islands: Janzen 1975), and increased predation as the habitat becomes more structurally suited to predators (Schultz 1992), e.g. arachnid predation (Foelix 1982, Uetz 1991). The predator guild appears better represented in three of the invaded communities (but not in tussock/*Calluna* or flax/*Calluna*) because of their more complex architectural structure (Chapter 2). Specialty root feeders, cicada larvae and Scarabaeidae larvae (Chapter 4), have not been adversely affected by *Calluna* invasion; they appear to have incorporated *Calluna* into their diet.

The positive correlations (Fig. 3.14 a,b,c) between abundance and plant architecture and successional rank and between phytophage abundance and plant architecture, imply that, in some respects, *Calluna* is actually beneficial to the invertebrate community. This is probably a consequence of the change in the type of invertebrates frequenting the invaded habitats, compensating for 'missing' herbivore components.

The comparison with southern England's and northern Spain's phytophagous fauna implies that there are many feeding niches 'open' in the *Calluna* habitats in Tongariro National Park. This stands favourably with respect to the potential introduction (another invasion) of a biological control agent, or even a suite of them. Fears of competition with native herbivorous invertebrates can be dismissed; a biocontrol agent monophagous on *Calluna* will be using otherwise non-utilised resource. Spiders, however, appear to have adopted *Calluna* in the Park readily, and seem as diverse in Tongariro National Park *Calluna* as the heath spiders of southern England. Their impact, as predators, on the biocontrol agent can not be predicted easily.

Seasonal variation

The prediction of less seasonal variation in *Calluna* invaded site assemblages because of added shelter provided by the structure of *Calluna* was not observed. Thysanoptera, Homoptera, and Heteroptera abundances responded to seasonal vegetation changes (e.g. new shoot growth and flowering). Thysanoptera (thrip) numbers increased dramatically as they made use of the seasonal abundance of *Calluna* pollen and nectar. These Thrips may be *Ceratothrips erica* , *Calluna* Thrips (Webb 1989), which have been recorded on *Calluna* in New Zealand (Mound and Walker 1987), and may explain their capacity to utilise *Calluna*. Homoptera and Heteroptera are plentiful in the tussock habitat over summer, but not in the invaded habitat, again supporting the suggestion that most phytophages have not 'host shifted' onto *Calluna*. In the manuka the Homoptera peak in numbers in early spring and again in February, but this does not happen in its partnered site. Possibly the higher number of Heteroptera (mainly predators) keeps the Homoptera populations low in the manuka/*Calluna*. The spider taxa are a summer feature of *Calluna* but spiders in general are more abundant over winter in tussock grasslands. The increase in spider abundance in summer in *Calluna* is solely a result of the increase in orb-web spinning spiders; this should bring increased predation pressure in these habitats at a time when many species of adult insects are mating and dispersing (flying).

Diversity

Diversity is predicted to increase with increasing structural complexity of vegetation (Southwood, Brown and Reader 1979), though this hypothesis comes from studies dealing with 'natural' successional progression rather than perturbation and novel (new in the history of the ecosystem) change. Intuition suggests that there should be a disparity in the diversity of the indigenous habitats because of their different successional status. There was, however, only a weak negative correlation (Table 3.9) of diversity with successional rank and plant architecture. It appears that the more complex the plant structure, the lower the invertebrate diversity, which is opposite to most other research findings (Lawton 1978, Lawton and Schröder 1977, 1978, Southwood *et al.* 1979, Lawton 1983, Strong, Lawton and Southwood 1984); this may be an artefact of the diversity measures used, however, because both total abundance and phytophage abundance positively correlated with plant architecture and successional rank (Fig. 3.14a,b). The partnered habitat comparisons of diversity (Fig. 3.2a,b) suggest that *Calluna* invaded habitats normally held more diverse assemblages (excepting flax and *Gleichenia*), which is puzzling considering that invertebrate diversity was not positively correlated with plant architecture; yet addition of *Calluna* increased a habitat's structural complexity (Fig. 2.10, Chapter 2).

The different diversity measures used gave rise to different interpretations on the diversity in each habitat. These differences arise because of the focus on different features; the Shannon measure is weighted for species richness and its evenness component is not weighted to 'favour' common or rare taxa in the data (Magurran 1988). The Simpson index (being a dominance index) is weighted towards the abundances of the common species. The only disagreement between the two measures was with the tussock and tussock/*Calluna* site, (Shannon index difference = 0.4 in favour of the invaded, Simpson index difference = 3 in favour of non-invaded tussock). Tussock appears more diverse in the Simpson but less in the Shannon. This is because the tussock/*Calluna* site, though having fewer species, had better evenness in distribution of numbers over all its species, whereas in the tussock site there were many 'rare' species and a pool of common species. The Simpson index counters the effect of the pool of rare species, and, focusing on the pool of common species, shows that the tussock site exhibits a more even distribution than the smaller pool of common species in the tussock/*Calluna* site. Over all the trend was an increase in invertebrate species diversity after invasion of *Calluna*.

Common invertebrates respond first to invasions

White (1987) suggests that the common species will first feelthe effects of a change in habitat conditions while the rare will persist. This is because the rare species are usually utilising uncommon resources and so have excellent search patterns and other 'skills' enabling them to cope with low apparency, and low frequency of resources. The common species, on the other hand, usually use the most abundant set of resources and have not developed such acute search and acquisition behaviour. This, in the adult insect, is now seen as the crucial factor determining success of a population (Ohgushi 1992). Thus an invasion of the type seen in Tongariro National Park, with *Calluna* drastically lowering the indigenous vegetation frequency, apparency, and abundance, but not often causing local extinctions (Chapman 1984), should greatly affect the common invertebrates. The data collected supports this hypothesis (Table 3.3). Changes between indigenous and invaded sites that were noticeable, and that is evidence for effects to common species, were abundance losses in the groups Formicidae, Stenopelmatidae, Psyllidae, Carabidae, and Staphylinidae, all of which are common species in their respective habitats. As well as losses, though, there were also gains in abundance in invaded sites of Phoridae, Mycetophilidae, Scarabaeidae and orb spiders, normally not so common in indigenous habitats.

Abundance distributions in assemblages

Abundance distribution data are often fitted to general models for descriptive purposes. Of the many models available at least half are not based on ecological theory (as are Geometric series, Broken stick), but rather are statistical descriptors, (e.g. Negative Binomial, Log Series, Log Normal). Nevertheless, adherence of an abundance pattern to a particular model implies a set of features expected of the habitat and resource allocation where the data were gathered.

The Geometric series states that the first colonising species will get a proportion (K) of a resource, suggesting that it pre-empts that fraction, while the second gets a similar fraction of what is left, and so on. This model assumes that the abundance of a species is proportional to its K fraction. The problem is that this last assumption is probably not true (Gray 1987). The model has been found to fit only communities poor in species, such as early successional systems or where extreme pollution or 'harsh' environments exist (Whittaker 1975). The fit of the abundance distributions from all the habitats to this model implies they were all experiencing 'harsh' environmental conditions and, for tussock, were in an early successional state (Rogers 1991).

The 'Broken Stick' Model, now abandoned in its original form (MacArthur 1966), suggests that resources are divided at the same time and at random. Allocations can be ranked into decreasing order. Thus abundance of a species was proportional to the size of the segment of the 'stick' (resource) a species got. Now the 'stick segments' are thought of as proportional to 'niche dimensions'. Adherence to the Broken Stick Model implies an even distribution of the major resources and thus of abundances (Gray 1987, May 1975). None of the habitat assemblages in this study fitted the Broken Stick model. This adds to the contention that 'in any assemblage the majority of species are rare, a number are moderately common, and very few are very abundant' (Magurran 1988). Generally any large, species 'rich' assemblage has this pattern and adheres to the log normal distribution. So it was in this study. If invasion was causing large scale detrimental disturbance the expectation would be for distributions to shift from log normal to geometric (or log series) distributions (assuming that the habitats are not so 'harsh' as to invoke a geometric distribution). The results did not support this hypothesis. Rather the reverse; the indigenous habitat assemblages, as well as fitting the log normal, better fitted the log series (cf. Table 3.6). The log series distribution (like the geometric) results from a process of niche pre-emption where a few species 'capture' most of the resources. This is indicative of early successional and 'harsh' environment assemblages (May 1975, Whittaker 1969, Whittaker & Woodwell 1972). Either because the indigenous habitats can be considered as earlier ranked successionally than their invaded partners (e.g. tussock is earlier than tussock/*Calluna*), or, because of their lower architectural complexity, they are harsher environments for invertebrates. The trend from log series distributions in the indigenous habitats to log normal distributions in the invaded habitats would support this contention and imply that the invaded habitat assemblages are more 'robust' assemblages, with better development and deployment of resources over more taxa; ie. a more 'stable' food web.

Conclusions

There was no decrease in diversity after invasion, in fact it generally increased (Fig 2 a,b). The abundance of spiders did correlate with the architectural complexity increase as predicted (R = 0.608), as did total abundance of invertebrates, and favoured the *Calluna* invaded sites (R = 0.668). Evenness of abundances also favoured the *Calluna* invaded sites. Distributions of abundances may be changing to log normal rather than log series, meaning a more even distribution of resources among species. This is probably because of the different 'style' of assemblage formed, one with less emphasis on nutritional plant resources, suggesting “vacant” niches, and more utilisation of the enhanced structural resources. The abundance of herbivores was most negatively affected.

The feeding guild structures have changed with establishment of the invader to a more even distribution of taxa in guilds. In the pollen eating guild, thrip numbers increased where ever *Calluna* was present. Predators generally were in higher numbers in *Calluna* invaded sites while herbivores were lower; prey/predator ratios were seldom different, the only difference being between flax and flax/*Calluna*. Other guilds were variable, or were not at all different. There is a shift to 'tourist' type invertebrates (those who utilise plant structure, but are generally heterotrophic and mobile (Moran and Southwood 1982)) in the *Calluna* habitat, but the assemblage is still indigenous and appears functionally stable.

The tussock grassland's invertebrate assemblage has been, of all the habitats studied, the most affected by the invasion of *Calluna*. Historically there has been little quantitative documentation on changes in tussock grassland fauna, what early work there is being principally descriptive (Hilgendorf 1917). What there is suggests that insect abundance in tussock grasslands of South Island was in the past greater, and I expect in the North Island too. Grasslands in the mid-altitude (<1000m) tend to be seral communities (White 1987, Scott *et al* .1979) and as such may change. This is certainly the case in Tongariro National Park, with its volcanoes and long history of human occupation (Rogers 1990). Insect decline in these types of systems has been associated with depletion of short tussock grasslands (Dick 1940) and in high country around Lake Hawea between 1920-1935 and 1950-55 (White 1987). Perhaps in Tongariro National Park's tussock grassland, as in the South Island, as seral changes occurred and the seral invertebrate assemblages 'peaked'; they then began to decline in abundance as grasslands became herb/grasslands then shrub/grasslands. Thus the invertebrate assemblages in Tongariro National Park may be in a state of chaos. The introduction of *Calluna* has at once accelerated the normal seral transition (as evidenced by the increased height, and structural complexity), and forced large initial abundance changes in the invertebrate assemblages. With establishment of *Calluna* in the plant community, the seral succession has stabilised allowing some stability and maturation in the invertebrate assemblage.

In Tongariro National Park invaded invertebrate assemblages respond well to large scale habitat change. Though herbivores 'suffer' resource shortages, most do not become extinct (though this study is ~80 years after the initial invasion). Rather, the assemblages shift their resource emphasis as other resources (e.g. structure) become available; new 'users' supply old and new predators and the 'food web' is maintained in functioning order. That is not to say that fundamental change has not occurred; a large new resource now exists relatively untouched; and a normally vital group of any community web - the herbivores - is much reduced; but the systems remain viable and operational. The new *Calluna* system still holds an indigenous assemblage, an important consideration as far as conservation ethics are concerned. Though the new invertebrate assemblage of the 'uniform' habitat, *Calluna* heath, (reported here as more diverse than any one native system, as 'balanced, and as stable, or more stable; Chapter 5), it represents only one assemblage type in the Park. Since *Calluna* appears to be spreading, removing native habitats which are successionally more initial and accelerating succession to shrubland, the variability of habitats in the Park is decreasing. So too, is the heterogeneity of invertebrate assemblages being decreased. The mosaic of assemblages will not be maintained if *Calluna* continues to spread.

Chapter 4

Impact of native herbivore feeding on *Calluna vulgaris*

ABSTRACT

New Zealand's phytophagous fauna could be pre-adapted to *Calluna* since it is a small leaved, low nutrient, high tannin plant much like many of the sub-alpine native plants, or the fauna, because of its long isolation, specialisation, and 'tight' coevolutionary association with the native vegetation, may be unable to shift host plants.

If feeding on *Calluna* is occurring then this 'challenge' may be affecting *Calluna's* performance, and hence competitive ability. To test if feeding on *Calluna* by some native invertebrates was possible, and to examine the impact of native herbivory on *Calluna*, two sets of experiments were done. Laboratory trials were done involving two prominent herbivores (manuka beetle and alpine grasshopper). Their performance (weight change), preference for, consumption of, and damage to, *Calluna* was measured and compared to that of *Hebe stricta* and two forms of manuka. In field experiments, areas of *Calluna* had either their roots protected from insect attack or the entire plant protected (through the use of a systemic insecticide). An additional treatment mimicked the damage level expected by a large population of the prospective biological control agent.

The results show that manuka beetle eats 2- 3 times more *Calluna* than *Hebe* or manuka, and grasshoppers eat 10 - 20 times more *Calluna* . No insect found any one plant satisfactory enough to maintain or put on weight. Manuka beetles performed best on manuka taken from the Park, while grasshoppers performed best on a diet of *Calluna* . Both insects did more feeding damage to *Calluna* than any other offered plant.

In the exclusion trials all the protected treatment's shoots grew more than the control shoots, though the difference was not statistically significant (C.I. 95%). Plants totally protected from insect herbivory grew 5.406 g dry matter over the time of the experiments, those root protected grew 4.362 g dry matter, and the controls grew 4.008 g dry matter. *Calluna* , Defoliated to simulate the potential biocontrol agents damage, achieved a positive growth response (4.793 g dry matter).

It appears that there are some native fauna with 'plastic' diets, able to shift hosts, but there is still a large food resource under utilised. Grasshopper and manuka beetle populations per hectare are calculated, and, with biomass of current year's shoot crop data, estimates of consumption per hectare are made. These two herbivores are estimated to consume ~ 0.6 to 3 % of a year's *Calluna* shoot crop. Addition of the biological control agent is predicted to increase this figure to around 20 % with the possibility of it being much higher if the agent experiences an extended population explosion. Unfortunately the literature reports that *Calluna* is un-challenged by herbivory levels damaging < 50 %.

INTRODUCTION

The interactions of invertebrate herbivores and their plant resources is a little understood, yet very important, realm of biology (Schultz 1992). Many plant-insect interaction studies have been done to ascertain what determines host plant choice or what determines the range of monophagous to polyphagous feeding strategies (Thorsteinson 1960, Kennedy 1965, Levins and MacArthur 1969), or dietary shifts (Gould 1979, Rausher 1983). Most of this work, though, centres on horticultural and agricultural pest species and crop plants. The results of this research are useful to natural systems' ecologists, but there needs to be more work, specifically aimed at understanding plant resources and invertebrate behaviour (Samways 1994). As with many native systems in New Zealand there are no data on types of herbivores, their population sizes, fluctuations, or types of foliage and quantity eaten, in Tongariro National Park's variety of native habitats. *Calluna vulgaris* has been in the park at least eighty years (Bagnall 1982) and is often the dominant vegetation type. It is possible that some of the more polyphagous insects may have incorporated it into their diets, especially as the quantity and cover of *Calluna* (hence affecting the probability of encounter) has increased in the park (Chapter 2).

In cold, harsh climates insect herbivore assemblages are normally dominated by host plant specialists, which are sedentary and relatively unresponsive to variation in nutrient levels of host plants (McNeill and Prestidge 1982). Tongariro National Park offers such a habitat, with soils poor in nutrients and plants with low nutrient tissue levels, which are high in tannins (H. Outredge pers. comm.), slow growing, and small leaved (Eg. *Dracophyllum* spp., *Coprosma cheesmanii*, tussock grass).

This condition suggests two opposing consequences; New Zealand phytophagous insects in Tongariro National Park may be pre-adapted for *Calluna* as it is also a low nutrient, small leaved, slow growing food plant, with high levels of secondary chemicals; but alternatively it is also possible that the insects, being highly specialised from a long period of co-evolution with the native flora, will not have the plasticity to widen their host range to include *Calluna*.

Herbivorous attack may reduce plant growth, fecundity (Crawley 1982, 1983), or competitiveness (Bentley and Whittaker 1979). Effects on plant 'fitness' have been, and still are, widely debated (Belsky 1986, Crawley 1983, 1985, 1989, McNaughton 1979a,b, 1983, Karban and Myers 1989, Verkaar 1988). There have been cases where 'benefits' of defoliation have been suggested and measured (Owen 1980, 1981, Van der Meijden 1990, and an equal number of cases in which the benefits have been refuted (Doak 1992, Verkaar 1988). There appears to be a threshold of tolerance to insect herbivory before 'critical' damage is done, depending on external factors affecting the plant's vigour, i.e. competition stress, water and nutrient stress, and climate (McNaughton 1983, Verkaar 1988, Strauss 1991, Doak 1992). *Calluna vulgaris* (European heather) appears to be a species that benefits from limited defoliation. It can be stimulated to grow by levels of defoliation up to 80% before showing permanent 'ill' effects (death)(Grant and Hunter 1966). Grant and Hunter (1966) showed that defoliated *Calluna* added photosynthetic biomass and reduced the amount of woody tissue development, but did not discuss other aspects of plant performance (loss of stored energy, increased pathogen susceptibility, reduced fecundity) due to defoliation. In later studies Grant *et al.* (1978, 1982) suggested that 40 - 50% defoliation is beneficial to the maintenance of vigorous healthy heather, though these studies were based on vertebrate herbivory which induces much trampling damage. Brunsting (Brunsting 1982, Brunsting and Heil 1985) found that repeated attacks by the Chrysomelid beetle *Lochmaea suturalis* can overwhelm this tolerance to defoliation and result in death of plants in Europe (Berdowski and Zeilinga 1987). The importance of below ground herbivore damage to plant vigour has only recently received attention (Brown and Gange 1989a, b, Gange and Brown 1989) but there is a growing appreciation that a reduction in plant performance may be due to root damage.

Biological control of *Calluna* has been proposed as the most viable control option and will involve introduction of *Lochmaea suturalis*, heather beetle. The heather beetle is a small Chrysomelid reputedly monophagous on *Calluna* (cf. Chapter 6). Discovery of which of the native herbivores have adopted *Calluna* as a food source or those that could utilise it, combined with the quantity they consume in the *Calluna* heathlands of Tongariro National Park is also important as a prelude to biological control, and may aid monitoring the success of biological control. The possibility to do so after introduction will be confounded by that invasion.

The aim of this work is to explore the issues at two levels of resolution. The first asks:

1. are there native herbivores that have widened, or have the potential to widen, their host range to include *Calluna*;
2. is the consumption of *Calluna* by these insects comparable to that of the heather beetle;
3. given a choice would test insects prefer to eat *Calluna* over manuka, or *Hebe*;
4. what might be the consumption level, in terms of % annual shoot crop removed, of native and heather beetle feeding.

The second level is a field trial to measure the impact of native herbivores, both root and foliar, on *Calluna* growth. If impacts of feeding are measured then this will be evidence of the ability of some indigenous herbivores to expand their host range, even to something as novel as *Calluna*. In addition the level of utilisation of an invading species can be estimated. To these ends this chapter addresses the following hypotheses:

1. freedom from herbivore attack will enhance plant growth (measured by shoot tip growth);
2. foliar feeding herbivores have less effect on growth than root feeding herbivores;
3. simulated mass damage such as *Lochmaea suturalis* achieved in The Netherlands will result in no new shoot growth of *Calluna* for at least one season.

Lab feeding trials

Insect herbivory on *Calluna* in New Zealand would represent a host range shift for native herbivores. This work assesses whether this has occurred, and what the consumption levels might be.

This was done by isolating two prominent phytophagous insects in the Park, one whose adult numbers peak for a short period (manuka beetle: Scarabaeidae; *Pyronota festiva*), and the other whose numbers are more stable and who is generally present throughout the year (alpine grasshopper: Acrididae: *Sigaus piliferus*). The use of a generally acknowledged polyphagous insect (White 1978, Bernays and Simpson 1989), in the Acrididae, should ensure observation of feeding on *Calluna* if there is likely to be any from any insect at all. Observations in the laboratory were made on the ability of these insects to survive on, their preference for, and their quantitative consumption of *Calluna vulgaris, Leptospermum scoparium,* (manuka), and *Hebe stricta* (*Hebe*). The native plants used are common shrubs, found with, and physiognomically similar to, *Calluna*. (cf. plant architecture, Chapter 2). Some nursery grown specimens of *Leptospermum* were used to enhance the observation of flexibility of diet using a subtle difference (a with-in species, variety, difference).

Rather than using the standard approach of excised pieces of plant material, whose water conditions may change dramatically from the normal, especially over prolonged tests, and thus greatly influence the insects feeding, I used intact plants. By using a whole plant I hoped to simulate food material changing naturally in nutritional value and chemical composition, such as production of deterrents, during the feeding trials.

Herbivory impacts

Differential growth of *Calluna* when freed from herbivore damage will indicate the extent of native herbivore 'control' of growth in *Calluna*. The effect on *Calluna* foliage productivity of native phytophagous insects was measured via the differential growth rate of shoots of *Calluna* after removal of either root or both root and shoot herbivore 'loads'. Chemical insecticides were used to protect some plots from grazing (Brown and *et al.* 1987a&b), while others were mechanically defoliated to levels expected by the proposed bio-control agent *Lochmaea suturalis* (Cameron *et al.* 1944, Brunsting and Heil 1985).

METHODS

Feeding trials

The purpose was to measure the survival, preference, and possible nutritive gain (i.e. weight) of two commonly occurring herbivores when given diets of purely *Calluna* compared to their performances on two native plants (*Hebe* and manuka). Preference was tested by allowing the insects the opportunity of access to two plant types.

Experimental system

Calluna plants (ca. 1 year old) were collected from the Park from a recent burn site (~5 years previously) near the Waihohonu River road end. Roots were washed free of substrate before being bagged (PB 8 sized bag) in a mixture of sand, pumice and peat (1:2:2), and approximately 10 grams per bag of Osmocote (6 month release formula, Grace Seria International products) as supplementary nutrient. The seedlings were then established in a glasshouse and grown for approximately one year. Two manuka (*Leptospermum scoparium*) varieties were used: one from the Park, collected as small shrubs, and the other a garden cultivar, ('Palmers' Garden center, Albert street, Palmerston North). The *Hebe* species used (*H. stricta*) came from the same garden suppliers. All were sprayed 14 days prior to testing with "Attack", a broad spectrum insecticide ('Watkins' cf. Walton and Walton 1994) to remove any possible insects already on them, and then washed down with water. The experiments were done between November through to February when insects are available from the field. Plants were watered once a day and were kept on a bench in the laboratory (as it was too hot in a glasshouse for the insects) during the experiment (thus receiving lower light levels than ambient, ie. they received around 165 $\mu Em^{-2}s^{-1}$ of light during much of the day (10 am - 3pm)).

There were two sorts of tests, starvation trials, and location choice tests. For both tests, chambers were suspended by a network of strings and clamp stands over growing fresh shoots. Several chambers were placed on one plant (cf. Photo 4.1, Fig. 4.1). The starvation chambers were plastic screw top pottles (volume = 225 mls), in which three mesh covered ventilation holes (radius 23 cms) had been cut. The base had a keyhole slit to allow a shoot (or shoots) to be inserted into the chamber without a gap for insect escape. On the bottom, filter paper collected the frass and damp cotton wool supplied moisture (Fig. 4.1, Photo 4.2a). Two shoots of *Calluna* or one of either *Hebe* or manuka of approximately equal foliage mass were inserted into a chamber.

The choice experiment chambers were the same except that there were two chambers attached together with no interceding wall (Fig. 4.2, Photo 2b). Choice tests were only done between *Calluna* and a 'native' plant. The two experiments used different insects each time, but the same plants.

Fig. 4.1 Starvation test chamber design

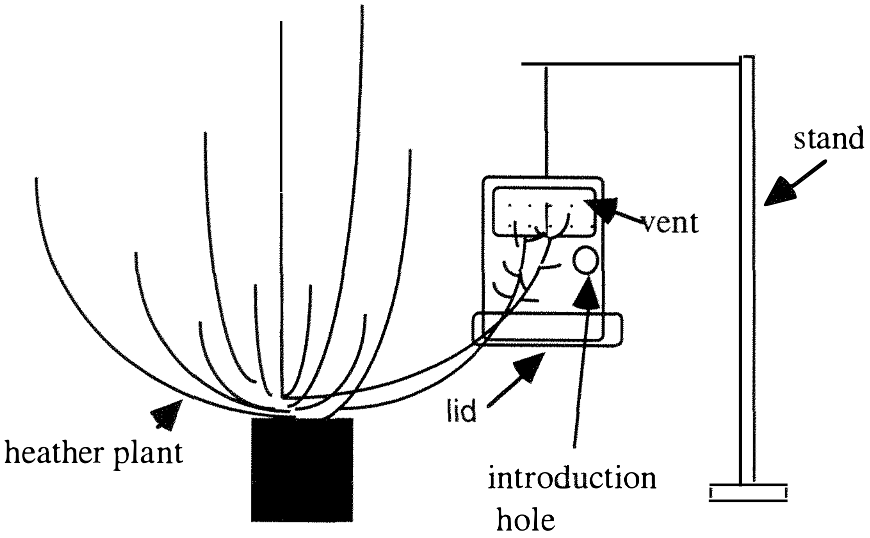
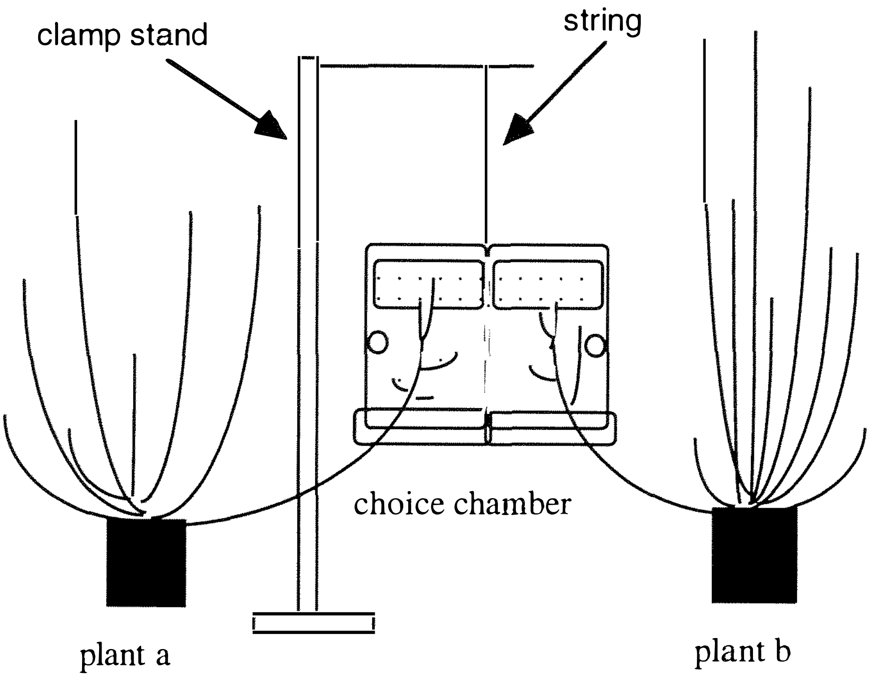


Fig. 4.2 Choice test chamber design



Experimental layout involved one plant of each of *Calluna*, *Hebe*, and nursery manuka, with four starvation test chambers and one choice test chamber for the manuka beetles, and only two starvation chambers and one choice test chamber of the grasshoppers (Fig. 3.3). In the second 'run' of the experiment a Park manuka plant was added to the starvation tests.

Fig. 4.3 Experimental layout of plants and chambers for each insect type for each run of the experiment

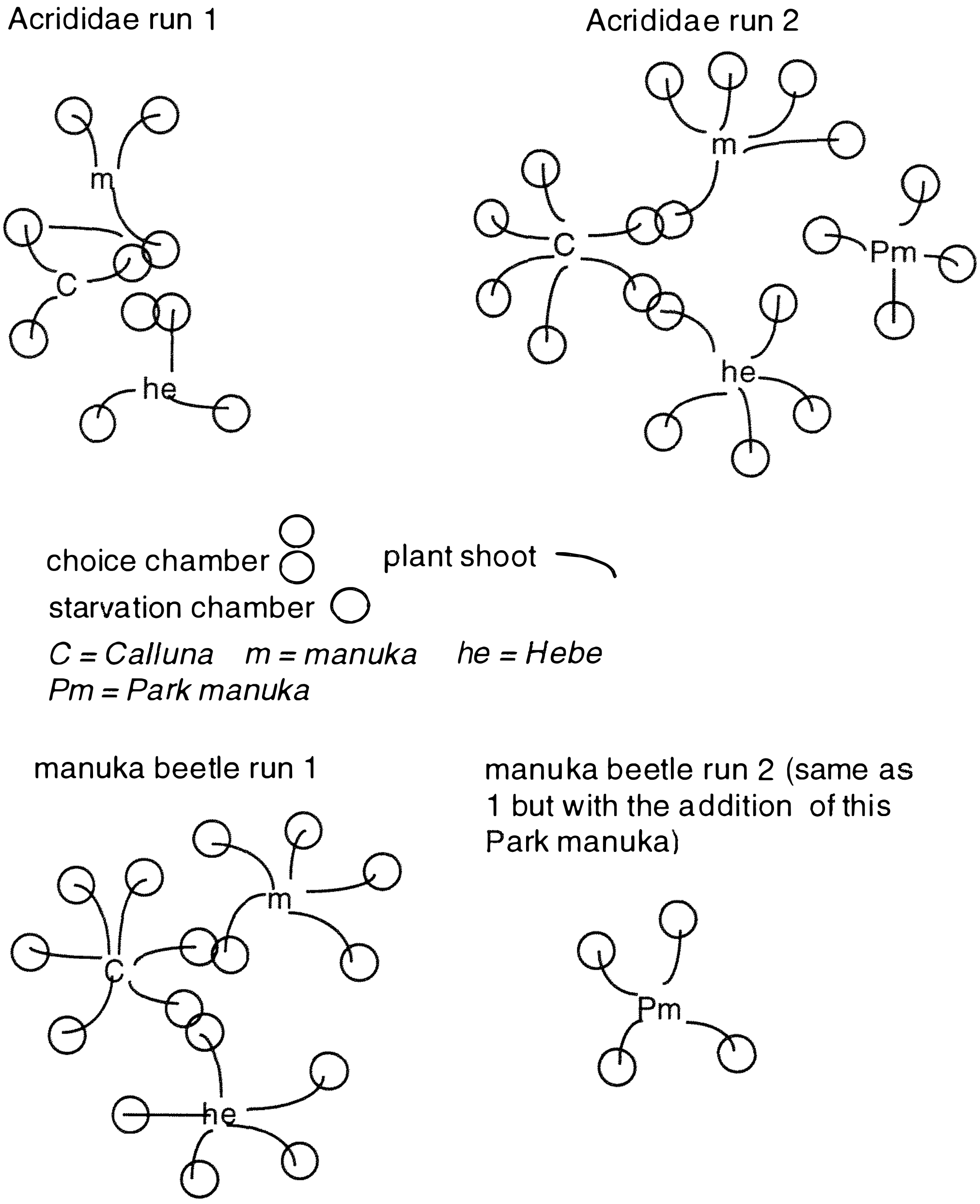
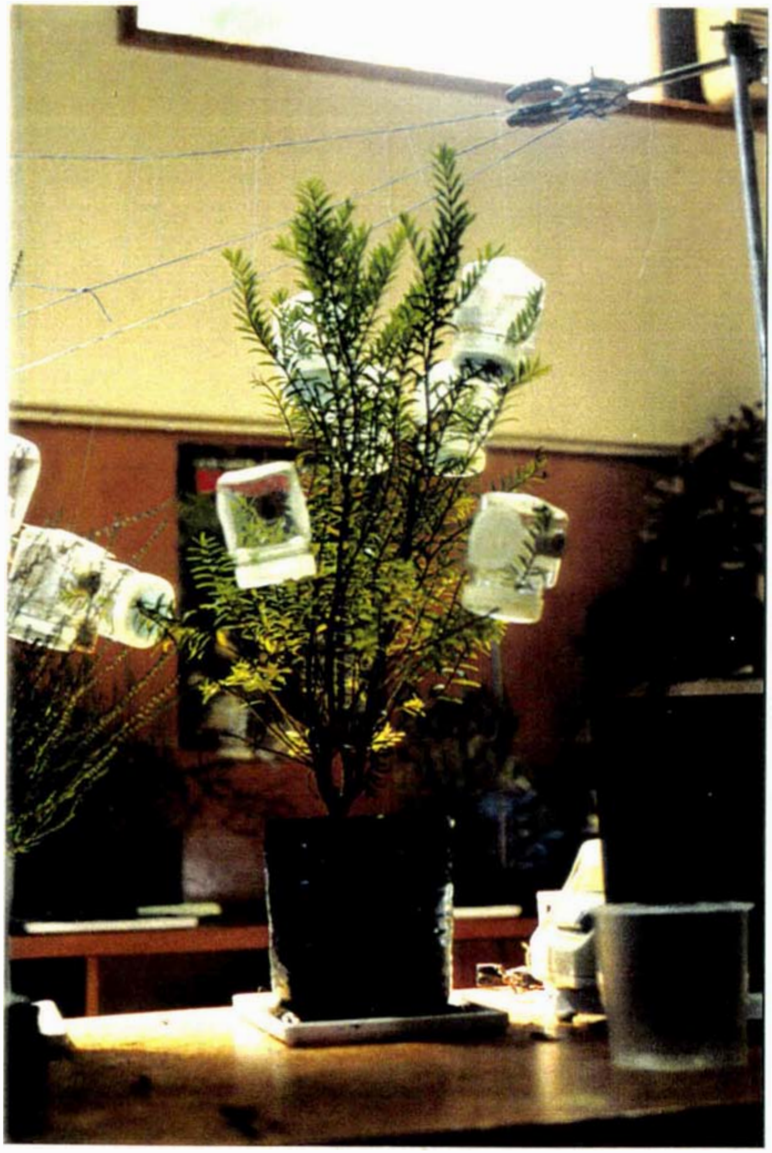
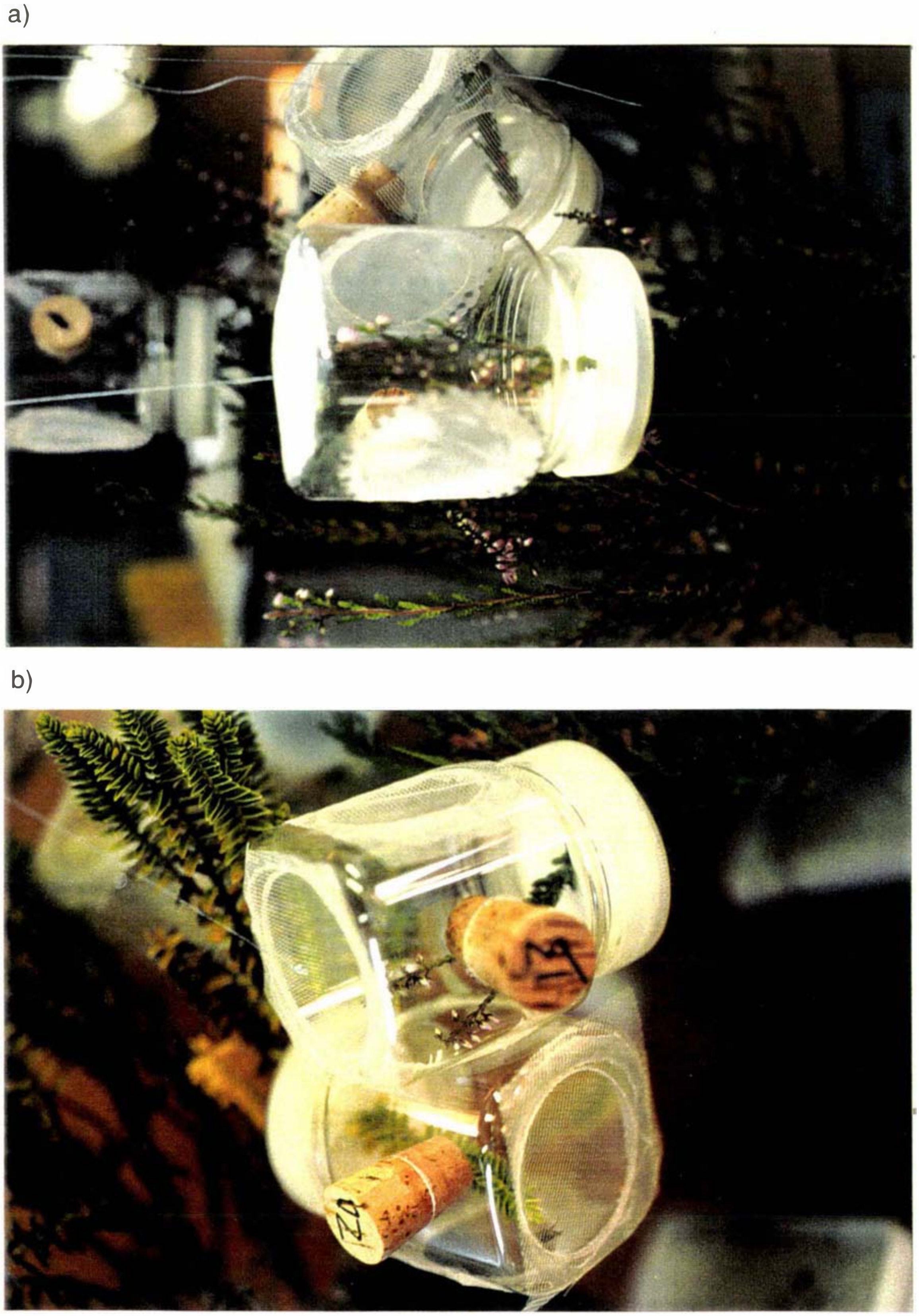


photo 4.1

Feeding trial arrangement of a *Hebe* plant and test chambers supported by string scaffolding.



photos 4.2a, 2b Test Chambers a) Standard feeding chamber. b) Choice chamber where insects can travel between chambers to different plants.



Experimental insects were caught by sweep-netting and hand collecting in the field (grasshoppers from the tussock grasslands on the Desert Road side of the Park, manuka beetles from *Calluna* heathlands around site 11; Fig. 2.1, Chapter 2. They were transferred to pottles and kept in a chilly bin until back in the lab (~4 hours). The insects were then starved, but allowed water, for 24 hours while stored at $5^{0}C$ and then they were weighed and introduced into the chambers. One grasshopper or two manuka beetles were put into each chamber. Choice chambers had twice the number of insects as starvation tests, as these had twice the space, and twice the plant material.

The experiments ran for 5 days or until the insects died. Three times a day (9am, 2pm, 7pm) 10 minute observations were made to ascertain if the insects were alive and where the insects were in the choice chambers; observations of which chamber the insects were in are presented as cumulative occurrence graphs. After 5 days the frass particles in the chambers were counted. Average frass produced over the same time without food was also measured using 10 insects that had been through the 'stand-down' period but which were then kept in vials with no food. At the end of the experiment all insects were weighed again. Acrididae survived the 5 days in the chambers and live weight could be measured at the beginning and end of the test period. The manuka beetles died in large numbers during the first or second night and were thus much lighter at 'harvest' time due to subsequent water loss than when they actually died. Consequently a correlation was derived between live and dry weight of beetles to give an estimated dry weight of the beetles at the start of the experiment with which to compare the final dry weight. This was done by weighing field-collected beetles (n = 200) after their 24 hour stand-down period, then drying them in a oven (60 ^{0}C for 3 days) and reweighing. The predictive equation was:

predicted initial dry weight = -0.00152 + 0.382 * initial live weight (r sq = 93.4%, P=0.000).

The leaves from the shoots enclosed in the chambers were collected and counted, and the number damaged counted. The damaged leaves were individually scored for percentage leaf area removed, giving a mean level of leaf damage per plant per test per grasshopper or per 2 beetles.

To estimate the biomass of plant material eaten by the insects, 200 leaves, not used in the chambers were collected haphazardly from each test plant type and fresh weighed. Using these figures to give an average weight of a leaf and the percent damage scores for the insects a consumption quantity can be estimated. The mean amount consumed by an insect (**g**) in the test period was calculated as:

$$\mathbf{g = W*D*N}$$

where W = mean weight per leaf of that plant type
D = mean proportion of damage to a leaf
N = mean number of leaves damaged.

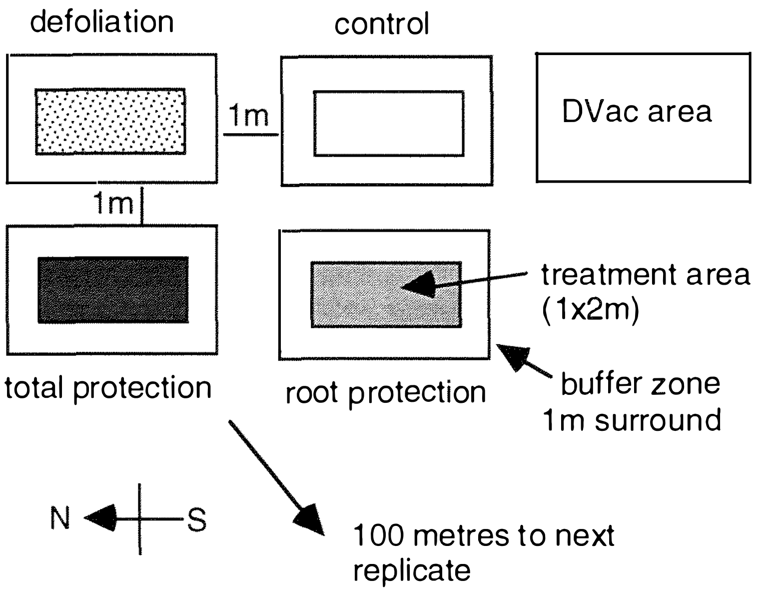
Field exclusion trials: Herbivory impacts

This experiment was designed to measure the growth response of *Calluna* in the form of shoot tip elongation, after alleviation of herbivore pressure on roots and on the whole plant, and to observe the response to large scale foliage damage.

In *Calluna* dominated vegetation 200m west of the base of Pukeonake (Fig. 2.1, Chapter 2) four replicate plots were installed. Each successive plot was 100 metres south-west of the last. Each replicate plot consisted of four equal sized (1 by 2 metre) areas (Fig. 4.4). Each area received one of four randomly assigned treatments (see below), and had a buffer area of 1 metre in width on all sides (total area 3m x 4m). The experiment ran from November through to April 1993 (6 months) over the growing season.

Fig. 4.4

Exclusion experiment layout showing positioning of plots



Prior to the treatments being applied the abundance and type of herbivores initially present at the site was measured. For above ground invertebrates, D-Vac sampling (Tecumseh Products company U.S.A.) was used in a temporary plot within each replicate.

Root herbivory was hard to measure non-destructively. I observed that Cicada (a prominent root feeder) exuviae (Homoptera: Cicadidae) were present in and at the bases of *Calluna*, tussock, *Dracophyllum*, and manuka plants. Cicada larvae were discovered in the soil amongst the roots of a small sample of plants, having exuviae at their bases. Assuming that 'hatched' exuviae at the base of a bush represent the presence of, and correlate with, the number of cicada larvae that have fed on the roots of that plant, then the number of exuviae will give an index to the amount of root feeding by cicadas for each type of plant. From plants around the Park, including near where this experiment took place, eighty *Calluna*, 60 tussock, 40 *Dracophyllum*, and 20 manuka bushes bases (including a 10 cm radius adjacent the plant on the soil and litter) were examined for the presence and number of cicada exuviae.

Treatments

Four treatments were applied to each replicate:

1. Root protection: Diazinon granules ("Yates soil insect killer" 50g kg^{-1} in pellet form) were used. This organo-phosphate is known to kill a wide range of invertebrates but in this form is designed to kill Scarabaeidae larvae and porina larvae. Application rate was 29 gm^{-2}, about 6 times as concentrated as is recommended for garden use. The pellets were sprinkled liberally, but evenly over the soil of those plots randomly assigned as root protection plots. The manufacturer recommended re-treatment after two months, and so this was done. There was no need to water in the pellets as rain fell after each application. The buffer zones were also treated.

2. Total plant protection: The systemic insecticide Dimethoate "RogorE" (Walton and Walton 1994) was used in a wettable powder form. Being systemic, the insecticide is absorbed into the plant and translocated to most tissues, effectively protecting all parts of the plant, though roots, especially secondary roots, may receive little (McGregor, pers. comm.). This insecticide, as well as being broad spectrum against phytophagous insects, also has miticidal activity. The recommended concentration for orchard use is approximately 600 ml/400L /ha (Walton and Walton 1994), so I used double the normal concentration, i.e. 0.25 $cm^3L^{-1}m^{-2}$). Spraying was done with a back-pack hand pump sprayer on calm days every two weeks from the initial spraying at the start of the experiment. Each plot (including the buffer zones) received one litre of spray. An effort was made to spray in the late afternoons to minimise Apididae (honey bee) poisoning.

3. Defoliation: This treatment simulated extensive foliage damage. The amount of foliage removed was calculated based on information of *Lochmaea suturalis* feeding (Brunsting 1982); 2000 beetles m^{-2} is the level reported from The Netherlands that results in *Calluna* death. One *Lochmaea* beetle requires approximately 151 mg of *Calluna* from hatching to laying eggs; 2000 beetles therefore require around 302 g of *Calluna* . My plots are one metre by two metres and therefore I estimate that 604 grams were to be removed to simulate retarding levels of herbivore damage. Using a hand held spring balance foliage

material was clipped haphazardly off most of the *Calluna* plants in the plot until the desired weight was removed.

4. Control plots: These plots had no treatments but were pegged out and managed as all others bar the chemical or mechanical alterations.

Measuring responses

To measure shoot growth an initial 100 shoots at each plot were marked using a cardboard template which sheltered the top 1 cm of the shoot while lime green fluorescent paint was sprayed on an open patch in the template to mark the boundary of the 1 cm zone. From each plot an initial 50 of the marked shoots were randomly sampled (cut) and collected for dry weight measures immediately. The other 50 were collected at the end of the experiment (6 months later) and dry weight obtained.

Analysis

Analysis of variance is used to find statistically significant differences between the food plants offered in the lab feeding trials. Pearson correlations were conducted to show any relationships between plant damage and insect weight change or frass output. The choice of location (plant type) trials are compared using a Chi square contingency table and graphed for visual comparison. Consumption of food plants by the insects is calculated using the mean number of leaves damaged per food plant type per insect type, the mean percent damage per leaf per food plant per insect type, and the mean weight of a leaf per food plant type. The herbivore impact field trial is assessed using an ANOVA.

RESULTS

FEEDING TRIALS

Insect survival and profit

The Acrididae (grasshoppers) survived the 5 day test period. The manuka beetles rarely lived longer than three days in the feeding chambers. The majority of subjects lost weight (mean ~22 % weight lost) (Fig. 4.5 a, b).

For the manuka beetle the variation in weight change between individuals is widest when fed on *Calluna*, spanning all other results (Fig. 4.6 a). Weights were best maintained on a diet of manuka taken from the Park, with the nursery grown variety giving the greatest loss in body weight (Fig. 4.6 a). An ANOVA on weight change versus plant diet indicated that there was no statistical difference in change of weights of beetles based on food plant ($R^2 = 0.181$, n = 32, Df = 3, F = 2.06, P = 0.128). Frass production was also the same ($R^2 = 0.09$, F = 0.922, P = 0.443).

For the grasshoppers, *Calluna* as food resulted in the least weight lost (80 % of initial weight maintained). *Hebe* was the next best, followed by manuka (Fig. 4.6 b). The differences between food types were, however, not significant at the 5% level ($R^2 = 0.044$, n = 57, Df = 2, F = 1.257, P = 0.293). The amount of frass produced was not statistically significantly either ($R^2 = 0.1$, F = 2.985, P = 0.059).

Diet preferences

To indicate difference in damage level, and thus preference for chewing, Chi square contingency tables were used (Table 4.1). The Park manuka and nursery manuka are pooled due to low numbers. A plant was considered chewed, category 'yes', if more than four leaves of *Calluna* or manuka, or two of *Hebe*, had feeding damage. The analysis suggests no food plant preferences for manuka beetles ($Chi^2 = 2.588$, $P > 0.05$), but grasshoppers did appear to favour *Calluna* foliage ($Chi^2 = 20.36$, $P < 0.05$).

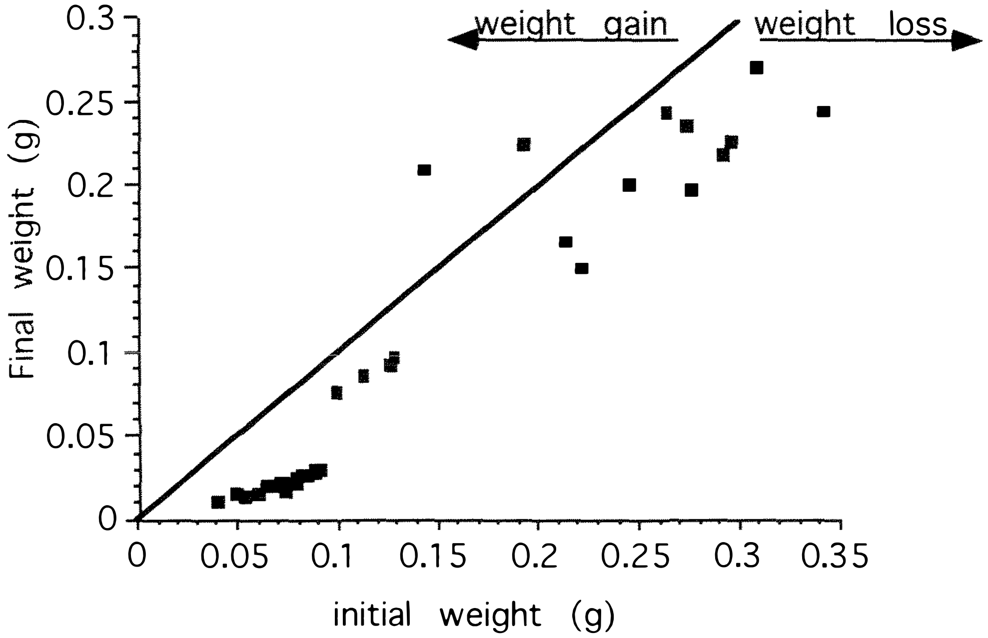
Table 4.1 Manuka beetle and grasshopper feeding preference. Data are pooled from both feeding trial runs. Park manuka and manuka data have been pooled.

beetle damage	*Calluna*	Hebe	manuka
- present	**6**	**2**	**4**
- absent	**8**	**9**	**15**
grasshoppers damage			
- present	**21**	**5**	**10**
- absent	**1**	**13**	**11**

Fig. 4.5 Insect weight gain, or loss, in the feeding tests (all insects on all plants). Each point represents one insect's change in weight, over either 3 (manuka beetle) or 5 (grasshopper) days.

manuka beetle

a)



grasshopper

b)

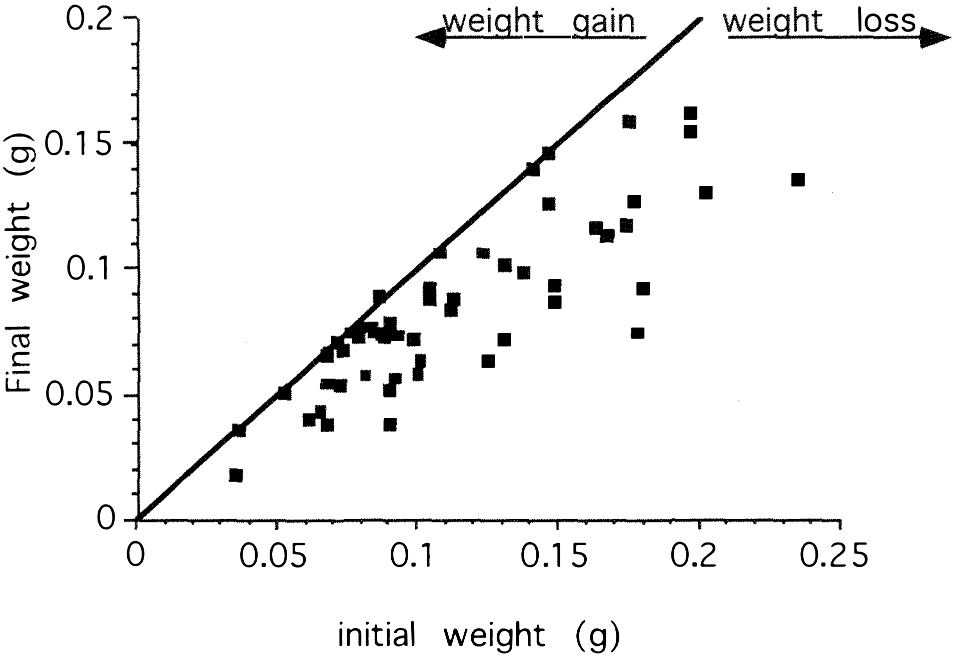
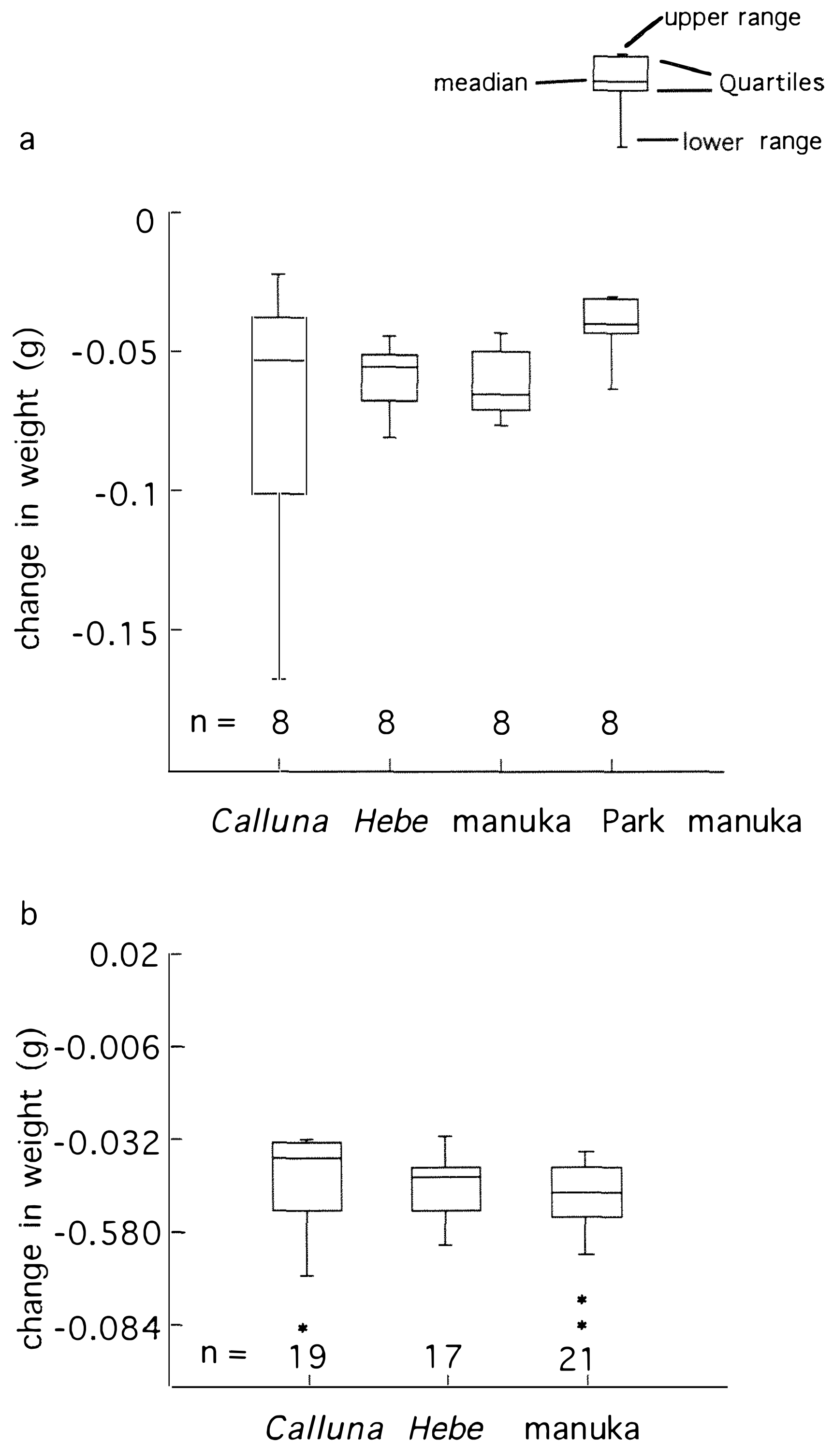


Fig. 4.6

Box plot of change in weight of manuka beetles (a) and grasshoppers (b) in relation to food plant type.



The amount of chewing damage was related to plant type for beetles (R^2 = 0.401, n = 32, F = 6.261, P = 0.002) and grasshoppers (R^2 = 0.383, n = 57, F = 16.771, P = 0.000). Bonferroni range analysis showed that beetles and grasshoppers damaged *Calluna* more than any other food plant. Damage to plants was not correlated with insect weight change (Table 4.2). It is more strongly associated with the amount of frass produced. There was also a weak, but not significant, negative correlation between frass and weight change in the grasshoppers. The frass-damage correlation implies that the large amounts of frass seen in the *Calluna* chambers (mean = 19.5 pellets) compared to *Hebe* (6.4), manuka (~1) and park manuka (4.6) were actually from feeding (ingestion) of *Calluna*, and not just 'vandalistic' damage.

Table 4.2 Pearson correlation matrix of feeding measures; numbers in bold, upper right, are grasshopper correlations, lower left in 'Roman' text are manuka beetle correlations. * = values significant at $P \leq 0.05$

	Weight change	Plant damage	Frass
Weight Change		**0.379**	**0.432**
Plant Damage	0.063		**0.764** *
Frass	-0.252	0.357	

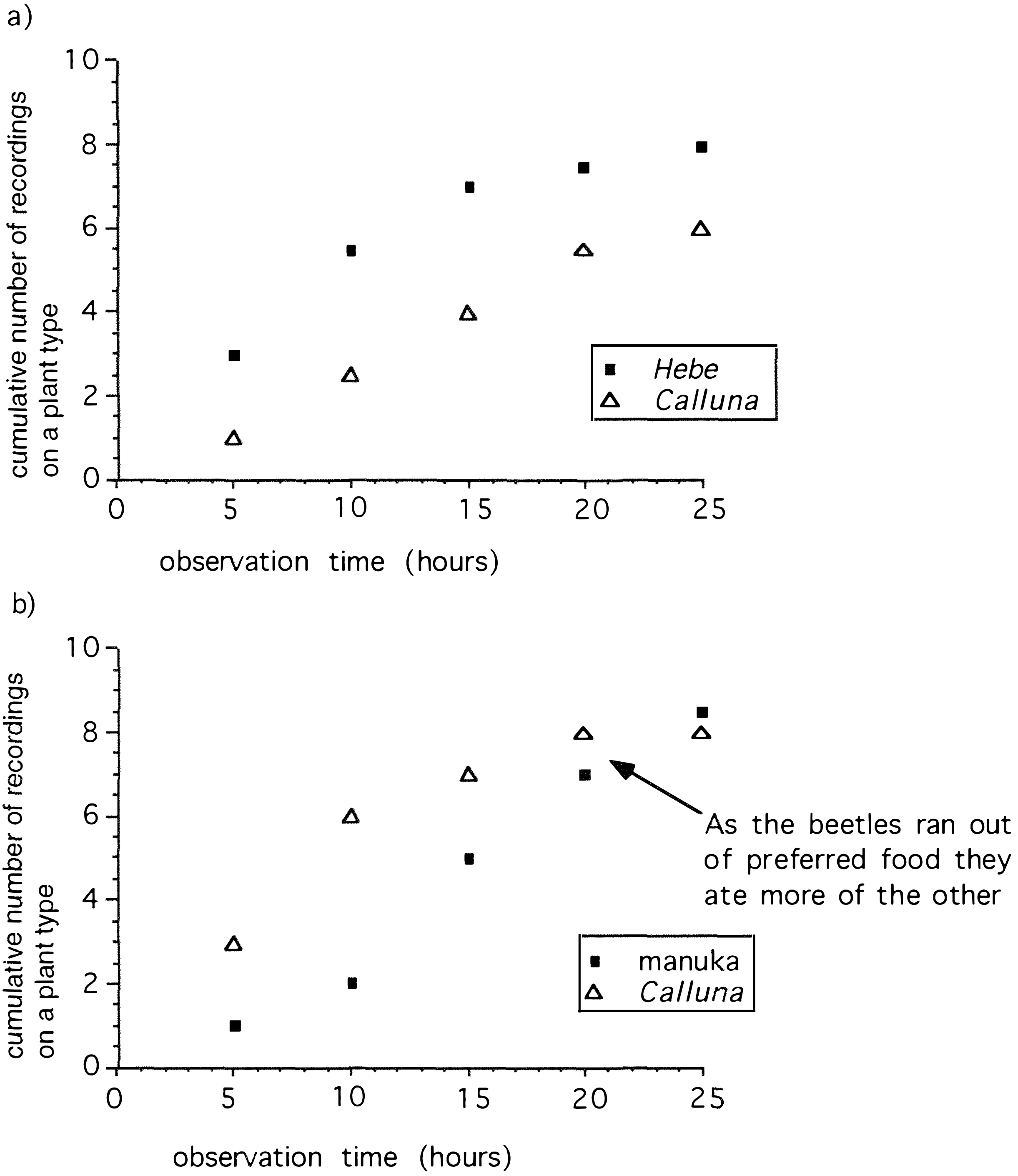
Location during choice tests

Manuka beetles were more often found on *Hebe* than *Calluna* (Fig. 4.7 a), but were more often on *Calluna* than manuka, until the *Calluna* had been stripped, evident at the end of the observation time as the data values became more similar (Fig. 4.7 b).

The grasshoppers were found equally on both *Hebe* and *Calluna* until the *Calluna* foliage was stripped, evident after ~ 40 hours (Fig. 4.8 a), and then progressively more often on *Hebe*. They were always more often found on *Calluna* than on manuka (Fig. 4.8 b).

Fig. 4.7

Manuka beetle preference for foliage visited in choice chambers; observed over a period of 25 hours.

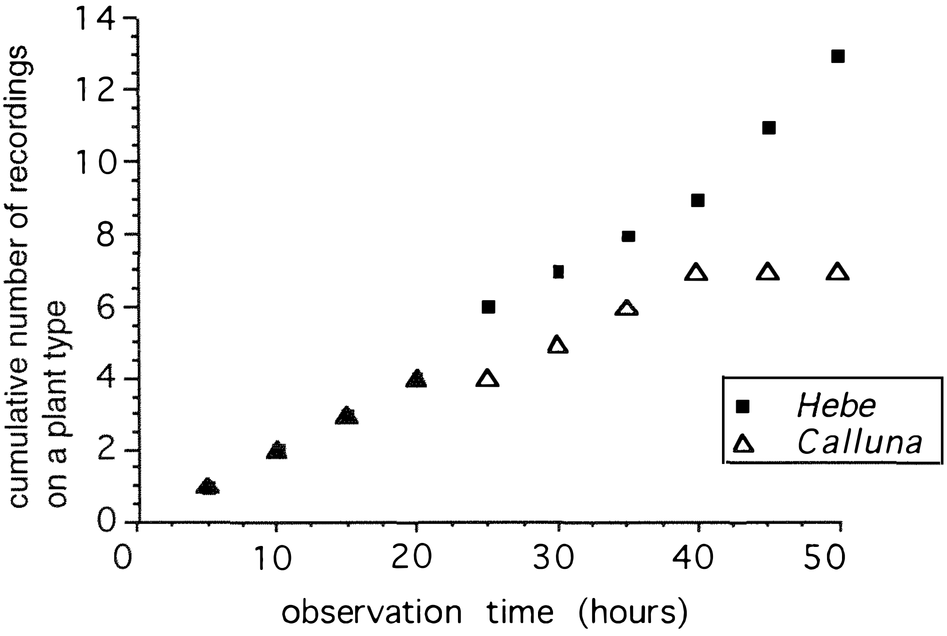


As the beetles ran out of preferred food they ate more of the other

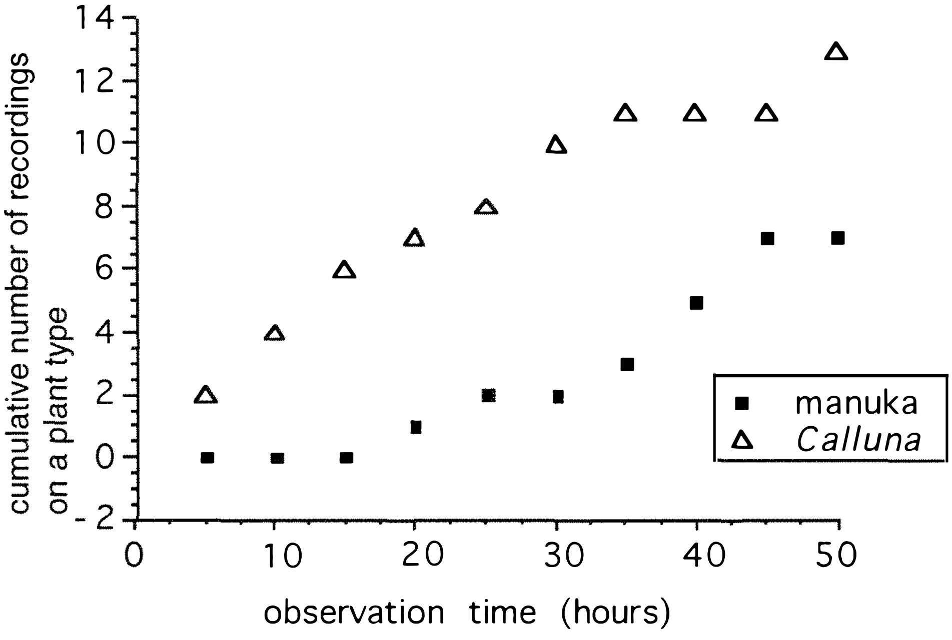
Fig. 4.8

Grasshopper preference for foliage visited in choice chambers; observations taken over a period of 50 hours.

a)



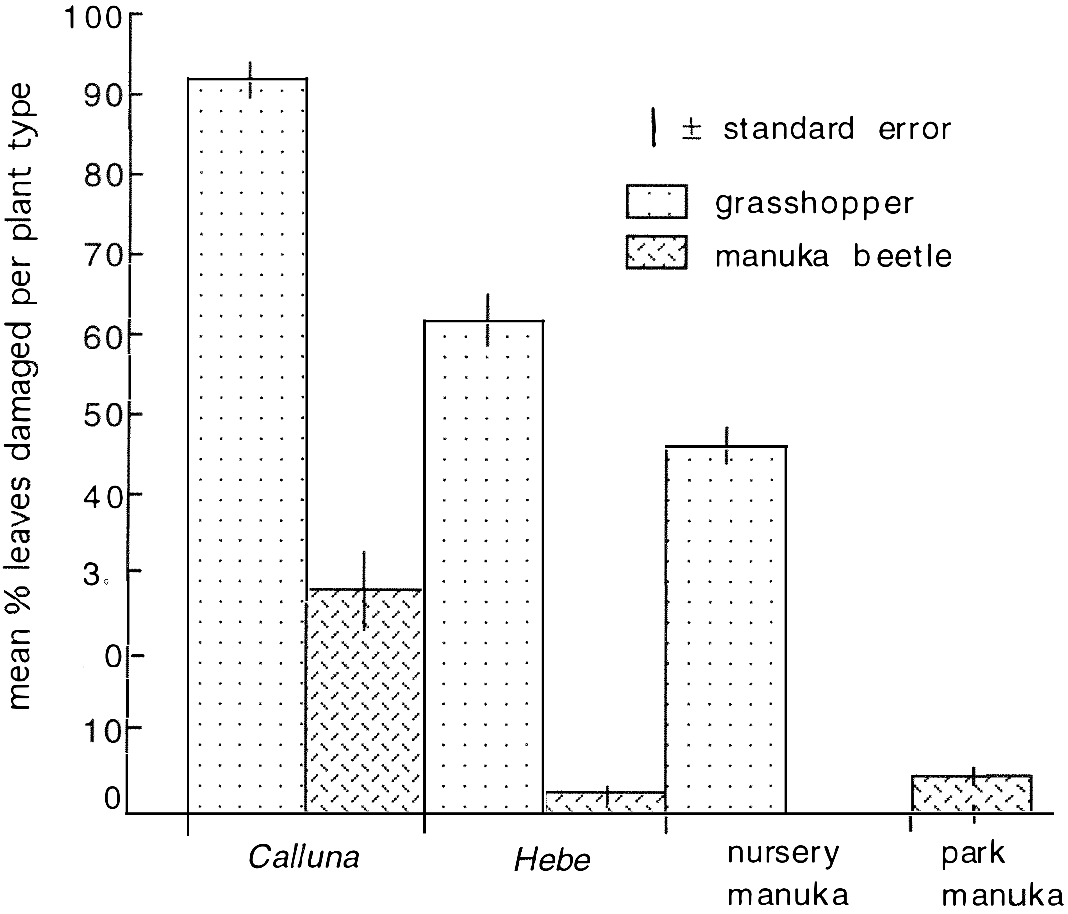
b)



Quantity of plant material consumed

Grasshoppers did approximately four times as much damage to plants as did manuka beetles (T=13.44, Df=31, P < 0.005). They also did one third to one half times more damage to *Calluna* than to either of the other food plants (Fig. 4.9, P <0.003), and sampled 2 to 4 times more leaves than the beetles. The beetles damaged *Calluna* more than Park manuka (P = 0.071), and more Park manuka than *Hebe* (P = 0.044), but did not damage nursery manuka (Fig. 4.9).

Fig. 4.9 Difference in the mean percent damage (area removed) of leaves from test plants per insect type over the test period.



The *Hebe* leaves were largest and heaviest, offering the most food per unit (leaf), and thus a possible reason for the lower mean number of leaves eaten (Table 4.3). On average grasshoppers consumed six times more *Calluna* and *Hebe* than beetles, but only half as much manuka (Table 4.3).

Table 4.3

Average weight of a leaf (from a measure of 200 leaves per plant type), mean damage of a leaf, mean number of leaves eaten over the test period, and calculated biomass eaten by insect type per day. Values in ( ) are standard errors of the means, (note: very small for leaf weight).

insect	plant	mean leaf weight (g) n = 200	mean % damage to a leaf	mean number of leaves eaten	biomass consumed (g)
manuka beetle	*Calluna*	0.0046 (0.0)	13.93 (1.90)	12.5 (2.44)	0.00267
	Hebe	0.015 (0.0)	5.75 (0)	4 (0)	0.00115
	manuka	0.0015 (0.0)	12.86 (3.03)	7 (2.02)	0.00045
grass - hopper	*Calluna*	as above	64.45 (8.06)	27.2 3.56)	0.01612
	Hebe		20.02 (6.30)	16.7 (4.05)	0.0067
	manuka		24.33 (3.45)	28.1 5.11)	0.00021

HERBIVORE EXCLUSION TRIAL

Above ground herbivore load

The above ground herbivore abundance was low, with only 6 sucking and 5 chewing insect taxa in three 1mx2m area samples of *Calluna* (Table 4.4, but see Chapter 3). The most abundant organisms were mites, though their feeding mode (herbivorous ?) is not certain.

Table 4.4 The type and number of herbivores found at initiation of the exclusion experiments.

Herbivores	number of taxa	abundance	feeding mode
Aphididae	1	1	suck sap
Delphacidae	1	2	suck sap
Coccoidae	1	3	suck sap
Thysanoptera	1	14	pollen/nectar
Acrididae	1	1	chew foliage
Lepidoptera sp.1	1	2	chew foliage
Lepidoptera sp.2	1	1	chew foliage
Ephydridae	1	1	chew foliage
Mite	8	57	?
Total	16	82	

Root herbivore survey

There is some herbivore pressure on the plants, normally un-observed, through root herbivory. Tussock supported the highest mean number of cicada larvae closely followed by *Calluna* (Fig. 4.10). ANOVA tests showed variance in number of cicada exuviae explained by plant species was close to statistical significant (F = 2.562, Df = 3, P = 0.056). Size of plant was not correlated with number of exuviae (Pearsons corr. R = 0.063, P= 0.375).

Exclusion trial

For every treatment there was an increase in dry weight of shoots i.e. growth, through leaf number increase and stem growth (Table 4.5). In all cases the final dry weights were at least double the initial, and often as much as three or four times greater, reflecting summer growth (Fig. 4.11).

ANOVA showed that treatments did not have an effect on growth of *Calluna* (P = 0.945, Df = 3 at 95% C.I.).

Table 4.5 Average change in weight of *Calluna* shoots in the experimental plots. Number in ( ) is standard error of the mean. Growth per treatment area = % cover x weight change.

Treatment	mean change in weight/shoot (g dry weight)	Mean % *Calluna* cover	growth (g dry weight) per treatment area (m^2)
root protection	0.0574 (0.0071)	76	4.362
defoliated	0.0639 (0.0131)	75	4.793
total protection	0.0569 (0.0003)	95	5.406
control	0.0549 (0.0042)	73	4.008

Fig. 4.10

Mean number of cicada exuviae found at the base of surveyed plants (lines are one standard error).

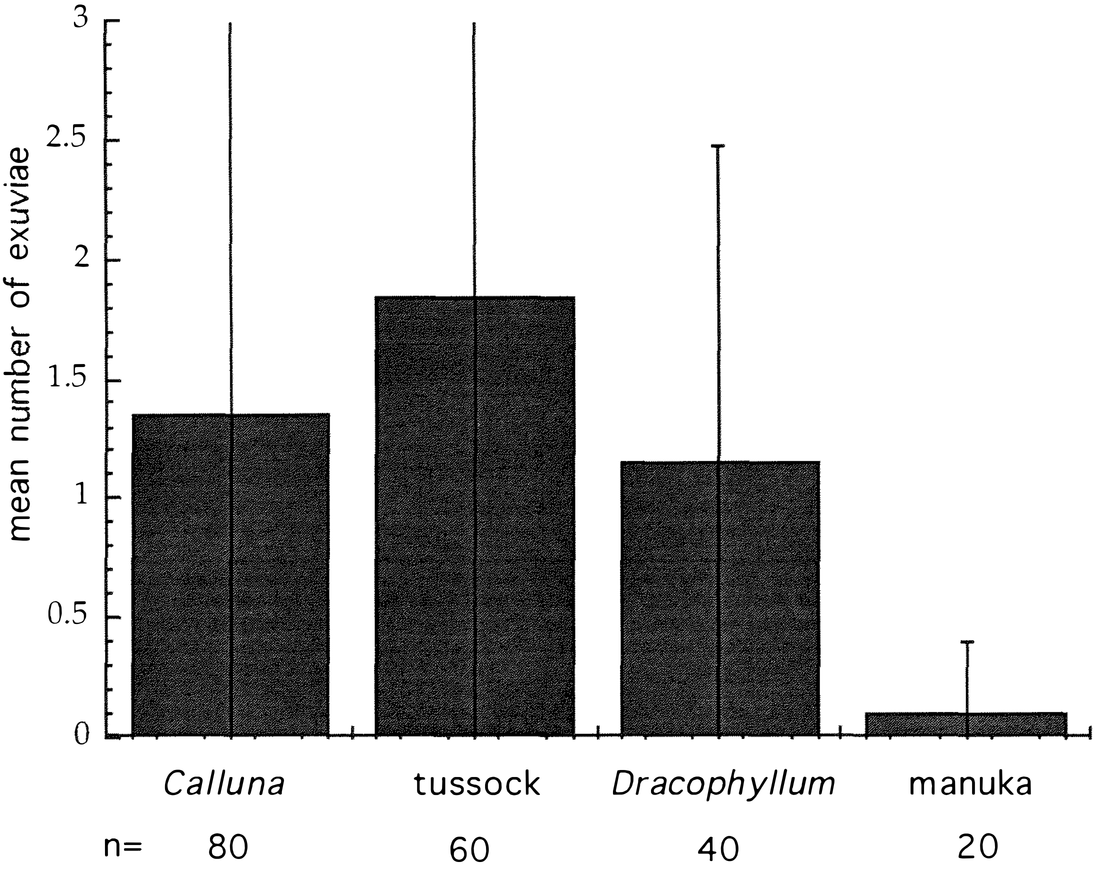
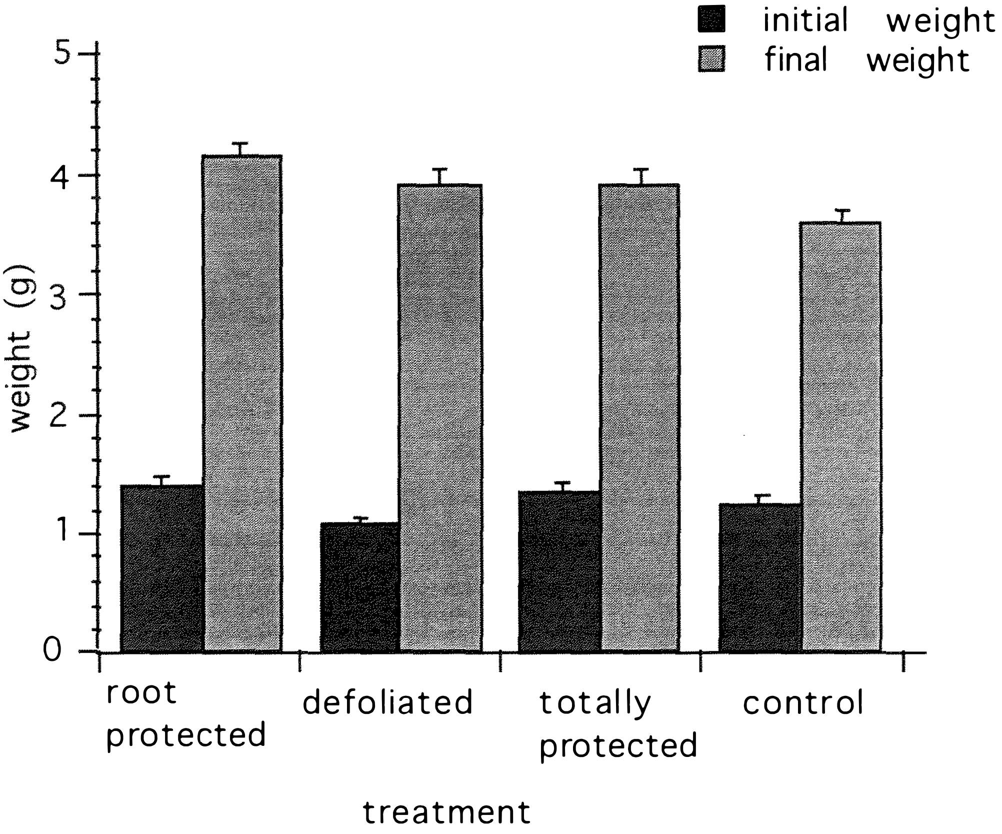


Fig. 4.11

Initial and final weights of untreated shoots 6 months after the whole bush was exposured to the treatments (bars are one standard error). Protection was by 3 applications of Diazinion, and 11 applications of 'Rogor E'.



DISCUSSION

Examination of the insect feeding and native herbivore 'challenge' to *Calluna* suggests that some elements of the native assemblages studied are 'plastic' in their diets and that the evidence here has use in predicting the resource availability to the proposed biological control agent, the monophagous defoliating beetle, *Lochmaea suturalis*.

Insect feeding

Probably insects need a range of food types from which to gain all the elements of a healthy diet; this tends to be the case for polyphagous insects (Fraenkel 1953, Chapman and Bernays 1978, Scriber 1984). Virtually all insects in the feeding tests lost weight, regardless of food type. Grasshoppers best maintained their weight when fed on *Calluna*, while the manuka beetle lost least weight on Park manuka. This perhaps is expected since Park manuka is the "preferred" diet of the manuka beetle. It is possible that the insects receive no more nutriment from *Calluna* than the other plants, but did receive more water. Nursery manuka resulted in the greatest weight losses. Thus no one plant species in these tests offered a complete diet, so maintenance of weight was rare. Further, the native plants offered may not have been the most ideal ones to use, especially for the grasshoppers, and, though water was supplied and temperature remained within the insects' experience range, perhaps the environmental conditions were not suitable, or the stress of capture too great.

Calluna plants received the most damage (chewed and removed material). More *Calluna* leaves were sampled by grasshoppers than any other plant, and the damage done to each leaf was far greater than to any other species' leaves. The manuka beetle sampled equal numbers of leaves from the different plant types, but damage was most severe to *Calluna* leaves. A manuka beetle is only a third as damaging as a grasshopper. There appears to be a preference for *Calluna* foliage, or the *Calluna* has milder deterrents that caused much more sampling of many leaves. Whichever the reason both types of insect chewed more *Calluna* than *Hebe* or manuka.

Frass production indicated that ingestion of plant material was occurring rather than simply repeated sampling because of diet dissatisfaction. The frass data for grasshoppers support the preference and damage data in that they show *Calluna* as being the most ingested plant species - one third to one half times more so than *Hebe* or manuka.

The insects' choice of foliage contradicts some of the above statements. Both insect types were either as likely, or, for beetles, more likely to be on (and thus, perhaps, feed on) *Hebe* than *Calluna*, when given the choice. Grasshoppers were as likely to be on *Hebe* as *Calluna* until the *Calluna* shoots were stripped of leaves. This happened much sooner to *Calluna* than *Hebe*, whose larger leaves take longer to severely damage; but also there appeared to be less damage to the *Hebe* leaves even though time spent by the insect on each plant was evenly distributed. Nursery manuka was never the favoured choice; perhaps this is because insects a) needed little manuka to satisfy hunger and spent more time exploring or b) did not accept manuka at all.

Insect consumption

Manuka beetles ate ~2-5 times more *Calluna* than *Hebe* or manuka, (yet did best on Park manuka) over the three day period. Grasshoppers showed a similar trend, only they ate 10-20 times more *Calluna* than *Hebe* or manuka over a five day period.

Using the consumption values estimated as a base, I can extrapolate to predict consumption over a six month period spanning summer. I expect a grasshopper to consume 0.0806 g *Calluna* x 36 (since there are 36 periods of 5 days in 6 months) = 2.9 grams of *Calluna*. Knowing the population density of grasshoppers in an area of *Calluna* would then allow a rough estimate of the biomass of *Calluna* removed through grasshopper feeding (assuming they ate as much *Calluna* in the field as in the lab). The invertebrate survey (Chapter 3) suggests there are at least 22 grasshoppers per 100m^2. In one hectare a rough estimate would be 2200 grasshoppers. Thus the amount of *Calluna* eaten would be:

22000 x 2.9 g = 63800 g (**63.8 kg**)

The same approach can be used for the beetle, except that I will consider only one month of the survey data, mid December through to mid January. This is when the adults are in very large numbers (for mating and at flight time), i.e. densities of 225 beetles per m^2. Thus in one hectare there would be 56500 beetles, each chewing 0.008 grams of *Calluna* in the 3 days measured, which multiplied by 10 (for one month) gives a value of

56500 x 0.0801 g = 4525.65 g (**4.5 kg**)

Beetle damage for the rest of the warm months (say 5) at a lower densities (1000 per ha) would equal **1.13 kg**.

Total grasshopper and beetle biomass removal for the warmer six months of the year is estimated at 63.8 + 4.5 + 1.13 = **69.43 kg.** These are wet weight values. For comparative purposes with other studies, dry weight of *Calluna* is 83% of wet weight. So dry weight consumption = **57.63 kg**.

With the data on biomass from Chapter 2 and using an estimate of current shoot/total biomass ratio (18%) (Chapman and Bannister 1994) to gain an estimate of the standing crop of 'green' shoots (Table 4.6) an estimate can then be made of the percentage of *Calluna* 's standing crop the two herbivores eat.

Table 4.6 Total standing biomass and current year's shoot biomass of *Calluna* in areas around Tongariro National Park.

	Desert Road sth	Desert Road nth	Bruce Road	Mangatepopo	National Park
biomass (kgha^{-1})	19800	52,600	238,000	190,000	150,000
current year's shoot biomass (kg/ha)	3564	9360	42840	34200	27000

Grasshoppers on the Desert Road side of the Park are in very large numbers, much more than estimated here. Thus the Desert Road loses ~ 63 kgha^{-1} per six months from defoliation with a standing crop of either 3564 or 9360 kgha^{-1}. Thus the percentage defoliation is ~ 0.67% to 1.77%. On the western side of the Park defoliation is 69.43 kgha^{-1} and the *Calluna* current shoot biomass ranges from 27000 to 42840 kgha^{-1}, giving defoliation percentages ranging from 0.16% to 0.26%. These figures are nowhere near Grant and Hunter's (1966) 40 or 80% defoliation levels required to inflict 'real' damage. The figures presented here are in accordance with White's (1978) estimates of grasshopper consumption in grasslands of 1-2% or, rarely, 6% consumption of annual primary production.

The above calculations allow comparison of the consumption levels of the biological control agent, *Lochmaea suturalis*, of *Calluna*. And so the 'natural' impact and the added impact of the control agent can be estimated.

Table 4.7 Consumption of *Calluna* over a six month feeding period of *Lochmaea suturalis* (in 'out-break' mode) in the Netherlands (from Brunsting 1982), with New Zealand comparisons, and estimated above ground current years increment.

agent	consumption (kg dry matter/ha) Netherlands	consumption (kg dry matter/ha) New Zealand
Adults	197	grasshopper 52.9
		beetle 4.7
Larvae	344	unknown
Total	542	57.6
Sheep graze (0.8/ha)	350	
current year's standing crop	18000	3600-43000

Thus, competition and interference aside, one might expect the combined efforts of *Lochmaea*, manuka beetle, and grasshoppers (disregarding any other natives that may be feeding on *Calluna*) to remove 600 kg of current year's *Calluna* shoots over one hectare in six months. This amounts (using Table 4.7 values) to ~1.4% to 16.7% defoliation. Of course the total intake of the insects measured here and in Brunsting's study is less than the potential amount of food available to them in the field; certainly grasshoppers had often stripped all the *Calluna* in a test chamber before the end of a 5 day trial. Thus this is likely to be an underestimate.

Calluna growth and herbivory

The release from herbivory had no beneficial effect. The damage level of clipping removed as much biomass of *Calluna* as does the bio-control agent at damaging population levels, though without the addition of chemical substances involved when isects feed, and so I expected the *Calluna* to be, at least, if not more, retarded by this treatment, considering also that clipping removes much more structural tissue (wood) than does insect feeding. The fact that it wasn't suggests that the co-requisite features of the habitat that cause the death of large areas in The Netherlands in conjunction with the beetle, (over fertilisation, drought, unusual frosts) did not occur at the experimental sites in the Park, and perhaps will not occur after establishment of bio-control agent, even if the agent can maintain substantial levels of defoliation. An important consideration, however, is that this experiment measured only short term responses. It is possible that the substantial regrowth seen could not have been sustained over a long period, and that the plants may have 'weakened' themselves by expending important reserves in re-establishing their foliage, creating a situation where they may suffer some time in the future, as is the case in some tussocks after burning (Mark 1979).

Threshold damage

The native herbivores alone are not reaching the threshold damage level of *Calluna*. Nor would *Calluna* still be successfully spreading in the Park if it were 'challenged' by herbivory. Addition of the bio-control agent can only boost the level of defoliation, though if it does not attain 'out-break' proportions, the gain in damage to *Calluna*, though additional, will be minimal.

Native phytophagous diet plasticity

The fauna on *Calluna* in the Park is much reduced (in taxa and abundance) than that normally found in its native habitats of western Europe and the United Kingdom, especially the phytophagous insects that feed on *Calluna*, (cf. Chapter 3). Because *Calluna* is an introduced 'weed', it will have escaped its 'normal' herbivore load and have established in New Zealand with little grazing, or pathogenic pressure. The defoliation percentage calculations support this. Obviously some of our native insects have, however, managed to incorporate it into their diets (at least *in vitro*), exhibiting some plasticity.

Testing other groups, Lepidoptera, weevils, Psyllids, and other Homopterans, would better examine the concepts that New Zealand insects are generally slow to change or totally inflexible, or that

Calluna is an inappropriate host, for which the native insect herbivores may have no pre-conditioning and no plasticity to cope with it. This experiment has only scratched the surface.

Conclusion

Some insect herbivores have, at least *in vivo*, managed to incorporate *Calluna* into their diets, and have not been deterred by *Calluna's* secondary chemicals (Jalal *et al.* 1982) or its novel growth form. The results imply that many other insects may have, or are, managing to utilise *Calluna* as a food source. Since root feeding may be even more detrimental to a plant (Brown and Gange 1989a), and the Cicadidae survey showed there to be a high level, relative to natives, of probable root herbivory (not to mention manuka beetle larvae, which are root feeders and most likely to feed on *Calluna* roots too), the damage estimates presented here are conservative. It is unlikely that the native herbivore pressure alone impacts detrimentally on the performance of *Calluna*. Addition of the heather beetle will enhance herbivore impact, but other environmental stresses (e.g. frosts, droughts) will most likely need to be concurrent with herbivory before *Calluna* stands will actually die.

Chapter 5

Testing predictions about community stability through measures of Resilience, Persistence, and Consistency

ABSTRACT

The native tussock grassland invertebrate assemblages of Tongariro National Park have co-evolved with the vegetation community for 1000's of years. The current grassland habitats have been in existence for over 400 years (Rogers 1990). The question can be asked whether these assemblages are more or less stable than the assemblages formed in the wake of disturbances; those developed after invasion and dominance of European heather, *Calluna vulgaris.* Both have different developmental histories and, presumably, different complexities. Measures of their complexity, resilience, persistence, and consistency (i.e. stability) can offer some evidence as to the communities' robustness in the face of disturbance, and give indication as to their recovery time and ability to recover to their original state.

Measures of resilience, persistence, consistency, i.e. stability, and community complexity are hard to apply and harder to interpret, with the interaction between complexity and stability often being unpredictable. Logistic constraints, not the least of which are time and expert background knowledge (eg. taxonomic knowledge), mean some areas (ie. complexity measures) are 'loose'. The results of any such study need careful scrutiny and cautious acceptance.

Though these measures are complex and controversial in interpretation, they are, nevertheless, more progressive ways of attempting to understand community dynamics. In two existing invertebrate assemblages, one native (tussock grassland) the other in a *Calluna* heathland (post invasion), I have attempted, through the application of a disturbance event (intense insecticide application), to measure the speed of faunal return (resilience) and the structure of the reformed assemblages (consistency). These measures aim to address the questions:

1. how do native invertebrate communities respond to a disturbance (on a small scale);
2. what is the time factor involved in re-establishment;
3. is reformation to a similar (original) state.
4. how do, by comparison, the 'new' *Calluna* communities (those replacing tussock) respond, given their differences in complexity, and time of co-existence with their habitat.

Hopefully this type of approach will offer a new way of viewing our native invertebrate assemblages, providing some idea (if not predictive power) as to native systems robustness and also the ability of native communities to return to areas now dominated by *Calluna*, should control measures of this 'weed' prove effective.

The initial estimate of complexity for both habitats (as an indicator of stability) went against prediction. The assumption that the tussock grasslands invertebrate assemblage, having a longer co-evolutionary history, is more complex and more stable, proved wrong. Complexity based on number of species, connectence, and evenness of abundance in feeding guilds was greatest in *Calluna* heathland invertebrate assemblages. The rate of return of invertebrates was faster in *Calluna* heathlands (7 taxa per week compared to 3 taxa per week in tussock grassland, and 24 individuals/week compared to 16). However, the time for return of taxa and abundance to their initial state (resilience) was fastest in tussock grasslands (3 weeks *versus* 3.5 weeks); the additional time taken in *Calluna* is probably because of the greater number of taxa and abundances in its original state than in tussock. Consistency, the adherence of the returning taxa to the original composition, was best in tussock grasslands (63% of the taxa were consistent with the original as compared to 44% in *Calluna*). But abundances, though complicated by seasonal progression, show *Calluna* assemblages to 'fill up' with individuals closer to original numbers (89% compared to 55% in tussock). This level of consistency in tussock and poorer rate of return, I believe, is the result of the longer history of association between the components of the assemblage of tussock grasslands. Stability, from a 'functional' assemblage aspect, I interpret as greatest in *Calluna* heathlands invertebrate assemblages, because, though it was measurably more complex, the strengths of associations between invertebrates was less directed than in the tussock grasslands assemblage. This 'relaxed' interaction template means the returning fauna could reform at a faster rate. The evidence suggests that the strategy of 'survival' of the tussock grasslands invertebrate assemblage leans more towards resistance than resilience.

Key words: Stability, resilience, persistence, consistency, community complexity, disturbance.

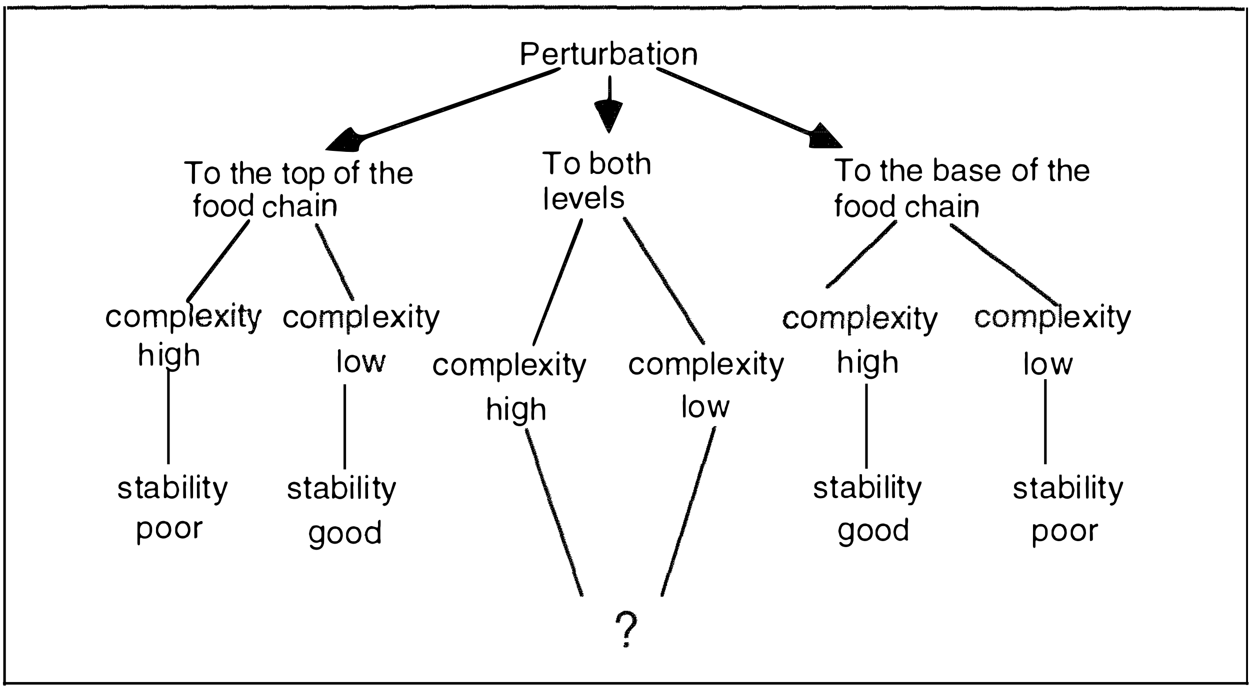
INTRODUCTION

Stability and complexity

Stability is a controversial concept in ecology (Margalef 1968, Pimm 1984). Pimm (1984) describes how the concept of complexity and its effect on stability has changed since the 1970s. Conventional wisdom asserts that simpler ecosystems are less stable than more complex ones (Begon *et al.* 1986). MacArthur (1955) suggested that the multiplicity of pathways for energy to reach a consumer implied failure of any one pathway would be less severe on that consumer and on the system as a whole. Elton (1958) also put forward evidence of pest outbreaks in agricultural systems (ones simplified by humans), and of the ease of invasions into small, remote, and thus species-poor, islands. Both are examples of the instability of simpler systems. For a summary of this evidence see Begon *et al.* (1986).

Since the 1970s, especially as ecological modelling has developed, and field studies have accumulated, ideas have moved to support the opposite contention: that complexity is inversely related to stability. Early 1970s models were weakened by predators that existed without prey, and predator loops where A eats B , B eats C and C eats A. Later models resulted in less sharp transitions from stable to unstable states, but still implied greater complexity equalled greater stability (Begon *et al.* 1986). Other models, termed 'donor controlled' systems, in which food supply affects, but is not affected by, consumers, found stability to increase with increasing complexity (DeAngelis 1975). Detritivore systems adhere to this type of model, as do seed and nectar feeding systems and some phytophagous insect systems (Lawton 1987). Species deletion models (Pimm 1979) illustrated that the effect on complexity of loss of species depended on which trophic level that species occupied. These models predicted that stability increased with decreasing complexity, but only if the species removed was from the 'top' of the food pyramid (e.g. a top carnivore). Basal removal (e.g. a plant or herbivore) resulted in decreased stability . The current situation is summarised in figure 5.1.

Fig. 5.1 *Predicted relationships between stability, complexity and perturbation. After a perturbation, one, several or all levels of the trophic structure may be adversely affected. The effect of the perturbation is dependant on the system's stability, predicted on the bottom tier, depending on whether the community has high or low complexity.*



Overall the trend today seems to be to accept that an increase in complexity generally leads to a decrease in stability. It is generally acknowledged that no single relationship is appropriate to all communities, and real community structure and response is still a distance from modellers' grasps.

Complexity is a collective term for structural and interactive attributes of an assemblage of organisms. Given that complexity is a large determinant of the stability of a system (Clements and Shelford 1939, Flaherty 1969, Collier 1973, Hurd and Wolf 1974), and that opinion about its effect is divided (Hairston *et al.* 1968, Orians 1974a,b, Goodman 1974), it should be the first level of observations when approaching research on system stability. Its measure employs:

1) species richness (the number of species present);
2) evenness (the abundance distribution of the species);
3) connectence (the number of inter-specific interactions divided by those possible);
4) interaction strength (the mean magnitude of interactions).

From the first two measures come the diversity indices, whose use and forms are controversial, especially those that combine the two to form a single measure (Magurran 1988). The last two are the least often measured, due to the difficulty in obtaining, with certainty, good data for systems with many species.

Complex systems are those with high species richness, high evenness, and good connectence with strong interactions. The variability of abundance and interaction strengths, and the variations in the levels of connectence, not always observed by the researcher, can result in misleading measures. Low connectence between taxa, and low strength of interactions within a connectence web, can result in a more stable condition, because such an assemblage has the ability to rapidly re-colonise disturbed areas.

The features of complexity react in many ways to fluctuations in the environment of an ecosystem - usually called disturbances. We may measure the amount of change in these parameters to forecast implications as to the stability of the system.

System stability

Stability is a measure of a community's sensitivity to disturbance (Begon *et al.* 1986)). Stability can be expressed as consistency or persistence (Margalef 1968). Consistency means a degree of predictability in the structure or 'functional' structure of the community (abundance as well as taxon number). Persistence is the presence or absence of organisms (taxa) after a profound disturbance, implying continuity of relationships (see Holling 1973 and Connell and Sousa 1983 for discussions). For stability to exist there needs to be equilibrium points or limit cycles at which the system remains when faced with a disturbance, or to which it returns if perturbed (Fig. 5.2) (Holling 1973, Connell and Sousa 1983).

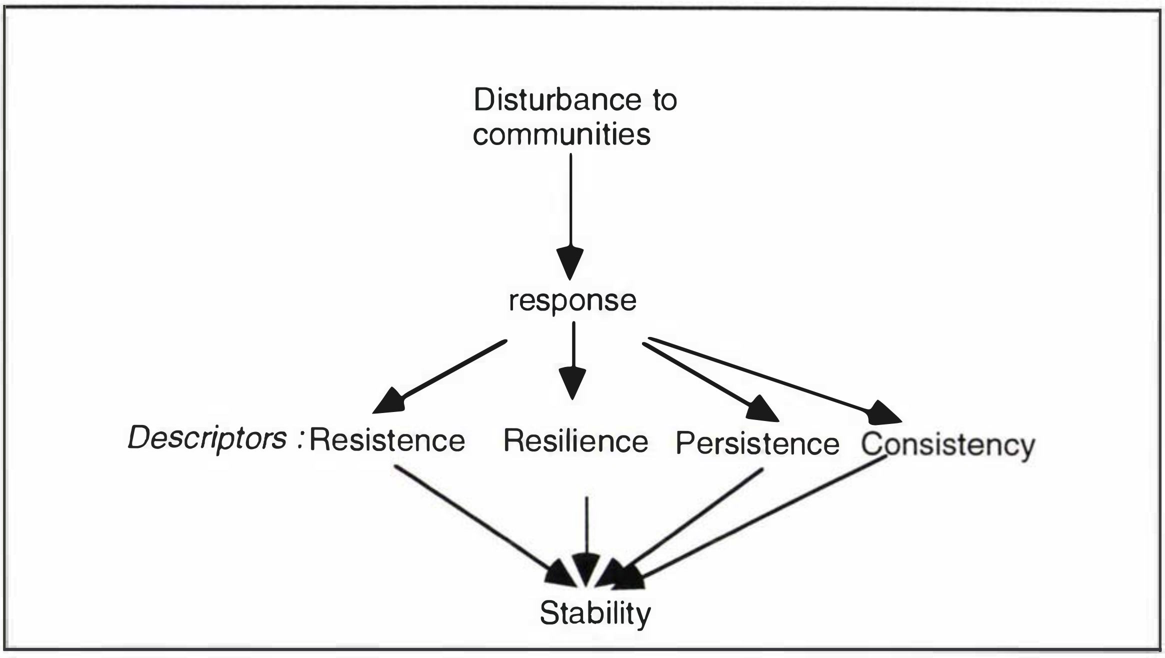
Stability, then, has two aspects:

1) resistance (or inertia, Sheehan 1981, Murdoch *et al.* 1974, Orians 1974a, 1974b);
2) return to 'equilibrium' after being perturbed.

The second aspect has 3 components:

1) rate of return described as elasticity, or resilience (Boesch 1974);
2) distance from which return is capable, termed amplitude (Orians 1974a) or malleability (Sheehan 1981);
3) consistency, the fidelity of the returned assemblages to the original structure.

Fig. 5.2 *The relationship between stability and complexity through its assemblage measures (descriptors).*



Choice of descriptors

There are many descriptors, though only a few are commonly used by most researchers (Fig. 5.2). Other workers considering changes in numbers without disturbances have some terms they use that are often similar, e.g. constancy (Orians 1974a,b, Whittaker 1974), conservatism and endurance (Margalef 1969); these are not considered further.

Resistance, persistence and resilience are the three most widely used and thus 'best' defined parameters of assemblage stability. There are still many varying definitions for these three descriptors, depending on the background, interests, motives, objectives, and schooling of the researcher involved. Stream ecologists have different concepts and preconceptions than a pollution ecologist, or a terrestrial systems (invertebrate-vertebrate) ecologist. The definitions adhered to in this chapter follow.

Resistance

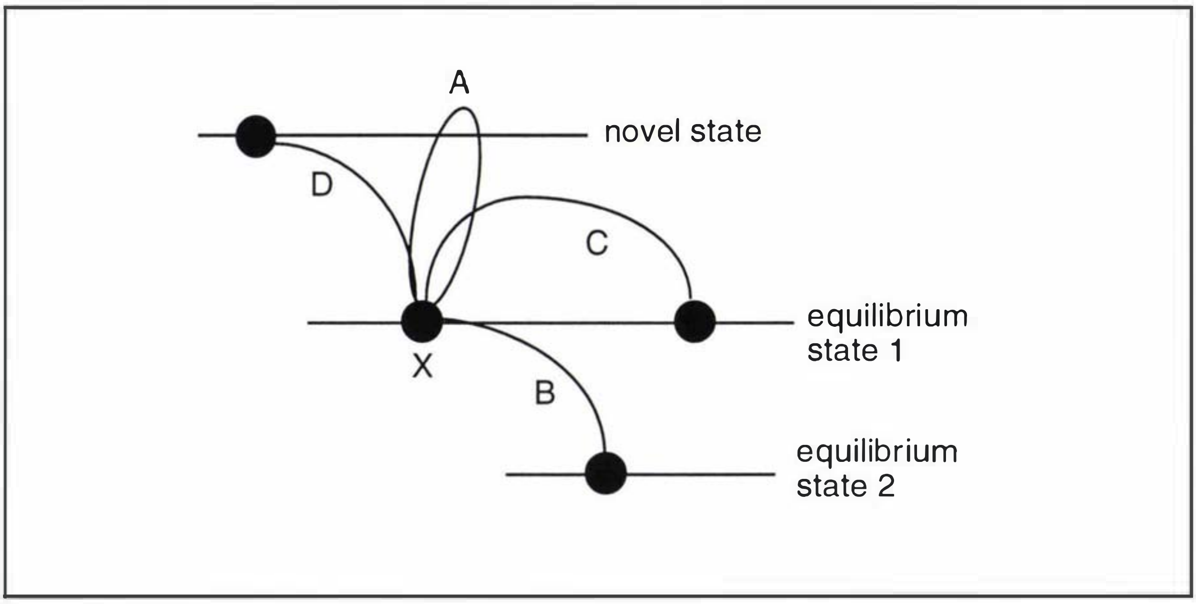
Resistance is the degree to which some attribute of an assemblage is changed following a perturbation (Pimm 1984, Peterson and Stevenson 1992), expressed as a percentage by Fisher and Grimm (1991) and Carpenter *et al.* (1992). Frank and McNaughton (1991) suggest resistance is opposition to change in species composition, one of the attributes of an assemblage.

Resistance appears to pertain to the degree of stubbornness of attributes when challenged with a perturbation; it measures the ability of organisms of a system to avoid [hide from] changing influences or to withstand them. It primarily depends on the timing and intensity of the perturbation.

Persistence or consistency

Holling (1973) suggests stability is a feature of resilience and persistence of components of a system. Sheehan (1981) stated that persistence was survival of a functioning ecosystem through time without reference to its condition. DeAngelis *et al.* (1989) and Pimm (1984) state persistence is the tendency for the components of a system to stay within specific bounds through time, though not necessarily having consistent values. All the above authors require existence of an equilibrium state or states, and return to any of these after a disturbance is an indication of persistence. This does not always mean return to the exact same condition (cf. Lewontin 1969 for discussion on 'original states'); this event is termed consistency. Figure 5.3 illustrates most of the possible states (A-D) that result after disturbance has been imposed on system X. After perturbation community 'X' may return to its original state (path A - exhibiting consistency) or to a new 'reference' state on the same equilibrium level (path C - exhibiting persistence). It may return to a new equilibrium level (i.e. path B) e.g. a 'lower' successional state, or (via. D) to a totally new state, perhaps without equilibrium.

Fig. 5.3 *The possible states an assemblage in system X might return to after disturbance.*



I believe the definition, or choice of terminology, largely depends on the type of system and on what criteria one wishes to impose. I shall refer to consistency as the reformation of the taxa present in the original assemblage (path A), and persistence as the return of taxa and abundances (assemblage structure) similar to those of the original state, but not requiring the fidelity of path A, i.e. the reformation of a functional assemblage similar to the original, but different (path C).

Resilience

Resilience is more complex. Some authors give it a dimension of time only; that is, a rate of return [to something?]. Others give it a rate and a 'persistence' component. All acknowledge that a terminal end point needs to be recognised at which timing can stop. Few discuss amplitude, which is the distance from which return is possible. DeAngelis *et al.* (1989) suggest resilence is the rate of return of the components of a system toward their original steady state (path A, Fig. 5.3) following a perturbation. Pimm (1984) and Carpenter *et al.* (1992) define resilience as how fast the variables return towards an equilibrium; which implies resilience is only a condition for systems originally having stability, and could either be paths A, B, or C in figure 5.3. Fisher and Grimm (1991) state it is the time to recovery of a pre-disturbance state (paths A or C). Holling (1973) submits that resilience determines the persistence of relationships within a system; thus it is a measure of ability to absorb changes of state variables and still persist. Yet again, Sheehan (1981) says it is a zone from which the system can return to a stable configuration (which appears to be amplitude rather than resilience as described above), and perhaps different from the original (any path of figure 5.3). Peterson and Stevenson (1992) recognise it as the ability of a system to return to some "reference" state (path C), following displacement or disturbance.

Resilience clearly has a rate component (all agree), but what the system will return to is contentious and really falls into the realm of persistence or consistency. Thus I shall define resilience as the rate of return to a steady state, and leave the condition of that state to the descriptors persistence and consistency.

A few other conditions have also been noted that pertain to resistance and resilience. Long lived organisms tend to be less resilient and more resistant (Pimm 1984). Longer food webs tend to be less resilient but more resistant (Carpenter *et al*. 1992). Larger organisms tend to be more resistant and less resilient (Fisher and Grimm 1991); hence the spectrum of scale is important.

Aim

The field of disturbance ecology and community stability is a complex, intriguing, controversial, and sometimes apparently convoluted one; an area that could occupy many thesis in itself. I have attempted to reconnoitre into this area to try a more progressive approach to filtering community differences between 'pristine' and invaded habitats, to offer some insight into response time and outcomes of 'old established' assemblages, and 'new' post-disturbance assemblages, after experiencing disturbances.

I aim to measure the complexity of assemblages in an area of tussock grasslands and *Calluna* shrub land at Tongariro National Park to illustrate the effect on assemblage complexity, and thus stability the invasion of *Calluna* has had. Then compare the rate of return of assemblages (resilience), and the level of consistency of each habitat assemblage after severe disturbance created by intense insecticide application. These measures will allow me to:

1) show how a native invertebrate community responds to a localised disturbance;

2) indicate the time factor involved for returning invertebrates;

3) demonstrate the strength of assemblage associations through the fidelity of the returning assemblage (consistency);

4) compare all these aspects between an 'old normal' system and a 'new' post-invasion system;

5) comment on the potential for re-establishment of tussock grassland invertebrate assemblages if *Calluna* control becomes successful.

The intense use of insecticide will negate any resistance feature because the disturbance will be severe and novel. The measurements of stability have spatial and temporal scales that, by Connell and Sousa's (1983) definition, seem impossible to measure without extensive, time consuming, long term observations. I have attempted to create a disturbance on a small local scale, without knowing if the existing assemblages are "stable". Because the experimentation was done within a National Park, the areas used are only small pieces of a large, relatively uniform habitat. This as it maybe, the return of invertebrates, primarily through movement (immigration) from surrounding habitat is still a measure of the larger community's ability to respond to disturbance.

Predictions

Predictions can be formulated about stability, i.e. resilience, persistence and consistency, based on the complexity of systems and their developmental history (e.g. the length of time of association between the components of the community), though Orians (1974a) warns of the "fruitlessness" of trying to measure this connectence between components and thus questions its usefulness as a tool.

The habitats and communities of the tussock grasslands of Tongariro National Park I treat, with respect to the invertebrate assemblages, as being closely co-evolved; this compares with the *Calluna* assemblage that has had only eighty years, at most, to develop. *Calluna vulgaris* (European heather) was introduced without its normal associates, especially its normal invertebrate fauna. Thus the *Calluna* community has developed from 'scratch' and is solely of reassembled native invertebrates.

Pimm (1984) summarised predictions based on modelling species richness and the degree of connectence, suggesting that stability at a local level is influenced by the number of species and their level of connectence. An assemblage containing many species will be less stable than one with fewer species; and an assemblage with strong connectence will be less stable than one with weak connectence. Similarly the greater the number of trophic levels the less resilient that assemblage will be (more levels to reform, with more difficulty, requiring more time). This follows on from thinking about time of co-evolution of assemblages; the longer the time of co-evolution, presumably, the more tropic levels will have developed. Consistency is affected in the same manner as resilience; it is harder to re-establish accurately a more complex system than a simple one, but on the other hand, a more complex system is one that may have set positions for its components (a template), making it easier to return to a previously established condition. Persistence is most likely to be better in less complex systems, where the return to a functional condition will be faster and simpler.

I support the contention that more highly co-evolved systems should tend to rely on resistance and not resilience (Sheehan 1981), as a perseverance strategy, because the effort involved in reforming such a system (a complex one with many trophic levels, well defined associations and 'tight' connectence), is much greater than of a simpler, perhaps 'younger' (evolutionarily), system. The invertebrate assemblage on *Calluna*, being younger in terms of association time, than on tussock, should not exhibit resistance as a perseverance strategy, whereas the assemblage in tussock should. Even if the *Calluna* invertebrate assemblage is more complex (admitting the lack of knowledge to accurately attain this measure) it, being newer and more transitory, should exhibit a better rate of return giving it better resilience than the tussock invertebrate assemblage. The more tightly co-evolved system of tussock grasslands, I believe, should have greater consistency, i.e. high fidelity of components. The more 'mobile' system of *Calluna* should exhibit better persistence, as it will not tend to adhere to a developed template of species connectence, and resource use, as does the tussock assemblage.

METHODS

Sites

Two habitat types were chosen, tussock grasslands and a comparable area of grassland invaded by European heather (*Calluna vulgaris*), now referred to as *Calluna* heathland (see Chapter 2 for basic vegetation descriptions and maps). The tussock grassland site was 200 metres west of the Desert Road near the Waihohonu track car park. The *Calluna* heathland site was ca. 400 metres east of the base of Pukeonake next to the Mangatepopo access road.

Experimental design

Three replicate blocks in each of the two habitat types (tussock grassland and *Calluna* shrub land) were pegged out at the corners to incorporate a 40 metre by 40 metre area (the treatment block). Within each of these areas 12 central, labelled, pegs were placed in a 4 X 3 grid, giving three treatments repeated four times, allowing 4 different harvest times (Fig. 5.4)

The treatments were three different sized circular disturbance areas of radius 0.5 metres (area 0.72m^2), 1 metre (3.14m^2) and 3 metres (7.06m^2) respectively. The treatments were cleared of invertebrates using insecticide applied by a backpack (the disturbance, applied in the first week of November 1993). In the centre of each treatment area a pit-fall trap was placed (see chapter 3) to monitor the return of the invertebrate fauna.

Controls

Invertebrate samples were taken using a D-Vac. A D-Vac is a vacuum device for sucking small invertebrates off turf into a net (Photo. 1). The device was designed for grasses and small prostrate shrubs. It operates best when a seal with the ground is formed. It has problems with taller, aggregated shrubs such as *Calluna* and therefore may not have been as efficient as in the tussock grassland. It was applied over plants and held down hard for 1 minute with slight rocking actions, then quickly up ended, and the net closed and removed. Five such samples per habitat per visit were collected as controls outside but near each block (Fig. 5.4.) to ascertain the "normal" invertebrate fauna, acknowledging that some of the larger animals (large Orthoptera, Carabidae, hunting spiders and nocturnal invertebrates) would not be represented using this collection method (N.Webb pers. comm.).

Control pit-fall traps were also placed in a line outside the blocks to measure the normal animal fauna, and their fluctuations, given the weather variability in any one week. There were 16 control traps in the *Calluna* and tussock which were emptied weekly, though throughout the experiment some traps were made ineffective through surface water run off. Prior to application of the treatments an initial fauna sample, collected using the D-Vac, and one week's pit-fall traps were used to assess the initial fauna, the base level of the assemblage to which it must return after the disturbance.

Fig. 5.4 Layout of a treatment block showing positions of treatments relative to each other and position of sampling events.

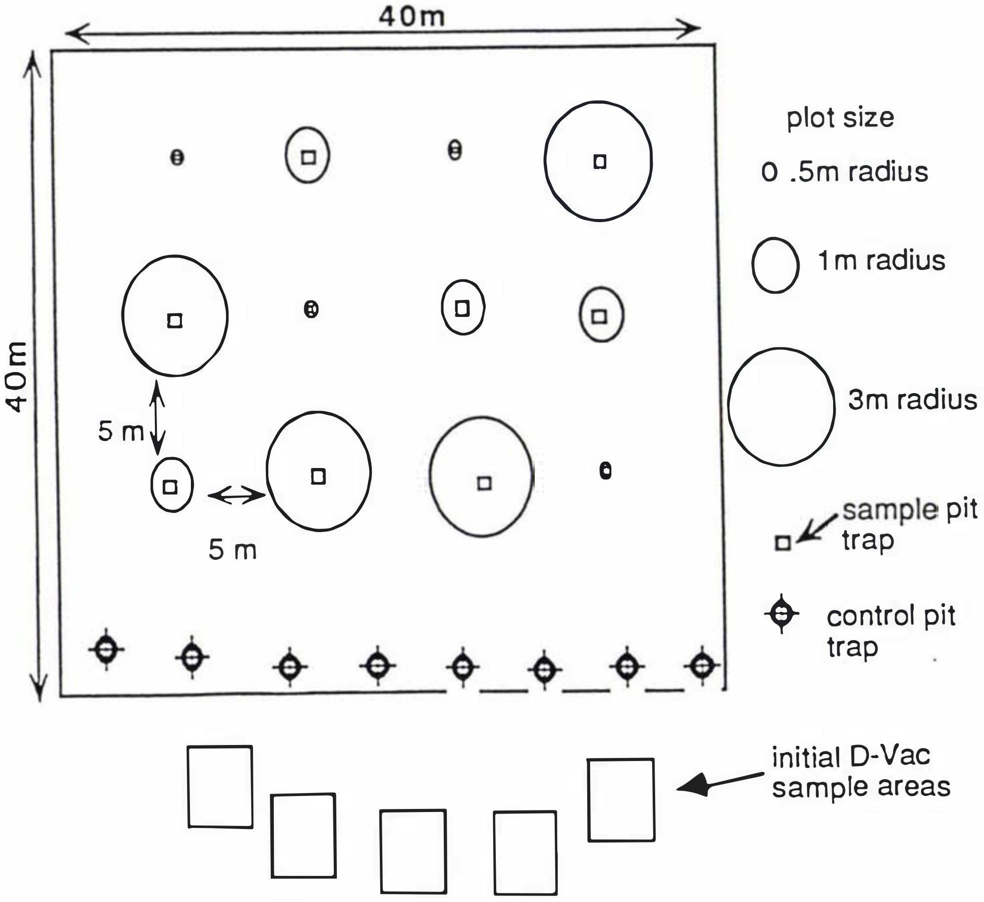


Photo 1

The D-Vac in action sampling returning fauna in the tussock grassland site. The method of sampling was better suited to the short tussock clumps than to the aggregated dense *Calluna* heathland.

Spraying treatments

The treatments were sprayed by backpack sprayer once only with "Watkins" Malathion at 4 cm^3l^{-1} (usual garden dose) at the start of the first week in November 1993. The residue effect is 14 days (Watson and Watson 1994), though less if heavy rain fall (of which there was none). Five litres of spray was required per block (i.e. $44.8m^2l^{-1}$)

Spray effectiveness was possibly reduced in *Calluna* (~80-90% kill) due to dense stem layering - thus there is a much better chance of avoiding direct spray in *Calluna* habitat for litter and sub-surface dwellers. Nevertheless sufficient spray was applied from various orientations to give as good a coverage as possible.

Sampling

Throughout the survey (4 week period) D-Vac and pit-fall trapping were used to monitor invertebrate return, on a weekly basis. Only one of each of the four rows in a block were D-vac-ed per week, a new row each week, to cause as little disturbance as possible. Thus one week's sample consisted of 12 pit-fall traps and five D-Vac samples per treatment block per habitat; a total of 36 pit-falls and fifteen D-Vacs per habitat. Trap catches were stored in 70% ethanol and hand sorted under a binocular microscope. Invertebrates were resolved to families, and morpho-species where possible.

ANALYSIS

Section 1: Initial assemblage complexity

Species richness and abundance

For species richness (the total number of taxa discovered from initial samples), a Chi-square contingency table was used to determine association of numbers of taxa in different guilds to habitat type (displayed in box diagrams).

The total abundances found, and abundances broken down into guilds are displayed. Chi-square contingency tables were used to test associations between abundances in guilds and the number of taxa present. T-test results comparing mean abundances in each guild are also displayed.

Guilds

The level of resolution for all taxa found was not uniform, i.e. the greater proportion were identified only to family, and most of these assigned to morpho-species only; still this collection has been better catalogued than that of chapter 3 due to its limited size (numerical). The problem was often exacerbated by the presence of previously undescribed taxa (Ian Andrews pers. comm.). The information on exactly what taxa eat what, or parasitise what, was not available. To overcome this problem when describing connectence, guilds of feeding type were constructed.

The guilds used were:

1. spiders
2. other predators
3. herbivores
4. scavengers
5. detritivores
6. hymenoptera (assumed parasites, except Formicidae)

The allocation of taxa to these guilds was based on information from the C.S.I.R.O. "Insects of Australia" (1991), and personal communication with New Zealand entomologists.

Randomisation tests

To establish if the differences observed in the number of taxa and abundance values between the habitats were chance, a Monte-Carlo simulation was run. The simulation consisted of random allotment of taxon number and abundance values from initial sampling of both habitats, into either tussock or *Calluna* habitats, and then measuring the difference for each of 1000 randomisations. The simulation resulted in the probability lines observed in figures 5.7 a & b of the results. On both figures the observed differences in taxa and in abundance from each trap event are drawn. From the plots the chance of the observed difference occurring between habitats can be evaluated.

Evenness and diversity

A Dominance measure, the Simpson index, and a Diversity index, the Shannon diversity index, were used to describe the distribution of abundances in taxa sampled, and the distribution of taxa in guilds. The Shannon diversity index incorporates an evenness weighting to species richness (Magurran 1988). The Simpson index (Magurran 1988) utilises evenness weighted to the most common taxa present in the sample data, thus lessening the effect a large pool of rare taxa has on the diversity measure.

Simpson index formula $\mathbf{D = \sum (ni*(ni-1))/(N*(N-1)}$

where ni = the ith taxon's abundance N = the total abundance.

The index is usually presented as 1/D because as D increases diversity decreases. The higher the value of 1/D the greater the evenness in distribution of abundances.

Shannon index formula $\mathbf{H = \sum pi*log(pi)}$

where pi = ni/N (proportion of the ith species).

Connectence

Food webs were constructed for both habitat assemblages. Connecting lines are subjective estimates of connectence, where the thickness of a line is based on the abundance of a guild, the number of taxa in each guild, and from field observation of feeding habit. The thicker the line the more connectence. A numerical rating can thus be made to compare connectence, and ratios of consumer connectence and predator connectence between the two habitats.

An index score was made based on the criteria in Table 5.1. The index enables the criteria used to be expressed on the same scale, with a correction weighting added for very large abundances (the effect of such abundances, I believe, is quite important). Thus a sum total for connectence could be made. Thus connectence = score A+B+C. Ratios of connectence for primary and secondary consumers can also be compared.

Table 5.1 Categories assigned to parameters for a connectence index based on the range of taxa, abundance, and number of connecting lines of the food web

number of taxa	score(A)	abundance	score(B)	incoming lines	score(C)
1-3	0	0-10	0	0-5	0
4-6	.1	10-20	.1	5-10	.2
7-9	.2	20-30	.2	10-15	.5
10-12	.5	30-50	.3	15-20	1
>20	1	50-100	.5		
		100-200	1		
		>200	2		

Complexity of the assemblages

From the above measures a decision could be made as to which community appeared the most complex. The habitat exhibiting the greatest species richness, highest evenness, and greatest connectence was considered the most complex.

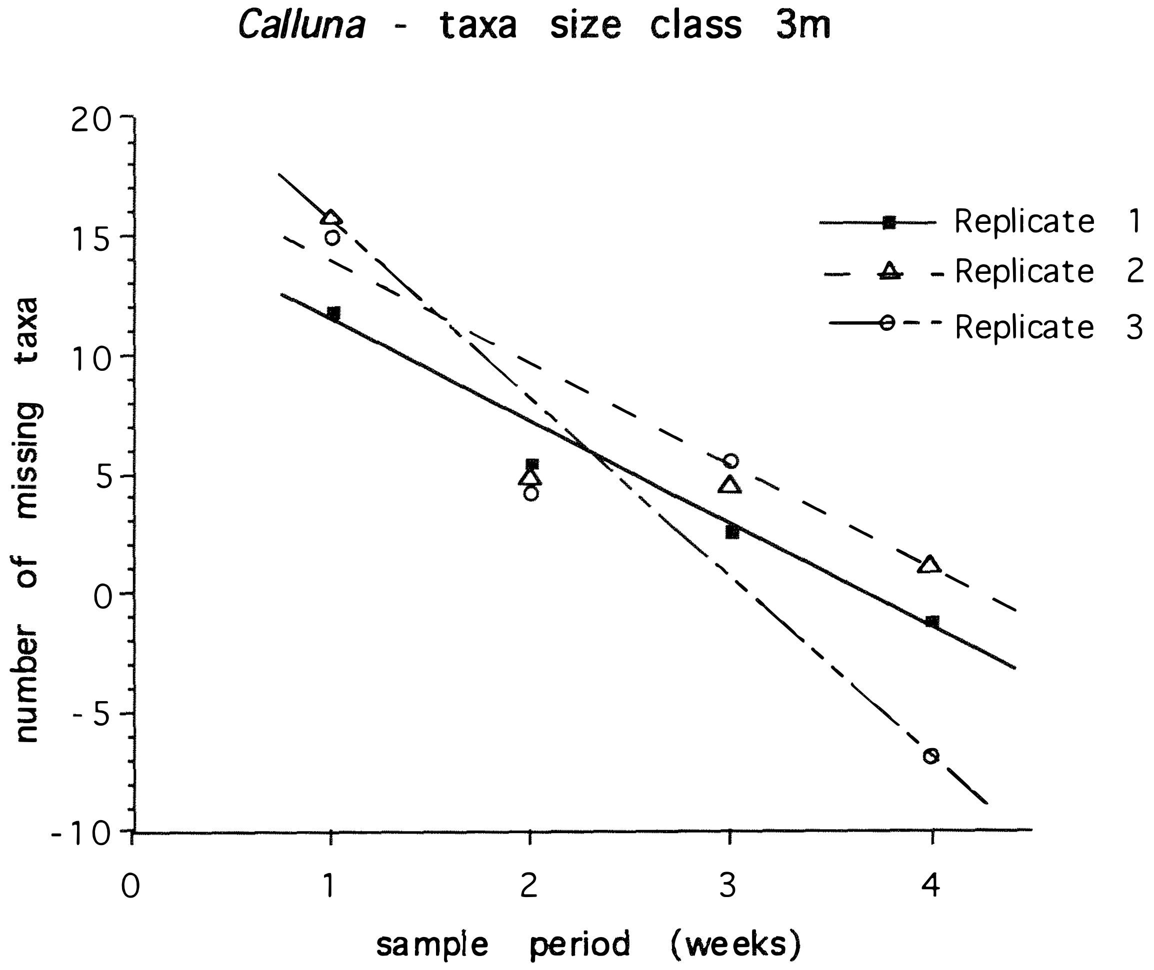
Section 2: Community stability

Resilience - The rate of return of invertebrates

The control pit-fall traps and D-Vac data were used to account for the variability in weekly catches; thus determining the 'reference' point at which there are zero 'missing' taxa. The weekly catches were subtracted from the mean weekly control catch values. This gives values that become closer to zero every week, provided there is return. This approach gave an 'end point' implying full return was achieved when the difference tends to zero.

The gradients for the rates of return were derived by plotting data from the rates of return into different sized disturbed areas for the 4 week period and doing regression analysis for each treatment replicate and habitat (Fig. 5.5). The gradients are presented as a table (Table 5.5).

Fig. 5.5 *An example of the plots made to determine the gradients of the different treatments for each block in each habitat.*



The gradients of each block for each size class (treatment) and habitat were then tested with disturbance size class as a covariate, by ANOVA (Systat 1988) to determine if the habitat, size of disturbed area and habitat-size interaction produced significant differences in the rates of return.

The lack of a significant difference (at the 5% level) in the size of disturbance treatments allowed data for each habitat from each treatment to be pooled, and a plot of these data done for taxa and abundance, to illustrate the overall habitat differences.

Finding the best descriptive Model to describe the rate of return

Several models were applied to the pooled size class data, both taxa and abundance in the search for the best descriptive model. R^2 values, signifying fit, were then used to determine the best model for the data.

models: where Y = the number of missing taxa, X = week after disturbance

1. Linear	$Y=a+b*X$
2. 2nd order Polynomial	$Y= a+b1*X+(b2*X^2)$
3. Logarithmic	$Y=a+b*\log(X)$

A good fit to the linear curve means that the taxa would return at regular intervals or at a constant rate throughout the period, which would imply that return is controlled by some sort of entry gate. A second order curve, by contrast, means that some species return faster than others, and rate of return declines as the community nears completion. This would be the logical model if dispersal or reinvasion rates were distributed along some normal curve. Of the two second order curves, the exponential decay curve is most likely to give the best fit, as the last species takes a long time to re-enter the community.

Consistency

Comparison of the returned assemblage composition through the abundance and type of taxa in each guild, with that of the initial abundance and types found for each habitat, allowed disparities between the initial and returned assemblages to be observed. Plots comparing the taxa and abundances in the two habitats before and after, and percentages of original components of the fauna illustrate the fidelity of the returning assemblages.

RESULTS

Section 1: Complexity of initial assemblages

These results are based on the assessment of the pre-treatment fauna.

Species richness

A third more taxa were found in *Calluna* than in tussock (Fig. 5.6). Spider species were the most common taxa caught in the greatest abundance. Separation into guilds showed that the tussock habitat held equal numbers of herbivores and Hymenoptera, more scavengers and fewer spiders, other predators, and detritivores. Approximately 50% of all the taxa of each guild except Hymenoptera and spiders were shared (Fig. 5.6).

The number of taxa present is dependent on the habitat type ($Chi^2 = 6.356$, $P < 0.05$). The number of taxa of spiders, detritivores, and scavengers appears to be the cause of this result (Fig. 5.6).

Abundance

Total abundances (Table 2) in guilds other than Hymenoptera and scavengers were greater in *Calluna*. In these two guilds, in tussock, one taxon contributed overwhelming numbers (ants contributed 75% of scavengers, and one taxon of Hymenoptera ~ 33%). In *Calluna* this dominance phenomenon also occurred in the spiders where one taxon (orb spinners) contributed ~ 48% of spider abundance. Total abundance was greatest in tussock, due to the large number of Formicidae. Abundance in guilds was not independent of habitat type ($Chi^2 = 140$, $P < 0.05$).

Mean abundance

T-tests (Table 5.2) of mean abundance show that differences in the mean number of individuals was not significant (95% C.I.), due to large variation in most of the samples. However, there certainly appears to be more detritivores in *Calluna* and more Hymenoptera in tussock.

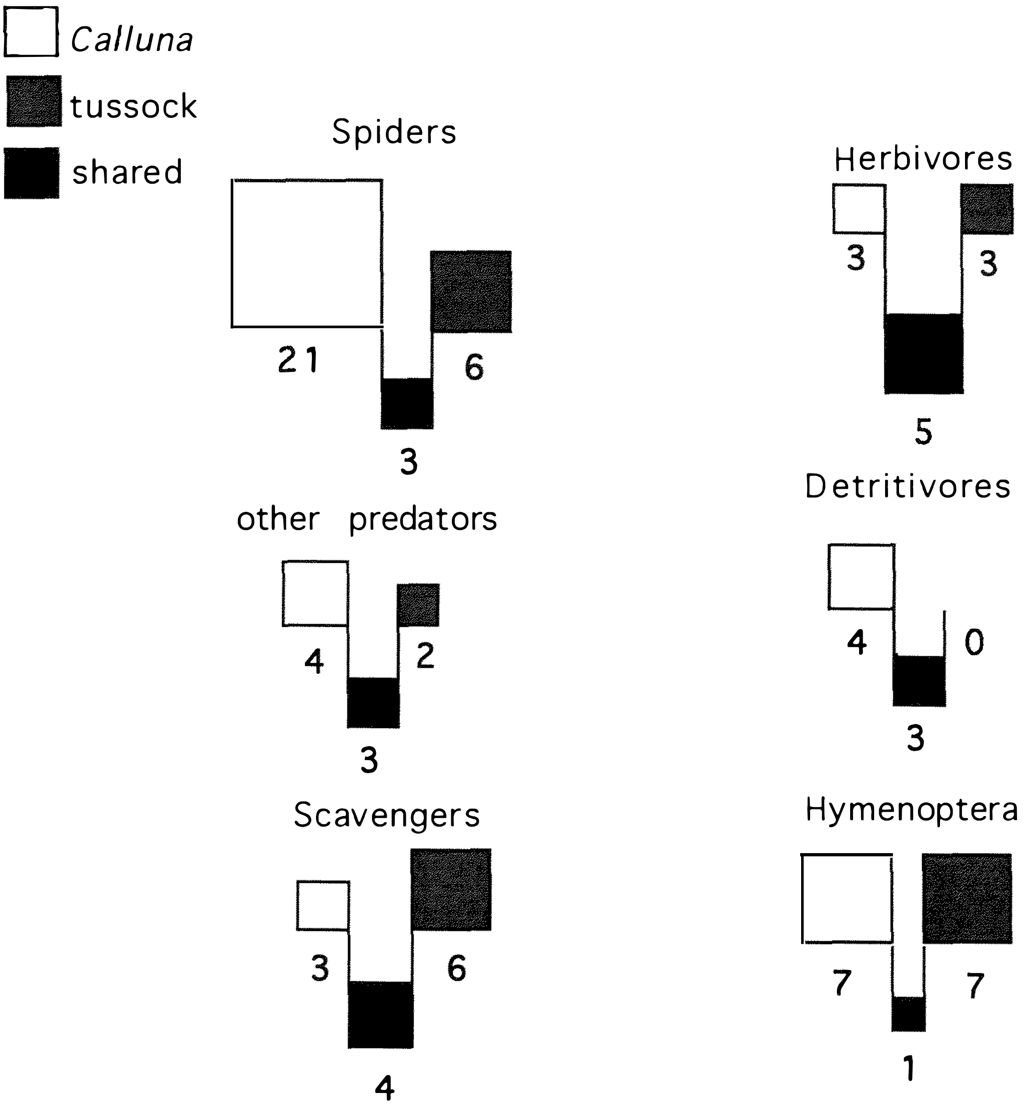
Table 5.2 Comparison of total abundances between habitats guilds. T-test values are for mean abundance of 5 initial D-vac and 16 pit-fall traps. Variation was high leading to no significant differences where they were expected

habitat	spider	predator	herbivore	scavenger	detritivore	Hymenoptera	total
Calluna	138	11	31	62	20	13	275
tussock	43	8	21	207	9	32	320
T-stat	-0.28	-0.09	0.17	0.14	-1.43	-1.25	
P-value	0.78	0.93	0.87	0.89	0.20	0.25	

Fig. 5.6

The number of taxa by feeding guild either unique to each habitat, or shared. Box size is proportional to the number of taxa (given below the box).

Total number of taxa *Calluna* = 61
tussock = 43



Monte Carlo randomisation tests

The Monte Carlo simulation produced results shown in figures 5.7a & b. On both figures the Monte Carlo differences (i.e. between the randomly assigned tussock taxon catch and that for *Calluna* for each trap event) are drawn. Both sampled differences fall at the extremes of the normally distributed data of the simulation implying the differences in assemblages are not due to chance, at 99+% and 99.5 +% probability for number and abundance respectively. Thus the habitats are different in numbers of taxa and their abundances.

Diversity - Evenness and dominance

The taxon evenness measure of the Simpson index (Fig. 5.8) and the output of the Shannon index (Table 5.3), illustrate the dichotomy of diversity measures. The *Calluna* assemblage is more diverse according to the Shannon index, even after removal of the spider component. The Simpson index, having no species richness weighting, reveals that the guild structure of *Calluna* is less even in its distribution of taxa in guilds than in tussock, having few dominant species. The evenness in abundances strongly favours the *Calluna* assemblage, i.e. the tussock assemblage has a few insects in large numbers. Removing the spider data from this index did not change this observation. A histogram of frequencies of occurrence of abundance of each taxon (Fig. 5.9) illustrates the difficulties in interpreting the Simpson index. The histogram of tussock seems to exhibit a more uniform spread of numbers (a 'J' curve distribution), while the *Calluna* assemblage has a non-continuous spread of abundance frequencies (Fig. 5.9). The Simpson index, because it is weighted for common species, however suggests that it is the *Calluna* abundance distribution that is least affected by dominance, i.e. most evenly distributed.

Table 5.3 Diversity measures of the Shannon diversity index.

	tussock	*Calluna*
All taxa		
No. species	43	61
No. individuals	318	275
Diversity	**2.313451**	**3.280825**
var	0.010065	0.006305
StDev	0.10033	0.079403
spiders only		
No. species	9	24
No. individuals	43	138
Diversity	**1.687522**	**2.164938**
var	0.020002	0.014539
StDev	0.141428	0.120578
taxa other than spiders		
No. species	34	37
No. individuals	275	137
Diversity	**1.953184**	**3.013518**
var	0.011728	0.007969
StDev	0.108297	0.089268

Fig. 5.7

Monte-carlo randomisation predictions of differences between the two sites (tussock & *Calluna*) for number of taxa and abundances. The actual differences observed are drawn to show the probable likelihood of them being due to chance, i.e. not 'real' differences.

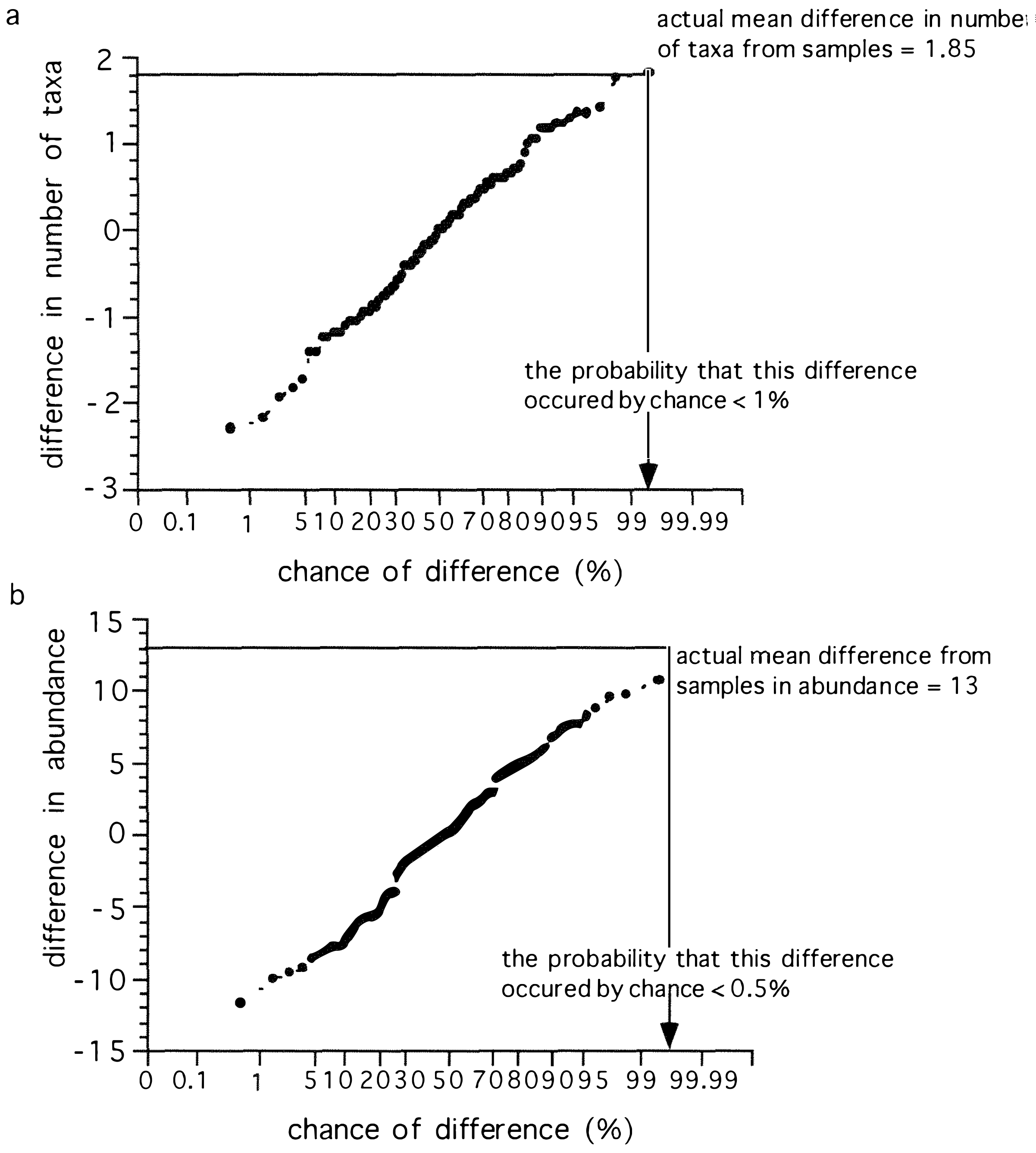


Fig. 5.8

Simpson index of dominance for taxon number in guilds and for abundances, for both habitats with and without the spider data, and for those habitats' spider components only.

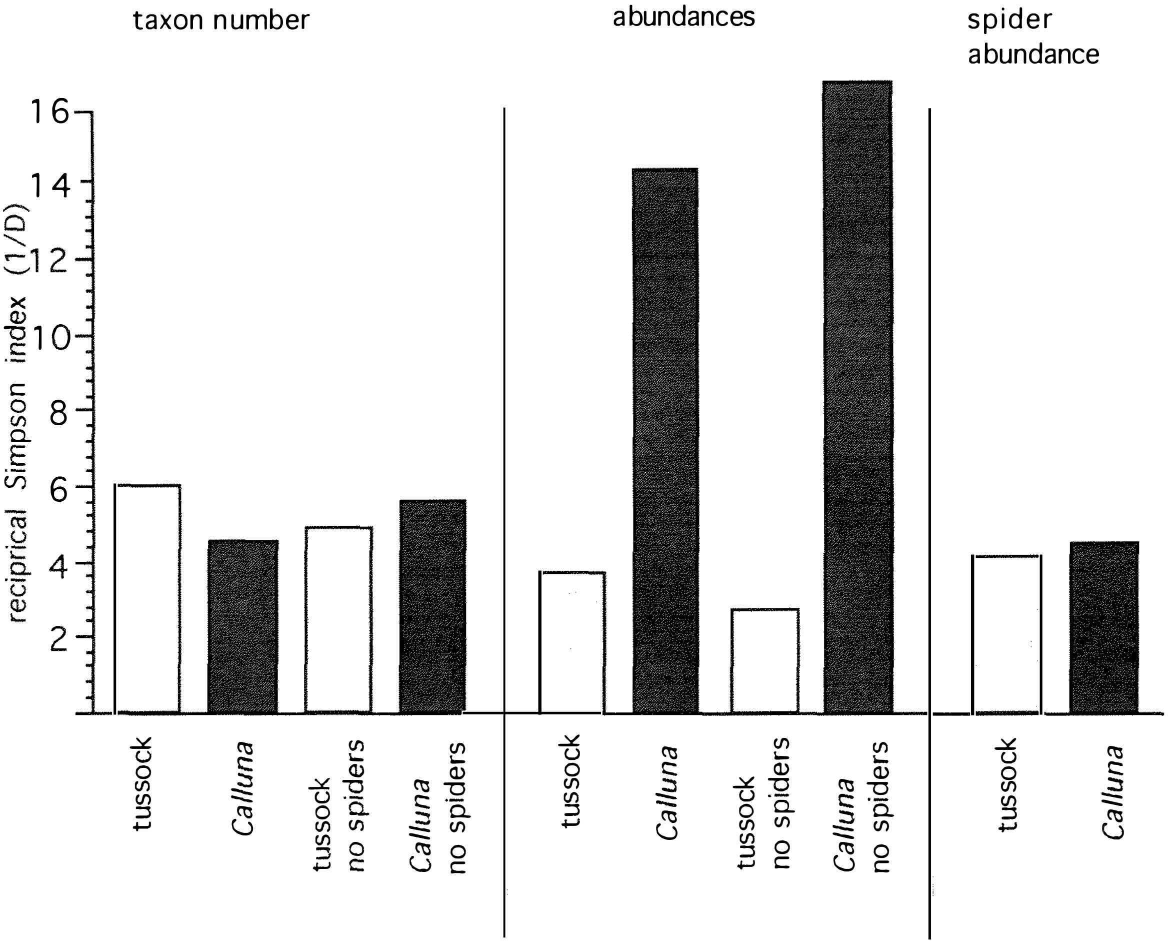
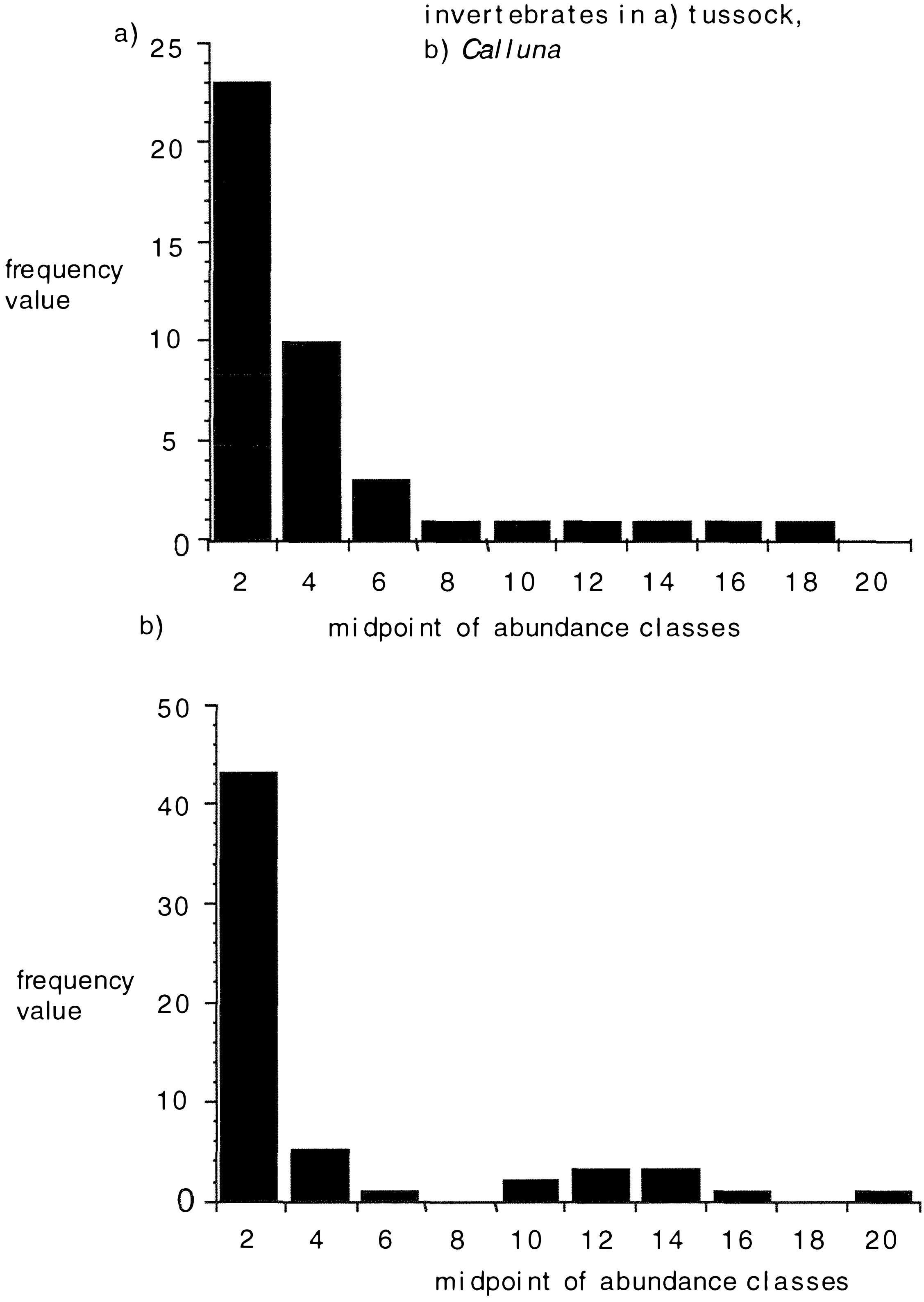


Fig. 5.9

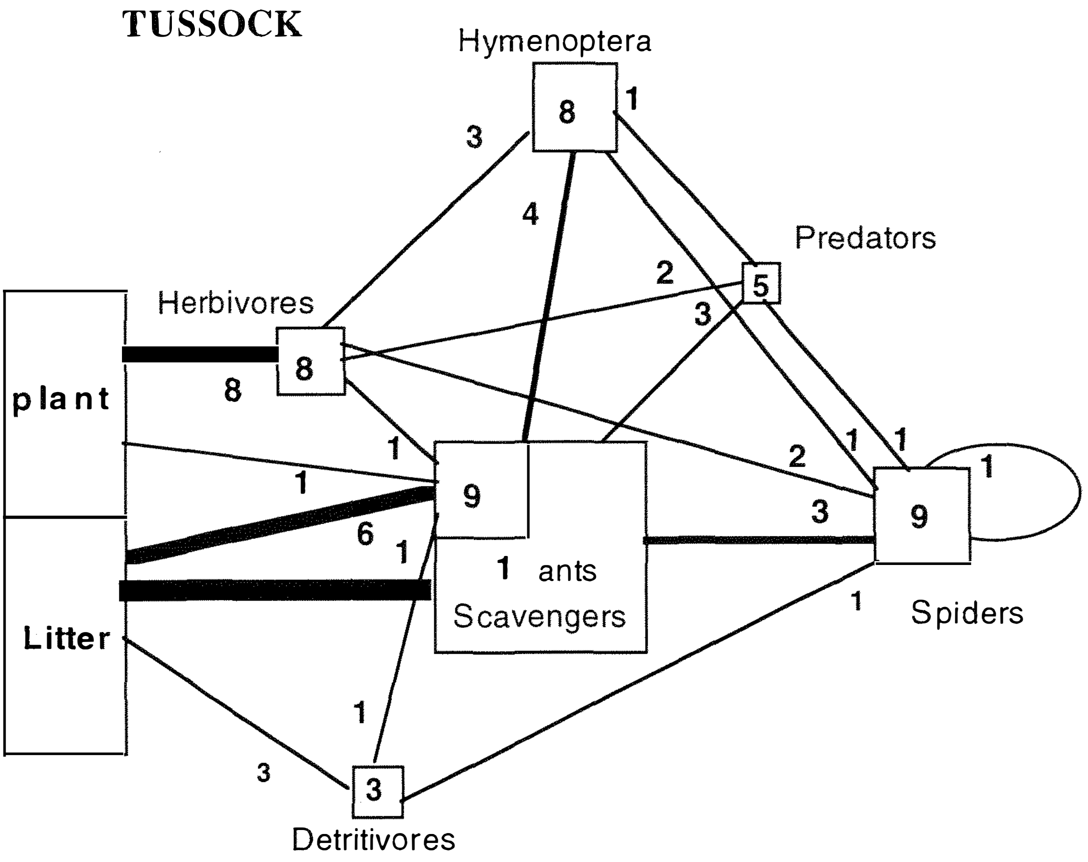
Frequency of abundance values of invertebrates in a) tussock, b) *Calluna*



Connectence

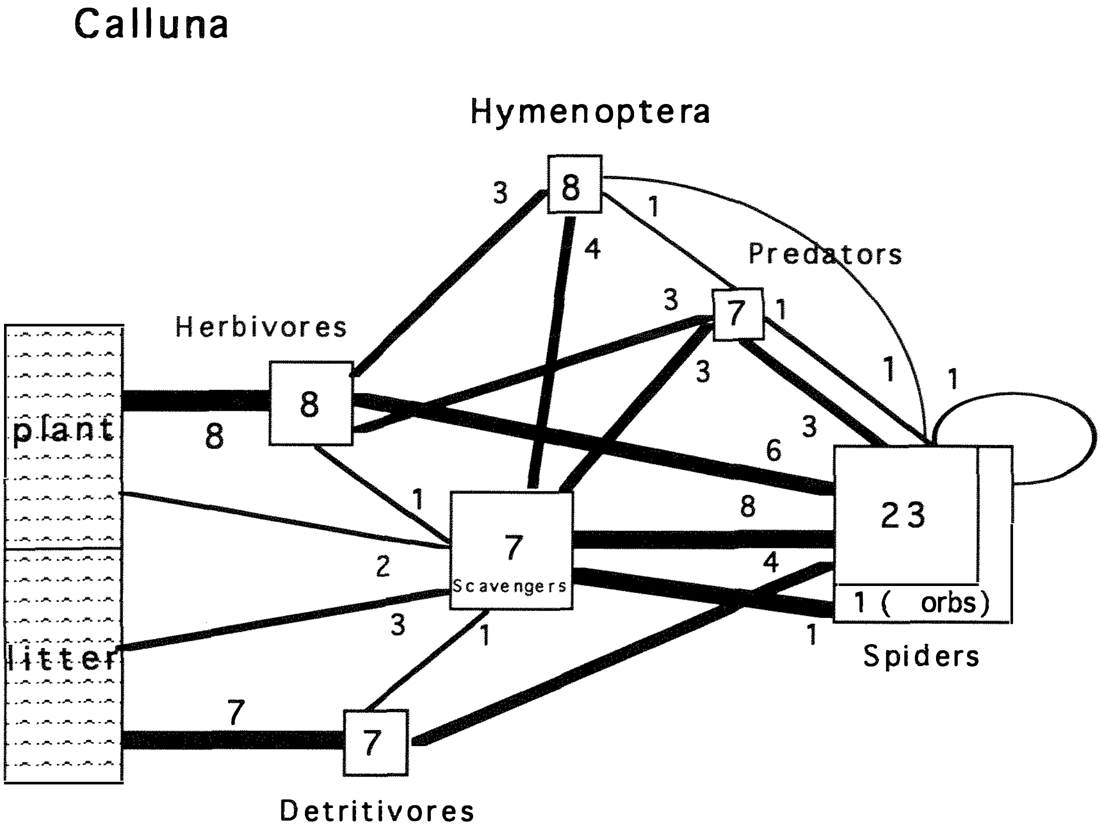
The connectence web for tussock (Fig. 5.10) shows generally weak connectence between predator, spider and detritivore guilds, and strong scavenger to litter connectence. This strength is mainly the product of one taxon, Formicidae. The web implies a good prey base only weakly utilised by the predators; and a strong producer-sarcophagous - consumer connectence.

Fig. 5.10 Connectence web for the tussock habitat's initial assemblage, based on abundance, taxon number and observation. Numbers in boxes are number of taxa. Thickness of lines represents the estimates of connectence (values are given next to them), based on taxa number, abundance, and observation. Size of boxes represent the abundance values for that guild. The box sizes of the plant and litter are arbitrary.



Calluna (Fig. 5.11) on the other hand, shows strong connections throughout the web, especially at the predator and detrital levels. The scavenger connectence is weaker (having lower abundance and thinner connectence lines), but predation on this level is also much more intense maintaining lower abundances than seen in tussock.

Fig. 5.11 Connectence web for the *Calluna* habitat initial assemblage, based on abundance, taxon number and observation. (cf. Fig. 5.10 description)



Connectence

The index values, following the criteria in table 5.1 of the methods, are presented in table 5.4.

Table 5.4 Connectence index values (based on criteria set in Table 5.1) for the two habitats and their 1^0 and 2^0 consumer components.

Habitat	Guild	Index	1^0 or 2^0 sub total	Total connectence	1^0 / 2^0 Ratio
Calluna				5.6	1.15
1^0 consumer	herbivore	.9	3		
	scavenger	1.7			
	detritivore	.4			
2^0 consumer	spider	2	2.6		
	wasp	.3			
	predator	.3			
tussock				4.4	3.0
1^0 consumer	herbivore	.6	3.3		
	scavenger	2.7			
	detritivore	0			
2^0 consumer	spider	.5	1.1		
	wasp	.5			
	predator	.1			

A ratio of first level consumers (1^0) and second level consumers (2^0) within habitats and between habitats shows the relative strengths of each habitat. In both habitats the 1^0 consumers show better connectence (higher subtotals), though three times as much in tussock, compared to an almost balanced situation in *Calluna* (Table 5.4). Making tussock the reference point (=1) for inter-habitat comparisons, *Calluna's* lower 1^0 consumer value (3 as opposed to 3.3 = 0.9 : 1 for *Calluna* : tussock) implies weaker connectence, while its 2^0 consumer level connectence (2.6 : 1.1) is very much stronger. Overall connectence (Total scores 5.6 : 4.4 or 1.27:1) is greatest in the *Calluna* assemblage.

Section 2 Rates of reinvasion

Extensive use of a D-Vac as the primary method of sampling provided a good estimate of the total diversity of the tussock and *Calluna* communities at this time of year, as is clear from a comparison o the Simpson and Shannon diversity indices derived from the long-term and more complex sampling of Chapter 3. There the Shannon and Simpson indices were 3.15 & 7 respectively in the tussock and 2.8 & 9 in the *Calluna*; here they were 2.3 & 6 and 3.2 & 5. The discrepancies were probably due to failure to sample the large ground dwelling invertebrates, and the more easily disturbed invertebrates.

Re-invasive species

Several species were noted to be fast reinvaders. Spiders were especially fast, in *Calluna* Lycosidae, Thomisicidae and Araneidae were particully fast as were Formicidae, Chironomidae, Sciaridae, Mycetophilidae, Collembola and amphipods. In the tussock grasslands only the spiders of the family Araneidae were evendent fast reinvaders but other invertebrates quick to reinvade were Formicidae, Delpacidae, Sciaridae, Pselaphidae, Ceratopogonidae, Chironomidae, and Collembola. Those slow to reinvade included Stenoplematidae, Elateridae, Carabidae, Cicadellidae and the Blattodea.

Resilience

The rate of return was expressed as changes in fauna over the four sampling periods after the disturbance. In both habitats the treatment in which the fauna (taxon number) was slowest to return was the largest area, while return was fastest in the smallest. There appears to be no difference in the rate of return of abundance into the different sized disturbance areas in *Calluna*, and only a slight difference, following the same trend as the taxa, in tussock (Table 5.5).

Table 5.5 The mean gradients of rate of return from three replicates for each of three differently sized disturbance areas in the two habitats.

	return gradients			
radius (m)	*Calluna* taxa	tussock taxa	*Calluna* abundance	tussock abundance
0.5	-7.72 ± 1.60	-3.08 ± 0.71	-23.97 ± 1.30	-16.10 ± 1.31
1.0	-6.10 ± 0.46	-1.84 ± 0.58	-26.9 ± 2.50	-15.60 ± 2.77
3.0	-4.99 ± 0.71	-1.19 ± 0.15	-26.7 ± 3.67	-11.25 ± 1.11

Analysis of variance (Table 5.6) demonstrated that the differences in rate of return between the habitat types were significant (at the 5% level) for the taxon number and abundance. Rates of return of abundances into different sized disturbances areas were not significant, but the rate of return of taxa into the different sized disturbance areas was significant at the 10% confidence level. The habitat-size interaction held no significant differences implying that the same trends in size to rate of return were occurring in both habitats.

Table 5.6 ANOVA of rates of return gradients for taxon number ($r^2 = 0.872$) and abundance ($r^2 = 0.806$) in tussock and *Calluna* habitats.

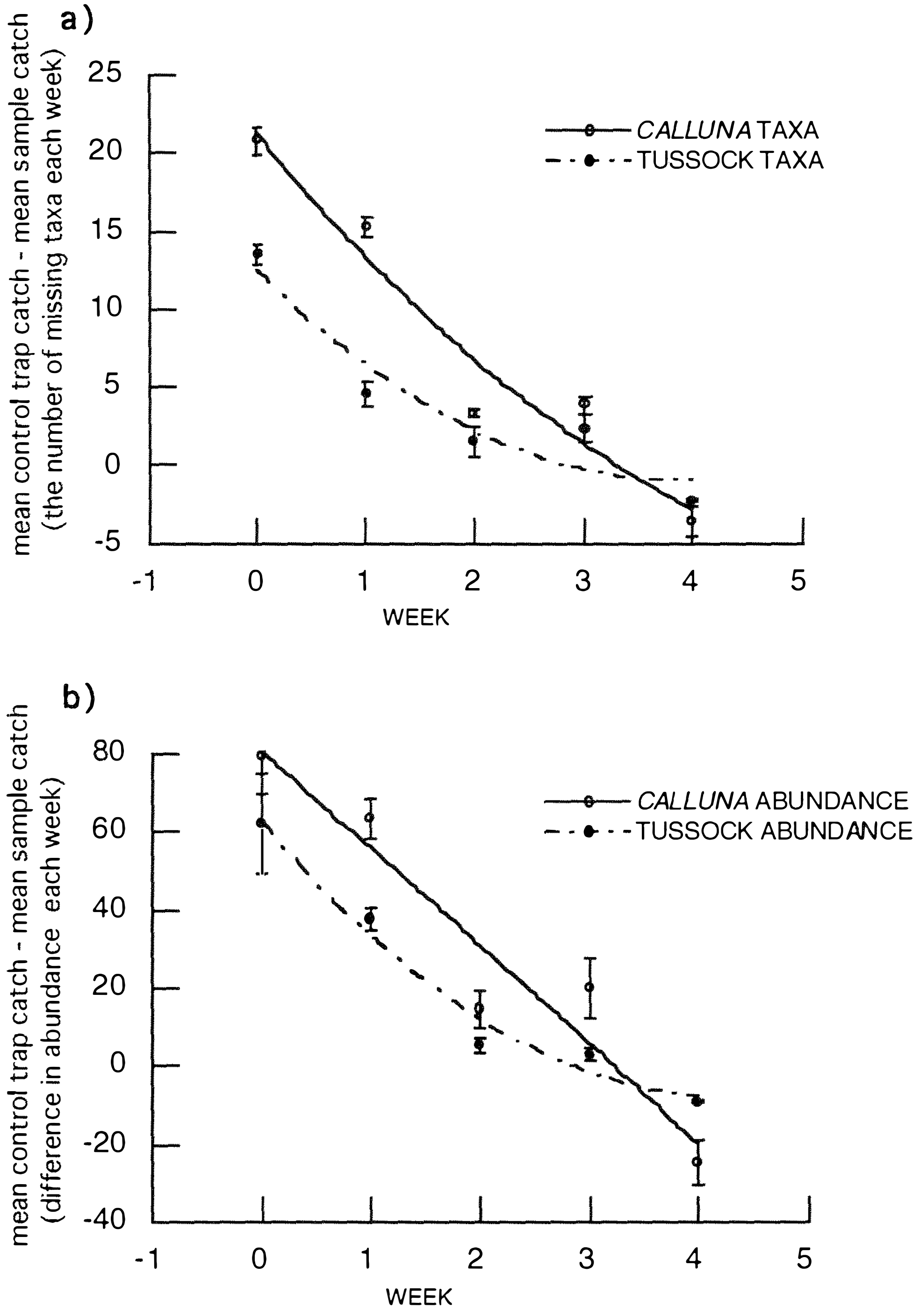
Taxon number	sum-squares	Df	mean-square	f ratio	P
habitat	56.676	1	56.676	64.378	0.000
size	5.471	2	2.735	3.107	0.085
habitat*size	1.672	2	0.836	0.950	0.416
replicate	2.412	1	2.412	2.740	0.126
error	9.684	11	0.880		
Abundance					
habitat	600.196	1	600.196	39.968	0.000
size	15.776	2	7.888	0.525	0.606
habitat*size	43.612	2	21.806	1.452	0.276
replicate	26.88	1	26.88	1.79	0.208
error	165.188	11	15.017		

To determine the habitat in which resilience was best (Figs. 5.12 a & b), the mean reinvasion sample catch was subtracted from the mean control trap catch each week over the 4 week period in tussock and *Calluna*. The taxon plot suggests that the time of return to 'normal complement' is different, tussock assemblages returning in about two and one half weeks, while the *Calluna* assemblage needed around three and one half weeks. The tussock habitat assemblage abundances reached the zero line first (reference point for return).

The graphs (Fig. 5.12) further illustrate the different gradients (rates) of return, the steeper gradient implying faster return in *Calluna* even though the *Calluna* assemblage returned later in time (based only on one point, the last week's catch) than the tussock assemblage. This is because the *Calluna* assemblage was more complex; there were more species to return in greater abundances.

Fig. 5.12

Overview of returning fauna numbers: a) number of taxa; b) abundances, throughout the 4 week period in tussock and *Calluna* habitats.



Model

The quadratic function (order 2: $Y=a+b1*X+b2*X^2$) best fitted both sets of data (Table 5.7), and is drawn on figures 5.12. a & b.

Table 5.7 R^2 values signifying the fit of three models used to describe the rates of return in both habitats.

fit of models	tussock taxa	*Calluna* taxa	tussock abundance	*Calluna* abundance
linear	0.91	0.96	0.96	0.96
quadratic	**0.95**	**0.97**	**0.99**	**0.96**
logarithmic	0.783	no fit	0.86	0.72

Consistency

Examination of the data through comparison of the initial taxa present and final taxa composition, (Figs. 5.13, 14), shows that tussock gained 5 new taxa and lost 18 while *Calluna* gained 16 new taxa and lost 36 of its original taxa (Table 5.8). Though these measures appear contradictory to the results of the rates of return (Fig. 5.12) where total return of taxa and abundances occurred, the data for those results used the weekly control traps as the returning point reference accounting for variation in presence due to weather. The data in figures 5.13 and 14 are based on initial catches before treatment and on the final catches within the disturbance areas.

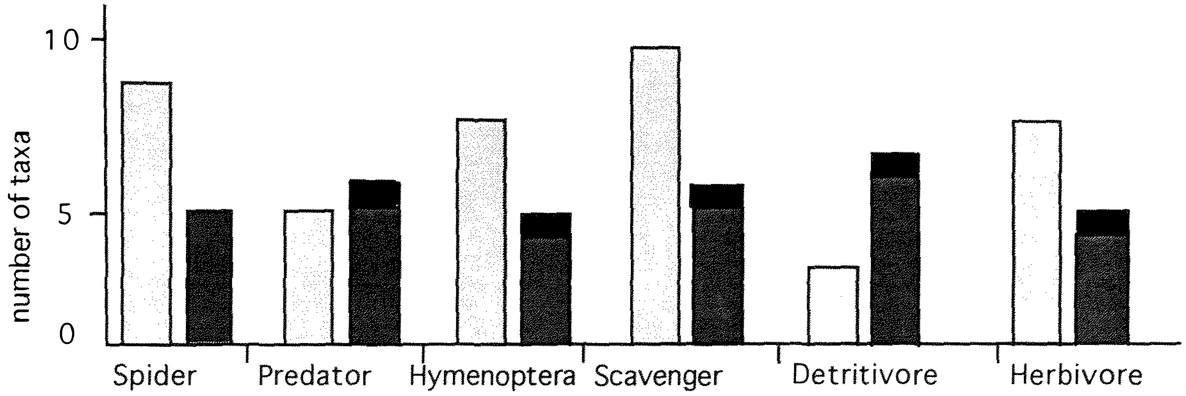
Table 5.8 Comparison of initial and final assemblages and the proportion of new taxa and original in the final assemblages

	habitat	initial number	final number	final as a % of initial	original taxa returned & as % of initial	number of new taxa
taxon number	tussock	43	32	74%	27 - (63%)	5
	Calluna	62	43	69%	27 - (44%)	16
abundance	tussock	320	177	55%		5 (3%)
	Calluna	275	245	89%		34(14%)

Percentages of returned taxa are approximately the same in tussock and *Calluna*, but the percentage of original taxa returned is much lower in *Calluna* . Thus the taxa in each guild returned more faithfully in tussock than in *Calluna* (Fig. 5.13). It is still apparent that in the tussock habitat, spiders, Hymenoptera (wasps), scavengers and herbivores are the main missing taxa, while *Calluna* showed losses in all guilds. Abundances (Fig. 5.14) returned closer to initial values in *Calluna* than in tussock for spiders, wasps, and scavengers. For scavengers this was due to the inability of the Formicidae, in tussock, to recover their initial large numbers. As the ants accounted for ~ 66% of the initial abundance, any hindrance to their return will have large impacts on the total abundance value of the assemblage. The return of the spider component in tussock was ~ 50% (taxa and abundance) of that of the original fauna with no new taxa. In *Calluna* ~ 50% of the original taxa returned plus the addition of 6 new taxa, bringing the total returned to ~70 % of the original fauna. Spider abundance was greater after the completion of the experiment, implying that the original inhabitants returned in greater numbers, which was the case for orb spinning spiders.

Fig. 5.13 The number of initial taxa in each habitat, and the number of original and new taxa found at the conclusion of the 4 week reinvasion period.

a) Tussock



b) *Calluna*

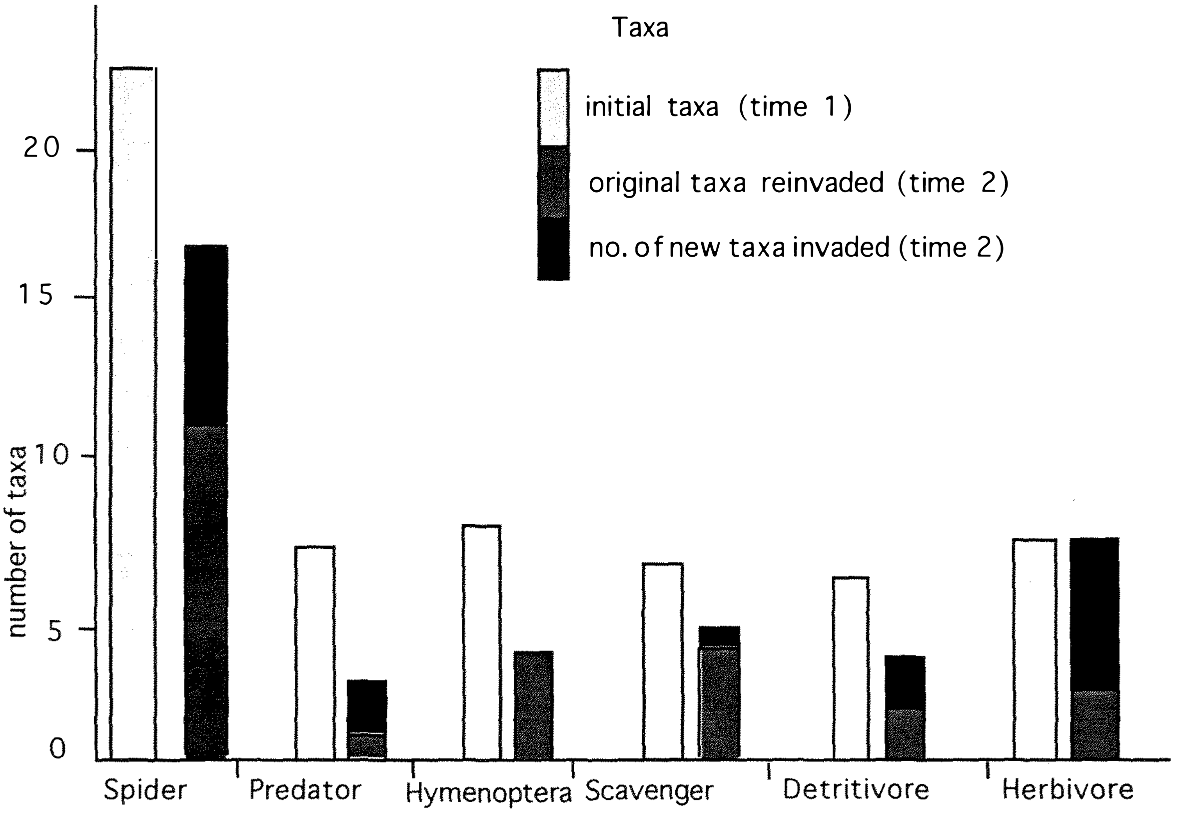
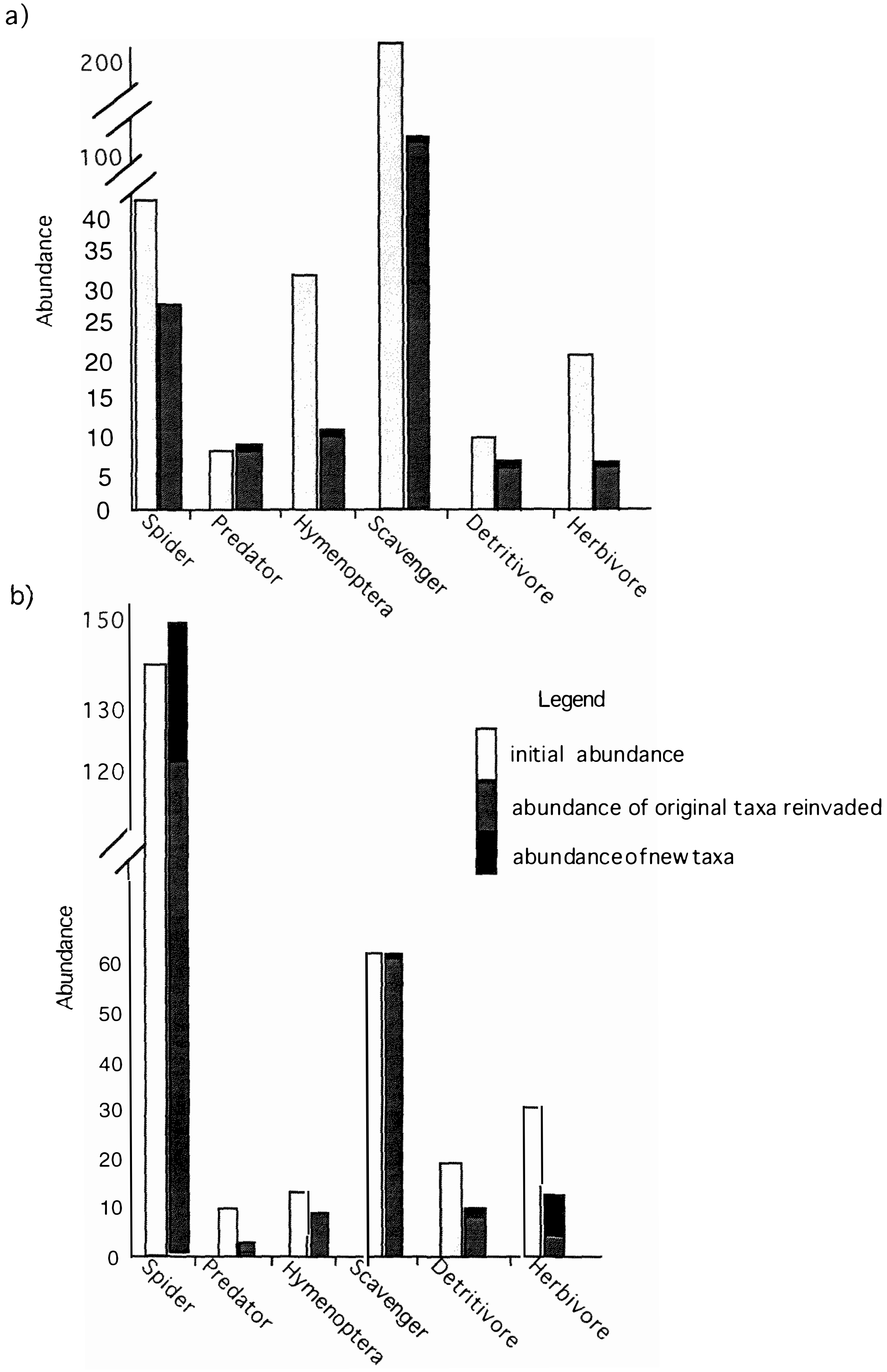


Fig. 5.14 Comparison of initial and final abundances of taxa from a) the tussock habitat and b) *Calluna* habitat.



DISCUSSION

This experiment set out to measure and compare the rate and fidelity of returning fauna after severe disturbance to the assemblages appropriate to two different habitats, one native, the other dominated by the invader *Calluna vulgaris*. Measures of the attributes of the assemblages before and after the disturbance allowed judgments to be made as to which assemblage was most complex, and so which should exhibit the best resilience, persistence and consistency, and hence stability.

Complexity

Complexity (the number of interactions - connections - in an assemblage) increases with increasing diversity, which increases with successional age (Margalef 1963, 1968, Flaherty 1969, Odum 1969, Hurd and Wolf 1974, Frank and McNaughton 1991). Thus complexity increase should lead to an increase in stability, but not all researchers agree - at least not as a general statement (Goodman 1974, Orians 1974a).

Complexity is formed from a combination of measures of species richness, abundance, evenness, and connectence. It is not often straight-forward. The measures themselves are multi-compartmented and do not always indicate the same trends. In this experiment species richness and evenness within guilds favoured *Calluna*, yet total abundance favoured tussock, as did evenness of abundances. Connectence measured better in *Calluna.* It was not obvious which of these measures of complexity to emphasise. I propose that the number of taxa present, the distribution of taxa in guilds, and the connectence, are more crucial than evenness of abundances and the total abundance, especially when total abundances are not very different. The measure of connectence already incorporates the abundance features. If the taxa that are the most prominent prey are in high abundance, the system's overall functioning (i.e the dependent trophic structure) is not compromised by rarification of other prey taxa (a 'bottom-up' stability). The presence or absence of a taxon will have greater effect on the system than the evenness of abundances.

Evidence of systems' complexity and stability

The Monte Carlo simulations showed that the differences between the two habitats were not due to chance, each habitat having its own assemblage, with respect to taxon number and abundances, reinforcing the long-term field invertebrate work of Chapter 3.

The breakdown of the assemblage differences by species richness, abundances, evenness, and connectence describes where and how those differences occur. The species richness results clearly demonstrate that the *Calluna* habitat was richer in the number of taxa, primarily through its more extensive spider fauna. Contrary to Chapter 3's summarised data, equal numbers of herbivores were sampled here, but this is probably due to the season (Spring) in which this experiment was done.

Separation of the taxa into guilds showed the strengths of each assemblage, the tussock having well developed ground fauna. Scavengers (especial Formicidae) and other Hymenoptera are very important elements of the tussock assemblage. The predominance of Formicidae in the tussock, not seen in the *Calluna*, may be a result of the plant architectural differences between the two habitats (see Chapter 2) and implies that ground scavenger functioning is much more developed in tussock grasslands. Predation, on the other hand, through spiders, is a component of the system that is much better developed in the *Calluna* shrub land, and may reflect the differential mobility capabilities of the two guilds.

The grouping of taxa into guilds allowed a different resolution of comparison when examining the abundance structure of each habitat. Total abundance values showed tussock to hold greater numbers of individuals but it became apparent that this was due to the predominance of only one taxon (i.e. Formicidae). Non-spider predators (beetles and flies) were similar in number, even though the enlarged spider fauna in *Calluna* must have been capturing a large proportion of this resource. This could mean that the replacement rate (through immigration and/or reproduction) of prey in *Calluna* is much higher than in tussock. Abundances of the other guilds (herbivores, detritivores and Hymenoptera (parasites)) showed similar totals.

By observing the evenness of taxa in guilds and the evenness of individual abundances, a feel for the 'balance' in assemblage composition can be gleaned. Diversity measures are contentious (Chapter 3). Many of the measures commonly employed give conflicting results (Hairston *et al.* 1968). It was just so in this experiment; the Shannon index suggested that the diversity was highest in *Calluna*, even without the spider fauna. The separation into measures of taxa evenness in guilds and evenness of abundances adds better resolution. The Simpson index applied to guilds and abundances, clearly showed that, while *Calluna* held better evenness of taxa over the guilds, the abundances of taxa were better spread in tussock. The histograms (Fig. 5.9) strongly support this allocation. Though both habitats showed the majority of taxa were present in low numbers, there was a very distinct 'J' curve 'tail' of abundances in tussock. *Calluna* was bimodal in distribution of abundances (cf. Chapter 3), suggesting that a few groups, orb spinning spiders, Chironomidae, Sciaridae, and Thysanoptera, were more able to exist in larger numbers, perhaps excluding others from maintaining higher abundances. The picture painted, then, of evenness of abundances appears to suggest that the tussock assemblage is more evenly distributed, but (and more importantly) that the *Calluna* assemblage has a more even distribution of taxa in its guilds.

Connectence in invertebrate field studies is not an easy parameter to measure. It usually requires in-depth information on each taxon present; its diet, habits, predators, mobility and strength of interactions. In New Zealand many taxa are not even taxonomically resolved, let alone their diets, habits etc. known. Thus attempts at this measure must be held, often, as rudimentary. Yet my index and webs based on field observations and elucidation of diets from related overseas fauna, supply useable information. The connectence webs with lines depicting food source, rather than energy flow, show that tussock has stronger connectence between its primary consumers (herbivores, detritivores and scavengers) and the producers and inert matter than does *Calluna*. The *Calluna* habitat clearly shows better connectence between the secondary consumer and primary consumer levels, through more taxa at greater abundances. The index supports this contention, illustrating *Calluna* as being ~ 90% as connected as tussock between primary consumer and organic resource and 230% more connected at the upper (secondary consumer) level. Connectence, then, is greater in the *Calluna* assemblage.

Stability

The stability of the initial assemblages (their temporal variability) was not known in this experiment. Further, the temporal scale of measurements of return were probably too short (Connell & Sousa 1983); though figure 5.12 does suggest that immigration into the areas had all but ceased, an additional week's sampling would have been better. Because I measured the rate of re-colonisation through local immigration rather than reconstruction from scratch, or involving long distant immigration, the length of time suggested by Connell and Sousa (1983), one turnover period (adult to new adult) was not necessary to observe a new assemblage of the same age structure as the original. Barrett (1968) illustrating insecticide stress on grassland ecosystems, using similar techniques, reported findings similar to this experiment; his treatment plot assemblages returned in ~ 5 weeks , the predacious insects returning faster than the phytophagous and the spider component returning in 3 weeks.

The assumption that the tussock habitat's assemblages are stable (through its long evolutionary history and successional age, (Margalef 1968, Hurd and Wolf 1974) is reasonable; the probability of the *Calluna*'s also being so is not outrageous because insect life is short and they can respond rapidly, though perhaps the *Calluna* assemblage exhibits what Hurd and Wolf (1974) describe as a "neutral stable state", one that oscillates about a lower, less stable, state of equilibrium, rather than a "stable state" such as the tussock.

Predictions of stability based on complexity, without an undisputable complexity measure, suggest that the tussock habitat should be more resilient (Margalef 1968, Odum 1969, Hurd and Wolf 1974), being less complex, and should show poorer consistency and perhaps better persistency, but despite having the longer co-evolutionary time it displays exactly the opposite. Indeed it was the *Calluna* habitats' assemblage which exhibited better resilience, but it clearly forms a 'newer' assemblage adhering less to a reference template. *Calluna* does however exhibit the better persistency of a functioning assemblage. This mix of results, I believe, can be explained by the evolutionary histories of the habitats. If the *Calluna* assemblage had the same evolutionary time to form as tussock (and did not progress successionally in this time), and had, through long term interactions of the components of its assemblage and plant resource, evolved to maximally use that resource and form strong dependencies on set interactions i.e. developed a template of assemblage structure, then it would have exhibited better consistency, but poorer resilience and persistence due its fixed form.

Because of its new (immature) coevolutionary nature the *Calluna* fauna return at a faster **rate** than tussock's. Consistency, however, was best in tussock, due to its longer evolutionary history, implying the formation of a reference template structure. Persistence favoured *Calluna*, as the numbers to form a new functioning group more completely were more easily acquired from the surrounding habitat than if it were adhering to a template of reconstruction (as in tussock).

This experiment has achieved my aims in that:

1) it has shown that native systems can recover from a small disturbance rapidly, in a 'balanced' fashion;
2) that the time factor involved (be it 'old' or 'new' systems) is only weeks, given the scale of the disturbance;
3) the consistency of the returned fauna in native, uninvaded systems was high (compared to post-invaded systems) demonstrating associations between assemblage members are strong, and well developed, more so than in the new post-invaded assemblages.

Further, resilience was better in small areas of disturbance no matter what the habitat (with respect to taxa), and the rate of return was greatest in *Calluna*, but because the initial assemblage was so much larger than tussock's it did not return totally in as fast a time (3 weeks as opposed to 3.5 weeks) - both resilience values were on a par with Barrett's (1968) findings. The tussock assemblage followed path A (consistency) in Figure 5.3, while *Calluna* adhered to path C (persistence) (Fig 5.3).

Implications

The change in habitat structure from tussock grassland to heather shrubland through extensive invasion by *Calluna* has dramatically changed the vegetative composition, the fundamental influence on the invertebrate composition (Southwood *et al.* 1979, Lawton 1978). The invasion has introduced a novel, prominent, dominant, competitive, vegetation type and pushed the native tussock grasslands to a new successional state, grassland to shrubland. This development has occurred at a far greater speed than would be normal (Rogers and Leathwick 1994); the effect on the developed invertebrate assemblage's stability has not been adverse, but has resulted in a loss of ability to maintain a consistent structure, yet increased the assemblage's functional persistence.

The developing fauna in this "new" habitat type (*Calluna*) differs markedly from the original, and is still in a state of flux as the new resources (physical structures, space, food) are 'being allocated' and more finely divided. There appears still to be room, and heterogeneity in existence of taxa, to allow more and different taxa to become part of the assemblage. The fact that the *Calluna* invertebrate assemblage shows good persistence, but not consistency, suggests that the assemblage is very 'plastic' - able to change dramatically, respond quickly, and reconstitute a functioning system admirably, without the 'hindrance' of a rigid template. This may be at the expense of the rarer, slower to breed and grow, monophagous invertebrates that were/are strongly associated with tussock, tightly co-evolved and unable to compete in the new system. This may make possible 'space' for a new herbivore, the heather beetle.

Yet the tussock grassland's assemblage, though not so 'plastic', did show it had the capacity to respond to a disturbance with great speed, and, importantly from a conservational aspect, was able to reconstitute the characteristic faunal assemblage conservation managers might expect. This is a promising sign of possible re-establishment of complete tussock grassland communities "when" successful control of *Calluna* is achieved. As long as there are areas of tussock grassland in "good' condition in the near vicinity of *Calluna* heathland, re-establishment should be a probable event when tussock is encouraged to reoccupy (through *Calluna* control) its previous range.

Chapter 6

The invasion process and its impacts in Tongariro National Park

Introduction

Invasions, though still 'naturally' occurring, are more widespread, more devastating and more common in this century than any other recorded (Elton 1958, Sykora 1990, Kornas 1990, di Castri 1990), primarily due to human expansion and developing technologies (Maillard & Raibaut 1990, *et al.* 1990, Townsend, 1991). Research and data are now coming to the fore on invasive species, on their characteristics (all above refs; Groves and Burdon 1986), and on community vulnerability to invasions. Less information exists on the full impact of these invasive species. This thesis describes such impacts on plant communities and their invertebrate assemblages indigenous to New Zealand, in Tongariro National Park.

Here I propose a possible general schematic sequence of temporal change for an indigenous system experiencing invasion to illustrate how there may be recurring invasions because of the initial invasion. The initial invader was the shrubby species, European heather, *Calluna vulgaris*, a fast spreading, *r* strategist (Barclay-Estrup 1970, Gimingham 1960, Gimingham *et al.* 1979), which entered via human mediation, thereby satisfying one of the primary criteria for an invading plant species listed in Table 1.1, chapter 1. In this particular example the importance of mulitiple introductions to the success of the invader can not be emphasised enough, and, as indicated for birds (C.J.Veltman), is a primary factor in the successful establishment of any invader into a new community. Indeed the establishment of *Calluna* took several years of plantings (introductions) and extensive pro-*Calluna* management (fires). Subsequent spread has not required deliberate human input, but instead has followed zones of human-generated disturbance.

Secondary invasions (brought on by the disturbance and formation of a new community) occured, conspicuously of the herbivores Psyllidae (Homoptera) and Thrips (Thysanoptera) as well as the 'tourist' insects (Diptera), and the web-spinning spiders (Araneidae), which were able to utilise the new resource created in the native communities by the presence of invasive *Calluna*. These invaders are characterised by high mobility and being generalist feeders (Table 1.1), and additionaly sre in some ways pre-adapted to the resource presented by *Calluna* which contributes to their success in this new environment.

The third possible invasion, that of the proposed biological control agent, is discussed below in the section on "The biology of the new invader". However Lochmaea suturalis has few of the characteristics of a successful invertebrate invader, but one major counter-balancing feature, that is its invasion will be human mediated into enemy free space onto a substantial, uncontested, unrestricted, food resource.

The invasion process

Figure 6.1 depicts a possible sequence of changes a system undergoes by way of response to plant invasion causing large scale disruption to the existing plant habitat. The scenario plotted is generalised and within each step there are many variations on what might happen to each compartment of the system and each component within each compartment.

The process is (Fig. 6.1):

Time 0 The indigenous system is at equilibrium, or changing with normal succession in response to endogenous disturbance patterns. There is a characteristic vegetation type with n_1 species having x_1 abundances that form the resource pool for the animal assemblage (in this case the invertebrate assemblage). Within the invertebrate assemblage there exists a trophic structure with y functional groups consisting of n_2 species with x_2 abundances interacting in z ways - forming a community. Between the two components lines can be drawn to represent resource use, the number of lines and their form (whole or dashed) relating to the stability of use. Within the habitat, the plant resource base, there is 'spare', unutilised, resource which may allow transient species, or species from other habitats to occasionally exist in the system. The whole model is of course dynamic in evolutionary time but 'stable' in the 'short' term.

Time 1 When invasion occurs, usually aided by human mediated disturbance, the invader establishes after a period of time and the 'old' resource base is changed. Often large proportions of the old resources are lost and replaced by new and usually novel ones. The replacement may result in a larger, smaller, or similar total resource base, but generally the usable resource available to the original dependents is reduced as the resource composition changes. The assemblage (Fig. 6.1) has a range of probable reactions: no change, loss or gain of species, loss or gain in abundances of species, immediate or delayed use of the new resource, trophic structure collapse, guild proportional shifts. Links may be lost between the assemblage and the resource base as local extinctions occur. As the new resource establishes another invasion may occur (invasion 2), an invasion of the new resource in their own habitat by the animals from the original assemblage.

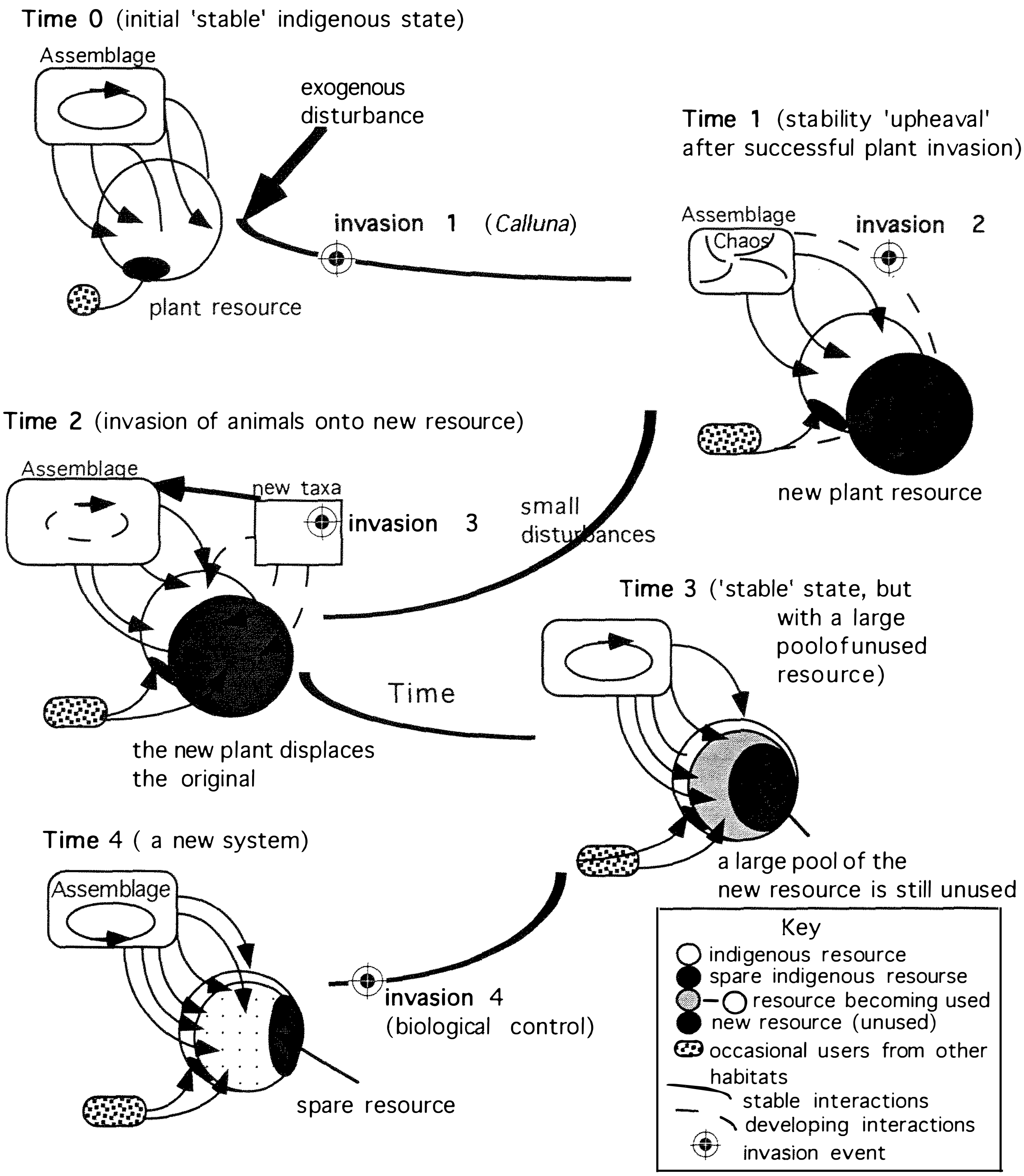
Time 2 After this state of flux, invasions onto the new resource by invertebrates from neighbouring habitats are more likely than usual. These occasional, or transient users may establish a permanent presence - replenishing locally extinct or reduced components of the original faunal assemblage. Taxa from other habitats may now be able to utilise the new resource (invasion 3) or usurp the old (competitive exclusion). Neighbouring habitats may be stressed or relieved demographically by these dispersals.

Time 3 After a period of time a new assemblage forms and stabilises as a functioning trophic structure (Heatwole and Levins 1972, Moran and Southwood 1982). There may now be new species, placing emphasis on different trophic levels. The resource base is better utilised than in time 1 or 2, but focus is on different features of that resource. The loss of plant resource initially present stabilises as the plant community establishes coherency in response to the stable animal assemblage. The amount of 'spare' resource is probably larger than the original condition because the plant invader will not be as well utilised as was the original plant resource. The system may appear, again, stable.

Time 4 This 'spare' resource is an 'invitation' to exotic 'invaders'; management can utilise this novel resource by introducing other invaders, i.e. biological control agents (invasion 4). These will ensure greater utilisation of the initial invader resource, perhaps adding beneficially to the indigenous invertebrate assemblages still in the invaded habitats, and a new stable animal assemblage will form, accommodating this final invader.

Fig. 6.1 Scenario of change as a community responds to invasion.

Starting with the initial indigenous habitat at time zero an exogenous disturbance may allow the invasion of an exotic (or native) species, in this case *Calluna*. Human aid can accelerate this phase so that the invasion is not gradual. After a period of time the invader's impact is evident. At time 1 the dependent assemblages tend to be experiencing many changes, and the system is prone to other invasions. Time 2 sees these new invasions from local sources (neighbouring habitats), and invasion of the new resource by original assemblage members. Time 3 is perhaps a long time (decade/s ?) after the invader established and the system is again functionally stable, but usually has resources that the indigenous fauna still can not utilise. There is room for further invasion, e.g human mediated (time 4).



Evidence for this model, the changes that actually occur in the compartments of the model (the assemblage and resource), can be gathered from the work done on *Calluna* invasion in Tongariro National Park. The evidence for the resource compartment comes from measures of plant diversity, frequency, apparency, abundance, architectural structure, and nutritional value. These describe the change in the indigenous 'resource base' and the new vegetation resource base after *Calluna* invasion (invasion 1), even though it has been 80 years since the initial invasion into parts of the Park. The assemblages of indigenous and invaded habitats were described through basic numerical data, diversity measures, trophic structures, and stability measures. These data provided information as to changes, and allow speculation on invasion events 2 and 3. At time 3 in the invasion sequence there is some utilisation of the new resource by indigenous invertebrates (those successful in invasion 2 and 3) and the community is relatively functionally stable. How much of the new resource is unutilised, available for introductions (invasion 4) of beneficial invaders, such as biocontrol agents, was measured in Chapter 4, and may be useful to management.

The data suggests

The resource base

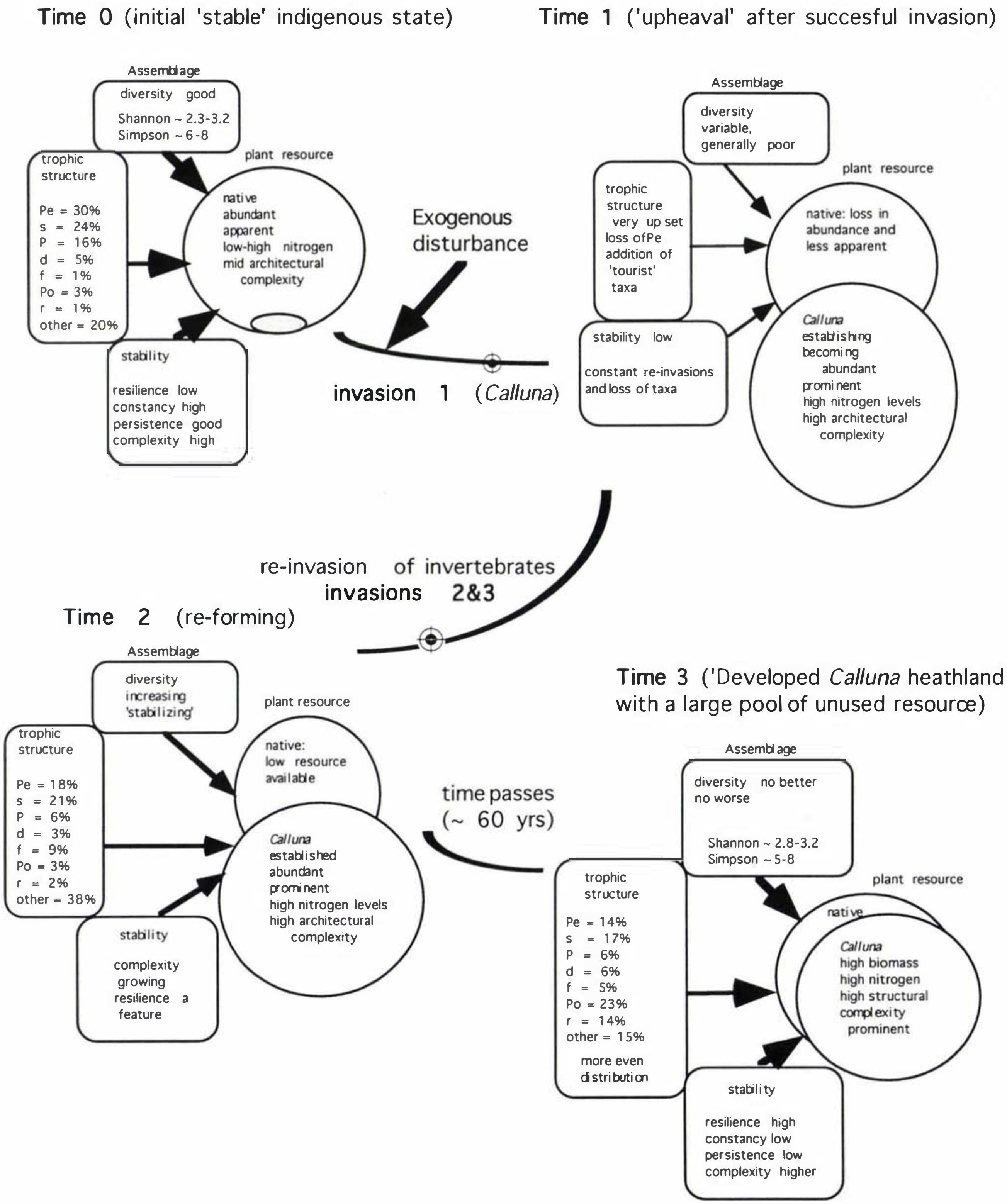
The data showed that the indigenous plant communities decreased in abundance (losing about 40% cover after invasion). Frequency, and hence visual appearance to invertebrates, of indigenous plants decreases (cf. Photographs 1 & 2 Chapter 2). This decrease is sometimes to the point of local extinction (Chapman 1984 pg 105), though none were recorded from the sites examined here. A large proportion of the indigenous resource base has gone, replaced by a *Calluna* resource. Invasion by *Calluna* has led to changes in the location and availability of minerals and nitrogen, *Calluna* being ~ 3 times 'richer' in nitrogen than tussock (Chapter 2, Fig. 2.7). The new resource, low on nutrient availability though high in nutrient value, has enhanced the structural features (architecture) of the habitats, i.e. the shape, height, number of leaves and branches: the pattern by which the vegetation occupies the volume of space about it (Chapter 2, Fig. 2.10). This has opened new resources that appear to favour invertebrates that utilise structural resources e.g. spiders, predatory Diptera. The repercussions to the 'invaded' herbivore invertebrates should be great as *Calluna* is a plant high in specific secondary compounds with a very monophagous fauna in Europe (Hopkins and Webb 1984, Webb and Hopkins 1984, Webb *et al.* 1984, Webb 1989a).

Calluna is less competitive in wet soils and soils that are not acidic (Gimingham *et al.* 1979, Jalal and Read 1983), though it appears that at the lower altitudes (< 1200 m) there are no habitats (discounting any above shrub in stature) immune to invasion; the process just takes longer in the wetter areas. The fact that *Calluna* takes longer to establish and dominate in habitats like the flax wetlands may give the invertebrate assemblages more time to 'adapt' to the changes.

Fig. 6.2
The evidence of change in a tussock community responding to *Calluna* invasion.

Note, the assemblage box of Fig. 6.1 is now divided into 3 boxes, showing features of the assemblage.

Pe = plant eater
s = scavenger
P = predator
d = detritivore
f = fungivore
Po = pollen eater
r = root eater



Disturbance and successional impacts on the invasion process

There are many major sources of natural (endogenous) disturbance in vegetation such as that at Tongariro National Park, including natural fires, volcanism, tephra, and lahar perturbations, tectonism, as well as the more widespread phenomena of forest dieback and climate change. Additional to these are ongoing exogenous disturbances, generated by humans, such as trampling, seed dispersal, fires, weed introductions, and perturbations through management by the Park managers, manipulating the ecosystem.

Each of these disturbances, depending on their frequencies and amplitudes, partially or completely resets successional processes within the Park. While the above model (Fig. 6.2) relies on an initial exogenous disturbance to launch the invasion process, it is predicated on an absence of future disturbances. In reality, given the dynamic nature of the ecosystem, such a stipulation might be only seldom obtainable. Consequently the model has its limitations, but even in the event of such disturbances, the end results of succession will probably be the same. Although chance order of re-entry of species may have destabilising effects, the competitive nature of *Calluna*, and its ability to displace native plants, will certainly guarantee it is successful, what ever the order of reinvasion. It remains to be seen whether the presence of the more vigorous defoliation achievable by the heather beetle, can alter this state of affairs.

Impacts on invertebrate assemblage structure

The diversity measures (Simpson and Shannon) suggest that the invaded communities increase in diversity, i.e. number of species increases and distribution of abundances of those species are more even, except in flax and tussock habitats (Chapter 3, Fig. 3.2). After invasion, abundance distributions of invertebrate species become less reverse J curve distributed (i.e. high numbers of low abundance taxa reducing rapidly to low numbers of high abundance taxa, often ending with a small rise caused by a few very successful taxa in high abundance), and more like Poisson distributions. The *Calluna* heathland assemblage has a bimodal distribution (Chapter 5 Fig 5.9, Chapter 3, Fig. 3.6). The Simpson index highlights this. It means that while a few species became locally extinct, others grew in abundance. The Coleoptera, Formicidae and Orthoptera were most negatively affected at these sites, i.e. the common invertebrates (Chapter 3, Table 3.1). This supports White's (1987) contention that it is the common invertebrate taxa that are first and most affected by plant invasions (chapter 3).

The positive correlation of architecture and invertebrate abundance (Chapter 3 Fig. 14) illustrates how some taxa have utilised the new resource and grown in abundance, e.g. web spinning spiders, which were less of a feature in the original assemblage. In habitats other than tussock the invasion of *Calluna* resulted in the presence of more invertebrate taxa. Their presence implies utilisation of the new resource.

If the new resource was being utilised by the new and old invertebrates as food then an expectation is that the herbivore guild should have increased in the invaded habitats. Study of this guild showed that generally herbivore frequency of occurance and abundances were depressed after invasion, The proportion of phytophagous insects dropping from 30% to 14% (Chapter 3, Figs. 3.10 to 3.12). This indicates that the new 'invaders' were utilising some elements of the old resource, or some structural, rather than nutritive, feature of the new resource. Only the proportion of pollen eaters dramatically increased (3% to 23%). The pollen eaters, solely Thysanoptera, are making extensive use of *Calluna* flowers for food. This is a good example of a species capable of fully utilising an otherwise un-utilised new resource and as a result experiencing population increases.

Predators generally increased while scavengers, detritivores, fungivores, and parasites were variable (Chapter 3, Figs. 3.10 to 3.12). The predator guild's variable enhancement was, where it occurred, through addition of predators capable of using the new resource structure, i.e. web spinning spiders. The trophic webs constructed in Chapter 5 (Figs. 5.10 and 5.11) clearly illustrate the differences in linkage strengths of predator and herbivore levels between un-invaded tussock and *Calluna* habitats, primary versus secondary consumer ratios being 3:1 in tussock and 1.2:1 in *Calluna.* Some of the species at time 2 (after invasions 2 & 3) of the model have now shifted host to incorporate *Calluna*, e.g. Thysanoptera, Scarabaeidae, Cicadidae. Others, specifically non-specialist guilds, whose abundances have flourished, or who represent a new taxon type (for that habitat), have migrated from neighbouring habitats. They have done so either because of the free resource, or the lack of once existing competition. These species, often referred to as 'tourist' taxa (Moran and Southwood 1982) are highly mobile non-specialist invertebrates usually belonging to the detritivore and scavenger guilds. Phoridae, Tipulidae, Muscidae, Tachinidae, Sarcophagidae, Dolichopodidae and Drosophilidae are examples of dipteran 'tourist' families that became more frequent after *Calluna* established (Chapter 3).

The invertebrate assemblage of established* Calluna *habitat

Though most of the invaded habitats explored here, I believe, are still moving through the invasion process and are in a state of 'flux', the *Calluna* dominated habitat data is evidence of the structure of the 'new' assemblage and resource system - time 3 of the model. After a length of time (~80 years) the system has probably reached some 'stability'. The guild structure has changed in that there is a more even distribution of taxon numbers within guilds throughout the entire trophic web (Chapter 5, Chapter 3). Pollen eaters are still prominent but predators are more even in proportion, as are herbivores (Fig. 6.2). There is high diversity, i.e. a high number of species and evenness in distribution. Though the species involved are different from the original indigenous habitat, the assemblage is still indigenous in composition, just generally more mobile and using different resources (i.e. the physical structure).

The stability of the new system (the definition for which can be found in Chapter 5) has reached a new 'equilibrium (Fig. 6.2). The evidence comes from comparing the 'pure' *Calluna* assemblage's rate of return, persistence, and fidelity of the returning fauna, to those of tussock habitats after disturbance (Chapter 5). The *Calluna* invertebrate assemblage exhibits better resilience but poorer consistency implying that the invertebrate assemblage of *Calluna* is more functionally stable than that of tussock, but the composition is not as constant. Tussock assemblages on the other hand return more slowly but with greater fidelity. Because the assemblages of the other indigenous habitats were not tested only inferences can be made about their stability. It would be reasonable to expect the same results as in the tussock for most, if not all the indigenous habitats, given their co-evolutionary histories, and thus perhaps tighter interactions between species. The new assemblage including *Calluna* can be considered, 'functionally', as stable, and more resilient to disturbance than indigenous ones. It may be that the indigenous habitats, especially tussock grasslands in Tongariro National Park, are inherently unstable because of their transitional, successional nature (Rogers and Leathwick 1994)

Resource availability for invasion of a biological control agent

The 'new' assemblage of *Calluna* heathlands in Tongariro National Park represents a diverse, 'stable' (resilient), indigenous, functioning, invertebrate community.

That some of the more polyphagous indigenous invertebrates have incorporated such a prominent food resource is not surprising. During surveying, Cicada larvae, Scarabaeidae larvae, Acrididae, Scarabaeid adults and Thysanoptera, were all observed feeding on *Calluna*. The invader, then, is starting to become part of the resource base. The preference for, and consumption of, this new resource was measured for grasshoppers (Acrididae: *Sigaus piliferous*) and the manuka beetle (Scarabaeidae: *Pyronota festiva*) in Chapter 4. Experiments revealed that both species found *Calluna* palatable; manuka beetles ate 2-5 times more *Calluna* than *Hebe* or manuka, while grasshoppers ate 10 - 20 times more *Calluna*. The proportion of the current shoot standing crop these insects are estimated to remove is between 0.4% and 2% (Chapter 4). Indeed exclusion experiments (Chapter 4) showed that the indigenous 'challenge' to *Calluna* was not substantial enough (even including root feeding invertebrates of which there are, in places, substantial numbers) to result in any measurable decrease in performance (as measured by shoot growth). This implies that there is a large resource untapped.

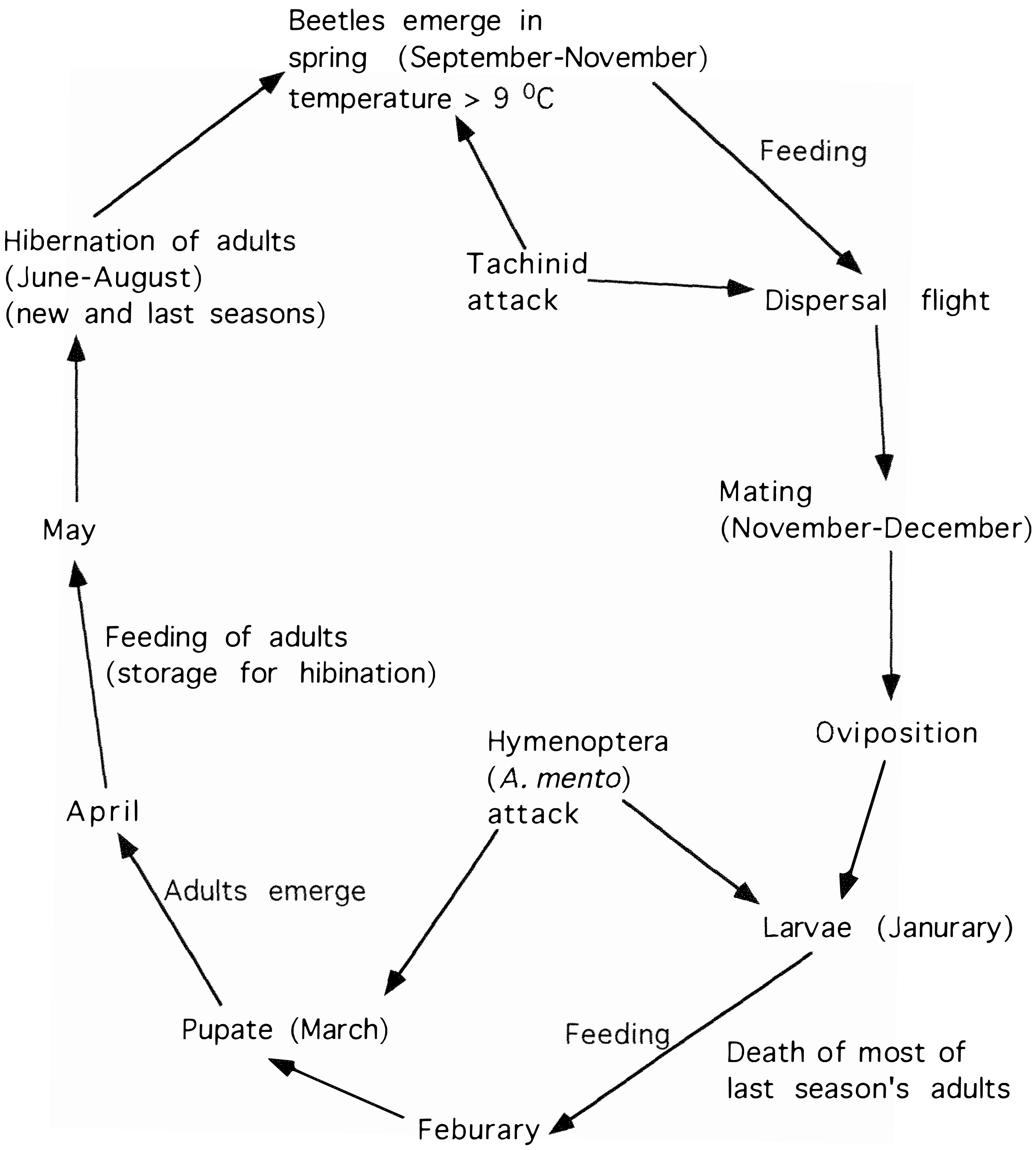
The fourth invasion (Fig. 6.1) could be an exotic invader, *Lochmaea suturalis*, introduced to combat the initial invader (*Calluna*). This beetle is a small (5 - 7 cm), brown, oval, chyrsomelid, reputedly monophagous on *Calluna* (but see Waloff 1987 and Syrett *et al*. 1994). The adults and larvae feed extensively on *Calluna* shoots, leaf, and 'bark', and of all the invertebrate feeders of *Calluna* has probably the potential for causing the most impact (Webb pers. comm.). It has been noted to damage populations of *Calluna* (Cameron *et al*. 1944, Brunsting and Heil 1985, Berdowski and Zeilinga 1987, N. Webb, S. Chapman, S. Fowler, S. McNeill pers. comm.). This beetle targets *Calluna* as its primary resource, and as I have shown, the *Calluna* resource in Tongariro National Park is both expansive, expanding (Chapman and Bannister 1990) and very under-utilised. There appears a 'niche' for such an organism; being both herbivorous and monophagous, it should fit into the indigenous assemblage, without being excluded by competition as can happen (Ehler and Hall 1982).

The biology of the new invader

Though *Lochmaea suturalis* does not have some of the most prominent attributes of other successful invertebrate invader species, i.e. rapid rate of increase, high mobility, polyphagy (see Chapter 1), it has one major redeeming feature: its introduction would be Human managed.

A univoltine beetle, in early spring the over-wintering adults emerge from hibernation in debris and moss at the bases of *Calluna* plants. They become active as the air temperature increases above 9^0C. Maximum population numbers are reached in mid summer (June to August in Europe). At this time both adults and the current year's larvae are feeding. There is another peak of feeding just before hibernation as the beetles build fat reserves for hibernation. Dispersal occurs when the temperature rises above 16^0C. Females exhibit oo-genesis flight syndrome; while flight muscles are large the eggs remain 'unripe'; when the flight muscles histolyse (usually after flight) the eggs mature. A large determinant of dispersal and fecundity is the food supply, poor food resulting in low or no egg production (Van Schaick Zillesen and Brunsting 1983). It has been suggested that the lack of food affects oo-genesis and this process, via hormonal methods, influences flight ability, and hence dispersal. Mating occurs from mid to late summer, after dispersal (Fig. 6.3).

Fig. 6.3 Life history of *Lochmaea suturalis*; dates are New Zealand estimates based on European data.



Predation and parasitism on *Lochmaea* should be much less in Tongariro National Park than in its 'natural' home. The reported parasites, the Tachinid *Degeeria collaris* (Fallen) and a Hymenopteran *Asecodes mento* (Walker), can parasite as much as 90% of a population of beetles in South England (Fowler pers. comm.). But, though there are native tachinids and parasitic Hymenoptera in the Park, their abundances are low, at least currently (Chapter 3). *Lochmaea's* main predators are Carabidae and Coccinallidae (Cameron *et al.* 1944); these are present in the Park in varying numbers depending on the habitat (Chapter 3) and may be a problem in the flax/*Calluna* communities. Perhaps of most concern is the fungus *Beauveria bassiana* which, when the beetle is in large numbers, can account for a large proportion of the population dying (Brunsting and Heil 1985). The fungus has been reported in the Park area (T. Bourner pers. comm.); what its impact will be is not known.

Influence on **Calluna** *dynamics*

Calluna of any age and condition is prone to attack by *Lochmaea* (Cameron *et al.* 1944). Young, vigorous, plants (up to 10 years old) are seldom killed; it is the older plants of poorer condition that suffer serious damage. Harsh environmental conditions (frost, drought) leave *Calluna* plants more prone to serious damage. Population levels of *Lochmaea* must be very high before *Calluna* stands are seriously damaged. There have been no recent observations of outbreaks of the beetle causing any extensive damage in the south of England (N. Webb, Chapman, S. Fowler pers. comm.). In the north, *Lochmaea* is all but discounted as a pest (R. Bunce pers. comm.); the last reports of damage come from Cameron *et al.* (1944) and Morrison (1938) in Scotland.

In The Netherlands outbreaks of the beetle are more common, occurring roughly in a ten year cycle. Densities of beetles reach upwards of 2000 m^{-2} at the 'hatching' foci; these disperse as a circular front (Brunsting and Heil 1985). Most damage is done at the end of the growing season and the *Calluna* has no chance to regenerate tissues. The following spring sees even larger numbers of the beetles, and it is in this season that plants are killed. Other factors, such as frosts and droughts, contribute to the 'success' of the beetle, but in The Netherlands the demise of *Calluna* heathlands is also attributed to over fertilisation of surrounding lands (*Calluna* being well adapted to 'poorer' soils and acid conditions), leading to more intense competition by grass species. Higher nutrient levels in the soil are thought to be reflected in the plants' nitrogen levels and this is believed to result in higher beetle infestations (Brunsting and Heil 1985). There is evidence in Tongariro National Park that *Calluna* develops a standard level of nitrogen in its tissues which is high regardless of soil levels (Chapter 2), so presumably nitrogen is not limiting.

Populations of *Lochmaea* do appear capable of destroying large areas of *Calluna*, given the co-requisites of environmental conditions, soil nutrients and competition.

Since there is a reduced herbivore load in the *Calluna* habitat in New Zealand, addition of this herbivore may have desirable repercussions for the entire trophic structure, as well as for control of

Calluna. It will allow 'freeing up' of minerals and nutrients 'tied' up in *Calluna* and supply a 'sedentary' addition to the food web (i.e. as Carabid, Tachinid and Coccinalid prey;(Cameron *et al*. 1944, Emberson 1988, perhaps creating additional complexity and stability.

Though the beetle is not indigenous it could become part of the trophic structure of a community type that will be in the Park for many years to come, perhaps to the point where *Calluna* heathlands and assemblages will be considered natural if not indigenous.

Management and Conservation

The key to conservation of invertebrates is the conservation of the habitats in which they live (Pyle *et al*. 1981). In New Zealand this is the mandate of the Department of Conservation (Edmonds 1989). The natural estate in New Zealand is at continual risk from invasion, but a distinction needs to be made as to whether it is conservation or preservation that is the ultimate goal. Usually this distinction is unnecessary because preservation of ecosystems surrounded by exotic landscape, subject to intensive human use and the inevitable motion of succession, is nearly impossible. Conservation however, means the maintenance of indigenous habitats in an indigenous state, recognising and allowing them to change in a natural way. Conservation of biological diversity, *per se*, isn't so much the aim as protection of native ecosystems, indigenous processes, and natural landscapes. By protecting these structures (habitat diversity), through disturbance and pest control, the components within will also continue to exist. Protection of rare and endangered species seems sometimes to be purely a luxury and an exercise in public relations. My findings suggest that the indigenous invertebrate assemblages in Tongariro National Park are not necessarily threatened to any extent by *Calluna* invasion, though over the long term, if *Calluna* continues to spread and replace indigenous habitats the diversity of these may drop to a level at which there will be losses of indigenous 'flavoured' assemblages.

Though no 'key stone' species (excepting *Calluna*) (Slocombe 1993) were identified, the data do provide insights into which invertebrate taxa are prominent in which habitat, and which appear most affected by invasion and modification of those habitats. No local 'extinctions' were recognised and the 'new' assemblages were still indigenous and may be viewed as assemblages that represent a successional stage similar to native heathlands (*Dracophyllum* and manuka serial stages). Differences were found, but it is my belief that the differences are not ‘conservationally significant’. Indeed the mosaic of habitats, and their rapidity of change (succession) (Rogers and Leathwick 1994) in the Park has meant quite a 'plastic' invertebrate assemblage structure, at once invasive yet also invasible.

The key features are, that indigenous 'integrity' is still intact, and stability and consistency is, if anything, better. With the introduction of the heather beetle (*Lochmaea suturalis*) careful monitoring will be necessary, but a sacrifice in the integrity of indigenous assemblages may be minor next to the benefits of controlling the spread of *Calluna* and the flow-on effects of re-establishment of the indigenous plant resource base. In time the *Calluna* and the heather beetle may become only small portions of the estate, and even seen as a natural part of the Park's ecosystem. This would make them the ultimate invaders.

REFERENCES

Aerts, R. (1989). Above ground biomass and nutrient dynamics of *Calluna vulgaris* and *Molinia caerulea* in a dry heathland. *Oikos* 56: 31-38.

Atkinson, I. A. E. (1981). *Vegetation map of Tongariro National Park.* Department of Scientific and Industrial Research, Wellington, New Zealand.

Auld, B. A.; Tisdell, C.A. (1986). Ecological and physiological characters of invading species. In:*Ecology of biological invasions*. Groves J.J.; Burdon, R.H. (eds) Cambridge University Press, Cambridge. 79-89.

Bagnall, A. G. (1982). Heather at Tongariro. A study of a weed introduction. *Tussock grasslands and Mountainlands Inst. Rev.* 41: 17-21.

Baker, H. G. (1965). Characteristics and models of Origin of weeds. In: *The genetics of colonizing species.* Baker, H. G.; Stebbins, G.L. (eds). Academic Press inc., New York. 147-172.

Bannister, P. (1981). Carbohydrate concentration of heath plants of different geographical origin. *Journal of Ecology* 69: 769-780.

Barclay-Estrup, P. (1970). The description and interpretation of cyclical processes in a heath community. *Journal of Ecology* 58: 243-249.

Barratt, S. C. H.; Richardson, B.J. (1986). Ecological and physiological characters of invading species. In: *Ecology of biological invasions.* Groves J.J.; Burdon, R.H. (eds). Cambridge University Press, Cambridge. 21-34.

Barrett, G. W. (1968). The effects of an acute insecticide stress on a semi-enclosed grassland ecosystem. *Ecology* 49(6): 1019-1035.

Bazzaz, F. A. (1975). Plant species diversity in old-field successional exosystems in southern Illinois. *Ecology* 56: 485-488.

Begon, M.; Harper, J.L.; Townsend, C.R. (1986). *Ecology: individuals, populations and communities.* London, Blackwell Scientific Publications.

Belsky, A. J. (1986). Does herbivory benefit plants? A review of the evidence. *The American Naturalist* 127(6): 870-892.

Bentley, S.; Whittaker, J.B. (1979). Effects of grazing by a chrysomelid beetle, *Gastrophysa viridula*,on competition between *Rumex obtusifolius* and *Rumex crispus*. *Journal of Ecology* 67: 79-90.

Berdowski, J. J. M.; Zeilinga, R. (1987). Transition from heathland to grassland: damaging effects of the heather beetle. *Journal of Ecology* 75: 159-175.

Bernays, E. A.; Simpson, S.J. (1989). Feeding and Nutrition: Biology of grasshoppers. *Journal of Natural History* 16: 261-266.

Bernays, E. A. (1981). Plant tannins and insect herbivores; an apprasial. *Journal of Ecological Entomology* 6: 353-360.

Boesch, D. F. (1974). Diversity, stability and response to human disturbances in estuarine ecosystems. *First international congress of ecology: Structure, functioning and management of ecosystems*, The Hague, Centre for agricultural publishing and documentation. 109-114.

Brown, V. K. (1982). The phytohagous insect community and its impact on early successional habitats. *5th International Symposium: Insect-Plant Relationships*, Wageningen. 205-213.

Brown, V. K.; Gange, A.C.; Evans, I.M.; Storr A.L. (1987). The effect of insect herbivory on the growth and reproduction of two annual *Vicia* species at different stages in plant succession. *Journal of Ecology* 75: 1173-1189.

Brown, V. K. (1991). The effects of changes in habitat styructure during succession in terrestrial communities. In:*Habitat Structures: the physical arrangement of objects in space*. Bell, S.S.;. McCoy, E.D. & Mushinsky, H.R. Chapman and Hall, London. First edition. 141-167.

Brown, V. K.; Gange, A. C. (1989a). Herbivory by soil-dwelling insects depresses plant species richness. *Functional Ecology* 3: 667-671.

Brown, V. K.; Gange, A.C. (1989b). Differential effects of above- and below-ground insect herbivory during early plant succession. *Oikos* 54: 67-76.

Brown, V. K.; Jepsen, M.; Gibson, W.D. (1988). Insect herbivory: effects on early old field succession demonstrated by chemical exclusion methods. *Oikos* 52: 293-302.

Brown, V. K.; Leijn, M.; Stinson, C.S.A. (1987b). The experimental manipulation of insect herbivore load by the use of an insecticide (malathion): The effect of application on plant growth. *Oecologia* 72: 377-381.

Brunsting, A. M. H. (1982). The influence of the dynamics of a population of herbivorous beetles on the development of vegetational patterns in a heathland system. *5th International Symposium: Insect-Plant Relationships*, Wageningen. 215-223.

Brunsting, A. M. H.; Heil, G.W. (1985). The role of nutrients in the interactions between a herbivourous beetle and some competing plant species in heathlands. *Oikos* 44(1): 23-26.

C.S.I.R.O. (1991). *The insects of Australia*. Melbourne, Melbourne University Press.

Cameron, A. E.; Hardy, J.W.; Bennett, A.H. (1944). *The Heather Beetle* (*Lochmaea suturalis*). Petworth, British field sports society.

Carpenter, S.R.; Kraft, C.E.; Wright, R.; He, X.; Soranno, P.A. & Hodgson, J.R. (1992). Resilience and resistance of a lake phosphorus cycle before and after food web manipulation. *The American Naturalist* 140(5): 781-798.

Chapman, H. M. (1984). The ecology of heather, *Calluna vulgaris*, in New Zealand; with particular reference to Tongariro National Park. PhD thesis, University of Otago, Dunedin, N.Z. 380 pp.

Chapman, H. M.; Bannister, P. (1990). The spread of heather, *Calluna vulgaris* (L.) Hull, into indigenous plant communities of Tongariro National Park. *New Zealand Journal of Ecology* 14: 7-16.

Chapman, H. M.; Bannister, P. (1994). *Calluna* performance in New Zealand. *New Zealand Journal of Ecology* 18(2): 109-121.

Chapman, R. F.; Bernays, E.A. (1978). Insect and host plant. *Proceedings of the 4th international Symposium: Entomological experimentaton and application* .

Chapman, S. B. (1967). Nutrient budgets for a dry heath ecosystem in the south of England. *Journal of Ecology* 55: 677-689.

Chapman, S. B.; Hibbles, S.; Rafarel, C.R. (1975). Net aerial production by *Calluna vulgaris* on lowland heath in Britain. *Journal of Ecology* 63: 233-258.

Chesson, P. (1978). Predator-prey theory and variability. *Annual Review of Ecology and systematics* 9: 323-347.

Clements, F. E.; Shelford, V.E. (1939). *Bio-ecology.* New York, John Wiley & sons Ltd.

Collier, B. D. (1973). *Dynamic ecology.* New Jersey, Prentice and Hall Inc.

Connell, J. H.; Sousa, W.P. (1983). On the evidence needed to judge ecological stability or persistence. *The American Naturalist* 121(6): 789-808.

Crawley, M. J. (1986). The population biology of invaders. *Phil. Trans. R. Soc. Lond.* 314(B): 711-731.

Crawley, M. J. (1989). Chance and timing in biological invasions. In:*Biological invasions: a global perspective.* Drake, J. A. John Wiley & sons Ltd, London. 407-423.

Crawley, M. J. (1982). *Herbivory: studies in ecology.* Oxford, Blackwell Scientific Publishers.

Crawley, M. J. (1983). *Herbivory: the dynamics of animal-plant interactions.* Oxford, Blackwell Scientific Publishers.

Crawley, M. J. (1985). Reduction of oak fecundity by low-density herbivore populations. *Nature* 314: 163-164.

Crawley, M. J. (1989). Insect herbivores and plant population dynamics. *Ann. Rev. Entomol.* 34: 531-564.

De Angelis, D.L. (1975). Stability and connectance in food web models. *Ecology* 56(1): 238-243).

DeAngelis, D. L.; Mulholland, P.J.; Palumbo, A.V.; Steinman, A.D.; Huston, M.A. & Elwood J.W. (1989). Nutrient dynamics and food-web stability. *Annual Review of Ecology and systematics.* 20: 71-95.

Denno, R. F.; Roderick, G.K. (1991). Influence of patch size, vegetation texture, and host plant architecture on the diversity, abundance, and life history styles of sap-feeding herbivores. In:*Habitat Structures: the physical arrangement of objects in space.* Bell,S. S.; McCoy, E.D. & Mushinsky, H.R. Chapman and Hall, London. First edition. 169-196.

di Castri, F. (1990). On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. In: *Monographic Biologicae.* Dumont, H.J.; Werger, M.J.A. Dordrecht, Kluwer Academic Publishers.

Dick, R. D. (1940). Observations on insect-life in relation to tussock-grassland deterioration. *The New Zealand Journal of Science and Technology* 22: 19-27.

Dickinson, K. J. M.; Mark, A.F.; Lee, W.G. (1992). Long-term monitoring of non-forest communities for biological conservation. *New Zealand Journal of Botany* 30: 163-179.

Doak, D. F. (1992). Lifetime inpacts of herbivory for a perennial plant. *Ecology* 73(6): 2086-2099.

Edmonds, A. (1989). Weed management: a conservation perspective. *Alternatives to the chemical control of weeds*, Forest Research Institute, Rotorua, New Zealand, Ministry of Forestry. vii-x.

Ehler, L. E.; Hall, R.W. (1982). Evidence for competitive exclusion of introduced natural enemies in biological control. *Environmental Entomology* 11(1): 1-4.

Elton, C. S. (1958). *The ecology of invasions by animals and plants.* London, Methuen & Co. Ltd.

Elton, C. S. (1966). *The pattern of animal communities.* London, Methuen & Co. Ltd.

Emberson, R. M. (1988). Biology of the heather beetle in Europe. In: *Heather control workshop*, Turangi, New Zealand, Department of Conservation. 26-30.

Fisher, G.; Grimm, N.B. (1991). Streams and disturbance: are cross-ecosystem comparisons useful? In: *Comparative analyses of ecosystems: patterns, mechanisms, and theories* . Findlay, J. L.; Cole ,G. S. Springer-Verlag, New York. 196-221.

Flaherty, D. L. (1969). Ecosystem trophic complexity and densities of the Willamette mite, *Eotetranychus willamettei* Ewing (Acarina: Tetranychidae). *Ecology* 50(5): 911-916.

Foelix, R. F. (1982). *Biology of spiders.* Massachusetts, Harvard University Press.

Forrest, G. I. (1971). Structure and production of north Pennine blanket bog vegetation. *Journal of Ecology* 59: 453-479.

Forster, R. R.; Forster, L.M. (1973). *New Zealand spiders: an introduction.* Hong Kong, Collins Bros & Co. Ltd.

Fox, M. D.; Fox, B.J. (1986). Ecological and physiological characters of invading species. In: *Ecology of biological invasions* . Groves J.J.; Burdon, R. H. (eds). Cambridge University Press, Cambridge. 57-67.

Fraenkel, R. (1953). The nutritional value of green plants for insects. T*ransactions of the 9th International Congression of Entomology.* 90-100.

Frank, D. A.; McNaughton, S.J. (1991). Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos* 62: 360-362.

Futuyma, D.J.; Keese, M.C.; Scheffer, S. (1993). Genetic constraints and the phylogeny of insect-plant associations: Responses of *Ophraella communa* (Coleoptera: Chrysomelidae) to host plants of its congeners. *Evolution* 47(3): 888 - 905

Gange, A. C.; Brown, V.K. (1989). Effects of root herbivory by an insect on a foliar-feeding species, mediated through changes in the host plant. *Oecologia* 81: 38-42.

Gimingham, C. H. (1960). Biological flora of the British Isles. *Journal of Ecology* 48:455-483.

Gimingham, C. H. (1988). A reappraisal of cyclical processes in *Calluna* heath. *Vegetatio* 77(1-3): 61-64.

Gimingham, C. H.; Chapman, S.B.; Webb, N.R. (1979). European heathlands. In: *Ecosystems of the world: heathlands and related shrubs: descriptive studies* . Specht, R.L. (ed). Elservier Scientific Publishing Co., Oxford. 365-413.

Goodman (1974). The validity of the diversity-stability hypothesis. *First international congress of ecology: Structure, functioning and management of ecosystems*, The Hague, Centre for agricultural publishing and documentation. 75-79.

Gould, F. (1979). Rapid host range evolution in population of the phytophagous mite *Tetranychus urticae* Koch. *Evolution* 33: 791-802.

Gouyon, P. H. (1990). Invaders and disquilibrium. In: *Monographic Biologicae.* Dumont, H.J.; Werger, M.J.A. Dordrecht, Kluwer Academic Publishers.

Grant, S. A.; Armstrong, H.M. (1993). Grazing ecology and the conservation of heather moorland: the development of models as aids to management. *Biodiversity and Conservation* 2: 79-94.

Grant, S. A.; Hunter, R.F. (1966). The effects of frequency and season of clipping on the morphology, productivity and chemical composition of *Calluna vulgaris* (L.) Hull. *New Phytologist* 65 : 125 - 133.

Grant, S.S.; Barthram, G.T.; Lamb, W.I.C.; Milne, J.A. (1978). Effects of season and level of grazing on the utilization of heather by sheep. 1: Responses of the sward. *Journal of the British Grassland Society* 33 : 289 - 300.

Grant, S.S.; Milne, J.A.; Barthram, G.T.; Souter, W.G. (1982). Effects of season and level of grazing on the utilization of heather by sheep. 3: Longer term responses and sward recovery. *Grass and Forage Science* 37 : 311 - 320.

Gray, J. S. (1987). Species-abundance patterns. *British Ecological Society Symposium*, 53-67.

Greenslade, P. J. M. (1983). Adversity selection and the habitat template. *American Naturalist* 122:352-365.

Groves, R. H. (1986). Ecological and physiological characters of invading species. In: *Ecology of biological invasions* . Groves J.J.; Burdon, R. H. Cambridge University Press, Cambridge. 137-150.

Groves, R. H.; Burdon, J.J (1986). *Ecology of biological invasions.* Cambridge, Cambridge University Press.

Hairston, N. G.; Allan, J.D.; Colwell, R.K.; Futuyma, D.J.; Howell, J.; Lubin, M.D.; Mathias, J. & Vandermeer, J.H. (1968). The relationship between species diversity and stability: an experimental approach with protozoa and bacteria. *Ecology* 49(6): 1091-1101.

Harte, J.; Levy, D. (1974). On the vulnerability of ecosystems disturbed by man. *First international congress of ecology,* The Hague, The Netherlands, Dr W. Junk B. V. Publishers. 208-236.

Heatwole, H.; Levins, R. (1972). Trophic structure stability and faunal change during recolonization. *Ecology* 53(3): 531-534.

Helsper, H. P. G.; Glenn-Lewin, D.; Werger, M.J.A. (1983). Early regeneration of *Calluna* heathland under various fertilization treatments. *Oecologia (Berlin)* 58: 208-214.

Helsper, H. P. G.; Klerken, G.A.M. (1984). Germination of *Calluna vulgaris* (L.) Hull *in vitro* under different pH conditions. *Acta Bot. Neerl.* 33(3): 347-353.

Hengeveld, R. (1988). Mechanisms of biological invasions. *Journal of Biogeography* 15: 819-828.

Herbold, B.; Molye, P.B. (1986). Intoduced species and vacant niches. *The American Naturalist* 128(5): 751-760.

Hilgendorf, F. W. (1917). Notes from Canterbury College Mountain Biological station, Cass. *Transactions and proceedings of the New Zealand Institute.* 50

Hobbs, R. J.; Gimingham, C.H. (1987). Vegetation, fire and herbivore interactions in heathland. In: *Advances in ecological research.* Academic Press, Ltd., London. 87-173.

Holdgate, M. W. (1986). Summary and conclusion: characteristics and consequences of biological invasions. *Phil. Trans. R. Soc. Lond.* 314(B): 733-742.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4: 1-23.

Hopkins, P. J.; Webb, N.R. (1984). The composition of the beetle and spider faunas on fragmented heathlands. *Journal of Applied Ecology* 21: 935-946.

Howarth, F. G.; Ramsey, G. W. (1991). *The conservation of island insects and their habitats.* London, Academic Press.

Hurd, L. E.; Wolf, L.L. (1974). Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. *Ecological monographs* 44: 465-482.

Jalal, M.A.F.; Read, D.J.; Haslam, E. (1982). Phenolic composition and its seasonal variation in *Calluna vulgaris. Phytochemisty* 21(6): 1397 - 1401.

Jalal, M. A. F.; Read, D.J. (1983). The organic acid composition of *Calluna* heathland soil with special reference to phyto- and fungitoxicity. II: Monthly quantitative determination of the organic acid content of *Calluna* and spruce dominated soils. *Plant and Soil* 70: 273-286.

Janzen, D. H. (1975). Host plants as islands. II: Competition in evolutionary and contemporary time. *The American Naturalist* 107(958): 786-790.

Karban, R.; Myers, J.H. (1989). Induced plant responses to herbivory. *Annu. Rev. Ecol. Syst.* 20: 331-348.

Kempton, R. A.; Taylor, L.R. (1974). Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. *Journal of Animal Ecology* 43: 381-199.

Kennedy, J. S. (1965). Mechanisms of host plant selection. *Annuals of Applied Biology* 56: 317-322.

Keys, H. (1991). Heather in the park. The beginnings. *Tongariro* 40: 13-19.

King, C. M. (1990). *The handbook of New Zealand mammals.* Oxford, Oxford University Press.

Kitching, R. L. (1986). Exotics in Australia - synopsis and strategies. In: *The ecology of exotic animals and plants (some australian case histories)* . R. L. Kitching. John Wiley and Sons, Chichester. 262-270.

Komas, J. (1990). *Plant invasions in Central Europe: historical and ecological aspects.* Dordrecht, Kluwer Academic Publishers.

Lawton, J. H. (1976). The structure of the arthropod community on Bracken. *Botanical Journal of the Linnean Society* 73: 187-216.

Lawton, J. H. (1978). Host-plant influences on insect diversity: the effects of space and time. Diversity of insect fauna: *Royal Entomological Sociey Symposium 9*, Blackwell Scientific Publishing, Oxford. 105-125.

Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* 28: 23-29.

Lawton J.H. (1987). Are there assembly rules for successional communities ? In: *Colonization, succession and stability. 6th British Ecological Society Symposium.* Gray, S. *et al.* (Eds). Blackwell Scientific Publishing.

Lawton, J.H.; Schröder, D. (1977). Effects of plant type, size of geographical range and taxonomic isolation on a number of insects associated with British plants. *Nature* 265: 137 - 140.

Lawton, J.H.; Schröder, D. (1978). Host-plant influences on insect diversity: the effects of space and time. In: *Diversity of insect fauna*: *Royal Entomolgical Society Symposium 9.* 105 - 125.

Laycock, G. (1966). *The alien animals.* New York, The Natural History Press.

Levin, S. A.; Paine, R.T. (1974a). The role of disturbance in models of community structure. *Ecosystem analysis and predictions: proceedings of a conference on ecosystems*, Alta, Utah. 56-67.

Levin, S. A.; Paine, R.T. (1974b). Disturbance, patch formation, and community structure. *Proc. Nat. Acad. Sci. USA* 71(7): 2744-2747.

Levins, R.; MacArthur, R. (1969). An hypothesis to explain the incidence of monophagy. *Ecology* 50(5): 910-911.

Lewontin, R. C. (1969). The meaning of stability. In: *Diversity and stability in ecological systems*, Brookhaven, National technical information service. 13-24.

Lodge, D. M. (1993). Biological invasions: lessons for ecology. *TREE* 8(4): 133-137.

Luff, M. L. (1975). Some features influencing the efficiency of pitfall traps. *Oecologia (Berl.)* 19: 345-357.

Lunberg, P.; Astrom, M. (1990). Low nutritive quality as a defense against optimally foraging herbivores. *The American Naturalist* 135(4): 547-562.

MacArthur (1955). Fluctuations of animal populations and a measure of community stability. *Journal of Ecology* 36: 533-536.

MacArthur, R. A. (1966). A note on Mrs Pielou's comments. *Ecology* 47: 1074.

MacDonald, A. J.; Kirkpatrick, A.H.; Hester A.J. & Sydes C. (1995). Regeneration by natural layering of heather (*Calluna vulgaris*): frequency and characteristics in upland Britain. *Journal of Applied Ecology* 32: 85-99.

Magurran, A. E. (1988). *Ecological diversity and its measurement.* Ryde, Croom Helm, Australia.

Maillard, C.; Raibaut, A. (1990). Human activities and modifications of ichyofauna of the Mediterranean sea: effect on parasitosis. In: *Monographic Biologicae*. Dumont, H.J.; Werger, M.J.A. Dordrecht, Kluwer Academic Publishers.

Major, J. (1988). Endemism: a botanical perspective. In: *Analytical Biogeography* . Myers, A. A.; Siller, P.S. Chapman & Hall, London. 117-148.

Margalef, R. (1963). Succesion in populations. *Advancing Frontiers of Plant Science* 2: 137-188.

Margalef, R. (1968). *Perspectives in ecological theory.* Chicago, University of Chicago Press.

Mark, A. (1979). Indigenous grasslands of New Zealand. In: *Ecosystems of the world: heathlands and related shrubs: discriptive studies* . Elservier Scientific Publishing Co., Oxford. 361-410.

May, R. M. (1974). General introduction. In: *Ecological stability* . Usher, M. B.; Williamson, M.H. Chapman and Hall Ltd., London. 1-16.

May, R. M. (1975). Patterns of species abundance and diversity. In: *Ecology and evolution of communities* . Cody, M. L.; Diamond J.M. (eds). Harvard University Press, Massachusetts. 81-120.

Mayr, E. (1965). The nature of colonization in birds. In: *The genetics of colonizing species* . Baker, H. G. ; Stebbins, G.L. (eds). Academic Press, New York. 29-47.

McNaughton, S.J. (1979a). Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist* 113: 691-703.

McNaughton, S.J. (1979b). Grassland-herbivore dynamics. In: *Serengeti: studies of ecosystem dynamics in a tropical savanna* . Sinclair, A. R. E.; Norton-Griffiths, M. University of Chicago Press, Chicago. 46-81.

McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. *Oikos* 40: 329-336.

McNeill, S.; Prestidge, R.A. (1982). Plant nutritional strategies and insect herbivore community dynamicsf. *5th International Symposium: Insect-Plant Relationships*, Wageningen. 225-235.

McNeill, S.; Southwood, T.R.E. (1978). The role of nitrogen in the development of insect/plant relationships. In: *Biochemical aspects of plant and animal coevolution* . Harborne. 77-98.

Meads, M. (1990). *Forgotten fauna*. Wellington, DSIR Publishing.

Michaux, J.; Cheylan, G.; Croset, H. (1990). Of mice and men. In: *Monographic Biologicae.* Dumont, H.J.; Werger, M.J.A. Dordrecht, Kluwer Academic Publishers.

Miller, G. R. (1979). Quantity and quality of the annual production of shoots and flowers by *Calluna vulgaris* in north-east Scotland. *Journal of Ecology* 67: 109-129.

Miller, G. R.; Watson, A. (1978). Heather productivity and its relevance to the regulation of red grouse populations. In: *Production ecology of some British moors and montane grasslands* . Heal, O. W.;. Perkins, D.F. Springer-Verlag, Berlin. 277-285.

Moore, N. W. (1962). The heaths of Dorset and their conservation. *Journal of Ecology* 50: 369-.

Moran, V. C.; Southwood, T.R.E. (1982). The guild composition of arthropod communities in trees. *Journal of Animal Ecology* 51: 289-306.

Morrison, G. D. (1938). The heather beetle (*Lochmaea suturalis*). *As cited in: The Heather Beetle (Lochmaea suturalis): its biological control* . Cameron, A. E.; Hardy, J.W.; Bennett, A.H. Petworth, British field sports society.

Mound, L.A.; Walker, A.K. (1987). Fauna of New Zealand Number 1 Terebrantia (Insecta: Thysanoptera). DSIR Wellington New Zealand.

Murdoch, W.W.; Evans, F.C.; Peterson, C.H. (1972). Diversity and pattern in plants and insects. *Ecology* 53: 819-829.

Newsome, A. E.; Noble, I.R. (1986). Ecological and physiological characters of invading species. In: *Ecology of biological invasions* . Groves J.J.; Burdon, R. H. (eds). Cambridge University Press, Cambridge. 1-21.

Odum, E. P. (1969). The strategy of ecosystem development. *Science* 164: 262-.

Ohgushi, T. (1992). Resource limitation on insect herbivore populations. In: *Effects of resource distribution on animal-plant interactions* . Hunter, M.D; Ohgushi, T.; Price, P.W. (eds). Academic Press Limited, London. 505.

Orians, G. H. (1974a). Unifying concepts in ecology. *First International congress of ecology, The Hague*, The Netherlands, Dr W. Junk B. V. 139-149.

Orians, G. H. (1974b). An evolutionary approach to the study of ecosystems. In: *Structure, functioning and management of ecosystems*. eds: van Dobben, W.H.; Gradwell, G.R. The Hague. 198-200.

Orians, G. H. (1975). Diversity, stability and maturity in natural ecosystems. In: *Unifying concepts in ecology* . Van Dobben, W. H.; Lowe-McConnell, R.H. Dr W. Junk B.V. The Hague. 139-150.

Owen, D. F. (1980). How plants may benefit from animals that eat them. *Oikos* 35: 230-235.

Owen, D. F. (1981). Mutualism between grasses and grazers: an evolutionary hypothesis. *Oikos* 36: 376-378.

Peterson, C. G.; Stevenson, R.J. (1992). Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology* 73(4): 1445-1461.

Pielou, E. C. (1975). Ecological Diversity. Pubs. John Wiley & Sons. New York. 165 pages.

Pielou, E. C. (1977). *Mathematical Ecology*. New York, John Wiley and sons.

Pimm, S. L. (1979). Complexity and stability: another look at MacArthur's original hypothesis. *Oikos* 33: 351-357.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature* 307: 321-325.

Power, M. E.; Marks, J.C. (1992). Variation in the vulnerability of prey to different predators: community-level consequences. *Ecology* 73(6): 2218-2223.

Prestidge, R. A.; McNeill, S. (1981). The role of nitrogen in the ecology of grassland Auchenorryncha. In: *British Ecological Society Symposium: Nitrogen as an ecological factor*, Oxford, Oxford Press. 257-281.

Pyle, R.; Bentzien, M.; Opler, P. (1981). Insect conservation. *Annual Review of Entomology* 26: 233-258.
Rausher, M. D. (1983). Ecology of host selection behaviour in phyptophagous insects. In: *Variable plants and herbivores in natural and managed systems* . Denno, R. F.; McClure, M.S. New York, Academic press, Chapter 7.

Robertson, R.A.; Davies, G.E. (1954). Quantities of plant nutrients in heather ecosystems. *Journal of applied Ecology* 2: 211-219.

Rogers, G. (1990). Conservation status and furture of North Island tussock grasslands. *Forest Research Institute Contract Report* FWE 90/34 (unpubl.). 15 p.

Rogers, G. (1991). Rates of shrub invasion of North Island tussock grasslands. *Forest Research Institute Report.* (unpublished).

Rogers, G. (1994). The rise and demise of *Calluna vulgaris* on the Pouakai Range, Egmont National Park. *New Zealand Botanical Society Newsletter* 38: 7-9.

Rogers, G. M.; Leathwick, J.R. (1994). North Island seral tussock grasslands. 2: Autogenic succession: change of tussock grassland to shrubland. *New Zealand Journal of Botany* 32: 287-303.

Roy, J. (1990). In search of the characteristics of plant invaders. In: *Monographic Biologicae*. Dumont, H.J.; Werger, M.J.A. Dordrecht, Kluwer Academic Publishers.

Safriel, U.H.; Riffe, U. (1983). Universal correlates of colonizing ability. In: *The ecology of animal movement.*: Swingland, I.R.; Greenwood, P.J. (eds). Oxford. Clarendon Press.

Samways, M. J. (1994). *Insect conservation biology.* London, Chapman and Hall.

Scanlan, A. B. (1961). *Egmont. The sory of a mountain.* Wellington, AD & AW Reed.

Schultz, J. C. (1992). Factoring natural enemies into plant tissue availibility to herbivores. In: *Effects of resource distribution on animal-plant interactions* . Hunter, M.D; Ohgushi, T.; Price, P.W. (eds). Academic Press Limited, London. 505-.

Scott, J. A.; French, N.R.; Leetham, J.W. (1979). In: *Perspectives in Grassland ecology.* N. R. French. Springer, New York. 89-106.

Scriber, J. M. (1984). Host plant suitability. In: *Chemical ecology of insects* . Bell, W. J.; Carde, R.T. 159-202.

Sheehan, P. J. (1981). Effects on community and ecosystem sturcture and dynamics. In: *Effects of pollutants at the ecosystem level* . Sheehan, P.J.; Miller, D.R.; Butler, G.C. ; Bourdeau, P.H. (eds). John Wiley & Sons. London. 51-99.

Slocombe, D. S. (1993). Implementing ecosystem based management. *BioScience* 43(9): 612-621.

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365.

Southwood, T. R. E. (1978). *Ecological methods with particular reference to the study of insect populations.* Oxford, Chapman & Hall.

Southwood, T. R. E. (1987). The concept and nature of the community. In: *Organisation of communities, past and present* . Gee, J. H. R.; Giller, P.S. Blackwell Scientific Publications, Aberystwyth. 3-27.

Southwood, T. R. E.; Brown, V.K.; Reader, P.M. (1979). The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society* 12(4): 327-348.

Southwood, T. R. E.; Moran, V.C.; Kennedy, C.E.J. (1982). The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* 51: 635-649.

Stenseth, N. C. (1979). Where have all the species gone ? On the nature of extinction and the Red Queen hypothesis. *Oikos* 39: 171-178.

Stinson, C. S. A.; Brown, V.K. (1983). Seasonal changes in the architecture of natural plant communities and its relevance to insect herbivores. *Oecologia* 56: 67-69.

Strauss, S. Y. (1991). Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* 72(2): 543-558.

Strong, D. R.; Lawton, J.H.; Southwood, T.R.E. (1984). *Insects on plants: community patterns and mechanisms.* Oxford, Blackwell Scientific Publications.

Sykora, K. V. (1990). History of the impact of man on the distribution of plant species. In: *Monographic Biologicae.* Dumont, H.J.; Werger, M.J.A. (eds). Dordrecht, Kluwer Academic Publishers.

Syrett, P.; Partridge, T.; Smith, L (1994). Biological control of heather, *Calluna vulgaris*, with the heather beetle, *Lochmaea suturalis.* Manaaki Whenua - Landcare Research (unpublished).

Systat. (1992). *Systat: statisics version 5.2 edition.* Evanston Illnois: Systat, Tnc. 724.

Thiele, H. U. (1977). *Carabid beetles in their environments.* Berlin, Springer-Verlag.

Thorsteinson, A. J. (1960). Host selection in phytophagous insects. *Annual Review of Entomology* 5: 193-218.

Townsend, C. R. (1991). Exotic species management and the need for a theory of invasion ecology. *New Zealand Journal of Ecology* 15(1): 1-3.

Tyler, G.; Gullstrand, C.; Holmquist, K.; Kjellstrand, A. (1973). Primary production and distribution of organic matter and metal elements in two heath ecosystems. *Journal of Ecology* 61: 251-268.

Uetz, G. W. (1991). Habitat structure and spider foraging. In: *Habitat Structures: the physical arrangement of objects in space*. Bell, S. S.; McCoy, E.D.; Mushinsky, H.R. (eds). Chapman and Hall, London. 1st edition, 325-348.

Usher, M.B. (1986). Invasibility and wildlife conservation: invasive species on nature reserves. *Philosophical Transactions of the Royal Society of London* 314(b): 695-710.

Van der Meijden, E.; Van Bemmelen, M.; Kooi, R.; Post, B.J. (1984). Nutritional quality and chemincal defence in the ragwort-cinnabar moth interaction. *Journal of Animal Ecology* 53: 443-453.

Van der Meijden, E. (1990). Herbivory as a trigger for growth. *Functional Ecology* 4: 597-598.

Van Schaick Zillesen, P. G.; Brunsting, A.M.H. (1983). Capacity for flight and egg production in *Lochmaea suturalis* (Coleoptera, Chrysomelidae). *Netherlands Journal of Zoology* 33(3): 266-275.

Verkaar, H. J. (1988). Are defoliators beneficial for their host plants in terrestrial ecosystems - a review? *Acta Bot. Neerl.* 37(2): 137-152.

Waloff, N. (1987). Observations on the heather beetle *Lochmaea suturalis* (Thomson) (Coleoptera, Chrysomelidae) and its parasitoids. *Journal of Natural History* 21: 545-556.

Walton, A.; Walton, T. (1994). *New Zealand agrichemical and plant protection manual.* Wellington.

Wardle, P. (1991). *Vegetation of New Zealand.* Cambridge, Cambridge University Press.

Watt, A. S. (1955). Bracken versus heather, a study in plant sociology. *Journal of Ecology* 43: 490 - 506

Watt, J. C. (1980). Notes on pitfall trapping on Headlong Peak, Mount Aspiring National Park. *New Zealand Entomologist,* 7(2): 184-191.

Webb, N. R. (1989a). The invertebrates of heather and heathland. *Botanical Journal of the Linnean Society* 101: 307-312.

Webb, N. R. (1989b). Studies on the invertebrate fauna of fragmented heathland in Dorset, UK, and the implications for conservation. *Biological Conservation* 47: 153-165.

Webb, N. R.; Clarke, R.T.; Nicholas, J.T. (1984). Invertebrate diversity on fragmented *Calluna-* heathland: effects of surrounding vegetation. *Journal of Biogeography* 11: 41-46.

Webb, N. R.; Hopkins, P.J. (1984). Invertebrate diversity on fragmented *Calluna* heathland. *Journal of Applied Ecology* 21: 921-933.

Welch, D.; Miller, G.R.; Legg, C.J. (1990). Plant dispersal in moorlands and heathlands in Britain. In: *Species dispersal in agricultural habitats* . Bunce, R. G. A.; Howard, D.C. NERC (ITE) Publications, 117-132.

White, E.G. (1978). Energetics and consumption rates of alpine grasshoppers (Orthoptera : Acrididae) in New Zealand. *Oecologia* 36: 259-261.

White, E. G. (1987). Ecological time frames and the conservation of grassland insects. *New Zealand Entomologist* 10: 146-152.

Whittaker, R. H. (1969). Evolution of diversity in plant communities. *Diversity and stability in ecological systems symposium*, Upton, New York, Brookhaven National Laboratory. 178-196.

Whittaker, R. H. (1974). The design and stability of plant communities. *First international congress of ecology, The Hague*, The Netherlands, Dr W. Junk, The Hague. 169-185.

Whittaker, R. H. (1975). The design and stability of some plant communities. In: *Unifying concepts in ecology*. Dobben, W.H.; Lowe-McConnell, R.H. Dr W. Junk, The Hague. 169-181.

Whittaker, R. H.; Woodwell, G.M. (1972). Evolution of natural communities. In: *Ecosystem Structure and Function*. J. A. Wiens. Oregon State University Press, Cornwallis.

Williams, K.; Keys, H. (eds). (1993). Heather control workshop. *Proceedings of the second heather control workshop*, Turangi, N.Z., Department of Conservation.

Wilson, F. (1965). Biological control and the genetics of colonizing species. In: *The genetics of colonizing species* . Baker, H.G.; Stebbins, G.L. (eds). Academic Press, New York. 307-329.

Wodzicki, K. (1965). The status of some exotic vertebrates in the ecology of New Zealand. In: *The genetics of colonizing species*. Baker, H.G.; Stebbins, G.L. Academic Press, New York. 425-460.

APPENDICES

Appendix 1: Plant species lists.

Appendix 1a: Plant Architecture measuring.

Appendix 2: Common and rare invertebrate lists.

Appendix 3: Lists of taxa by site (means and total abundances).

APPENDIX 1 Plant species list

Presence of the plant species at a site is denoted by an " *". A "!" indicates that there was only one seedling or small plant.

Sites 1 = tussock/*Calluna*; 2 = tussock; 3 = *Dracophyllum/Calluna*; 4 = *Dracophyllum*; 5 = *Gleichenia*; 6 = *Gleichenia/Calluna*
7 = manuka; 8 = manuka/*Calluna*; 9 = flax; 10 = flax/*Calluna*; 11 = *Calluna*

Plant species	1	2	3	4	5	6	7	8	9	10	11
Aciphylla squarrosa	*	*		*							*
Agrostis setifolia			*	*							*
Agrostis castellana							*		*		
Agrostis capillaris	*	*			*					*	
Anthoxanthum oduratum	*	*							*		
Aristotelia fruticosa							*				
Aristotelia serrata							*				
Astelia sp.							*				
Baumea tenax										*	
Blechnum pennamarina									*	*	
Blechnum capense									*		
Blechnum fluviatile									*		
Calluna vulgaris	*	!	*	!		*	!	*	!	*	*
Carex echinata					*	*					
Carex geminata					*	*					
Carpha alpina					*	*					
Cassina fulvida			*	*							
Celmisia gracilenta	*	*	*	*		*					
Celmisia glandulosa	*		*	*							
Celmisia spectablis			*	*							
Centaurea erythroea									*		
Chionochloa rubra	*	*	*	*						*	*
Chrysanthemum leucanthemum									*		
Cirsium vulgare									*		
Cladonia sp.							*				

Plant species	1	2	3	4	5	6	7	8	9	10	11
Coprosma "microcarpa"			*	*							
Coprosma cheesmanii	*	*									
Coprosma perpusilla	*	*									
Coprosma robusta							*				
Coprosma foetidissima							*				
Coprosma australis							*				
Coprosma rhamnoides							*	*	*		
Coprosma parviflora								*			
Coprosma propinqua									*		
Cotonia cotoneaster							*				
Crepis capillaris									*		
Cyathodes empetifolia										*	
Dracophyllum recurvum			*	*							
Dracophyllum filiformis	*			*		*		*			*
Dracophyllum subulatum		*	*	*	*					*	
Dracophyllum longifolium							*				
Drosera binata										*	
Elymus rectisetus		*									
Empodisma minus					*						
Epilobium sp.		*									
Euphrasia cuneata		*	*	*							
Gaultheria depressa							*			*	
Geranium microphyllum	*										
Gleichenia dicarpa					*	*					
Griselina littoralis								*			
Hebe sp.			*	*							
Hebe stricta							*	*	*		*
Hierachloe redolens			*						*	*	*
Holcus lanatus	*	*							*		*
Hypochaeris radicata		*	*	*					*		
Juncus sarophonus										*	

Plant species	1	2	3	4	fi5ve	6	7	8	9	10	11
Lachnogrostis filiforme	*	*	*				*				
Leontodon taraxacoides	*										
Lepidosperma australe			*		*	*			*		
Leptospermum scoparium						*	*	*	*	*	*
Leucopogon fraseri	*	*									
Leucopogon colensoi	*										
Libocedrus bidwillii							*	*			
Lotus peduculatus									*	*	
Luzula sp.		*									
Lycopodium fastigiatum	*	*	*	*							
Melicope simplex							*				
Muelenbeckia axillaris	*							*			
Mycelis muralis									*		
Mrysine divaricata							*				
Nothofagus solandri var. cliffoides								*			
Ourisa vulcanica	*	*									
Pentachondra pumila	*	*	*	*							
Phormium tenax						*	*	*	*	*	*
Phyllocladus alpinus					*		*	*			
Pimelea prostrata			*	*							
Pinus contorta	*	*									
Poa colensoi	*		*	*							
Poa cita	*	*	*					*	*		*
Podocarpus halli							*				
Polystichum sylvaticum									*		
Prunella vulgaris									*		
Pseudopanax simplex							*				
Pseudopanax arborea								*			
Pseudopanax colensoi							*		*	*	
Pseudowintera colorata							*				
Pteridium esculentum									*		
Pterostyus banksii								*		*	*

Plant species	1	2	3	4	5	6	7	8	9	10	11
Racomitrium lanuginosum	*	*	*	*							
Ranunculus repens									*		
Ranunculus acris									*		
Rhytidosperma sedifolia	*	*	*		*	*	*			*	
Rubus schmidelioides							*				
Sarothamnus scoparius									*		
Scirpus sp.										*	
Schoenus pauciflora					*		*				
Schoenus sp.					*						
Senecio jacobaea									*		
Thelymitra sp.	*	*									
Uncinia rupestris											*
Viola cunninghamii	*	*					*		*	*	
Wahlenbergia pygmaea	*	*	*	*							

APPENDIX 1a Example of the Plant Architectural Score Sheet.

Basically were there is a set of numbered box options, one chooses the approperate box, circling it, boxes with-out nubers are for measurements made by the observer. Each sections number total is calculated by adding all numbers choosen or measured, this is a sub total, in approperate boxes, the plants gross score is the total of the sub totals.

Plant		#	

STRUCTURE

interlinked	0 (none)	1 (few)	2 (some)	3 (many)	4 (very)

Neighbouring plants

branches errect	1	separate	1		
horrizontal	2	touching	2	surrounded	+5
1/2 & 1/2	3	interlinked	3	number	1-4

sub total

STEM & BUSH

one main stem	1	height	
many	2	radius	
number		height of first branch(s)	

number of 1^0 branches		>90 90 60-90 30-60 <30
number of 2^0 branches		>90 90 60-90 30-60 <30
number of 3^0 branches		>90 90 60-90 30-60 <30
		3 4 3 2 1

sub total

LEAVES

few spaced	1	few clustered	2	leaves found on which branch	
many spaced	3	many clustered	4	1st	2
heaps spaced	5	heaps clustered	6	1st & 2nd	4
leaves separate	1			many	6
leaves packed	2				

sub total

APPENDIX 2 Common and rare invertebrate lists

Mean number of common and rare taxa, their frequency in samples, and the Standard Error of the mean for each site. Following the "by site" tables, are listed, with mean number etc., the taxa that represent the common, or rare, groups. (f = number of times encountered; m = mean abundance over entire sampling period; Se = standard error of that mean).

SITE	common diptera			common coleoptera			common homoptera			common hemiptera		
	f	m	Se	f	m	Se	f	m	Se	f	m	Se
tussock/*Calluna*	94	3.6	0.72	29	4.17	1.68	18	1.5	0.23	9	3.89	2.1
tussock	113	3.5	0.48	31	4.39	1.75	34	3.03	0.59	14	5.43	3.5
Dracophyllum/Calluna	47	3.1	0.54	13	3.39	0.86	13	4.15	1.1	4	1.5	0.5
Dracophyllum	45	2.6	0.36	15	5.4	1.61	18	4.11	1.3	3	1.67	0.3
Gleichenia/Calluna	33	6.1	0.8	6	2	0.63	9	27.6	12.7	2	1	0.0
Gleichenia	22	3.5	2.29	1	2	-	14	6.5	2.8	1	1	-
manuka/*Calluna*	75	8.8	3.81	28	5.21	1.92	27	14.44	3.3	17	3.29	0.81
manuka	74	3.9	0.81	26	6.12	1.62	29	45.6	15.6	5	1.8	0.37
flax/*Calluna*	80	19.6	7.33	21	4.38	1.58	26	4.3	0.96	9	2.33	0.78
flax	103	5.0	0.79	53	24.3	7.39	27	3.26	0.53	3	1.67	0.33
Calluna	79	10.2	3.76	13	2.85	1.44	22	11.36	3.4	7	2.14	0.46

SITE	common orthoptera			common Arachnida			thysanoptera		
	f	m	Se	f	m	Se	f	m	Se
tussock/*Calluna*	20	4.1	1.05	32	9.44	2.71	18	30.8	15.4
tussock	25	10.0	3.71	25	16.24	5.19	11	3.18	0.75
Dracophyllum/Calluna	6	5.67	1.76	20	6.7	1.51	9	31.4	24.0
Dracophyllum	7	4.14	1.93	24	5.54	1.15	3	1.67	0.67
Gleichenia/Calluna	1	1	-	14	8.93	3.36	4	10.5	7.88
Gleichenia	-	-	-	13	9.08	5.26	-	-	-
manuka/*Calluna*	6	3	1.06	41	5.44	1.17	11	130.2	93.6
manuka	3	2	0.58	29	5.66	1.20	6	3.8	2.09
flax/*Calluna*	7	4.57	1.09	37	7.68	1.41	10	40.2	28.4
flax	5	1.2	0.2	26	7.04	2.80	8	3.5	0.87
Calluna	2	2	1	39	17.6	1.41	7	44.7	20.3

SITE	rare diptera			rare coleoptera			rare homoptera		
	f	m	Se	f	m	Se	f	m	Se
tussock/*Calluna*	9	1.89	0.77	4	2	0.71	-	-	-
tussock	14	1.29	0.16	10	1.6	0.4	3	1.33	0.33
Dracophyllum/Calluna	7	2.29	0.84	4	1	0.0	2	1	0.0
Dracophyllum	6	1.17	0.17	6	1.27	0.17	2	1	0.0
Gleichenia/Calluna	12	1	0.0	4	1.75	0.75	-	-	-
Gleichenia	3	3.33	1.2	3	1	0.0	-	-	-
manuka/*Calluna*	18	1.94	0.44	22	2.36	0.39	5	1	0.0
manuka	5	2.4	0.75	21	1.67	0.37	2	1.5	0.5
flax/*Calluna*	8	2	0.16	9	2.3	0.97	2	1	0.0
flax	20	1.25	0.40	21	4.76	1.51	3	1.33	0.33
Calluna	29	2.59	0.52	8	3.87	2.46	1	1	0.0

SITE	rare hemiptera			rare Arachnida		
	f	m	Se	f	m	Se
tussock/*Calluna*	1	7	-	22	4.4	1.25
tussock	1	1	-	23	5.7	20.3
Dracophyllum/Calluna	2	1	0.0	21	7.2	3.14
Dracophyllum	-	-	-	19	5.9	3.06
Gleichenia/Calluna	-	-	-	6	4.67	2.87
Gleichenia	-	-	-	7	1.43	0.297
manuka/*Calluna*	2	1.5	0.34	14	2.64	0.65
manuka	6	1.6	0.6	20	3.45	0.69
flax/*Calluna*	1	2.0	-	19	4.42	0.96
flax	2	2.5	1.5	22	2.27	1.48
Calluna	-	-	-	16	2.87	0.69

Taxa that comprise the common and rare groups
(No. = the number of times a taxon was encountered)

Common Diptera

taxa	No.	mean abundance	Std. error
Phoridae	68	16.07	6.03
Sciaridae	107	5.36	0.79
Mycetophilidae	77	15.7	7.48
Chironomidae	123	9.17	1.25
Chloropidae	34	3.85	0.75
Dolichopodidae	27	2.56	0.33
Empididae	26	1.96	0.28
Muscidae	43	3.65	1.10
Ephydridae	22	1.96	0.45
Tachinidae	31	2.65	0.62
Tipulidae	56	2.84	0.42
Tephritidae	28	2.89	1.02
Cecidomyiidae	35	1.71	0.19
Ceratopogonidae	29	2.66	0.38
Psychodidae	29	1.89	0.37
Trichoceridae	30	3.23	0.69

Rare Diptera

taxa	No.	mean abundance	Std. error
Drosophilidae	13	1.23	0.17
Cryptophagidae	2	2.5	1.5
Sarcophagidae	9	4.0	1.29
Asilidae	7	2.43	0.97
Calliphoridae	16	2.13	0.55
Sphaeroceridae	15	1.73	0.44
Lonchopteridae	9	1.22	0.15
Therevidae	2	2.0	1.0
Bibionidae	5	1.4	0.4

Agromyzidae	15	1.87	0.38
Anisopodidae	5	1.4	0.4
Sryphidae	6	2.0	0.82
Heleomyzidae	1	1.0	-
Pipunculidae	7	2.0	0.66
Simulidae	8	2.38	0.87
Scatopsidae	3	2.33	1.33
Stratiomyidae	2	1	-
Piophilidae	1	1	-
Lauxaniidae	1	1	-
Blephariceridae	1	1	-
Asteiidae	1	1	-
Anthemyiidae	2	1	0.0

Common Coleoptera

taxa	No.	mean abundance	Std. error
Carabidae	43	21.53	8.45
Staphylinidae	51	9.22	3.39
Curculionidae	46	2.84	0.57
Lathridiae	34	10.38	1.93
Pselaphididae	22	1.77	0.26
Chrysomellidae	23	1.52	0.24
Scarabaeidae	17	9.53	3.95

Rare Coleoptera

taxa	No.	mean abundance	Std. error
Colydiidae	3	2	0.0
Scolytidae	3	1	0.0
Cicindelidae	3	2.33	0.88
Elateridae	12	3.08	0.94
Scydmaenidae	8	1.5	0.5

Anobiidae	2	1	0.0
Dermestidae	1	1	-
Byrrhidae	1	1	-
Corylophidae	5	2	1.2
Attelabidae	2	1	0.0
Throscidae	2	1	0.0
Nitidulidae	2	1	0.0
Cerambycidae	7	1.43	0.20
Coccinellidae	8	8.25	3.64
Melyridae	9	3.33	0.62
Helodidae	7	1.29	0.18
Trogossitidae	10	1.2	0.13
Palacridae	1	1	-
Anisotomidae	5	6.4	3.76
Melandryidae	5	2	0.63
Hydrophilidae	2	1	0.0
Cleridae	1	1	-
Amphizoidae	2	2	1
Bruchidae	1	1	-
Mordellidae	1	1	-
Anthribidae	1	1	1.5
Inopeplidae	4	1.75	0.75
Cucujidae	2	1.5	0.5

Common Homoptera

taxa	No.	mean abundance	Std. error
Aphididae	44	2.34	0.32
Cicadellidae	49	3.39	0.85
Delpaecidae	14	1.21	0.16
Coccoidea	51	3.86	0.51
Psyllidae	79	28.8	6.14

Rare Homoptera

taxa	No.	mean abundance	Std. error
Meenoplidae	2	1	0.0
Machaerotidae	6	1.33	0.21
Cicadidae	4	1	0.0
Cercopidae	3	1.33	0.33
Flugoridae	3	1	0.0
Cixidae	1	1	-
Eurymelidae	1	1	-

Common Hemiptera

taxa	No.	mean abundance	Std. error
Miridae	21	5.0	2.46
Lygaeidae	32	2.66	0.50
Reduviidae	21	1.95	0.28

Rare Hemiptera

taxa	No.	mean abundance	Std. error
Largidae	6	2.83	0.95
Enicocephalidae	1	1	-
Coreidae	2	1	0.0
Pentatomidae	3	1	0.0
Nabidae	3	2.67	0.88
Mesoveliidae	1	1	-
Pyrrhocoridae	1	1	-
Dipsocoridae	1	1	-

Common Orthoptera

taxa	No.	mean abundance	Std. error
Rhaphidophoridae	24	2.63	0.40
Stenopelmatidae	21	4.0	0.90
Gryllidae	23	11.3	4.0
Acrididae	14	3.93	0.82

Arachnidae

These were identified only as morpho-species, and as such a list of ‘my’ names is of no additional infomation. However, there were 9 common taxa of spider, with a mean abundance of 6.7 with an Se of 2.03, While rare taxa are represented by 44 morpho-species with a mean abundance of 4.67 and Se of 2.53

APPENDIX 3 Lists of taxa by site (their mean and total abundances).

site one (tussock/*Calluna*) (total 1437= individuals)
ENCOUNTERS = the number of times this family was found from the 12 sampling times.
SE-MEAN = the standard error of the mean. * = no SE possible.

FAMILY or ORDER	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	7	4.00	28.000	1.57
Staphylinidae	8	3.12	25.000	1.03
Curculionidae	5	1.400	7.000	0.245
Lathrididae	1	1.00	1.000	*
Pselaphidae	2	1.500	3.000	0.500
Chrysomelidae	3	1.333	4.000	0.333
Colydiidae	1	2.0000	2.000	*
Scarabaeidae	3	17.7	53.000	15.7
Scolytidae	1	1.0000	1.000	*
Cicindalidae	2	2.0	5.000	1.50
Aphididae	4	1.0000	4.000	0.0000
Cicadellidae	5	2.000	10.000	0.548
Delphaecidae	2	1.500	3.000	0.500
Coccoidae	5	1.600	8.000	0.600
Psyllidae	2	1.0000	2.000	0.0000
Miridae	4	6.00	24.000	4.67
Lygaeidae	5	2.200	11.000	0.800
Largidae	1	7.0000	7.000	*
Rhaphidophoridae	5	1.800	9.000	0.374
Stenopelmatidae	5	2.000	10.000	0.548
Gryllidae	6	6.83	41.000	2.93
Acrididae	4	5.50	22.000	2.06
Phoridae	7	10.14	71.000	4.96
Sciaridae	17	3.824	65.000	0.928
Mycetophilidae	10	3.500	35.000	0.778
Chironomidae	11	6.55	72.000	4.75
Chloropidae	3	1.333	4.000	0.333
Dolichopodidae	4	2.000	8.000	0.408
Empididae	3	1.333	4.000	0.333
Muscidae	6	1.667	10.000	0.667
Ephydridae	3	3.00	9.000	2.00
Tachinidae	3	3.667	11.000	0.882
Tipulidae	7	2.429	17.000	0.649
Drosophilidae	1	1.0000	1.000	*
Cryptophagidae	1	1.0000	1.000	*
Tephritidae	7	1.571	11.000	0.297
Cecidomyiidae	7	1.286	9.000	0184
Ceratopogonidae	1	1.0000	1.000	*
Psychodidae	3	3.00	9.000	0.00
Trichoceridae	2	1.0000	2.000	0.0000
Sarcophagidae	2	1.500	3.000	0.500
Asilidae	1	8.0000	8.000	*
Calliphoridae	1	1.0000	1.000	*
Sphaeroceridae	2	1.0000	2.000	0.0000
Bibionidae	1	1.0000	1.000	*
Formicidae	12	19.	239.000	8.16
Thysanoptera	18	30.8	554.000	15.4
Blattodea	2.250	.629	9.000	

site 2 (tussock) (total individuals =1559).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	4	3.75	15.000	2.10
Staphylinidae	10	3.300	33.000	0.943
Curculionidae	3	1.333	4.000	0.333
Lathrididae	1	1.0000	1.000	*
Pselaphidae	5	1.800	9.000	0.374
Chrysomelidae	6	2.167	13.000	0.833
Colydiidae	1	2.0000	2.000	*
Scarabaeidae	2	30.5	61.000	24.5
Cicindelidae	1	2.000	2.000	*
Elateridae	1	1.0000	1.000	*
Scydmaenidae	3	2.33	7.000	1.33
Anobiidae	1	1.0000	1.000	*
Dermestidae	1	1.0000	1.000	*
Byrrhidae	1	1.0000	1.000	*
Attelabidae	1	1.0000	1.000	*
Aphididae	7	3.00	21.000	1.53
Cicadellidae	12	3.000	36.000	0.929
Delphaecidae	4	1.0000	4.000	0.0000
Coccoidae	8	4.62	37.000	1.55
Psyllidae	3	1.667	5.000	0.667
Meenoplidae	1	1.0000	1.000	*
Machaerotidae	1	2.0000	2.000	*
Cicadidae	1	1.0000	1.000	*
Miridae	7	9.00	63.000	7.01
Lygaeidae	5	2.200	11.000	0.800
Largidae	1	1.0000	1.000	*
Reduviidae	2	1.0000	2.000	0.0000
Rhaphidophoridae	1	2.0000	2.000	*
Stenopelmatidae	4	3.25	13.000	1.31
Gryllidae	14	15.29	214.000	6.34
Acrididae	6	3.50	21.000	1.15
Tettigonidae	1	2.0000	2.000	*
Phoridae	9	4.56	41.000	1.94
Sciaridae	16	6.94	111.000	2.72
Mycetophilidae	12	2.833	34.000	0.806
Chironomidae	8	2.125	17.000	0.611
Chloropidae	9	4.44	40.000	1.71
Dolichopodidae	7	2.571	18.000	0.649
Empididae	8	2.750	22.000	0.620
Muscidae	7	2.000	14.000	0.378
Ephydridae	5	1.600	8.000	0.600
Tachinidae	4	2.250	9.000	0.479
Tipulidae	9	4.11	37.000	1.09
Drosophilidae	1	1.0000	1.000	*
Tephritidae	7	3.29	23.000	1.13
Cecidomyiidae	6	2.000	12.000	0.516
Ceratopogonidae	2	5.50	11.000	4.50
Psychodidae	3	1.0000	3.000	0.0000
Trichoceridae	1	2.0000	2.000	*
Sarcophagidae	1	2.0000	2.000	*
Asilidae	3	1.0000	3.000	0.0000
Lonchopteridae	2	1.0000	2.000	0.0000

Therevidae	1	3.0000	3.000	*
Bibionidae	1	1.0000	1.000	*
Agromyzidae	3	1.333	4.000	0.333
Anisopodidae	1	1.0000	1.000	*
Asteiidae	1	1.0000	1.000	*
Formicidae	15	32.9	494.000	13.1
Thysanoptera	11	3.182	35.000	0.749
Blattodea	6	3.33	20.000	1.17
Lauxaniidae	1	1.0000	1.000	*

site 3 (*Dracophyllum/Calluna*) (total individuals =872.000).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	5	4.80	24.000	1.50
Staphylinidae	2	5.00	10.000	4.00
Curculionidae	1	3.0000	3.000	*
Pselaphidae	4	1.500	6.000	0.500
Scarabaeidae	2	2.50	5.000	1.50
Elateridae	1	1.0000	1.000	*
Scydmaenidae	2	1.0000	2.000	0.000
Throscidae	1	1.0000	1.000	*
Scaphidiidae	3	4.333	13.000	0.882
Aphididae	4	2.75	11.000	1.03
Cicadellidae	3	1.333	4.000	0.333
Delphaecidae	1	1.0000	1.000	*
Coccoidae	3	9.33	28.000	2.73
Psyllidae	2	5.00	10.000	2.00
Meenoplidae	1	1.0000	1.000	*
Cicadidae	1	1.0000	1.000	*
Miridae	1	1.0000	1.000	*
Lygaeidae	3	1.667	5.000	0.667
Largidae	1	1.0000	1.000	*
Enicocephalidae	1	1.0000	1.000	*
Rhaphidophoridae	2	2.50	5.000	1.50
Stenopelmatidae	3	8.33	25.000	2.73
Acrididae	1	4.0000	4.000	*
Phoridae	6	4.33	26.000	1.96
Sciaridae	6	2.333	14.000	0.955
Mycetophilidae	7	2.714	19.000	0.993
Chironomidae	7	2.571	18.000	0.997
Chloropidae	5	4.40	22.000	2.01
Dolichopodidae	2	1.500	3.000	0.500
Empididae	2	3.50	7.000	2.50
Muscidae	2	10.00	20.000	9.00
Tachinidae	4	2.250	9.000	0.250
Tipulidae	4	1.0000	4.000	0.000
Drosophilidae	1	2.0000	2.000	*
Tephritidae	2	1.500	3.000	0.500
Asilidae	1	3.0000	3.000	*
Calliphoridae	2	4.00	8.000	3.00
Therevidae	1	1.0000	1.000	*
Anisopodidae	1	1.0000	1.000	*
Syrphidae	1	1.0000	1.000	*
Formicidae	10	26.2	262.000	10.0
Thysanoptera	9	31.4	283.000	24.0

Blattodea	3	1.0000	3.000	0.000

site 4 (*Dracophyllum*) (total individuals = 709.000).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	5	5.80	29.000	2.27
Staphylinidae	3	3.67	11.000	2.19
Curculionidae	7	5.86	41.000	3.10
Scarabaeidae	1	20.000	20.000	*
Elateridae	1	1.0000	1.000	*
Throscidae	1	1.0000	1.000	*
Nitidulidae	1	1.0000	1.000	*
Cerambycidae	2	1.500	3.000	0.500
Scaphidiidae	3	2.0000	6.000	0.0000
Inopeplidae	1	1.0000	1.000	*
Aphididae	3	2.000	6.000	0.577
Cicadellidae	4	2.000	8.000	0.577
Delphaecidae	2	1.0000	2.000	0.0000
Coccoidae	3	7.33	22.000	3.48
Psyllidae	6	6.00	36.000	3.44
Machaerotidae	1	1.0000	1.000	*
Cicadidae	1	1.0000	1.000	*
Miridae	2	1.500	3.000	0.500
Lygaeidae	1	2.0000	2.000	*
Stenopelmatidae	5	4.40	22.000	2.68
Acrididae	2	3.50	7.000	2.50
Phoridae	5	5.00	25.000	1.76
Sciaridae	6	3.17	19.000	1.05
Mycetophilidae	5	3.400	17.000	0.927
Chironomidae	8	1.250	10.000	0.164
Chloropidae	3	5.33	16.000	1.86
Empididae	2	1.500	3.000	0.500
Muscidae	3	2.67	8.000	1.20
Ephydridae	1	1.0000	1.000	*
Tachinidae	2	3.00	6.000	2.00
Tipulidae	3	1.0000	3.000	0.0000
Drosophilidae	1	1.0000	1.000	*
Tephritidae	3	1.0000	3.000	0.0000
Cecidomyiidae	3	1.333	4.000	0.333
Trichoceridae	1	1.0000	1.000	*
Asilidae	1	1.0000	1.000	*
Calliphoridae	1	2.0000	2.000	*
Sphaeroceridae	1	1.0000	1.000	*
Syrphidae	1	1.0000	1.000	*
Heleomyzidae	1	1.0000	1.000	*
Formicidae	8	44.6	357.000	15.0
Thysanoptera	3	1.667	5.000	0.667

site 5 (*Gleichenia*) (total individuals = 242.000).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Curculionidae	1	2.0000	2.000	*
Helodidae	1	1.0000	1.000	*
Trogossitidae	1	1.0000	1.000	*
Cucujidae	1	1.0000	1.000	*
Aphididae	1	4.0000	4.000	*

Cicadellidae	5	4.00	20.000	1.82
Coccoidea	1	1.0000	1.000	*
Psyllidae	6	10.67	64.000	6.31
Miridae	1	1.0000	1.000	*
Phoridae	3	2.00	6.000	1.00
Sciaridae	2	1.0000	2.000	0.000
Chironomidae	5	15.00	75.000	7.67
Chloropidae	2	1.500	3.000	0.500
Muscidae	2	4.00	8.000	3.00
Ephydridae	1	1.0000	1.000	*
Tachinidae	1	1.0000	1.000	*
Tipulidae	3	1.667	5.000	0.667
Tephritidae	1	29.000	29.000	*
Ceratopogonidae	2	2.500	5.000	0.500
Lonchoopteridae	1	1.0000	1.000	*
Agromyzidae	1	4.0000	4.000	*
Pipunculidae	1	5.0000	5.000	*
Formicidae	2	1.0000	2.000	0.000

site 6 (*Gleichenia/Calluna*) (total individuals = 445).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Staphylinidae	1	1.0000	1.000	*
Curculionidae	1	2.0000	2.000	*
Lathrididae	1	1.0000	1.000	*
Chrysomelidae	1	1.0000	1.000	*
Scarabaeidae	2	3.50	7.000	1.50
Elateridae	1	1.0000	1.000	*
Coccinellidae	1	1.0000	1.000	*
Melyridae	1	4.0000	4.000	*
Helodidae	1	1.0000	1.000	*
Aphididae	1	3.0000	3.000	*
Cicadellidae	2	1.500	3.000	0.500
Psyllidae	6	40.3	242.000	17.0
Lygaeidae	1	1.0000	1.000	*
Reduviidae	1	1.0000	1.000	*
Acrididae	1	1.0000	1.000	*
Phoridae	1	5.0000	5.000	*
Sciaridae	2	2.00	4.000	1.00
Mycetophilidae	1	1.0000	1.000	*
Chironomidae	7	8.71	61.000	3.04
Chloropidae	1	1.0000	1.000	*
Dolichopodidae	2	2.500	5.000	0.500
Empididae	2	1.0000	2.000	0.0000
Muscidae	5	1.400	7.000	0.245
Ephydridae	1	1.0000	1.000	*
Tachinidae	2	2.00	4.000	1.00
Tipulidae	3	3.0000	9.000	0.0000
Tephritidae	2	1.500	3.000	0.500
Cecidomyiidae	1	1.0000	1.000	*
Ceratopogonidae	3	3.33	10.000	1.20
Calliphoridae	2	1.0000	2.000	0.0000
Sphaeroceridae	3	1.0000	3.000	0.0000
Bibionidae	1	1.0000	1.000	*
Agromyzidae	2	1.0000	2.000	0.0000

Syrphidae	1	1.0000	1.000	*
Pipunculidae	1	1.0000	1.000	*
Simulidae	2	1.0000	2.000	0.0000
Formicidae	2	3.50	7.000	2.50
Blattodea	4	10.50	42.000	7.88

site 7 (manuka) (total individuals = 1884).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	4	14.50	58.000	7.03
Staphylinidae	2	5.500	11.000	0.500
Curculionidae	9	2.000	18.000	0.471
Lathrididae	3	14.33	43.000	7.06
Pselaphidae	2	1.500	3.000	0.500
Chrysomelidae	3	2.000	6.000	0.577
Scarabaeidae	4	5.25	21.000	2.66
Scolytidae	1	1.0000	1.000	*
Elateridae	2	5.00	10.000	3.00
Scydmaenidae	1	1.0000	1.000	*
Anobiidae	1	1.0000	1.000	*
Corylophidae	1	1.0000	1.000	*
Attelabidae	1	1.0000	1.000	*
Cerambycidae	3	1.0000	3.000	0.0000
Coccinellidae	1	1.0000	1.000	*
Melyridae	2	3.00	6.000	2.00
Helodidae	2	1.500	3.000	0.500
Trogossitidae	3	1.333	4.000	0.333
Scaphidiidae	2	3.00	6.000	2.00
Anisotomidae	1	1.0000	1.000	*
Hydrophilidae	1	1.0000	1.000	*
Inopeplidae	1	1.0000	1.000	*
Aphididae	3	1.333	4.000	0.333
Cicadellidae	3	1.0000	3.000	0.0000
Coccoidea	0	3.900	39.000	0.900
Psyllidae	3	98.2	1277.000	29.0
Cercopidae	2	1.500	3.000	0.500
Miridae	3	2.333	7.000	0.333
Lygaeidae	1	1.0000	1.000	*
Largidae	1	4.0000	4.000	*
Reduviidae	1	1.0000	1.000	*
Coreidae	2	1.0000	2.000	0.0000
Pentatomidae	1	1.0000	1.000	*
Nabidae	1	1.0000	1.000	*
Rhaphidophoridae	3	2.000	6.000	0.577
Phoridae	5	5.40	27.000	2.86
Sciaridae	8	4.62	37.000	1.38
Mycetophilidae	5	3.20	16.000	1.32
Chironomidae	7	8.53	145.000	3.09
Chloropidae	1	1.0000	1.000	*
Dolichopodidae	1	3.0000	3.000	*
Empididae	2	1.0000	2.000	0.0000
Muscidae	2	1.0000	2.000	0.0000
Ephydridae	1	1.0000	1.000	*
Tachinidae	1	1.0000	1.000	*
Tipulidae	4	1.250	5.000	0.250

Tephritidae	2	1.0000	2.000	0.0000
Cecidomyiidae	4	1.500	6.000	0.289
Ceratopogonidae	9	2.222	20.000	0.401
Psychodidae	7	1.286	9.000	0.184
Trichoceridae	5	1.600	8.000	0.600
Calliphoridae	1	3.0000	3.000	*
Agromyzidae	1	2.0000	2.000	*
Pipunculidae	1	1.0000	1.000	*
Simulidae	1	1.0000	1.000	*
Scatopsidae	1	5.0000	5.000	*
Formicidae	4	2.750	11.000	0.854
Thysanoptera	6	3.83	23.000	2.09
Blattodea	3	1.000	3.000	0.000

site 8 (manuka/*Calluna*) (total individuals = 2930.000).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	4	22.0	88.000	10.9
Staphylinidae	5	2.600	13.000	0.812
Curculionidae	9	2.444	22.000	0.603
Lathrididae	1	3.0000	3.000	*
Pselaphidae	3	3.67	11.000	1.33
Chrysomelidae	4	1.0000	4.000	0.000
Colydiidae	1	2.0000	2.000	*
Scarabaeidae	3	2.000	6.000	0.577
Elateridae	1	7.0000	7.000	*
Scydmaenidae	2	1.0000	2.000	0.000
Corylophidae	1	1.0000	1.000	*
Nitidulidae	1	1.0000	1.000	*
Melyridae	2	4.00	8.000	1.00
Helodidae	1	1.0000	1.000	*
Trogossitidae	4	1.250	5.000	0.250
Scaphidiidae	1	3.0000	3.000	*
Phalacridae	1	1.0000	1.000	*
Anisotomidae	3	3.33	10.000	1.45
Malandryidae	2	2.00	4.000	1.00
Hydrophilidae	1	4.0000	4.000	*
Inopeplidae	1	4.0000	4.000	*
Cucujidae	1	2.0000	2.000	*
Aphididae	4	1.750	7.000	0.250
Cicadellidae	6	10.50	63.000	6.00
Coccoidea	3	1.0000	3.000	0.0000
Psyllidae	14	22.64	317.000	4.85
Machaerotidae	2	1.0000	2.000	0.0000
Cercopidae	1	1.0000	1.000	*
Flugoridae	1	1.0000	1.000	*
Eurymelidae	1	1.0000	1.000	*
Miridae	3	2.000	6.000	0.577
Lygaeidae	6	4.50	27.000	2.20
Largidae	1	2.0000	2.000	*
Reduviidae	8	2.875	23.000	0.549
Pentatomidae	2	1.0000	2.000	0.0000
Nabidae	1	3.0000	3.000	*
Mesoveliidae	1	1.0000	1.000	*
Pyrrhocoridae	1	1.0000	1.000	*

Rhaphidophoridae	6	3.00	18.000	1.06
Phoridae	7	45.7	320.000	39.5
Sciaridae	11	4.09	45.000	1.67
Mycetophilidae	3	4.33	13.000	2.03
Chironomidae	14	11.86	166.000	4.04
Dolichopodidae	3	1.333	4.000	0.333
Empididae	2	2.0000	4.000	0.0000
Muscidae	1	1.0000	1.000	*
Ephydridae	5	2.80	14.000	1.56
Tachinidae	3	1.0000	3.000	0.0000
Tipulidae	6	4.17	25.000	2.40
Drosophilidae	2	1.0000	2.000	0.0000
Cryptophagidae	1	4.0000	4.000	*
Tephritidae	4	1.750	7.000	0.479
Cecidomyiidae	2	1.0000	2.000	0.0000
Ceratopogonidae	5	2.400	12.000	0.748
Psychodidae	4	2.001.00	8.000	
Trichoceridae	5	7.00	35.000	2.05
Calliphoridae	2	1.500	3.000	0.500
Sphaeroceridae	2	4.00	8.000	3.00
Bibionidae	1	1.0000	1.000	*
Agromyzidae	3	2.67	8.000	1.67
Anisopodidae	1	1.0000	1.000	*
Pipunculidae	1	1.0000	1.000	*
Simulidae	1	3.0000	3.000	*
Scatopsidae	1	1.0000	1.000	*
Stratiomyidae	1	1.0000	1.000	*
Piophilidae	1	1.0000	1.000	*
Anthemyiidae	1	1.0000	1.000	*
Formicidae	6	20.50	123.000	9.41
Thysanoptera	11	130.2	1432.000	93.6
Blattodea	1	1.0000	1.000	*

site 9 (flax) (total individuals = 2116.000).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	7	92.9	650.000	44.3
Staphylinidae	16	22.6	361.000	10.2
Curculionidae	7	3.86	27.000	1.61
Lathrididae	17	14.18	241.000	2.84
Pselaphidae	2	1.0000	2.000	0.0000
Chrysomelidae	4	1.250	5.000	0.250
Scolytidae	1	1.0000	1.000	*
Elateridae	1	1.0000	1.000	*
Corylophidae	3	4.00	12.000	1.73
Cerambycidae	1	2.0000	2.000	*
Coccinellidae	6	10.67	64.000	4.48
Trogossitidae	3	3.67	11.000	1.33
Scaphidiidae	4	6.75	27.000	3.01
Melandryidae	2	2.50	5.000	1.50
Cleridae	2	1.0000	2.000	0.0000
Amphizoidae	1	1.0000	1.000	*
Inopeplidae	1	1.0000	1.000	*
Aphididae	10	3.300	33.000	0.684
Cicadellidae	2	1.0000	2.000	0.0000

Coccoidea	11	4.18	46.000	1.05
Psyllidae	4	1.750	7.000	0.750
Machaerotidae	2	1.500	3.000	0.500
Cicadidae	1	1.0000	1.000	*
Reduviidae	3	1.667	5.000	0.333
Nabidae	1	4.0000	4.000	*
Dipsocoridae	1	1.0000	1.000	*
Rhaphidophoridae	2	1.500	3.000	0.500
Stenopelmatidae	2	1.0000	2.000	0.0000
Gryllidae	1	1.0000	1.000	*
Phoridae	9	6.33	57.000	4.10
Sciaridae	17	9.00	153.000	3.35
Mycetophilidae	15	4.80	72.000	1.88
Chironomidae	15	7.53	113.000	1.61
Chloropidae	2	1.0000	2.000	0.0000
Dolichopodidae	2	1.500	3.000	0.500
Empididae	2	1.0000	2.000	0.0000
Muscidae	3	2.000	6.000	0.577
Ephydridae	2	1.0000	2.000	0.0000
Tachinidae	3	1.333	4.000	0.333
Tipulidae	8	2.875	23.000	0.718
Drosophilidae	2	1.0000	2.000	0.0000
Cecidomyiidae	8	2.625	21.000	0.596
Ceratopogonidae	3	3.67	11.000	1.45
Psychodidae	7	2.286	16.000	0.644
Trichoceridae	7	3.71	26.000	1.77
Calliphoridae	4	2.75	11.000	1.75
Sphaeroceridae	4	2.250	9.000	0.750
Lonchopteridae	3	1.333	4.000	0.333
Agromyzidae	2	2.00	4.000	1.00
Anisopodidae	1	3.0000	3.000	*
Syrphidae	1	1.0000	1.000	*
Pipunculidae	1	4.0000	4.000	*
Scatopsidae	1	1.0000	1.000	*
Lauxaniidae	1	1.0000	1.000	*
Formicidae	3	5.00	15.000	2.65
Thysanoptera	8	3.500	28.000	0.866

site 10 (flax/*Calluna*) (total individuals = 2510.000).

FAMILY	ENCOUNTERS	MEAN	TOTAL	SE-MEAN
Carabidae	3	2.67	8.000	1.67
Staphylinidae	2	1.500	3.000	0.500
Curculionidae	2	2.00	4.000	1.00
Lathrididae	8	7.50	60.000	3.94
Pselaphidae	1	1.0000	1.000	*
Chrysomelidae	1	1.0000	1.000	*
Scolytidae	4	3.75	15.000	1.38
Elateridae	2	6.00	12.000	4.00
Cerambycidae	1	2.0000	2.000	*
Melyridae	1	1.0000	1.000	*
Helodidae	1	2.0000	2.000	*
Trogossitidae	2	1.0000	2.000	0.0000
Melandryidae	1	1.0000	1.000	*
Bruchidae	1	1.0000	1.000	*

Aphididae	6	1.500	9.000	0.224
Cicadellidae	2	2.0000	4.000	0.0000
Coccoidea	6	1.833	11.000	0.477
Psyllidae	2	7.33	88.000	1.71
Fulgoridae	1	1.0000	1.000	*
Cixidae	1	1.0000	1.000	*
Lygaeidae	8	2.500	20.000	0.866
Largidae	1	2.0000	2.000	*
Reduviidae	1	1.0000	1.000	*
Rhaphidophoridae	5	4.00	20.000	1.14
Stenopelmatidae	2	6.00	12.000	3.00
Phoridae	8	18.0	144.000	14.2
Sciaridae	1	7.36	81.000	2.88
Mycetophilidae	2	81.2	974.000	44.8
Chironomidae	7	14.82	252.000	4.79
Chloropidae	5	7.80	39.000	2.73
Dolichopodidae	1	3.0000	3.000	*
Empididae	2	1.500	3.000	0.500
Muscidae	4	5.25	21.000	2.95
Ephydridae	1	2.0000	2.000	*
Tachinidae	2	1.0000	2.000	0.0000
Tipulidae	4	1.250	5.000	0.250
Cecidomyiidae	3	1.333	4.000	0.333
Ceratopogonidae	2	2.0000	4.000	0.0000
Psychodidae	2	1.500	3.000	0.500
Trichoceridae	4	4.00	16.000	2.38
Calliphoridae	2	1.0000	2.000	0.0000
Agromyzidae	2	1.500	3.000	0.500
Anisopodidae	1	1.0000	1.000	*
Syrphidae	1	2.0000	2.000	*
Pipunculidae	1	1.0000	1.000	*
Anthemyiidae	1	1.0000	1.000	*
Psilidae	1	1.0000	1.000	*
Formicidae	8	29.1	233.000	14.0
Thysanoptera	10	40.2	402.000	28.4
Blattodea	6	4.83	29.000	1.56

site 11 (*Calluna*) (total inidividuals = 1839.000).

FAMILY	ENCOUNTER	MEAN	TOTAL	SE-MEAN
Carabidae	4	6.50	26.000	4.50
Staphylinidae	2	1.0000	2.000	0.0000
Curculionidae	1	1.0000	1.000	*
Lathrididae	2	1.500	3.000	0.500
Pselaphidae	3	1.333	4.000	0.333
Chrysomelidae	1	1.0000	1.000	*
Scarabaeidae	5	50.8	254.000	43.9
Elateridae	2	1.500	3.000	0.500
Helodidae	1	1.0000	1.000	*
Scaphidiidae	4	2.250	9.000	0.479
Anisotomidae	1	21.000	21.000	*
Bruchidae	1	3.0000	3.000	*
Mordellidae	1	1.0000	1.000	*
Anthribidae	1	1.0000	1.000	*
Aphididae	1	1.0000	1.000	*

Cicadellidae	4	2.75	11.000	1.75
Delphaecidae	5	1.400	7.000	0.400
Coccoidae	1	2.0000	2.000	*
Psyllidae	11	20.82	11 229.000	5.51
Fulgoridae	1	1.0000	1.000	*
Lygaeidae	2	3.500	7.000	0.500
Reduviidae	5	1.600	8.000	0.400
Gryllidae	2	2.00	4.000	1.00
Phoridae	8	46.4	371.000	34.7
Sciaridae	11	3.82	42.000	1.11
Mycetophilidae	6	4.50	27.000	2.35
Chironomidae	14	14.21	14 199.000	4.91
Chloropidae	3	1.0000	3.000	0.0000
Dolichopodidae	4	4.75	19.000	1.44
Empididae	1	2.0000	2.000	*
Muscidae	8	7.50	60.000	5.24
Ephydridae	2	2.00	4.000	1.00
Tachinidae	6	5.33	32.000	3.00
Tipulidae	5	5.20	26.000	2.48
Drosophilidae	5	1.400	7.000	0.400
Cecidomyiidae	1	1.0000	1.000	*
Ceratopogonidae	2	1.500	3.000	0.500
Psychodidae	3	2.33	7.000	1.33
Trichoceridae	5	1.400	7.000	0.400
Sarcophagidae	6	5.17	31.000	1.78
Asilidae	1	2.0000	2.000	*
Calliphoridae	1	2.0000	2.000	*
Sphaeroceridae	3	1.0000	3.000	0.0000
Lonchopteridae	3	1.333	4.000	0.333
Bibioonidae	1	3.0000	3.000	*
Agromyzidae	1	1.0000	.000	*
Syrphidae	1	6.0000	6.000	*
Pipunculidae	1	1.0000	1.000	*
Simulidae	4	3.25	13.000	1.65
Stratiomyidae	1	1.0000	1.000	*
Blephariceridae	1	1.0000	1.000	*
Formicidae	3	12.33	37.000	8.09
Thysanoptera	7	44.7	313.000	26.3
Blattodea	4	2.500	10.000	0.645