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Statistical models of invertebrate distribution on Macquarie Island: a tool to assess climate change and local human impacts

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Abstract Sub-Antarctic islands are good model systems in which to study the ecological effects of human impacts, particularly global climate change and alien species. Invertebrates form a central component of these ecosystems. We conducted a stratified survey of 69 sites on sub-Antarctic Macquarie Island and used logistic regression models to describe the distribution of 14 abundant invertebrate species. We also developed a statistical model of windspeed based on topography. The distributions of individual species were described by different combinations of aspect, altitude and vegetation type. Ordination of sites based on species composition showed strong effects of altitude and vegetation on invertebrate assemblages. The species distribution models provide a tool for detecting, monitoring and predicting effects of climate change and alien species on biota and ecosystem processes.

Introduction

Two human impacts could have a great effect on the terrestrial ecosystems of sub-Antarctic islands: climate change, and the introduction of alien species. Indeed, the combination of these two impacts could have greater, if not more complicated, effects. We consider the ecological effects of climate change and alien species on invertebrates, which are the major group of animals in terms of both species and biomass, forming key structural and functional elements of sub-Antarctic ecosystems. We present a tool for assessing the impact of climate change

and alien species on the distribution of invertebrates on Macquarie Island.

Sub-Antarctic islands as model systems for climate change

Four characteristics make sub-Antarctic islands good model systems for studying the ecological effects of climate change on biota, and together suggest that effects will be manifested earlier and more clearly at sub-Antarctic islands than in other terrestrial ecosystems. First, significant changes in climate have recently been observed at sub-Antarctic islands. For example, air temperatures at Marion and Macquarie Islands increased by about 1°C from 1950 to 1985 (Adamson et al. 1988; Smith and Steenkamp 1990; Smith 1992). Second, in the southern hemisphere, climate change is predicted to be greatest in the Antarctic and sub-Antarctic. Recent runs of general circulation models predict that temperature rises in the sub-Antarctic could be twice the global average (Smith 1993). Third, terrestrial systems of sub-Antarctic islands could be particularly sensitive to climate change because of the ecological properties of islands (e.g. susceptibility to invasion, and limits to migration; Peters and Darling 1985; Vitousek et al. 1995). Fourth, because of their relatively simple ecosystem structure, low species richness and discrete physical boundaries, sub-Antarctic terrestrial systems are also more tractable to study. For example, on Macquarie Island an almost complete inventory of plants and invertebrates has been made (Greenslade and Wise 1986; Greenslade 1990; Orchard 1993). Because of the properties given above, important processes can be isolated and understood, and this has considerable heuristic value for understanding the ecological effects of climate change elsewhere on the globe.

Direct effects of climate are most likely to be manifested through increases in temperature and associated changes in solar radiation and precipitation. The spatial distribution of individual species can be expected to

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change on islands as the spatial distribution of suitable habitat changes (e.g. along temperature gradients associated with altitude). Indeed, if the migration required exceeds the physical limits of the island then extinction will follow (Peters and Darling 1985; Vitousek et al. 1995). At the ecosystem level, Smith and Steenkamp (1992) outlined a scenario for the effects of elevated temperature and CO₂ on Prince Edward Island. They predicted that primary production will increase. Invertebrates play a vital role in this scenario because many species increase rates of nutrient mineralisation (Smith and Steenkamp 1990; Smith and Steenkamp 1992). The activity of invertebrates also increases with temperature leading to a concomitant increase in nutrient cycling, which is necessary for the higher level of primary production to be realised (Smith and Steenkamp 1992).

Impact of alien species

Sub-Antarctic islands are particularly vulnerable to the introduction of alien species. Indeed, in the sub-Antarctic, alien species have had a profound effect on ecosystem processes or on the native biota of some islands (Brothers and Copson 1988; Crafford 1990; Chapuis et al. 1994). Species invasions tend to have greater effects on islands than mainland systems (D'Antonio and Dudley 1995). This is thought to be because islands have fewer species in functional groups, have more keystone species, and lack some functional groups entirely, making it more likely that invading species can fill under-represented functional roles (Cushman 1995; Fownes 1995). On sub-Antarctic islands, invertebrates could play a significant role as either the invading species or as species affected by the invader (for some contemporary examples, see Crafford and Chown 1990; Chown and Smith 1993; Ernsting et al. 1995).

Climate change could also enhance the impact of alien species. Naturally dispersed organisms, particularly insects, plant propagules and microorganisms continually reach sub-Antarctic islands (e.g. Gressitt et al. 1961; Marshall 1996). Accidental introductions by humans probably account for an even greater number of immigration events (Pugh 1994). Most organisms are probably unable to survive the harsh conditions when they arrive. For many species that do survive, conditions may be close to their physiological limits, so their range may be restricted or their population growth may be slow. Some examples of recent invertebrate invasions include the diamondback moth, which probably dispersed naturally to Marion Island (Crafford and Chown 1990), and two terrestrial crustaceans, which were probably introduced accidentally to Macquarie Island (van Klinken and Green 1992; Richardson and Jackson 1995). All are currently restricted to small areas. Ameliorated conditions due to climate change could mean that these species are able to spread more widely and reach higher population densities, resulting in changes to the distribution of resident species and ecosystem processes. In

addition, Smith (1993) speculated that alteration of atmospheric circulation patterns due to climate change could increase natural immigration rates. Thus, the net result of climate change could be that more species will arrive and more of these will find favourable physiological conditions and be able to establish successfully.

Empirical distribution models

Data on the spatial distribution of species and communities provide a baseline for detecting, monitoring and predicting effects of human impacts on biota and ecosystem processes. However, the distribution of invertebrates cannot be directly determined at a useful spatial resolution without an unrealistic field survey effort. Strategically designed sample surveys provide a means of empirically estimating the distribution of species. This approach involves selecting sample sites along gradients of biologically important variables, which can include climatic variables (e.g. temperature, rainfall, solar radiation, or surrogates such as altitude and aspect), hydrological variables (e.g. topographic position, wetness), or a range of others (e.g. habitat structure, disturbance history). Correlative statistical models are then constructed from the significant variables (Austin and Heyligers 1989; Austin et al. 1994). Recently, this approach has been used widely for vegetation and vertebrates. For example, distribution models developed for tree and vertebrate species have been used to assess reserve adequacy (Austin and Heyligers 1989; Margules and Stein 1989), to contrast species conservation and resource use (Lindenmayer et al. 1991), and as baseline data against which to monitor change (Buckland and Elston 1993).

In this paper we construct correlative statistical models relating frequency of occurrence of invertebrate species to some major environmental variables on sub-Antarctic Macquarie Island and consider ways in which these models can be used as a tool to assess and monitor climate change and local human impacts.

Materials and methods

The island

Macquarie Island (54°30'S, 158°57'E) lies approximately 1500 km southeast of Tasmania and 1450 km north of Antarctica, 240 km north of the Antarctic convergence. It is an oceanic island that has never been connected to a land mass (Williamson 1988). The island is rectangular (approximately 5.5 km by 34 km) and runs roughly north to south (Fig. 1). It consists of an undulating plateau (150–300 m above sea level, highest point 433 m) bounded by scarps that fall to a narrow, low-lying coastal fringe. The island regularly experiences strong westerly winds. The climate is cool and moist and remarkably uniform because of the extensive surrounding oceans (e.g. mean monthly temperature 3.3–7.0°C, Selkirk et al. 1990).

For the purposes of this study we recognised six structurally different vegetation types (based on Selkirk et al. 1990): short grass (*Agrostis*, *Luzula*, *Uncinia*, *Festuca* dominated), tall grass (*Poa foliosa* dominated), herbfield (*Pleurophyllum hookeri* dominated), feldmark (gravel-covered bare ground with bryophytes and the

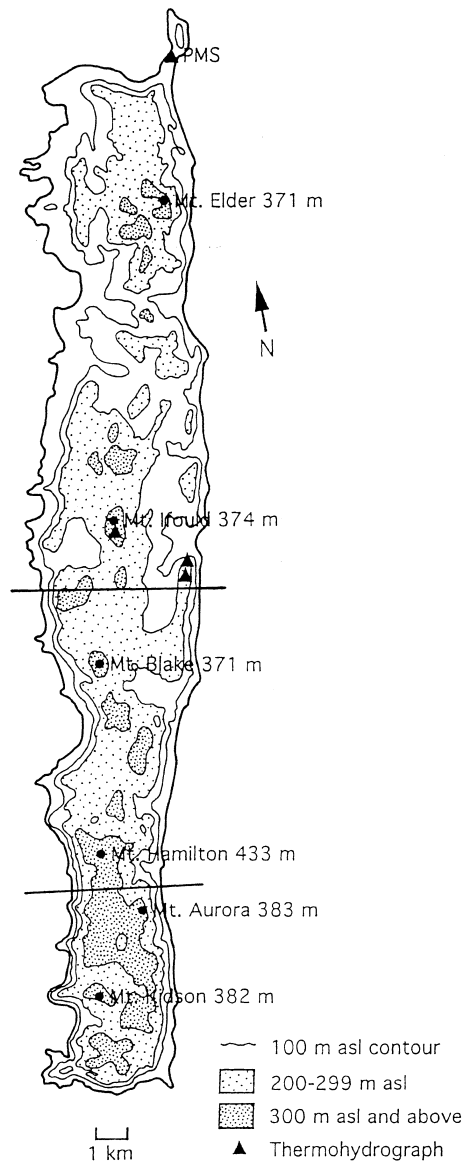


Fig. 1 Map of Macquarie Island showing altitude classes, the location of thermohydrographs, major mountains and permanent meteorological station (PMS). Boundaries between blocks are shown. Block 1 is to the north (asl above sea level)

cushion plant *Azorella macquariensis*), mire (water table close to surface, dominated by bryophytes and *Juncus*), and *Stilbocarpa* (*Stilbocarpa polaris* dominated).

The terrestrial, free-living invertebrate fauna comprises approximately 168 species, not including tardigrades or nematodes. Of these species, the mite fauna is the only component that is not well known. There are thought to be about 90 species of mites and 31 species of Collembola (Greenslade 1990). We consider neither of these groups in this paper. The fauna that we focus on here, the remaining 47 species, includes insects, oligochaete worms, molluscs, crustaceans and spiders.

Survey design

We used a stratified sample survey of 69 sites (Table 1). We sampled two aspects (east, west), two topographic positions (slopes and

drainage lines), four altitudes (0–100 m, 100–200 m, 200–300 m, over 300 m), and six vegetation types (described above). Ideally the design would have included replicated combinations of all of the above variables. However, not all vegetation types occurred at all four altitude classes, so we amalgamated altitude and vegetation to give a single variable ALTVEG, which had 12 categories (Table 1). We divided the island spatially from north to south into three blocks (Fig. 1). Within each block we replicated each ALTVEG combination twice, crossed with aspect (Table 1). We also recorded whether a site was a slope or a drainage line (topographic position) and dispersed topographic position among sites where possible. Some ALTVEG combinations did not exist in some blocks. We compensated by placing extra replicates of those combinations in other blocks (Table 1). However, we were not able to compensate for all missing combinations, giving a total of 69 sites.

At each site we placed three pitfall traps (3 cm diameter, 10 cm depth, glass) 3 m apart and one yellow-pan trap (10 by 13 by 5 cm). The pitfall traps were half-filled with ethylene glycol to which we added a few drops of detergent to break the surface tension. The yellow-pan traps were half-filled with water and had a few drops of detergent added. All traps were opened for 6 weeks from 1 February to 15 March 1994 (summer). We also conducted a timed hand search of 20 min at each site for four taxa (*Derocerus reticularis*, *Phrixognathus hamiltoni*, *Eudonia mawsoni*, *Oligochaeta*).

In addition to surveying invertebrates, we measured temperature and windspeed during the period of the survey. Windspeed was measured using a hand-held anemometer, twice at each survey site, during the period of the survey. For each measurement, a reading was taken every minute for 10 min at about 1.8 m above ground level. We measured temperature at four altitudes (0 m, 150 m, 250 m, 350 m) with thermohydrographs in standard meteorological screens. The 0-m station was installed within the compound of the permanent meteorological station; the 150-m and 250-m stations were positioned on the unnamed peak just south of Green Gorge hut, and the 350-m station was installed on Mt Ifould (Fig. 1). Temperature data were calibrated against data collected by the permanent meteorological station.

Data analysis

We derived statistical models for 14 taxa (11 species and 3 higher taxa), which were trapped at a minimum of 10 sites each. We also analysed species composition data, which included 20 taxa, using a multivariate approach.

Species distribution models

We chose to analyse presence/absence of species, rather than abundance, to avoid biases of pitfall trapping in vegetation types that are structurally different from each other (Greenslade 1964; Melbourne et al. 1997). We used logistic regression, a type of generalised linear model, because the data were binary (McCullagh and Nelder 1989; Nicholls 1989).

We tested for the significance of vegetation type, altitude, aspect, topographic position and block. Model fitting took place in two steps. First, the full model was fitted including all of the above variables. Each variable was then dropped one at a time. A variable was considered significant if the change in deviance associated with dropping that variable exceeded the chi-squared critical value, at $P < 0.05$, for the number of degrees of freedom that the variable conferred (McCullagh and Nelder 1989). Once the significant main effects were established we tested for the significance of first-order interactions between those variables. Unless both altitude and vegetation type were significant, the modelling process ended there. Otherwise, as we were unable to fit the interaction between altitude and vegetation type, we fitted a second model, which tested for the significance of ALTVEG instead of altitude and vegetation type. An example analysis summary table, showing both models, is presented in Table 2. The distribution of a given species was de-

Table 1 Survey design, showing combinations of altitude and vegetation type (ALTVEG), aspect (east, west), topography (*sl* slope, *dr* drainage) and block at which animals were collected. Some combinations did not exist in some blocks (*blank cells*)

	Block 1		Block 2		Block 3	
	East	West	East	West	East	West
ALTVEG						
1 Short grass 0–100 m	sl	sl	sl	sl	dr	sl
2 Tall grass 0–100 m	dr	sl × 2	sl	dr	sl	sl
3 Herbfield 0–100 m	sl and dr	sl and dr				
4 Mire 0–100 m	dr	dr	dr	dr	dr	dr
5 <i>Stilbocarpa</i> 0–100 m	sl	dr	sl	sl and dr	dr	dr
6 Short grass 100–200 m	dr	sl and dr	sl	sl and dr	sl	
7 Tall grass 100–200 m	sl	sl	sl	dr	dr	dr
8 Herbfield 100–200 m	sl	sl				
9 Mire 100–200 m	dr	dr	dr	dr	dr	dr
10 Short grass 200–300 m	dr	dr	sl	dr	sl	sl
11 Feldmark 200–300 m	sl	sl	dr	dr	sl	sl
12 Feldmark 300 m +	sl	sl	sl	sl	sl	sl

scribed by the final model, which included only the significant variables.

Multivariate analysis of species composition

All multivariate analyses were performed using PATN 3.3 (Belbin 1994). The effect of environmental variables on species composition was investigated as follows (Belbin 1991a; Clarke 1993). First, the species composition of each survey site was compared with all other sites using the Czekanowski association measure (equivalent to the Bray-Curtis measure for presence-absence data). Second, hybrid multi-dimensional scaling (HMDS) was used to ordinate sites based on the association values (Faith et al. 1987; Belbin 1991b; Belbin 1994). A cut-value of 0.90 was used for HMDS based on inspection of a histogram of the association values (Belbin 1994). A two-dimensional solution was obtained from 100 random starts using a stopping rule of a maximum of 50 iterations or a minimum stress difference of 0.005. Although the stress value of the two-

dimensional solution was high (0.23), an inspection of the three-dimensional solution (stress = 0.15) suggested that the two-dimensional solution adequately represented the main features of the ordination. Third, to determine whether there were significant effects of vegetation type, altitude, aspect, or topographic position, we calculated group centroids and performed permutation tests. To perform permutation tests, we used the analysis of similarity (ANOSIM) test described by Clarke (1993) but used the metric association values rather than ranks, as described by Belbin (1994). This latter approach provides a test with more statistical power than the test based on rank (Belbin 1994). Fourth, we classified species into groups of co-occurring species using the association measure “Two-Step” (Austin and Belbin 1982) and the flexible-UPGMA clustering algorithm (Sneath and Sokal 1973; Belbin 1994). We calculated the affinity of each species group with each ALTVEG class as $P/(E \times S)$, where E is the number of survey sites in the ALTVEG class, S is the number of species in the species group, and P is the number of cells in the $E \times S$ matrix where a presence was recorded.

Windspeed and temperature

We used multiple regression to model hand-held windspeed, which we measured on 74 occasions, and included most of the sites in the survey. We tested for the significance of aspect, altitude, region, and two covariates: PMS windspeed (windspeed at the permanent meteorological station) and PMS wind direction (wind direction at the meteorological station). PMS windspeed accounted for temporal variation in windspeed, thus allowing us to compare sites that were measured at different times. Even though the wind direction was consistently from the west and northwest, as a precaution we tested for an effect of wind direction using records from the permanent station as a covariate. We included region in all models because readings were taken by walking transects across the island from east to west (transects equal regions). Usually we were only able to take windspeeds for one region per day. Since readings taken on the same day were likely to be more similar to each other than those taken on different days, we included region in the model to account for this structure in the data.

Model fitting took place as follows. First, the full model was fitted including all of the above variables. Each variable was dropped from the model one at a time and then replaced if significant. P -values were calculated from variance ratios and a variable was considered significant when $P < 0.05$. We then tested for the significance of interactions between significant variables and covariates. Predicted windspeed across the island was described by the final model, which included only the significant variables, as

Table 2 Summary of logistic regression analysis. The example given here is for *Eudonia mawsoni* (larvae). Model fitting took place in two steps. First (model 1), the significant main effects were established. When both altitude and vegetation type were significant we fitted a second model (model 2), which tested for the significance of ALTVEG (*df* degrees of freedom)

Variable	<i>df</i>	Deviance change	<i>P</i>
Model 1			
Altitude	3	14.38	0.005
Vegetation type	5	40.45	0.001
Aspect	1	5.74	0.02
Topography	1	1.46	0.2
Block	2	2.68	0.3
Residual	56		
Total	68		
Model 2			
ALTVEG	11	49.08	0.001
Aspect	1	5.30	0.03
Topography	1	1.42	0.2
Block	2	2.08	0.3
Residual	53		
Total	68		

well as region. Departures of the data from model assumptions were determined by viewing histograms of the data, plots of residuals versus fitted values, and plotting residuals as a normal order probability plot. We logged the response variable (hand-held windspeed) and PMS windspeed because the variance was found to increase systematically with windspeed.

Temperature data collected from the four thermohydrographs were calibrated against the permanent meteorological station temperature data. We calculated the difference between the temperature at 0 m and each height (150 m, 250 m, 350 m) every 6 h for the period 15 February to 15 March 1994 and then calculated the mean and standard error of these differences.

Fig. 2 Distribution models for 11 invertebrate taxa on Macquarie Island, from logistic regression. The probability of occurrence of each species/taxon in six vegetation types, *Stilbocarpa* (*St*), short grass (*SG*), tall grass (*TG*), herbfield (*Hf*), mire (*Mi*), feldmark (*Fm*), two aspects, east (*E*), west (*W*), and four altitude classes, 0–100 m (0–1), 100–200 m (1–2), 200–300 m (2–3), above 300 m (3+). Shading indicates altitude, see panel of *H. antarctica* for key. Those species for which the combined variable ALT-VEG was significant have lines joining the points, showing the effect of altitude within vegetation type. Only the significant variables describing the distribution of a taxon are presented, except for aspect, which is presented for all taxa. Standard errors are shown. Five species for which the probability of occurrence was significantly different between aspects can be identified because their error bars do not overlap

Results

Species distribution

Twenty-two taxa were captured by pitfall and yellowpan trapping. Excluding mites and Collembola, a further 21 species known to occur on Macquarie Island were not caught in our survey. For 7 species of the 22 taxa captured, few individuals were caught. Distribution models

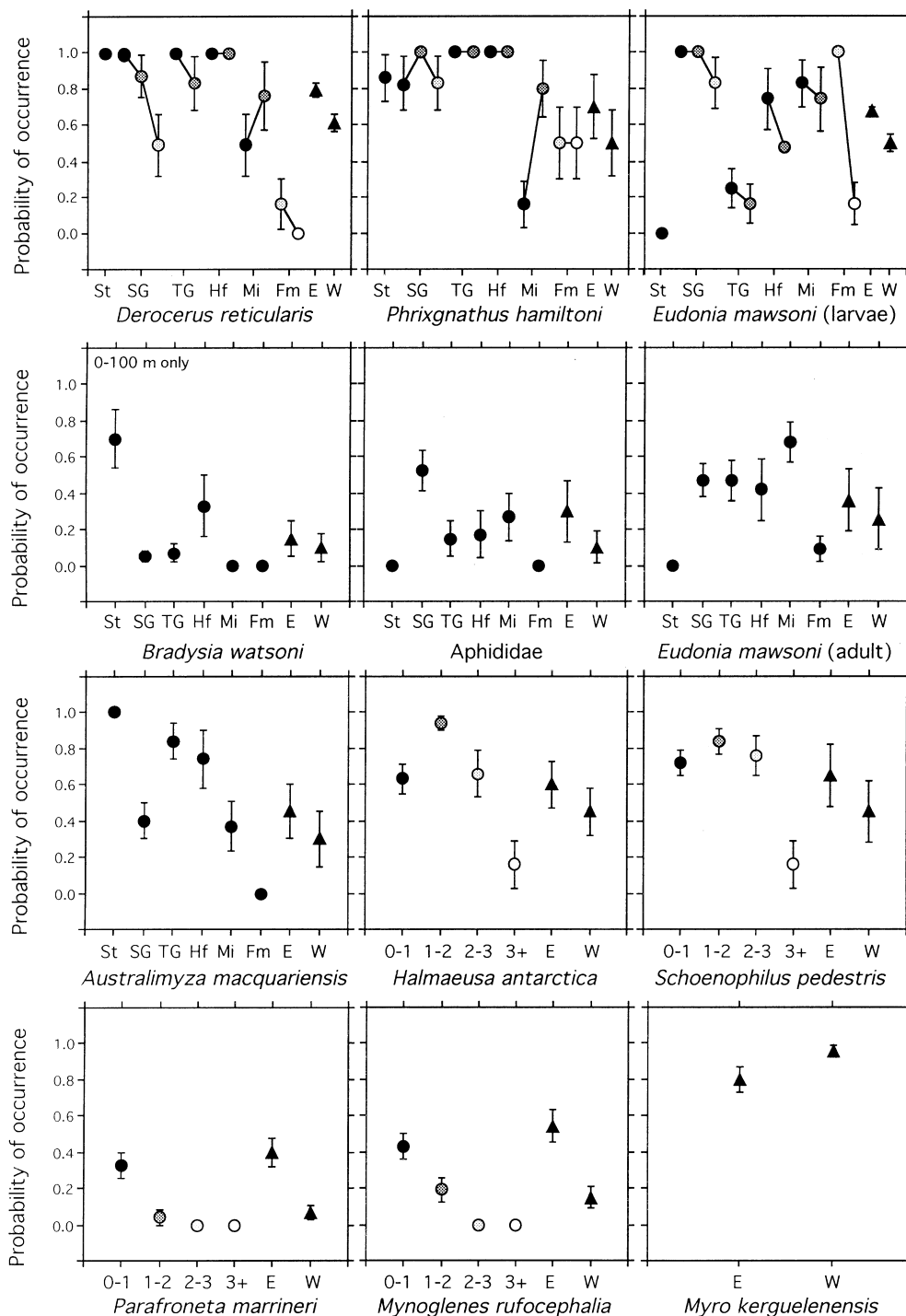


Table 3 Logistic regression analysis for 14 invertebrate taxa: *P* values for environmental variables. ALTVEG was fitted (model 2) instead of altitude and vegetation type (*Veg.*) when both altitude and vegetation type were significant (see Table 2). For these cases

we have also given *P* values for model 1 in parentheses. The empirical distribution model for each taxon contained only those variables that were significant at $P < 0.05$ (*Topo.* topographic position)

	Species	Altitude	Veg.	Block	ALTVEG	Aspect	Topo.
Mollusca	<i>Derocerus reticularis</i>	(0.05)	(0.05)	0.6	0.001	0.02	0.5
	<i>Phrixgnathus hamiltoni</i>	(0.06)	(0.003)	0.3	0.01	0.7	0.3
Hemiptera	Aphididae	0.6	0.01	0.2		0.1	0.08
Thysanoptera	<i>Physemothrips chrysodermus</i>	0.6	0.07	0.7		0.9	0.1
Coleoptera	<i>Halmaeus antarctica</i>	0.08	0.1	0.8		0.2	0.4
Diptera	<i>Psychoda</i> spp.	0.2	0.7	0.2		0.8	0.7
	<i>Bradysia watsoni</i> ^a	(0.001)	0.003	0.4		0.5	0.2
	<i>Schoenophilus pedestris</i>	0.03	0.1	0.008		0.6	0.4
	<i>Australimyza macquariensis</i>	0.2	0.05	0.2		0.4	0.4
Lepidoptera	<i>Eudonia mawsoni</i> (adult)	0.5	0.03	0.002		0.4	0.6
	<i>Eudonia mawsoni</i> (larvae)	(0.005)	(0.001)	0.3	0.001	0.03	0.2
Araneae	<i>Myro kerguelensis</i>	0.7	0.5	0.1		0.001	0.6
	<i>Parafroneta marrineri</i>	0.006	0.7	0.3		0.005	0.1
	<i>Mynoglenes rufocephalia</i>	0.05	0.9	0.6		0.003	0.3
Oligochaeta	<i>Lumbricina</i>	0.1	0.9	0.4		0.2	0.8

^a *B. watsoni* was never caught above 0–100 m, so ALTVEG was not fitted. The final model was restricted to 0–100 m and included vegetation type only

were not developed for these species because there were too few data but they were included in the multivariate analysis. They were: *Austrosocus insularis* (Psocoptera), *Stenomalius sulcithorax* (Coleoptera), *Erioptera pilipes*, *Coelopella curvipes*, *Icaridion nigrifrons*, *Ephydrella macquariensis* (Diptera), and *Antarctopria latigaster* (Hymenoptera).

The distribution of most taxa was described by one or more of altitude, aspect and vegetation type (Table 3, Fig. 2). The distributions of three taxa (Aphididae, *Eudonia mawsoni* adults, *Australimyza macquariensis*) were determined by vegetation type alone (Fig. 2). For these taxa, feldmark vegetation was consistently not favoured; otherwise we can generalise little other than to say that different species were associated with different vegetation types.

The distributions of two species were determined by altitude alone (Fig. 2; *Halmaeus antarctica*, *Schoenophilus pedestris*) and the distributions of two other species were determined by altitude and aspect (Fig. 2; *Parafroneta marrineri*, *Mynoglenes rufocephalia*). Generally, the probability of occurrence for these species decreased with increasing altitude. The two spider species (*P. marrineri* and *M. rufocephalia*) did not occur above 200 m. *H. antarctica* and *S. pedestris* were both most likely to occur at 100–200 m. The distributions of four species (*D. reticularis*, *Phrixgnathus hamiltoni*, *Eudonia mawsoni* larvae, *Bradysia watsoni*) were determined by a combination of vegetation type and altitude (Fig. 2). *B. watsoni* was found only at 0–100 m and was more likely to occur in *Stilbocarpa* and herbfield. For *D. reticularis*, *P. hamiltoni* and *E. mawsoni* larvae there was a difference among vegetation types but, generally, the

probability of occurrence also declined with altitude. However, there were some exceptions. For example, the snail *P. hamiltoni* was more likely to occur in mire sites between 100 and 200 m than at mire sites below 100 m.

Four species were more likely to occur at east-facing sites than at west-facing sites (Fig. 2; *D. reticularis*, *E. mawsoni* larvae, *P. marrineri*, *M. rufocephalia*). All of the remaining eight taxa in Fig. 2 were also more likely to occur at east-facing sites, although in these cases there was not a significant difference between east and west. One species, the spider *Myro kerguelensis* was more likely to occur at west- than east-facing sites. *M. kerguelensis* was the most widely distributed species and had the highest probability of any species at sites above 300 m (Fig. 2).

Two species showed spatial trends in their occurrence from north to south (Fig. 3a). Adults of the moth *E. mawsoni* were most likely to occur in the northernmost third of the island and least likely to occur in the southernmost third of the island, and the fly *S. pedestris* was also least likely to occur in the southern third of the island.

The distribution of three taxa was not predicted by any of the variables that we tested for (Fig. 3b; *Physemothrips chrysodermus*, *Psychoda* spp., Oligochaeta). For these taxa, the probability of occurrence was the same for all sites, regardless of vegetation type, altitude, aspect or topography.

Species composition

Ordination of sites based on species composition clearly showed the strong effects of altitude and vegetation on

invertebrate assemblages (Fig. 4) and these were confirmed by the permutation tests (altitude $P < 0.001$, vegetation type $P < 0.001$, ALTVEG $P < 0.001$). The effect was particularly strong for altitude alone (Fig. 4b), although the altitude signal may in part be strengthened by covariance with vegetation type. Nevertheless, the altitude signal remained strong within vegetation type (Fig. 4c). Two other patterns are evident from the ordination. First, differences in species composition between vegetation types were greater at sea level than at 100–200 m (Fig. 4c). Second, there was some suggestion that structural attributes of the vegetation may be important, with a gradient from tall vegetation types to low vegetation types (Fig. 4c; rank height as follows: *Stilbocarpa* > tall grass > herbfield > short grass > mire > feldmark). We did not find an effect of topographic position ($P = 0.577$) on species composition and although the ANOSIM test for aspect was close to significant ($P = 0.056$), no difference was evident in the ordination. Block had a significant effect on species composition ($P = 0.045$), displaying a gradual change in species composition from north to south, although considerable variance was evident in the ordination. This result appeared to be a real spatial effect rather than a result of pseudoreplication with respect to herbfield.

Classification of species on the basis of co-occurrence suggests three main groups (Fig. 5). Group 1 contains species that were both widespread and common. Group 2 contains species that tended to be restricted to lower altitudes and were less common. Group 3 consists of two Diptera known to be associated with kelp and that were uncommon in the survey. Examination of the affinities of groups for different altitude and vegetation classes provides one striking pattern that is not obvious from the ordination (Fig. 6): i.e. a distinct invertebrate assemblage is associated with *Stilbocarpa* compared to other vegetation types. Species in group 2 had a higher

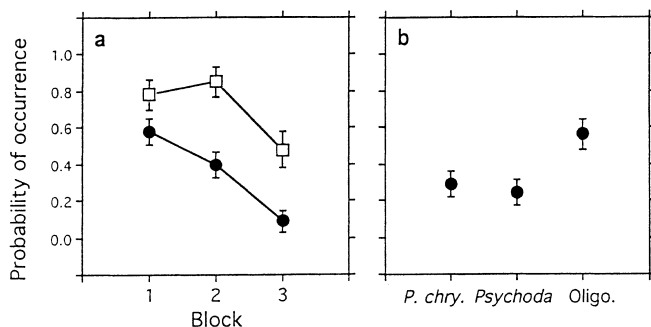


Fig. 3 a Spatial trend in the distribution of two species from north to south. Adults of the moth *Eudonia mawsoni* (circles) were most likely to occur in the northernmost third of the island and least likely to occur in the southernmost third of the island. The fly *Schoenophilus pedestris* (squares) was least likely to occur in the southern third of the island. **b** The distribution of three taxa *Physemothrips chrysodermus* (*P. chry.*), *Psychoda* spp. (*Psychoda*), *Oligochaeta* (*Oligo.*), was not predicted by any of the variables that we tested for. For these taxa, the probability of occurrence was the same for all sites, regardless of vegetation, altitude, aspect or topography

affinity with *Stilbocarpa* than other vegetation types but species in group 1b were never caught. Also, *Stenomalium sulcithorax* was highly associated with *Stilbocarpa* (Fig. 6). It was caught at six out of seven *Stilbocarpa* sites and only at one other site in the survey. It was not appropriate to model *Stenomalium sulcithorax* using the single species approach because it was confined to one altitude and one vegetation type.

Temperature and windspeed

Windspeed on Macquarie Island increased with altitude; it was calmest at sea level and windiest above 300 m

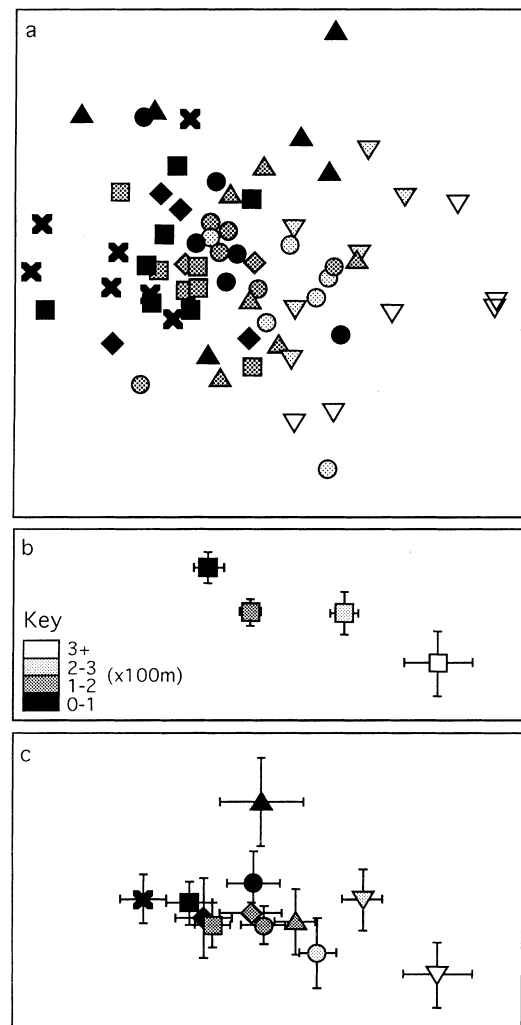
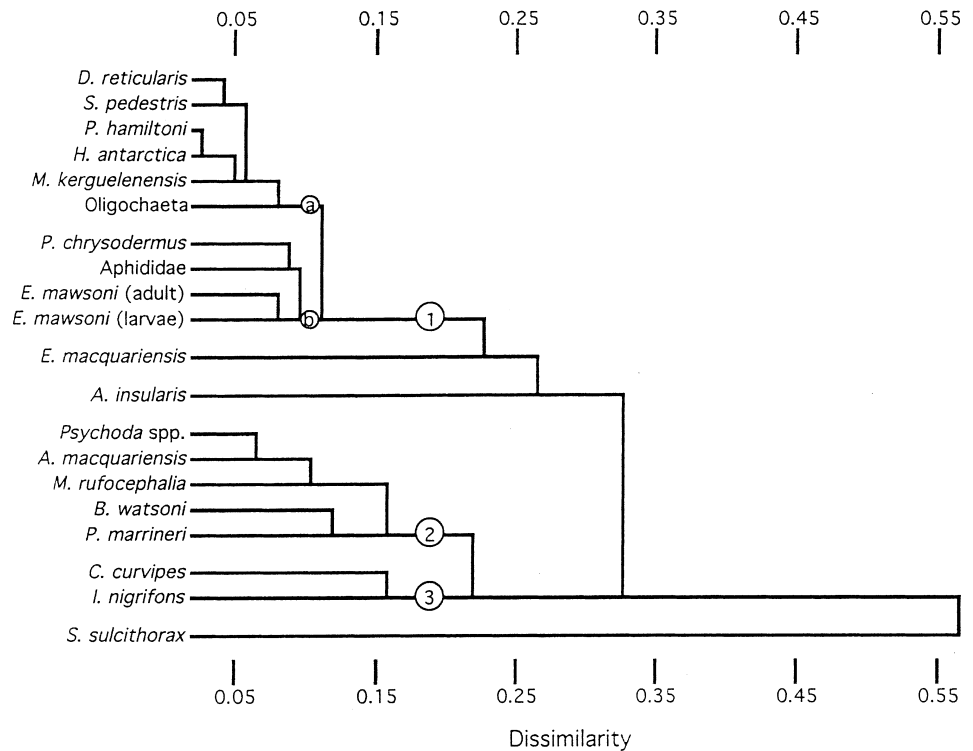


Fig. 4 The effect of vegetation type and altitude on species composition (presence/absence) at sites in the survey. The ordination is a two-dimensional solution from HMDS. The distance between points in this ordination space represents the degree of dissimilarity in species composition. **a** The 69 survey sites. **b** Group centroids (mean and standard error) for each altitude class. **c** Group centroids (mean and standard error) for each ALTVEG class. Symbols indicate vegetation type (except in **b**): short grass (circles), tall grass (squares), *Stilbocarpa* (crosses), mire (triangles), feldmark (upside-down triangles), herbfield (diamonds). Shading indicates altitude. Axes are scaled equally

Fig. 5 Classification of species based on co-occurrence. To group species together, we cut the dendrogram at the six group level. At this level, three species groups (1–3) were recognised along with three individual species. Group 1 was further divided into two subgroups (a, b). The classification was achieved using flexible-UP-GMA with the two-step association measure (dissimilarity)



(Fig. 7a, Table 4), although there was little difference between windspeeds at 100–200 m and 200–300 m (Fig. 7a). It was not windier on the west-facing parts of

the island than the east-facing parts, and windspeed did not differ between north and south (Table 4). Hand-held windspeed was strongly correlated with windspeed at the permanent meteorological station (Table 4).

The mean temperature on Macquarie Island dropped with increasing altitude (Fig. 7b): it was warmest at sea level and coolest at 350 m. However, the relationship between temperature and altitude was not linear. Temperature difference rose more steeply than predicted between 0 and 150 m, and rose less steeply than predicted above 150 m.

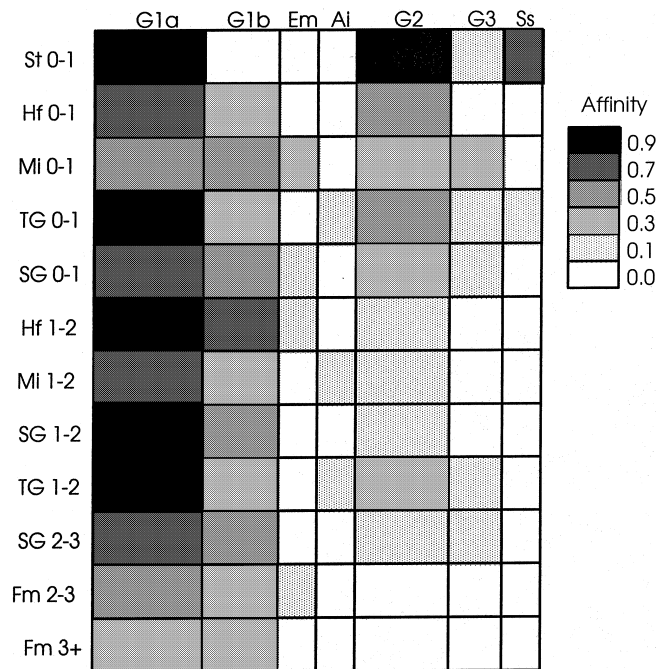


Fig. 6 Affinities of species groups with altitude/vegetation classes. Species groups as in Fig. 5. Group 1a (G1a), Group 1b (G1b), *Ephydrella macquariensis* (Em), *Austropsocus insularis* (Ai), *Stenomalius sulcithorax* (Ss). Vegetation types: *Stilbocarpa* (St), herbfield (Hf), mire (Mi), tall grass (TG), short grass (SG), feldmark (Fm). Altitudes in 100-m units

Discussion

Species distribution models as monitoring tools

The distribution models, along with the basic survey design, form the basis for monitoring changes in the distribution of invertebrate species on Macquarie Island. Changes in the distribution of species can be monitored by repeating the survey and testing whether the relationship between distribution and explanatory variables changes with time. In addition to the single species models, change in species assemblages can be monitored using a multivariate approach (Clarke 1993).

One application of the models is to predict the presence or absence of species at sites not included in the survey. This is useful because localised impacts will not necessarily coincide with survey sites and some impacts will initially only affect localised areas of the island, even if they eventually affect the whole island. For example,

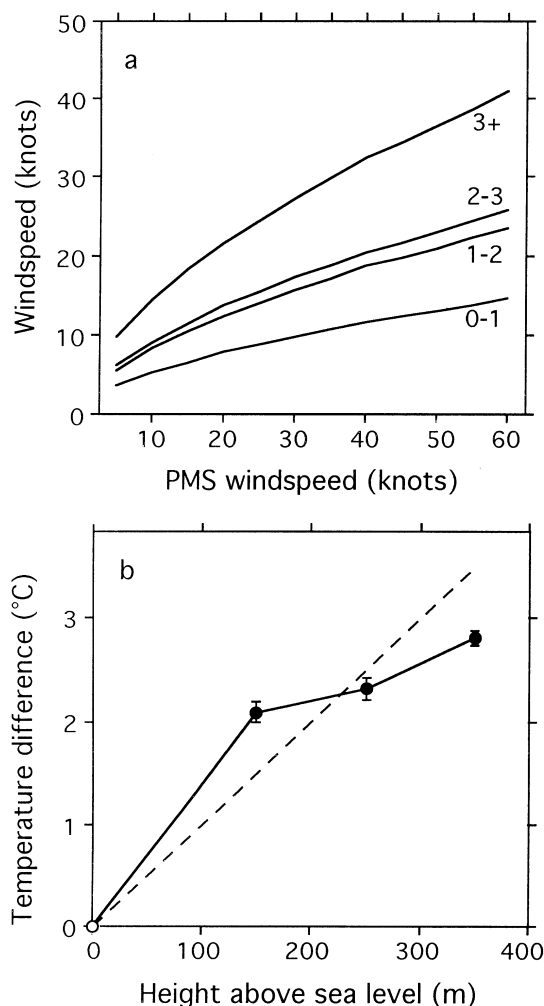


Fig. 7 a The effect of altitude on windspeed for four altitude classes: 0–100 m, 100–200 m, 200–300 m, and above 300 m. Predictions are shown from a multiple regression model. The windspeed at a given point on the island, at a height of 1.8 m, is related to the windspeed recorded at the permanent meteorological station as follows: $\ln(\text{windspeed}) = 0.582 \ln(\text{PMS windspeed}) + b$ where $b_{0-100 \text{ m}} = 0.301$, $b_{100-200 \text{ m}} = 0.773$, $b_{200-300 \text{ m}} = 0.866$, $b_{\text{above } 300 \text{ m}} = 1.330$. **b** The mean number of degrees Celsius lost with height above sea level during the invertebrate survey period, summer 1994. Standard errors are shown. The dashed line represents a lapse rate of 1°C for every 100 m gain in altitude estimated in two previous studies (Taylor 1955; Jenkin 1975). Locations for thermohydrographs at each altitude are given in Fig. 1

an alien species may be introduced to a part of the island that was not surveyed. Then, the models can be used to predict the baseline occurrence of native species at that location, allowing the impact of the alien species on native species to be assessed. This approach can also be used over a wider extent to produce maps of the probability of occurrence of each species for the whole island, by coupling the statistical models to maps of the explanatory variables (Buckland and Elston 1993; Lindenmayer et al. 1994, 1995). While distribution maps are not necessary for monitoring, they could be useful for predicting effects of human impacts when the spatial

Table 4 Summary of multiple regression analysis of windspeed by environmental variables (*df* degrees of freedom). A variable was considered significant when $P < 0.05$

Variable	<i>df</i>	Variance ratio	<i>P</i>
Aspect	1	1.61	0.21
Altitude	3	6.90	0.001
Region	5	2.23	0.070
Log _e PMS windspeed	1	11.04	0.002
PMS wind direction	1	0.00	0.97
Aspect.Altitude	3	0.45	0.72
Aspect.Region	5	1.29	0.29
Altitude.Region	13	1.34	0.23
Altitude.Log _e PMS windspeed	3	0.79	0.50
Residual	38		
Total	73		

arrangement of local populations is considered to be important to population and community processes (e.g. metapopulation dynamics; Hanski and Gilpin 1997).

Species distribution models as prediction tools

To use our statistical models to predict the effects of climate change on the distribution of species, climate information at the landscape and microclimate scales is required (Weiss and Murphy 1993). Our measurements of windspeed and temperature indicate considerable variation in these variables at the landscape scale, probably resulting from topographic effects. For example, we found that windspeed increased with altitude and the relationship between temperature and altitude was different to studies done at other locations on the island. To develop climate change scenarios for the terrestrial environment, a hierarchical approach could be used in which regional predictions from general circulation models are used as input to generate landscape-scale estimates of climate, based on topography. For example, Moore et al. (1993) described terrain models to estimate solar radiation and temperature at a scale appropriate to that required for Macquarie Island. The resulting distribution of environmental variables could then be coupled to our statistical models to predict the distribution of species on the island under the new climatic regime.

Refinements to our models would be necessary if they were to be used to predict the effects of climate change on the distribution of species. In our survey we found significant effects of altitude, aspect and vegetation type on the distribution of invertebrate species. These variables are probably surrogates and in each case a number of causal variables, both biotic and abiotic, could be implicated. It would be critical to determine the causal variables involved because outcomes may be different depending on the variable. For example, we found that eight species were less likely to occur as altitude increased. However, the effects of altitude could be due to either temperature or wind exposure or a combination,

since both of these variables change with altitude. Small differences in temperature have been shown to have large effects on the population dynamics of arctic insects (Strathdee et al. 1993). However, in our study, four affected species were flying animals, which may have limited opportunities for flight at exposed sites. Also, species composition appeared to change along a gradient from tall to short vegetation types, which may also reflect an exposure gradient. Thus, to predict the effects of climate change on the distribution of species, empirical approaches would have to be devised to decouple the effects of temperature and wind exposure.

Similarly, the effect of vegetation type, which affected the distribution of seven taxa, could be due either to the microclimate of the vegetation or to feeding requirements or other aspects of the animal's life history. For example, five species had a strong association with *Stilbocarpa polaris*, which forms a low, closed canopy and thus creates a buffered microclimate that is moister and less windy than elsewhere. However, at least one of these species, *Bradysia watsoni*, a small fly, is known to feed on *S. polaris*. A small-scale experimental approach and microclimate characterisation would be needed to assess the relative roles of these factors before predictions about climate change could be made.

Finally, we found aspect to be important to the distribution of invertebrates. Four species were more likely to occur at east-facing sites and the same pattern, although not significant, existed for all taxa except *Myro kerguelenensis*, which was more likely to occur at west-facing sites. Wind is the most obvious factor that varies with aspect, since the prevailing wind is from the west. However, we did not find a difference in windspeed between west and east (see also Peterson and Scott 1988). The fact that aspect does not appear to affect species assemblages, in contrast to individual species, suggests that species' tolerances are not important in explaining west-east differences and possibly indicates a mechanism operating at a spatial scale larger than the site scale. One hypothesis consistent with this observation is that there is a dispersal bias due to the prevailing wind direction.

To understand and predict the ecological effects of climate change, monitoring and process studies from a range of spatial scales are needed (Root and Schneider 1995). In contrast, terrestrial studies in the sub-Antarctic and Antarctic have tended to concentrate on small spatial scales and predictions rely on scaling up. Larger scale studies are also required, particularly at the landscape scale. We propose that the next phases of a strategy to monitor and predict the effects of human impacts at Macquarie Island should include the construction and validation of topoclimate models, monitoring of microclimate in different vegetation types, and experiments to test hypotheses generated from our species distribution models.

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