INTRODUCTION

Community structure and the question of coexistence of species have produced one of the most enduring and prominent themes of ecology (Hutchinson 1957, MacArthur 1972, Stubbs & Wilson 2004). Many of the hypotheses put forward as explanations of why species are able to coexist centre on the niche concept (e.g. Hutchinson 1961, MacArthur & Levins 1967, Tilman 2004). We investigate the question of coexistence and community structure as a result of ecological processes in saltmeadow vegetation using relative abundance distributions and stochastic niche apportionment models. Saltmeadow vegetation was selected because it is a classic harsh environment and considerable controversy surrounds the nature of biotic interactions, and hence community structure, in stressful or harsh environments (e.g. Terborgh 1973, Wiens 1977, Grime 1979, Callaway 1995, Chesson & Huntly 1997); much of this debate centred on saltmeadow communities (e.g. Whittaker 1991, Bertiess & Hacker 1994, Emery et al. 2001, La Peyre et al. 2001, Stubbs & Wilson 2004). To increase the generality of our conclusions, an inter-continental and multi-scale approach was used. Saltmeadow vegetation was sampled in 3 biogeographical regions, i.e. New Zealand, South America and southern Europe, and compared at both the community
scale (within site) and at the intercontinental scale (across sites).

Niche apportionment models are classified as either deterministic models, those that give a single set of relative abundances, or stochastic models, those that encompass some degree of variation (Tokeshi 1990, Hubbell 2001). Early work was largely based on the fit of observed data to deterministic models, such as the broken-stick, geometric series, general lognormal, and Zipf-Mandelbrot (see Whittaker 1972, May 1975, Frontier 1985, Wilson 1991). These models are largely statistical in origin, and there are different biological interpretations for each model, so that if a model is shown to fit many different communities, it is unclear whether this is due to the model’s flexibility or an underlying and general rule of community structure (May 1975, Tokeshi 1993). The different number of parameters required to fit the various models (Wilson 1991) further complicates objective comparison of these models. However, the main failing of deterministic models is that, as each model only has one realisation, it is possible to compare the mean of several observed replicates with the model prediction but not the variance. Stochastic mechanistic models may provide both a mean and a variance to compare with the observed data, and because they are mechanistic in nature, they have a greater potential to provide valuable insight into the processes behind community structure (e.g. Sugihara 1980, Tokeshi 1990, Mouillot et al. 2000, Hubbell 2001, Mouillot et al. 2003, Tilman 2004). Consequently, as niche-oriented models are explicitly related to an ecological process, they have an advantage over deterministic models, which have the inherent problem of requiring a post hoc ecological explanation. Following MacArthur (1957), niche-oriented models tend to be expressed in terms of a stick or unit volume which represents the total available resource of a community. This total resource is then divided amongst the species within the community following some mechanistic rule. In MacArthur’s (1957) broken-stick model (Hypothesis I, non-overlapping niches) the total resource was divided simultaneously between the existing species, using a uniform random distribution. In contrast, the niche-apportionment models introduced and developed by Tokeshi (1990, 1993, 1996, 1999), and used here, all exhibit sequential division of the resources. Tokeshi argues this is a more ecologically realistic approach, as it is unlikely that all the species of a community would arrive simultaneously and then jostle for resources. Although Tokeshi (1990, 1993, 1996, 1999) suggests that his sequential MacArthur fraction (MF) model ‘produces the same result as the broken-stick model’, the average outcome of the 2 models is actually different. Despite the ready interpretability of the mechanistic approach of Tokeshi, niche-apportionment models remain an inferential tool. Demonstrating that the species abundance pattern produced by a particular mechanism or division process is not significantly different from the observed pattern is not sufficient evidence to prove that the mechanism actually did produce the pattern – only that it might have (Naeem & Hawkins 1994). However the mechanistic niche-apportionment models do seem to offer a step forward in our understanding of which processes may produce community structure (Naeem & Hawkins 1994, Tokeshi 1999).

Traditionally, niche-apportionment models have been fitted with either density data (e.g. Bersier & Sugihara 1997) or biomass data (e.g. Mouillot et al. 2003) or both (Tokeshi 1990). To date, Tokeshi’s models have not been used with vascular plant communities. One possible reason for this is that both biomass and density data are time-consuming and difficult to collect for most plant communities. Although some authors have suggested that biomass is the only appropriate abundance measure for community structure work (e.g. Wilson 1991), it is inappropriate to directly measure biomass in most natural systems as it destroys the system it seeks to conserve and becomes impractical when the biomass is too great (e.g. forest). Moreover, the measurement of density is also problematic, not only because of the considerable variation in individual size (Mouillot et al. 2003) but also because of the difficulty in defining an individual in plant communities that contain clonal species or modular individuals. Some authors (e.g. Mason et al. 2002) have suggested counting modules (e.g. leaves, ramets or tillers) rather than individuals; however, even these differ greatly in size and are often more time-consuming to count than individuals. Tokeshi (1993 p. 134) suggested that any measure of abundance that was deemed appropriate might be used. In studies of short vegetation, point-quadrat cover data provides a practical compromise. It is a time-efficient estimate of cover (Smartt et al. 1976) that is objective, does not require individuals of a species to be distinguished, and is non-destructive—an often crucial consideration in many conservation and/or management studies (Glatzle et al. 1993). Critically, there is also evidence to suggest that cover is proportional to biomass or energy (e.g. Greig-Smith 1964, Sugihara 1989, Chiarucci et al. 1999, Guo 2001), and strong correlations have been found between density and cover data (e.g. Loya 1972).

Scale and resolution are 2 aspects of sampling that are particularly likely to affect the fit of field data to simulated models and consequently the perception of coexistence rules within communities. In this sense scale has been referred to as ‘extent’ (e.g. Palmer & White 1994, Dunjan et al. 2002). Resolution may be seen as the power or limits imposed by the sampling
(Dungan et al. 2002). In order to evaluate the effect of scale and resolution on the fit of Tokeshi’s niche-apportionment models to vascular plant communities, 2 levels of resolution and 2 scales were used: the intercontinental scale (observations across communities, where individual sites are the replicates); and the community scale (observations within communities, where quadrats within the individual sites are the replicates). The bounded nature of point-quadrat data means that it may be particularly sensitive to resolution (Greig-Smith 1964, Smartt et al. 1976). In the context of discrete bounded data the resolution is the range of possible abundances. With point-quadrat data the resolution of a site with replicate quadrats is equivalent to the number of points used in each quadrat. At the intercontinental scale resolution is still the number of points used in each quadrat (25 or 100), but a mean was taken over the 10 quadrats in each site. The importance of maintaining the same resolution has previously been recognised by Eilertsen et al. (1990), who used local frequency data combined with ordination gradients to investigate community structure. However, the influence of resolution on niche-oriented models does not appear to have been investigated. The impact of resolution on the final ecological conclusions may be particularly important when the resolution is low.

The aim of this study was to search for rules governing plant community structure using Tokeshi’s niche-apportionment models. Saltmeadow vegetation from 3 biogeographical regions was used to uncover community structure rules. Two different levels of resolution and scale were used to test the robustness of both the method and any rules uncovered. Three specific questions were asked: (1) Can a niche-apportionment model fit observed plant data, and is there any consistency over different saltmeadow sites? (2) Does the fit to different niche-based coexistence rules depend on the resolution used to measure the species abundances? (3) Do the niche-based coexistence rules at the intercontinental scale mirror those of the community scale?

### MATERIALS AND METHODS

#### Study system
Six saltmeadow sites were sampled in 3 biogeographical regions, New Zealand, Southern Europe and South America (Table 1, Anderson 2006). Sites included in the present study all fall in between the mid-tide line and the mean high-water neap-tide line and correspond roughly to what Partridge & Wilson (1988) termed the ‘middle marsh saltmeadow’ or simply ‘meadow’. *Selliera radicans* Cav., was among the dominant species at all the southern hemisphere sites. Both *Selliera radicans* and *Samolus repens* (Forster et Forster f., Pers., were the dominant species at Mehuin, Queule, and Blueskin Bay; with the addition of *Schoenus nitens* (R. Br.) Hook. f. at the latter, and *Selliera radicans* alone at Savvedra. At Maremma, *Halimione portulacoides* (L.) Aell. was the dominant species; and at Porto Vecchio, *Parapholis incurva* C. E. Hubb., *Athrocnemum macrostachya* (Moric.) et Delponte, and *Limonium vulgare*...
Mill. were dominant. Saltmeadow sites are subject to repeated inundation with saline water (Chapman 1960), and the main abiotic stress is therefore the high salinity of the soils (measured as soil conductivity). However, saltmeadow vegetation tends to be fairly stable, as it is generally associated with some kind of protection from the full forces of wind and sea: in estuaries, to landward of barrier islands or spits, in the lee of promontories and near extensive areas of shallow water (Chapman 1960). Both maritime/estuarine and brackish riverbank salt marshes were included in the present study. Maritime/estuarine saltmeadows exist below the high-tide mark and are sheltered in some way from direct wave action (e.g. inside a semi-enclosed or shallow harbour or bay). Brackish riverbanks occur on the lower stretches of rivers, extending from the estuarine marshes to the brackish riverbanks (e.g. inside a semi-enclosed or shallow harbour or bay).

Saltmarsh sites are subject to re-peated inundation with saline water (Chapman 1960), and the main abiotic stress is therefore the high salinity of the soils (measured as soil conductivity). However, saltmarsh vegetation tends to be fairly stable, as it is generally associated with some kind of protection from the full forces of wind and sea: in estuaries, to landward of barrier islands or spits, in the lee of promontories and near extensive areas of shallow water (Chapman 1960). Both maritime/estuarine and brackish riverbank salt marshes were included in the present study. Maritime/estuarine saltmeadows exist below the high-tide mark and are sheltered in some way from direct wave action (e.g. inside a semi-enclosed or shallow harbour or bay). Brackish riverbanks occur on the lower stretches of rivers, extending from the estuarine marshes to the brackish riverbanks (e.g. inside a semi-enclosed or shallow harbour or bay).

Saltmarsh sites are subject to re-peated inundation with saline water (Chapman 1960), and the main abiotic stress is therefore the high salinity of the soils (measured as soil conductivity). However, saltmarsh vegetation tends to be fairly stable, as it is generally associated with some kind of protection from the full forces of wind and sea: in estuaries, to landward of barrier islands or spits, in the lee of promontories and near extensive areas of shallow water (Chapman 1960). Both maritime/estuarine and brackish riverbank salt marshes were included in the present study. Maritime/estuarine saltmeadows exist below the high-tide mark and are sheltered in some way from direct wave action (e.g. inside a semi-enclosed or shallow harbour or bay). Brackish riverbanks occur on the lower stretches of rivers, extending from the estuarine marshes to the brackish riverbanks (e.g. inside a semi-enclosed or shallow harbour or bay).
Random fraction (RF): Tokeshi’s RF model is similar to the MF model. However, after the first random break, the segment to be divided is chosen at random with each segment having an equal probability of being selected. This is the sequential breakage model of Sugihara (1980) and the sequential breakage algorithm type III of Naeem & Hawkins (1994). It gives a lognormal distribution of abundances (Sugihara 1980). Ecologically, this represents a new or ‘invading’ species taking part of the niche of an existing species, with all the existing species equally likely to be invaded.

Random assortment (RA): The segment to be divided is chosen at random, and the other segment is preserved from further division. Ecologically, the preserved segment represents niche pre-emption by a species, the remaining part represents unoccupied niche space. According to Tokeshi (1990, 1993), this model may be seen as the result of either ‘non-correspondence between niche apportionment and species abundance’ or as ‘non-hierarchical, dynamic apportionment of niche in a variable environment’. Tokeshi (1990, 1993) intended this as a ‘null’ or ‘neutral’ model where the abundances of the species varied independently of each other, the niche was assumed to be unsaturated and competitive relationships were not ‘structuring’ the community.

Dominance pre-emption (DP): The DP model represents the extreme opposite of the DD model. Under the DP model, after the first random break the segment chosen to be divided is always the smallest. This means that the largest segment produced at each division is preserved from further division, producing a high degree of dominance, i.e. low evenness. Ecologically, this represents resource pre-emption by a dominant species.

Fitting procedure. The procedure used to fit these models here is that used by (Mouillot et al. 2003). It is a modified and improved version of that first proposed by Tokeshi (1993). The method proposed by Tokeshi does not allow for the rejection of communities whose variance is larger than the one expected from the model, and it is sensitive to the number of species or ranks. Bersier & Sugihara (1997) introduced a randomization test to overcome these problems. This procedure was further improved by Cassey & King (2001). However, their procedure was species-oriented, i.e. species identities are assumed to be important. Thus, the mean and the variance of each species across the replicates produce the observed relative abundance distribution, which is then compared with the stochastically generated models. In contrast, the procedure used in the present study is process-oriented. The models assume no consistency in species ranks across replicates, the species of each replicate are ranked independently and the mean and variance for the relative abundance of each rank are calculated across all replicates. These observed means and variances are then compared with the values generated by a large number of simulations (9999 in each case) according to each model. A model is considered not to be rejected when the p-value for both the mean and variance are greater than 0.05 (Mouillot et al. 2003). Although Tokeshi (1993) has argued that either interpretation might be equally valid, the process-oriented approach allows the examination of the relative abundance distribution to be separated from the question of rank consistency between the species—a concept which may be explicitly addressed using a distinct randomisation procedure (e.g. Mason et al. 2002).

RESULTS

The RF and RA models were the models which most often fitted both the mean and the variance (Table 2). At the community scale (within site) the RF model fitted 5 of the 6 saltmeadows with both the low resolution data (i.e. not Maremma) and the higher resolution data (i.e. not Blueskin Bay). The RA model fitted 4 of the 6 sites with both the low and high resolution. However, at the intercontinental scale only the RF model was accepted, all other models were significantly different from the observed data (Table 2). The DD, MF and DP models were significantly different (p < 0.05) to the species-abundance pattern of all 6 sites at both the community scale and the intercontinental scale, using both the low resolution (25) and the high resolution (100) (Table 2). To illustrate these results we chose to present data for the RF (Fig. 1) and RA (Fig. 2) models at the intercontinental scale with low resolution for both the means (Figs. 1a,c & 2a,c) and the variances (Figs. 1b,d & 2b,d). The observed relative abundance distribution for both the mean and variance of the observed data clearly fall well within the 95% confidence interval of the RF simulation model (Fig. 1a,b), but the tail end of the observations exceed the 95% confidence interval for the RA simulation model (Fig. 2a,b). This can be seen even more clearly from the frequency distribution of the test statistic values for the mean and the variance of the 2 simulations. The observed test statistic falls within the distribution for the RF model (Fig. 1c,d) but the observed statistic is an outlier when compared to the distribution for the RA model (Fig. 2c,d). Note that the test-statistic values are dependent on both the model and the observed values. Thus, it is normal to have different observed statistics for the same data but for 2 different models. The test-statistic includes a comparison to simulated distributions and is not 100% derived from the observed data.
Table 2. Comparison of saltmeadow vegetation and Tokeshi’s niche apportionment models. The models were: dominance decay (DD), MacArthur fraction (MF), random fraction (RF), random assortment (RA) and dominance pre-emption (DP). Comparison of the observed and simulated data is based on both the mean and variance of the relative abundances of the species ranks for saltmeadow vegetation at 2 scales and at 2 resolutions. At the community scale 6 saltmeadow sites were compared. Models that could not be rejected (both 2-tailed mean and variance \( p \geq 0.05 \)) are in bold: \( p \) given for mean and variance (var.) where \( p \) for the mean >0.001. *\( p < 0.001 \)

<table>
<thead>
<tr>
<th>Scale &amp; site</th>
<th>Resolution</th>
<th>Model</th>
<th>Mean</th>
<th>Var.</th>
<th>Mean</th>
<th>Var.</th>
<th>Mean</th>
<th>Var.</th>
<th>Mean</th>
<th>Var.</th>
<th>Mean</th>
<th>Var.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blueskin</td>
<td>25</td>
<td>*</td>
<td>*</td>
<td>0.106</td>
<td>0.102</td>
<td>0.735</td>
<td>0.234</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mehuin</td>
<td>25</td>
<td>*</td>
<td>*</td>
<td>0.085</td>
<td>0.139</td>
<td>0.213</td>
<td>0.068</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saavedra</td>
<td>25</td>
<td>*</td>
<td>*</td>
<td>0.246</td>
<td>0.419</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Queule</td>
<td>25</td>
<td>*</td>
<td>*</td>
<td>0.140</td>
<td>0.872</td>
<td>0.061</td>
<td>0.407</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maremma</td>
<td>25</td>
<td>*</td>
<td>*</td>
<td>0.011</td>
<td>0.111</td>
<td>0.010</td>
<td>0.039</td>
<td>0.001</td>
<td>0.026</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porto Vecchio</td>
<td>25</td>
<td>*</td>
<td>0.002</td>
<td>0.271</td>
<td>0.259</td>
<td>0.233</td>
<td>0.133</td>
<td>0.183</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blueskin</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.012</td>
<td>0.071</td>
<td>0.113</td>
<td>0.097</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mehuin</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.311</td>
<td>0.136</td>
<td>0.667</td>
<td>0.057</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saavedra</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.357</td>
<td>0.069</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Queule</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.108</td>
<td>0.720</td>
<td>0.047</td>
<td>0.901</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maremma</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.072</td>
<td>0.069</td>
<td>0.088</td>
<td>0.086</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porto Vecchio</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.328</td>
<td>0.151</td>
<td>0.437</td>
<td>0.538</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercontinental</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saltmeadow</td>
<td>25</td>
<td>*</td>
<td>*</td>
<td>0.552</td>
<td>0.160</td>
<td>0.002</td>
<td>0.001</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saltmeadow</td>
<td>100</td>
<td>*</td>
<td>*</td>
<td>0.146</td>
<td>0.576</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 1. Observed means (A) and variances (B) for the ranks at the intercontinental scale using the low (25) resolution (△). 95% confidence intervals are given for the random fraction (RF) model (solid lines). Frequency distribution of the test statistic values for the mean (C) and the variance (D) of the RF model produced by the randomization procedure; observed values are indicated by an arrow on the distribution and are not significantly different from the RF model, which therefore cannot be rejected.
DISCUSSION

The RF and the RA models were accepted more often than the more extreme DD, MF or DP models. This is in general agreement with the findings of the few existing small-scale studies: epiphytic chironomid communities (Tokeshi 1990), larval chironomid assemblages (Fesl 2002), macrobenthic communities (Formentin et al. 1997), parasite communities (Mouillot et al. 2003), and parasitoid communities (Naeem & Hawkins 1994).

Resolution

With the exception of the effect of sample size on density data (e.g. Simpson 1949, Peet 1975), the effect of resolution on various abundance measures and data analyses has not been well studied (Dungan et al. 2002). The bounded nature of point-quadrat data may make models particularly susceptible to the influence of resolution, but also allows the ecologist to predetermine and standardize the resolution used in samples or studies, thus allowing valid comparisons. Tests of the effects of resolution showed that higher resolution improved the discrimination between the models (Table 2) and higher resolution data resulted in the rejection of the RF model for Blueskin Bay and the RA model for Queule. However, with high resolution, both the RF and the RA models were accepted for Maremma whilst low resolution resulted in the rejection of all models for this site. This difference between the 2 levels of resolution may be related to the very low species richness of the site at Maremma (Table 1). However, at the intercontinental scale, all models except the RF were rejected at either resolution. This suggests that resolution may be more important at the smaller, community scale than at the larger, intercontinental scale. This may simply be an effect of statistical power. At the intercontinental scale there are more species per replicate and the relative abundance per replicate would also show less stochastic variation (since the relative abundance of each species would combine the data from all the quadrats from a site).
The difference observed between the 2 scales of observation may therefore be largely due to sampling effort per se rather than an intrinsic effect of scale.

**Community scale**

At the community scale the RF model was accepted for 5 of the 6 saltmeadow communities at both the low and high resolution. The ecological interpretation of this model is that the niche or species to be ‘invaded’ is chosen at random with each available species equally likely to be chosen irrespective of its abundance (i.e. the size of its niche). Tokeshi (1996) suggests that this may be the result of ‘species with narrow niches being more likely to pursue the tendency of specialization’ balancing out the ‘trend of species with a wider niche to experience a higher chance of habitat fragmentation and isolation’ and therefore speciation (i.e. there is an equal likelihood that segments will be chosen from species with larger or smaller niches). Intuitively, the RF model seems to be a more realistic scenario than a model in which the abundances of the available species determines with which the ‘invading’ species competes, as is the case in the DD, DP and MF models. Ecologically, it seems more likely that an ‘invading’ species would compete with an available species that is most similar in resource use (MacArthur & Levins 1967) rather than the most abundant species (DD), the least abundant species (DP) or proportionally more with more abundant species (MF). Fesl (2002) examined both species-oriented and process-oriented models. He found that only the RF model fitted his larval chironomid communities when he used the process-oriented model and the entire community, as in the present study. Tokeshi (1990) found that the RF model fitted epiphytic chironomid communities when based on density but not biomass, while Naem & Hawkins (1994) found that the RF model fitted parasitoid communities. Ecologically, Tokeshi (1990, 1993) argues that the RF model suggests that there is some hierarchical structure, i.e. within the saltmeadow communities. If this is a general rule, then the same model may explain the relative abundance patterns of quite different communities. However, it has been shown that the RF model leads asymptotically to a lognormal distribution of abundances. Sugihara (1980) first brought to our attention the link between a random sequential breakage model (the RF model) and the lognormal distribution, and he suggested this was evidence for a hierarchical community structure. However, mechanisms other than a sequential breakage may also lead to a lognormal distribution of abundance. For instance, if the abundances of the species are determined by several variables acting multiplicatively but independently, this will also lead to a lognormal distribution (May 1975). Another example is the Unified Neutral Theory of Biodiversity and Biogeography proposed by Hubbell (2001), which shows that communities of functionally equivalent species undergoing random drift may in some circumstances display patterns of abundance distribution that are very close to lognormal. The multiplicity of potential mechanisms leading to the lognormal may explain why this distribution is so prevalent among ecological communities. Unfortunately, this also makes it impossible to determine which of these mechanisms is responsible without additional evidence.

Tokeshi (1990, 1993) suggests that the RA model may fit when there is no correspondence between the species niches and the species abundances or as a ‘non-hierarchical, dynamic apportionment of niche under a highly variable environment’. However, if species abundances were not related to their niches, all 5 models should be rejected. In the present study, although the RF model was the most frequently accepted, the RA model was accepted for 4 of the 6 saltmeadow sites. Consequently, the ecological interpretation of the RA model must also be considered for some saltmeadow sites at the community scale. This model has previously been found to fit parasite communities in fishes (biovolume data; Mouillot et al. 2003) and in epiphytic chironomids (biomass and density data; Tokeshi 1990). Mouillot et al. (2003) suggested that the RA model was a suitable explanation for fish parasitoid communities because of their dynamic and unsaturated nature. Blueskin Bay was the only saltmeadow site for which the RA, but not the RF, model was accepted. This site had both the highest abiotic stress (measured by the conductivity of the soil) and the highest levels of nutrients (soil NPK; Table 1). The high nutrient levels at Blueskin Bay may reflect nutrient enrichment from the adjacent farmland and indicate that this site is more disturbed than the others. However, the RA model also fitted the 3 sites with the lowest conductivity: Mehuin, Maremma and Porto Vecchio (Table 1); whereas the remaining 2 sites, Saavedra and Queule, were rejected for the RA model but not the RF model.

**Intercontinental scale**

At the intercontinental scale, the 6 sites were used as replicates in order to determine whether there was evidence of a global pattern in the community structure of saltmeadow vegetation. Despite the very different species composition and vast spatial distance between the 6 sites, the RF model was the only model accepted, thus providing some evidence of a global pattern. The
consistency of this result with that found at the community scale suggests the possibility of some element of self-similarity in the construction of saltmeadow vegetation. Saltmeadow is widely acknowledged to be a stressful or harsh abiotic environment due to its high salinity. C-S-R theory maintains that the importance of competition is reduced in stressful (including saline) habitats (Grime 1979). As the saltmeadow vegetation in the present study fits the RF model, hierarchical structuring of the community is likely, and this suggests that competition may play some part in community structure of at least some stress communities (cf. Naeem & Hawkins 1994). Although one of the 6 saltmeadows rejected the RF model at the community scale, the saltmeadow vegetation as a whole fitted the RF model. This suggests that there may be a general rule, which may include biotic interactions, at least for saltmeadow vegetation. However, given the link between the RF model and the lognormal distribution of species abundance, this ‘consistency’ may only suggest that the law of large numbers is at play (i.e. a statistical explanation rather than a biological one). What is clear is that all of the extreme models (DD, MF and DP) were significantly different from all the observed data for both resolutions at both the community and the intercontinental scale.

Acknowledgements. B.J.A. thanks C. Jara-Vergara, R. Ohlemüller, N. Mason and J. Wilson for assistance in the field, C. Ramirez, A. Chiarucci, C. Lusk, M. L. Castelli and M. L. Pozzo Di Borgo for assistance in locating suitable sampling sites and P. Bannister, A. Chiarucci, J. Clark, V. Clarke, B. Lowe, C. Lusk, O. Missa, R. Ohlemüller, C. D. Thomas, and one anonymous reviewer for comments on the manuscript and invaluable discussion. We acknowledge a grant to B.J.A. from the Miss H. E. Hellaby Indigenous Grasslands Trust, BRAP, and a University of Otago Research Grant. B.J.A. was supported by a FORST Bright Future award, and UKPopNet.

LITERATURE CITED


Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway

Submitted: June 18, 2007; Accepted: October 24, 2007
Proofs received from author(s): December 28, 2007