



Correlates of vascular plant species richness in fragmented indigenous forests: assessing the role of local and regional factors

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Abstract: Both local and regional factors determine local species richness. We investigated the relative role of local (13 soil and tree stand structure variables) and regional factors (19 climate, land cover and geographic location variables) in determining the richness of several vascular plant functional groups in indigenous forest fragments in southeastern New Zealand. The predictor variables explaining the largest fraction of the variation in species richness were identified using a backward and forward stepwise procedure, with adjustments for the number of variables and testing for multicollinearity. The total proportion of variation explained by local and regional factors was highest for tree species richness (54.1%) and lowest for herbaceous species richness (28.2%). We found differences between the functional groups in the extent to which species richness was explained by local vs. regional factors, but both showed some ability to explain the species richness of all functional groups. The abundance of the strongly competitive tree species *Nothofagus menziesii* (silver beech) had a strong negative effect on total, tree and herb species richness, but it had only minor effects on woody and fern species richness. Once the effect of this local variable was accounted for, the remaining variation in tree and woody species richness was mainly explained by regional variables. Herbaceous and fern species richness, on the other hand, was strongly correlated with local as well as regional variables. We emphasize the importance of using a fixed plot size when the relative effects of local and regional factors on patterns of species richness are to be compared and evaluated.

Abbreviations: AIC – Akaike Information Criterion; CV – Coefficient of Variation; dbh – diameter at breast height; PCA – Principal Component Analysis; VIF – Variance Inflation Factor.

Nomenclature: Allan (1961).

Introduction

Plant community structure at the plot level in fragmented habitats is determined by a complex of local and regional processes (e.g., Ricklefs 1987, Huston 1999). Understanding the relative importance of local vs. regional factors in determining local features such as species richness is not only crucial for relating biodiversity patterns to potential processes (Gaston 2000), but may in fact hold the key for understanding global biodiversity patterns (Huston 1999). However, the issue has, so far, hardly been explored, and very rarely quantitatively assessed. In communities with a wide range of functional species groups, different groups are likely to respond differently to environmental factors, and it may be misleading to analyse just the richness of the whole plant community (Austin et al. 1996, Ohlemüller and Wilson 2000, Godefroid and Koedam 2003).

Species richness and its determinants in fragmented ecosystems have received considerable attention since the formulation of MacArthur and Wilson's (1967) equilibrium theory of island biogeography. Once ecologists had overcome the initial temptation to treat fragmented ecosystems as true islands (Lomolino 2000), the often considerable influence of the landscape matrix on within-fragment vegetation structure has increasingly been recognised (Turner 1989, Haila 2002). Some studies have investigated the effect of the landscape matrix on the plant species richness of entire fragments or nature reserves (e.g., Metzger 1997, Dumortier et al. 2002, Pyšek et al. 2002), but this approach confounds species/area relationships with differences in within-fragment heterogeneity. Only a few studies have used the more rigorous approach of comparing the effects of local and regional factors on species richness in plots of fixed size (Huston 1999, Ross et al. 2002).

Table 1. Response variables showing vascular plant species richness of different plant species groups in 20 m × 20 m sampling plots.

| Response (richness) variable | Description | Range | Mean |
|------------------------------|---|---------|------|
| TOTAL | Total number of species (native + exotic) | 17 – 59 | 36.6 |
| NATIVE | Number of native species | 16 – 56 | 34.4 |
| WOODY | Number of all woody species (native + exotic) | 8 – 27 | 17.1 |
| TREE | Number of native woody species with dbh ≥ 10 cm | 1 – 16 | 8.5 |
| HERBACEOUS | Number of non-woody species (native + exotic) | 6 – 36 | 19.5 |
| FERN | Number of fern species (native + exotic) | 1 – 19 | 10.8 |

This study uses plots of fixed size to address three issues for the vascular plant species richness in remnants of indigenous forest in southeastern New Zealand: (1) the relative importance of local vs. regional factors in determining plant species richness in the sampling plots; (2) the most important environmental factors (out of those measured) and (3) the differences in these relations between total species richness and the species richness of five functionally different plant groups.

Methods

Study area and vegetation sampling

We compiled complete species lists from 143, 20 m × 20 m, sample plots in 61 remnants of indigenous forest in the study area in southeastern New Zealand (Ohlemüller 2003). These temperate forests comprise two main types: southern beech forests, dominated by the highly competitive species *Nothofagus menziesii* (silver beech), and mixed conifer/broadleaved forests with species such as *Podocarpus hallii*, *Dacrydium cupressinum*, *Melicactus ramiflorus*, *Fuchsia excorticata* and *Griselinia littoralis* (Wardle 1991). The study area comprised a coastal band of approximately 95 km length and 20 km width, ranging from 45° 30' S to 46° 13' S in latitude, 169° 57' E to 170° 46' E in longitude, and 0 to 880 m above sea level in altitude. Forest remnants were chosen, and sampling plots located, according to a proportional random sampling scheme (Hirzel and Guisan 2002), keeping the number of sampling plots per environmental region (Leathwick et al. 2003) approximately proportional to its area.

Model formulation

We inferred determinants of species richness from fitted Generalised Linear Models (GLMs) – an extension of linear models (McCullagh and Nelder 2000, Guisan et al. 2002). As with many biological count data (Vincent and Haworth 1983, McCullagh and Nelder 2000), the residu-

als of the response variables here followed an approximately Poisson distribution. GLMs were therefore fitted with Poisson errors and a log link function. The Poisson distribution was confirmed by scaling factors of approximately 1 for all models (Crawley 1993). We follow the latter author's definitions of the various models fitted:

- *Null model*: model with no variables (intercept only).
- *Maximal model*: model with all available predictor variables.
- *Minimal adequate model*: model with a parsimonious subset of variables, which explains a high amount of variation with a small number of variables.

Response variables

Total richness as well as the species richness of five further, functionally different, plant groups was modelled (Table 1). These five groups were: native (comprising all species present in New Zealand at the time of European settlement, c. 1840 AD), woody (all species with any woody parts), tree (all woody species with at least one individual in that plot with a stem diameter at breast height (dbh) of ≥ 10 cm), herbaceous (all non-woody species) and fern species (all fern and tree-fern species). Apart from the native and tree species groups, all groups comprised native as well as exotic species.

Predictor variables

Altogether, 32 predictor variables from five categories were used (Table 2): 13 of these were local variables (factors) and considered to influence the vegetation at a local level (soil, stand structure), whereas the other 19 were regional variables (climate, land cover, geographic location) and considered to influence the vegetation in the sampling plots from the surrounding area.

Table 2. Predictor categories and variables.

| Predictor categories (a-e) and variables | Unit | Type | Min | Max | Mean |
|--|---------------------------|------------|---------|---------|---------|
| LOCAL FACTORS: | | | | | |
| <i>a) Soil</i> | | | | | |
| pH | n/a | continuous | 3.53 | 6.92 | 5.36 |
| Organic matter | % | continuous | 4.80 | 72.77 | 16.99 |
| Cation exchange capacity | Mmol | continuous | 6.06 | 22.20 | 12.33 |
| Fertility | g biomass | continuous | 1.26 | 2.66 | 1.88 |
| Gravel | log(%) | continuous | 0 | 1.84 | 0.97 |
| Soil heterogeneity | mean CV | continuous | 0.03 | 0.41 | 0.15 |
| Ground heterogeneity | n/a | ordinal | 1 | 5 | 2.83 |
| <i>b) Stand structure</i> | | | | | |
| Tree density | n/a | integer | 14 | 112 | 49.78 |
| Proportion of trees > 40 cm dbh | log(%) | continuous | 0 | 1.78 | 0.81 |
| Tree size differentiation | n/a | continuous | 0.05 | 1.23 | 0.27 |
| Number of tree fern individuals | n/a | integer | 0 | 29 | 3.02 |
| Total tree basal area | log(cm ²) | continuous | 3.82 | 4.85 | 4.39 |
| Relative abundance <i>N. menziesii</i> | % | continuous | 0 | 100 | 13.42 |
| REGIONAL FACTORS: | | | | | |
| <i>c) Climate</i> | | | | | |
| Mean annual temperature | [°C] | continuous | 7.23 | 10.66 | 9.40 |
| October vapour pressure deficit | [kPa] | continuous | 0.27 | 0.44 | 0.36 |
| Minimum temperature | [°C] | continuous | -0.30 | 4.28 | 1.39 |
| Rainfall:pot. evaporation ratio | n/a | continuous | 1.22 | 3.36 | 2.28 |
| Mean annual solar radiation | [MJ /m ² /day] | continuous | 12.12 | 12.69 | 12.39 |
| Mean annual humidity | [%] | continuous | 74.87 | 81.08 | 77.50 |
| <i>d) Land cover</i> | | | | | |
| Area pasture 2500 m radius | ha | integer | 21 | 1878 | 798 |
| Area planted forest 2500 m radius | ha | integer | 0 | 936 | 298 |
| Area shrubland 2500 m radius | ha | integer | 0 | 1174 | 218 |
| Area indig. forest 2500 m radius | ha | integer | 0 | 1810 | 343 |
| Area pasture 500 m radius | ha | integer | 0 | 307 | 97 |
| Area planted forest 500 m radius | ha | integer | 0 | 299 | 16 |
| Area shrubland 500 m radius | ha | integer | 0 | 317 | 89 |
| Area indig. forest 500 m radius | ha | integer | 0 | 317 | 94 |
| Distance to nearest edge | log(m) | continuous | 1.18 | 3.29 | 2.01 |
| Fragment area | log(ha) | continuous | 0.27 | 3.76 | 2.17 |
| Perimeter:area ratio | log | continuous | -2.71 | -1.30 | -2.05 |
| <i>e) Geographic location</i> | | | | | |
| Northing | NZ projection | integer | 5444100 | 5518500 | 5479325 |
| Easting | NZ projection | integer | 2272900 | 2335000 | 2307225 |

(a) *Soil*. The soil variables pH, percent organic matter, cation exchange capacity, fertility and percent gravel (Table 2) were measured from three soil samples taken at random positions within each sampling plot. These variables were selected to characterise the physical and chemical attributes of each sampling plot at local level. Detailed descriptions of the soil analyses can be obtained from the author. Soil heterogeneity was calculated as the mean co-

efficient of variation of the above five soil variables. Ground heterogeneity was estimated visually on an ordinal scale from 1 (even ground, low heterogeneity) to 5 (very rugged, high heterogeneity).

(b) *Stand structure*. The stand structure variables (Table 2) were derived from measurements of all trees, i.e., woody species with a stem dbh of ≥ 10 cm. These were

Table 3. Pearson's correlation coefficient (r) between the original climate and geographic location variables and the first three PCA axes (named 'Radiation', 'Temp_mean' and 'Temp_min').

| | Radiation | Temp_mean | Temp_min |
|-----------------------------------|-----------|-----------|----------|
| Eigenvalue | 0.445 | 0.239 | 0.215 |
| Cumulative variance explained [%] | 44.5 | 68.4 | 89.9 |
| Variable | | | |
| Climate | | | |
| Mean annual temperature | - 0.216 | + 0.945 | 0.106 |
| October vapour pressure deficit | - 0.722 | + 0.292 | - 0.478 |
| Minimum temperature | - 0.153 | + 0.256 | 0.926 |
| Rainfall:pot. evaporation ratio | 0.004 | - 0.877 | 0.302 |
| Mean annual solar radiation | - 0.912 | - 0.150 | - 0.307 |
| Mean annual humidity | 0.889 | + 0.258 | 0.065 |
| Geographic location | | | |
| Northing | - 0.910 | - 0.102 | 0.047 |
| Easting | - 0.720 | + 0.002 | 0.657 |

tree density, i.e., the number of trees with a dbh ≥ 10 cm, the proportion of large trees (dbh ≥ 40 cm), the size differentiation of the tree individuals (Lee et al. 1999) with values close to 1 indicating equal distribution of tree sizes, the number of tree ferns (indicating a strong shading effect), total basal area and the abundance of *Nothofagus menziesii* (silver beech), a competitive species which is known to be a strong potential determinant of vascular plant species richness in New Zealand's forests (Ogden 1995, Leathwick et al. 1998). To avoid circularity, certain stand structure variables were not included as predictors of species richness for certain plant groups (e.g., tree density for tree species richness).

(c) *Climate*. The set of six climate variables (Table 2) was chosen on the basis of their relevance to the physiology of New Zealand tree species (Leathwick et al. 1998). They were derived from national climate models interpolated from climate station data (Leathwick and Stephens 1998). It could be argued that climate is more a local than a regional factor, but following Huston (1999) it was considered here as a regional factor, since it was derived from regional-scale models (Leathwick et al. 2003).

(d) *Land cover*. Eleven land cover variables (Table 2) describing the vegetation cover surrounding the sampling plots were derived from the New Zealand land cover database LCDB1 (Ministry for the Environment 2001). The area of four land cover classes (pasture, planted forest, shrubland, indigenous forest) surrounding each plot was calculated within a concentric neighbourhood size of 2500 m and also at 500 m radius. Additionally, three simple indices relating to fragment shape and isolation were calculated: distance from the centre of the sampling plot

to the nearest forest edge, fragment area and the perimeter:area ratio of the forest fragment in which the plot was located.

(e) *Geographic location*. The geographic location (Northing, Easting) of the sampling plots was included to check for any spatial determinants of species richness which might be independent of the above environmental factors.

Stepwise variable selection

The climate and geographic-location variables showed high intercorrelation and were therefore combined via a standardised, unrotated PCA. The first three PCA axes (named after their most highly correlated factors 'Radiation', 'Temp_mean' and 'Temp_min': Table 3) are by definition uncorrelated and were then used as surrogate predictor variables.

A forward and backward stepwise variable selection procedure based on the Akaike Information Criterion (AIC) was used to identify a set of variables that explained most of the variation in species richness of each plant group (Venables and Ripley 1999). Significance of the reduction in deviance of each variable was determined by analysis of variance using the approximate χ^2 distribution of the deviance (McCullagh and Nelder 2000, Crawley 1993). Multicollinearity, i.e., intercorrelation of the predictor variables retained in the minimal adequate models was checked with variance inflation factors (VIF):

$$VIF_i = 1 / (1 - R^2)$$

Table 4. Minimal adequate models of species richness, showing variables in order of selection in stepwise procedure. L = local variable, R = regional variable, p = probability, VIF = variance inflation factor, jack. r = jackknifed correlation between observed and predicted species richness, D^2_{adj} = proportion of total deviance explained, adjusted for number of variables.

| Predictor variables retained in minimal adequate models | Null deviance | Effect | Deviance reduction | p (χ^2) | VIF | jack. r | D^2_{adj} |
|---|---------------|--------|--------------------|----------------|------|---------|-------------|
| TOTAL SPECIES RICHNESS | 187.29 | | | | | 0.56 | 0.367 |
| (L) Relative abundance of <i>N. menziesii</i> | | – | 33.23 | <0.0001 | 3.87 | | |
| (L) Ground heterogeneity | | + | 21.85 | 0.0002 | 1.73 | | |
| (R) Area of surrounding pasture (2500 m) | | + | 8.34 | 0.0039 | 3.77 | | |
| (R) Fragment area | | + | 6.47 | 0.0109 | 7.69 | | |
| (R) 'Temp_mean' | | + | 3.15 | 0.0758 | 2.88 | | |
| (R) Area of surrounding shrubland (500 m) | | + | 3.23 | 0.0724 | 2.41 | | |
| NATIVE RICHNESS | 208.59 | | | | | 0.62 | 0.437 |
| (L) Ground heterogeneity | | + | 48.35 | <0.0001 | 1.73 | | |
| (L) Relative abundance of <i>N. menziesii</i> | | – | 21.04 | <0.0001 | 3.87 | | |
| (R) Area of surrounding shrubland (2500 m) | | + | 14.58 | 0.0001 | 4.28 | | |
| (R) Fragment area | | + | 7.52 | 0.0061 | 7.69 | | |
| (R) Area of surrounding pasture (2500 m) | | + | 4.22 | 0.0400 | 3.77 | | |
| (R) Area of surrounding shrubland (500 m) | | + | 2.94 | 0.0864 | 2.41 | | |
| WOODY RICHNESS | 127.94 | | | | | 0.57 | 0.360 |
| (R) Fragment area | | + | 17.12 | <0.0001 | 8.16 | | |
| (R) Area of surrounding pasture (2500 m) | | + | 11.10 | 0.0009 | 3.77 | | |
| (R) Area of surrounding shrubland (500 m) | | + | 9.75 | 0.0018 | 2.47 | | |
| (R) 'Temp_min' | | – | 4.09 | 0.0430 | 2.74 | | |
| (L) Relative abundance of <i>N. menziesii</i> | | – | 6.85 | 0.0089 | 3.87 | | |
| TREE RICHNESS | 223.03 | | | | | 0.70 | 0.541 |
| (L) Relative abundance of <i>N. menziesii</i> | | – | 65.75 | <0.0001 | 3.87 | | |
| (R) Fragment area | | + | 26.71 | <0.0001 | 7.69 | | |
| (R) Area of surrounding shrubland (2500 m) | | + | 14.26 | 0.0001 | 4.28 | | |
| (L) Tree size differentiation | | – | 7.61 | 0.0058 | 2.39 | | |
| (R) Area of surrounding indig. forest (2500 m) | | + | 4.11 | 0.0426 | 3.09 | | |
| (R) Area of surrounding pasture (2500 m) | | + | 3.77 | 0.0521 | 3.77 | | |
| (R) Area of surrounding shrubland (500 m) | | + | 3.58 | 0.0584 | 2.41 | | |
| HERBACEOUS RICHNESS | 176.49 | | | | | 0.47 | 0.282 |
| (L) Relative abundance of <i>N. menziesii</i> | | – | 24.90 | <0.0001 | 4.11 | | |
| (R) Area of surrounding indig. forest (500 m) | | – | 12.58 | 0.0004 | 4.83 | | |
| (R) Area of surrounding pasture (2500 m) | | + | 4.63 | 0.0315 | 3.99 | | |
| (L) Number of tree fern individuals | | + | 4.13 | 0.0419 | 1.58 | | |
| (L) Ground heterogeneity | | + | 8.54 | 0.0737 | 1.78 | | |
| (R) Distance to nearest edge | | – | 3.03 | 0.0815 | 3.70 | | |
| FERN RICHNESS | 174.83 | | | | | 0.58 | 0.339 |
| (R) Area of surrounding shrubland (2500 m) | | + | 33.34 | <0.0001 | 4.49 | | |
| (L) Total tree basal area in plot | | + | 7.71 | 0.0055 | 4.16 | | |
| (L) Relative abundance of <i>N. menziesii</i> | | – | 8.42 | 0.0037 | 4.10 | | |
| (L) Fertility | | – | 4.34 | 0.0372 | 3.66 | | |
| (L) Gravel | | + | 9.55 | 0.0020 | 1.71 | | |

where R^2 = multiple regression coefficient of variable 'i' on all other variables. A VIF < 10 is generally accepted as showing a degree of multicollinearity low enough for the results of the variable-selection procedure to be reliable (Freund and Wilson 1998).

Model evaluation

The goodness of fit of the models was assessed using the adjusted D^2 value (D^2_{adj}), a measure of the proportional deviance reduction weighted by the number of predictors in the model (Guisan and Zimmermann 2000).

D^2_{adj} values range from 0 to 1, high values indicating that a large proportion of the variation (deviance) in the response variable is explained by the model (Table 4).

The predictive accuracy of the models was assessed using jackknifing: each of the 143 sampling plots was in turn omitted from the dataset, a model was fitted using the remaining sampling plots, and the fitted model was then used to predict the species richness of the omitted plot. The correlation between observed and predicted species richness was expressed by Pearson's r (jackknifed r in Table 4).

Results

Model accuracies and variation explained

Total variation explained by the maximal models (Fig. 1) was similar to the total variation explained by the minimal adequate models (Table 4) indicating that the predictor variables omitted from each minimal adequate model contained little additional predictive power. Both total variation explained by the minimal adequate model and its predictive accuracy were highest for tree species

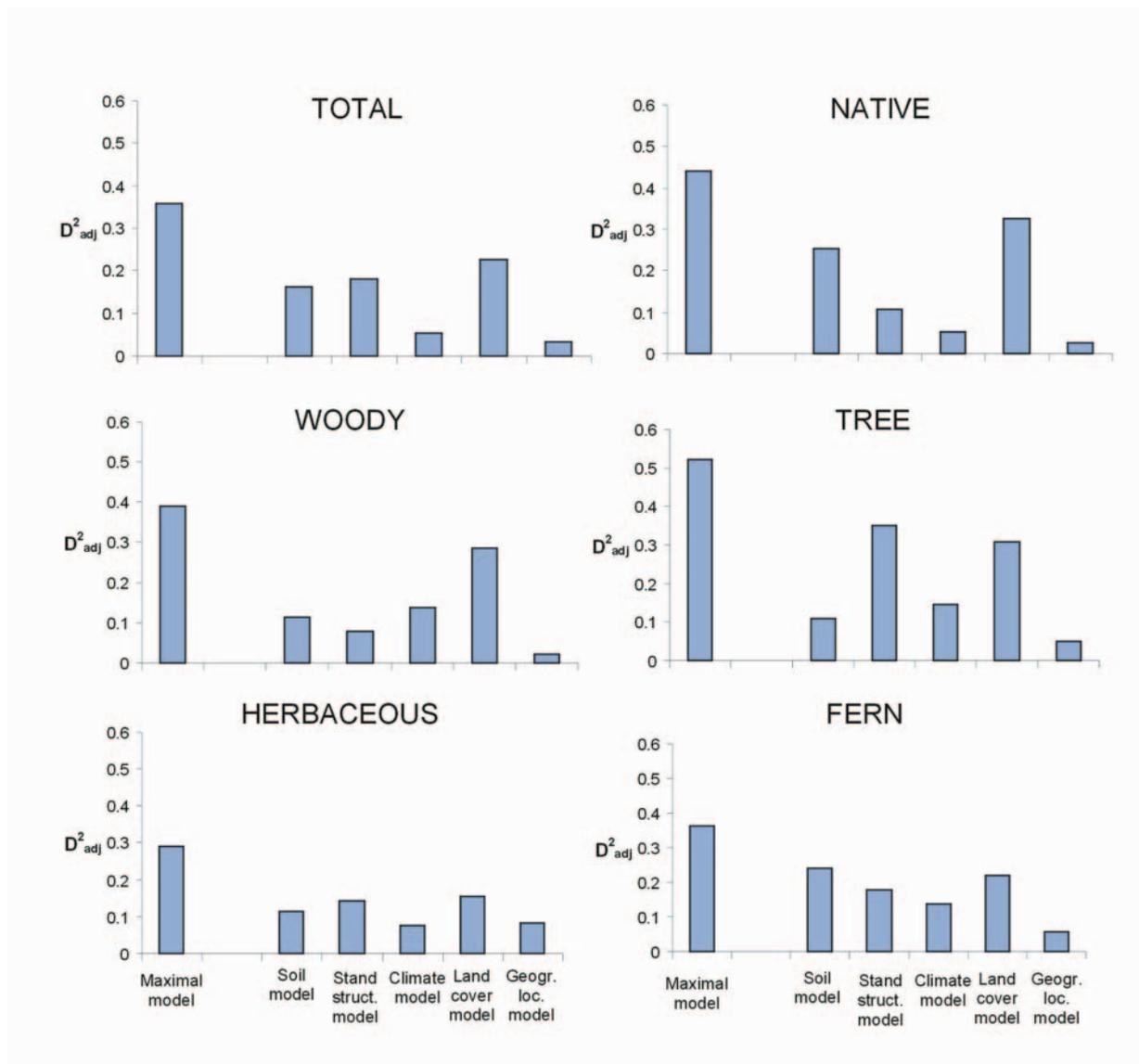


Figure 1. Model evaluation of maximal model (including all 32 predictor variables) and predictor category models, judged by the proportion of deviance explained, adjusted for the number of predictor variables used (D^2_{adj}).

richness ($D^2_{\text{adj}} = 0.541$, $r = 0.70$) and lowest for herbaceous species richness ($D^2_{\text{adj}} = 0.282$, $r = 0.47$) (Table 4).

Local factors

Both local and regional variables reduced the variation in species richness significantly for all six plant species groups (Fig. 1). The two local variable categories, soil and stand structure, explained 10–20% of the variation for most functional groups, and each *ca.* 15% of the total species richness (Fig. 1). For total and native richness, the two variables from those categories selected first for the minimum adequate model were the abundance of silver beech (leading to lower richness) and ground heterogeneity, leading to higher richness (Table 4). These two variables were important to a lesser extent for other functional groups.

Regional factors

The land cover variables explained the greatest amount of variation for the native, woody and (marginally) herbaceous plant groups by criterion D^2_{adj} (Fig. 1). For the other two groups, trees and ferns, the stand structure and soil models respectively were marginally more effective. The effectiveness of the land cover variables could be seen also in their representation in the minimal adequate models (Table 4). In contrast, the climate variables explained only small amounts of variation in species richness for all plant groups.

Though local variables were the more important for tree and native species, once the effect of these variables was accounted for, a number of regional variables explained further significant amounts of variation (Table 4). Woody species richness, on the other hand, appeared to be determined mainly by regional factors. Variation in tree species richness was explained primarily by abundance of *Nothofagus menziesii*, a local variable, but also by two regional variables, fragment area and the area of surrounding shrubland.

Discussion

Model accuracies and variation explained

Up to 54% (using D^2_{adj}) of the total variation in species richness was explained by the investigated variables, the maximum being for tree species richness, and the minimum (28%) being for herbaceous species richness. Though low, these values are intermediate to high relative to the proportion of variance explained (10–50%) in regional-scale vegetation generally expected in models of this type (Ohmann and Spies 1998). In a cultural landscape, such as the one studied here, forest composition

and species richness at a particular site is determined not only by the fundamental niche of the species (i.e., physiological responses to environmental factors such as climate, soil) but often to a much greater extent by the surrounding land cover and disturbance and historical factors, which are often difficult or impossible to quantify (Guisan et al. 1998, de Blois et al. 2002). Therefore, when forests with different disturbance histories are included, a high degree of uncertainty in the vegetation/environment relationship is to be expected (McCune and Allen 1995, Dumortier et al. 2002, Ross et al. 2002).

Local factors

Local variables explained most of the variation in species richness in four out of six species groups, especially the abundance of *Nothofagus menziesii* (silver beech) and ground heterogeneity (Table 4). Abundance of *Nothofagus menziesii* explained most of the variation in total, tree and herbaceous plot species richness, indicating a strong competitive component in local determinants of these groups. These results are consistent with the few quantitative accounts of tree alpha-diversity in New Zealand's indigenous forests (Ogden 1995, Leathwick et al. 1998, Bellingham et al. 1999). It has been suggested that the strong competitiveness of *Nothofagus menziesii* is based on mechanisms such as the shade tolerance of its seedlings, the acidity of its leaf litter, and its ectomycorrhizal symbiosis compared to the endomycorrhizal symbiosis of most other New Zealand tree species (Leathwick and Austin 2001). However, the latter authors suggest that the effect of these competitive interactions of *N. menziesii* changes in magnitude along environmental gradients.

Higher ground heterogeneity, another local variable, resulted in higher total and native species richness (Table 4), possibly due to the creation of additional microhabitats. Other local factors such as the number of tree fern individuals and the total basal area of trees were important possible determinants of herbaceous and fern species richness (Table 4). Dupré and Ehrlén (2002) similarly found that herbaceous species composition of forest fragments in Sweden was controlled mainly by local factors, though they added that animal-dispersed species were more affected by the regional factor of fragment area.

Our results are in accordance with the distance decay analyses by Nekola and White (1999) drawn from large scale forest distributions in Canada. In their study, tree species composition at particular sites showed a significantly slower decay in floristic similarity with increasing distance between sites than did herbaceous species, indicating that tree species distribution is controlled by factors acting at larger scales, whereas herbaceous species

are likely to be controlled by small scale, local factors. In a study of forest fragments in Belgium, the inclusion of local soil factors clearly improved the predictive accuracy of models of plant species richness (Dumortier et al. 2002). Another aspect for the flora involved in this study is that diaspores of the tree species are mostly bird-dispersed, and hence those species are likely to be influenced by regional factors, but those of non-woody species are generally not bird-dispersed, which may imply less dispersal limitation, and a greater role for local factors at the site.

Regional factors

The climate models explained only small amounts of variation in species richness, and a climate factor was rarely included in a minimal adequate model (Fig. 1, Table 4). In contrast, Leathwick et al. (1998) found that forest tree species richness across New Zealand was determined primarily by temperature and solar radiation. This may be due to the narrower climatic range in the present study. However, species composition (rather than species richness) in the investigated plots was driven mainly by climate variables (Ohlemüller 2003).

The land cover variables explained high amounts of variation, in particular for woody, tree and native species richness (Fig. 1). This could be because both a larger fragment and a larger surrounding area of forest/shrubland can give a larger species-pool, which applies especially to native and to woody species (Table 4). However, we also observed the opposite effect, namely that the area of pasture surrounding a plot is positively correlated with woody species richness in the plot. This may be explained with a crowding effect (Kareiva 1987, Collinge and Forman 1998), in that highly isolated forest patches within large areas of pasture act as foci for seed-dispersing animals, in particular birds.

A large area of indigenous forest/shrubland surrounding a fragment could give a microclimate more suitable for certain species groups. This might explain the highly significant positive effect of the area of surrounding shrubland on fern species richness within the plots. Several studies have claimed a strong influence of the surrounding landscape matrix on the species composition of fragments for both plants (Bastin and Thomas 1999, Honnay et al. 1999, Bullock et al. 2002) and animals (Pickett and Cadenasso 1995, Steffen-Dewenter et al. 2002), but very few (e.g., Ross et al. 2002) have investigated actual plant species richness at the plot level and its correlation with regional variables. Vellend (2003) concluded that in many cases the proportion of surrounding forest in a land-

scape can indeed account for large amounts of explained variation in species richness at plot level in a forest patch.

Limitations and future work

In this study, climate models derived from large-scale interpolations were used. However, the ideal climate values would be actual records from each plot, taken over several decades. Since such records were not available, it was and will be necessary to use interpolated climate models, as done in the present study.

The variables identified here via stepwise variable selection clearly differ in their ability to explain the observed variation in species richness, although, as in all regression-based analyses, correlation does not prove direct causal relationship. Our aim was to find predictive models, using the AIC criterion to account for the number of variables included (alternative criteria to AIC are available). Multicollinearity between variables (Mac Nally 2002) still means that other combinations of variables might yield deviance reductions similar to the ones in the models constructed here, though the variance inflation factors suggested this was not a large problem with our dataset.

Future work could study the effects of spatial scale on the observed species richness patterns. For example, at smaller plot sizes, herbaceous species richness may have been predicted with higher accuracy. Investigating the effect of scale on the accuracy of predictions of species richness of functionally different plant groups may lead to new insights into the processes maintaining biodiversity of these plant groups.

Conclusion

Plot records of a fixed area are essential when investigating possible local and regional determinants of species richness (Huston 1999). A complex of both local and regional variables can explain variation in the richness of various plant groups. The landscape matrix has a demonstrated effect, and should be included in distribution models of species and communities in fragmented landscapes (Austin et al. 1996, Haila 2002). Revegetation efforts can use a climate-based predictive distribution model to identify areas in which certain species or communities are most likely to establish, but with the addition of the landscape matrix these models could adjust re-vegetation plans towards areas closer to a dispersal source, that are likely to have high diaspore influx (lower replanting effort would be necessary).

The species richness of different functional groups in the forest system investigated was likely to be determined

by both local and regional factors. The low degree to which the climate variables explained tree species richness contrasts with their ability to predict species composition and the richness of exotic species. It suggests that there are tree species-pools of approximately equal size adapted to a range of climate conditions.

We conclude that there is a measurable difference in the effect of both local and regional factors on vascular plant species richness at plot level (20 m × 20 m) in the indigenous forest fragments investigated here. The recognition of these differences may be important for the conservation and management of functionally different plant groups in areas with fragmented indigenous vegetation.

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