Modelling Responses of New Zealand's Indigenous Forests to Global Warming

J. R. LEATHWICK[1], D. WHITEHEAD[2], M. MCLEOD[1]

Manaaki Whenua - Landcare Research, [1]Private Bag 3127, Hamilton and [2]P.O. Box 69, Lincoln, New Zealand

Summary. Data from 14 500 plots are used in conjunction with estimates of current climate and other site conditions to develop a model allowing prediction of likely effects of global warming on New Zealand's native forests. Relationships between 35 major forest species and environment are modelled using Generalised Additive Models, with mean annual temperature, temperature seasonality, mean annual solar radiation, an integral of cumulative annual water deficit, lithology, and drainage used as predictors. The resulting regressions are used to predict species distributions for points on a 5 km grid across New Zealand, and predictions for all species are combined and clustered to form groups of similar composition. Substantial improvements in model predictions for the four *Nothofagus* species, which are ill-adjusted to climate, are made through the incorporation of parameters to detect residual spatial autocorrelation by indicating whether each species occurs on other adjacent plots. Predictions for other species are improved through the incorporation of a term modelling interaction with the patchily distributed but locally dominant *Nothofagus* species. Predictions formed using data perturbed to represent an overall 2°C rise in temperatures indicate that a substantial disequilibrium is likely between current forest pattern and future climates. Future work will focus on modelling the dynamic processes likely to occur as a result of this disequilibrium.

1. INTRODUCTION

The potential impacts of both elevated temperature and atmospheric carbon dioxide concentration on natural vegetation are the subject of an increasing literature [e.g., Prentice et al. 1992, Solomon and Shugart 1993, Lenihan 1993, Brzeziuecki et al. 1995], and remain issues of major ecological significance. A number of studies of potential impacts at global to regional scales are contributing to the GCTE Core Research Programme [Steffen et al., 1992], with investigation of how environmental variables control the distribution of species an important component of this work. Regional studies are important providing the greater levels of detail required for incorporation into models operating at the global scale. New Zealand is placed particularly well as a site for such research, since it has wide latitudinal and climatic ranges, and extensive areas of relatively intact and intensively sampled natural forests.

Generally, New Zealand's forests occupy sites with mild, moist climates; the former forests of the drier eastern parts of both islands are severely reduced in extent following burning by Maori before the arrival of Europeans [McGlone 1983]. Sites that are warmer and receive higher solar radiation are dominated generally by broadleaved trees, with only scattered emergent conifers [Leathwick 1995]. Dominance by conifers is generally restricted to Quaternary surfaces or extensive plateaux formed during cataclysmic rhyolitic eruptions. Forests on cooler sites and/or those with lower solar radiation are generally dominated either by combinations of conifer and broadleaved species or by southern beeches of the genus *Nothofagus* [Wardle 1984].

The objective of the work reported here was to develop a model to relate forest composition to major climate and edaphic factors. The following constraints were applied:

- The model should be based on analysis of the relationships between individual species and the environment (as opposed to community-based), to accommodate the likely differing responses of species to changing environmental conditions [e.g., Lenihan 1993].

- The model should be robust in its assumptions concerning the nature of species:environment relationships. Austin and Gaywood [1995] and Leathwick [1995] have demonstrated that symmetrical gaussian responses between species and environmental gradients, although widely assumed and computationally attractive, occur less frequently than is often supposed.

- Climatic variables used in the analysis should be closely linked to physiological processes [Prentice et al. 1992, Lenihan 1993].

2. DATA USED FOR MODELLING

Forest composition data used in this study were taken from two sources. The first was an extensive national timber inventory undertaken between the mid 1940s and late 1960s, when timber volumes were measured on nearly 15 000 one-acre (0.4 ha) plots. Approximately 10 500 of these were selected, covering the majority of the indigenous forest of the North Island and much of the lowland forest in the South Island. They were supplemented by a further 4000 plots, each 0.04 ha, from catchment surveys in South Island high-country forests. In the analysis, the data used were summarised to the numbers of trees with a diameter exceeding 305 mm diameter at 1.4 m above ground level for each species, and a variable indicating plot size. Estimates of climate variables for all the plots were derived from mathematical surfaces fitted to climate station data for New Zealand using BIOCLIM by Mitchell [1991]. These consisted of monthly estimates of mean daily maximum and minimum air temperature, precipitation, and daily solar radiation, and were transformed before analysis into forms more relevant to plant

growth and distribution, as follows:

Light, which is the key determinant of potential plant growth, was typified for each plot by converting monthly solar radiation estimates to a single annual estimate, i.e., mean annual solar radiation.

Temperature characteristics for each plot were typified by two variables. The overall temperature conditions, which together with water availability regulate growth processes, were described using mean annual temperature. Winter minimum temperatures, which strongly influence plant survival, were described by an index calculated by subtracting mean annual temperature from mean July minima after both had been converted to standard deviation units [Leathwick 1995]. Negative values indicated that the climate was more continental, and positive values indicated a more maritime climate.

Available *water* at each plot was described using an annual integral of root zone water deficit, calculated using a simple daily water balance model incorporating climate and soil characteristics. The root zone water storage S_j on day j is given by

$$S_j = S_{j-1} + P_j - E_j - D_j \qquad (1)$$

where P_j, E_j, and D_j are the daily precipitation, evaporation, and drainage, respectively. Soil texture and rooting depth for each plot were estimated by overlaying plot coordinates onto soil maps [New Zealand Soil Bureau 1968]. The available water holding capacity and the relationship between water content and water potential for the soil at each plot were estimated from parameters for the water retention function given by Clapp and Hornberger [1978]. Daily precipitation was estimated by dividing the monthly BIOCLIM precipitation estimates into equal daily amounts. Evaporation comprises $E_t + g \beta P$, where β is the fraction of precipitation intercepted by forest canopies set to a typical value of 0.25 [Whitehead & Kelliher 1991], and g is an empirical coefficient set to 0.8 [Giles et al. 1984]. E_t was calculated from estimates of available energy at each site (A), as

$$E_t = \varphi \; \alpha \; A \; \frac{\varepsilon}{[(\varepsilon + 1)\lambda]} \qquad (2)$$

where the coefficient α is 0.7 for forest, and ε and λ are the change in sensible heat content of saturated air, and the latent heat of vaporisation at the appropriate temperature, respectively [Spittlehouse 1989]. The coefficient φ reduces E_t as root zone water content decreases. It is set equal to 1 when the root zone water storage is at "field capacity" and decreases linearly to reach 0 when root zone water storage reaches "permanent wilting point" [Whitehead & Kelliher 1991]. Daily values of A were calculated from estimates of solar radiation [Spittlehouse 1989] from the BIOCLIM model. Drainage was assumed to be zero while the root zone water content was below field capacity, and when this value was exceeded all surplus additions of precipitation were assumed to be drainage. The components of the water balance were calculated on a daily basis and, to allow comparison between sites with different soil characteristics, S_j was converted to root zone water potential. When this fell below

field capacity the daily values were summed to give an annual integral of water deficit for each plot.

Two additional variables indicating edaphic conditions at each plot were also used in the analysis. The underlying lithology for each plot was determined by overlaying plot coordinates onto a digital copy of the 1:1 000 000 geological map of New Zealand [Anon. 1972a,b]. A subjective three-class categorisation of site drainage was taken from the original data.

3. BUILDING INITIAL CLIMATIC MODELS

Initial models describing relationships between the distribution of 35 species and the six environmental variables were developed using the technique of Generalised Additive Models (GAMs) developed by Hastie and Tibshirani [1990] and implemented in Splus. In order to eliminate the large number of zero observations beyond the environmental limits of species, the data were restricted to 100 observations beyond the upper and lower limits for species occurrence in relation to each climatic variable. Multiple regression models were then developed using a backwards stepwise procedure. Because of widespread problems with over-dispersion, all models were specified using an option which allows the scale factor to be estimated from the data. The significance of removal of individual terms was tested using scaled changes in deviance, which are distributed similarly to an F-statistic. Once finalised, regression equations were used to calculate an independent set of predictions using estimates of the same environmental variables for positions on a 5 km grid across New Zealand, and results were compared with actual distributions. Finally, predicted values for all 35 species were combined into a single matrix and clustered using a non-hierarchical technique to define groups of similar composition.
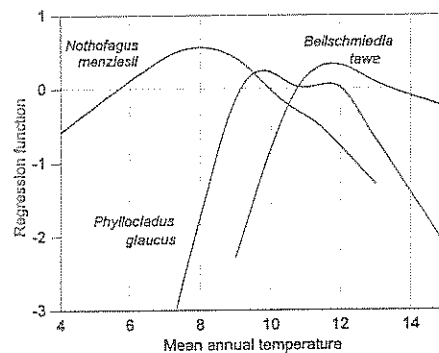

Figure 1: Fitted smooths for three species in relation to mean annual temperature (°C).

For the majority of species, all six environmental variables were retained as significant terms in the final regression equation. Many of the fitted regression functions for continuous variables were of a form not easily approximated by conventional parametric techniques (e.g., Fig. 1). Temperature and solar radiation were generally the variables most strongly correlated with species distribution, followed by the integral of root zone
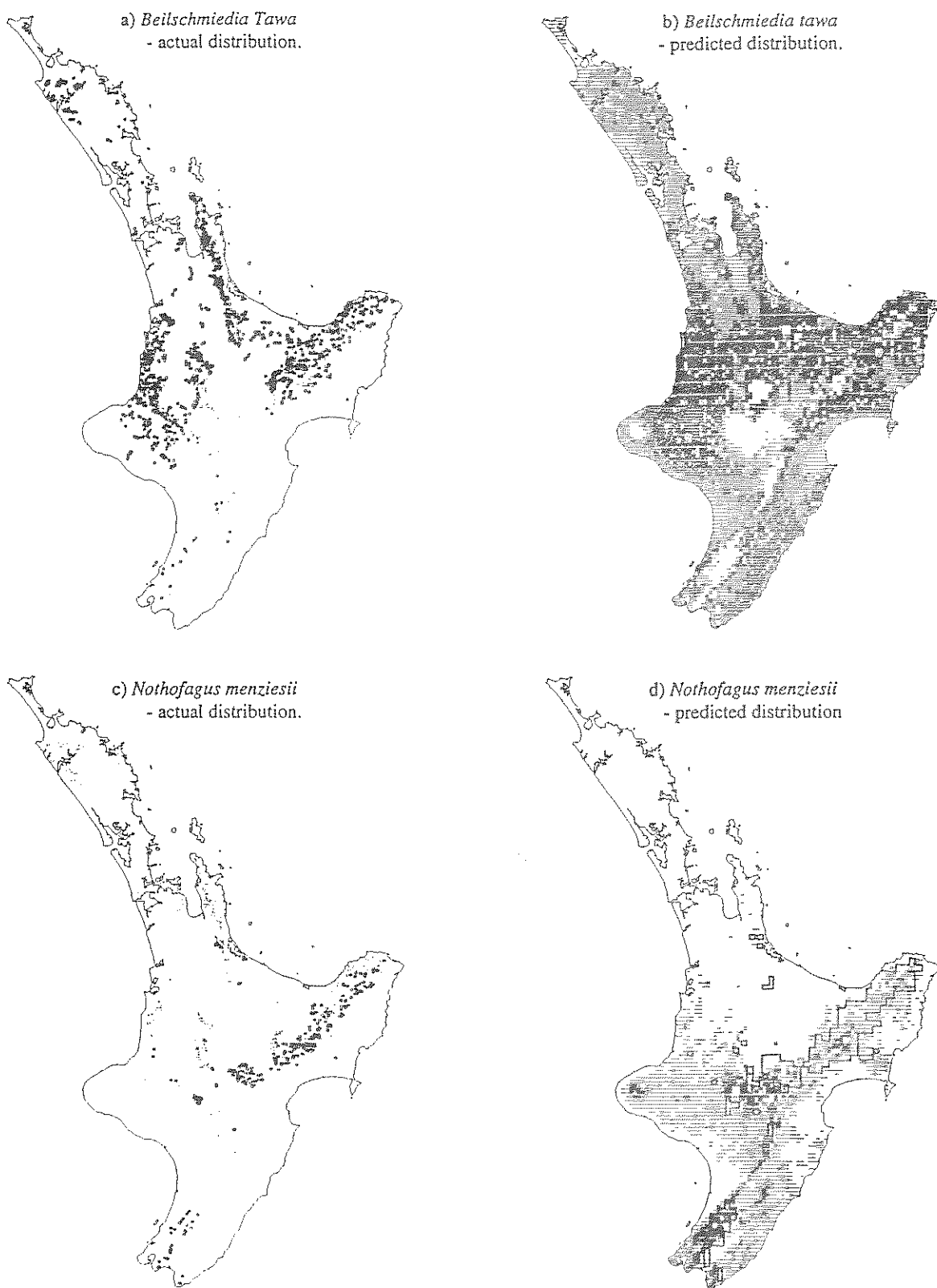
Figure 2: Actual and predicted distribution of *Beilschmiedia tawa* and *Nothofagus menziesii* in the North Island. In (a) and (c), actual occurrences are shown by a 'o', and absences by a dot; in (c) the distribution as mapped by Wardle [1984] is shown by bold lines. In (b) and (d), increasing intensity of shading indicates increasing predicted density in steps of 1-2, 3-5, 6-10, 11-20, and >21 stems/0.4 ha plot.

water deficit and lithology; drainage generally played a minor role. For many species there was close agreement between current distribution and that predicted across the 5 km grid (e.g., Fig. 2(a) & (b)). For others, however, and most notably for the four *Nothofagus* species, there were marked discrepancies (e.g., Fig. 2(c) & (d)). As a consequence, when predictions for all 35 species were combined, the resulting groups failed to separate adequately the current distribution of *Nothofagus*-dominant forest communities from the others. Clearly, an alternative approach is required if we are to adequately model the distribution of these 'difficult' species.

4. MODELLING *NOTHOFAGUS* DISTRIBUTION

The strongly clumped current distribution of *Nothofagus* species, with boundaries not aligned to any apparent climatic gradients, suggested that other processes were also strongly determining their distribution. The conceptual framework developed by Legendre [1993] for handling spatially autocorrelated ecological data provided a useful paradigm for further progress. Legendre suggested that where species distribution is controlled to some degree by environment, the spatial patterning or autocorrelation can be partitioned into two components, one explained by the patterning in the available environmental data, and the other independent. The independent component can be attributable either to 'missing' environmental parameters, to other life history-related factors such as competition, predation, or disturbance dynamics, or to historical events.

In order to determine the magnitude of this 'independent' component for each species, we used the procedure described by Borcard and Legendre [1994]. For each species we tested the significance of adding to the basic environmental model a presence/absence variable indicating for each plot whether that species occurred on other plots within a 2.5 km radius.

Scaled reductions in residual deviance varied markedly between species, but were statistically significant for all 35. For some species the reductions were of the order of several tens of thousands of units (Table 1). Notably, ratios of the deviance explained by the spatial variable to that explained by the environmental variables alone were much higher for the *Nothofagus* species than for other widespread species, confirming our suspicion that non-environmental factors also had an important influence on their distributions.

More important, at a practical level the resulting regression equations allowed much more realistic recovery of the current distribution of these species (Fig. 3). This was done by using existing maps [Wardle 1984] to establish whether each *Nothofagus* species occurred within a square surrounding each 5 km grid point, the resulting variable paralleling the 'proximity' variable used to develop the original regression equation. As a consequence, the resulting predictions for the four *Nothofagus* species were effectively adjusted point by point to take account of whether or not that species occurred in the vicinity. Although problems could arise for some species when attempting to make predictions in a changed climate for which no prior knowledge of species distribution exists, constraining the *Nothofagus*

species to their current range when making predictions in the near future is ecologically realistic, given the well known conservatism of their dispersal [e.g., Rogers 1989].

Table 1: Summary of changes in deviance for major species. Total dev. = total deviance (x10^5); Env. dev. = deviance accounted for by fitting environmental variables (x10^5); Spat. dev. = increase in deviance explained after adding spatial variable (x10^5); Env./Spat = ratio of Spat. dev. to Env. dev.

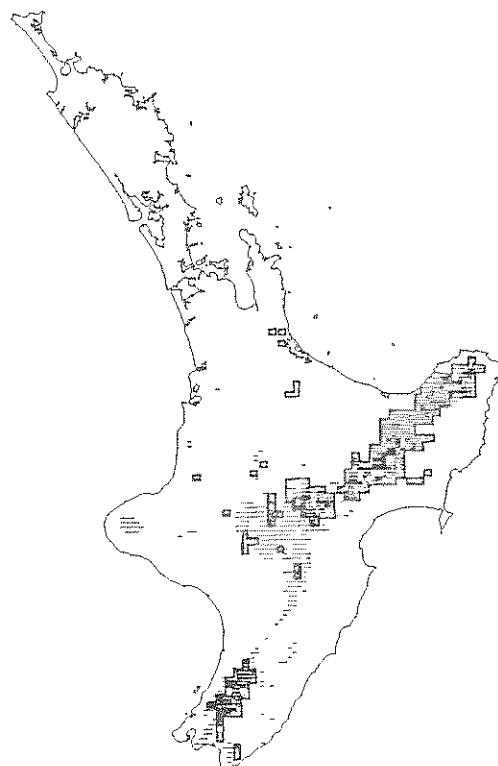| Species	Total dev.	Env. dev.	Spat. dev.	Spat./ Env.
Beilschmiedia tawa	1.14	0.49	0.04	0.08
Dacrydium cupressinum	2.04	1.11	0.02	0.01
Nothofagus fusca	1.48	0.57	0.28	0.50
N. menziesii	2.04	0.75	0.44	0.59
N. solandri	1.26	0.44	0.19	0.48
N. truncata	13.5	0.54	0.26	0.48
Prumnopitys ferruginea	0.75	0.27	0.01	0.05
Weinmannia racemosa	1.97	0.64	0.07	0.12

Figure 3: Predicted density of *Nothofagus menziesii* using spatial autocorrelation model - shading corresponds to increasing density, as for Fig. 2.

5. INCORPORATING COMPETITION EFFECTS

Although a substantial improvement was evident in the predictive map of forest communities, with the *Nothofagus*-dominant communities much more realistically modelled, the predictions for some non-*Nothofagus* communities were still deficient. In order to resolve this problem, we tested to see if the distribution of non-*Nothofagus* species could be more accurately predicted by taking account of interaction effects between them and the strongly competitive but patchily distributed *Nothofagus* species.

We did this by adding to each of the individual species regressions a variable indicating the total number of *Nothofagus* trees in each plot. Scaled decreases in deviance varied widely, but were statistically significant for all but one species, and exceeded 200 for nearly half, indicating substantial and widespread interaction effects between *Nothofagus* and other species. Although most species declined in number as *Nothofagus* numbers increased (e.g., *Beilschmiedia tawa* - Fig. 4), a small number of species typical of infertile soils were most numerous on plots with low to moderate numbers of *Nothofagus* (e.g., *Phyllocladus glaucus* - Fig. 4).

Predictions from the individual regressions were then recalculated across the 5 km grid for all species, with an additional predictor variable indicating predicted total density from the regressions for the *Nothofagus* species. Results showed marked improvement, both for species with strong negative and strong positive association with *Nothofagus* species (e.g., Fig. 5). Combined results from this refined model substantially recovered New Zealand's existing forest pattern.
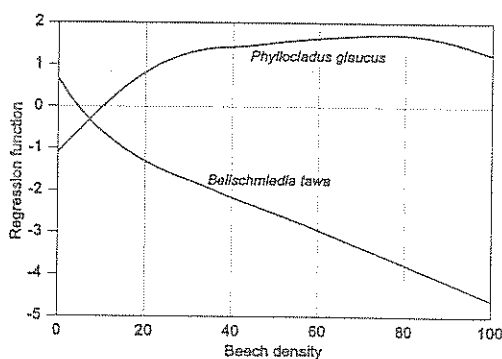

Figure 5: Predicted density of *Beilschmiedia tawa* after fitting *Nothofagus* competition effect - shading corresponds to increasing density, as for Fig. 2.

Figure 4: Fitted smooths for two species in relation to *Nothofagus* density.

6. PREDICTIONS OF CHANGE

Once the regression models successfully recovered New Zealand's current forest pattern, a revised set of environmental variables were created for the 5 km grid points assuming an overall elevation of temperature by 2°C. Both temperature and precipitation estimates were altered using the New Zealand scenarios of Mullan [1994], which provide regional patterns of change in temperature and precipitation in relation to wider scale changes in mean annual temperature. Estimates of the integral of root zone water deficit were then recalculated using the new temperature and precipitation estimates. Finally, predictions were formed for each species with this 'perturbed' environmental dataset, and the results were combined and classified to give an indication of likely changes in forest community patterns.

Comparison of current forest pattern, as recovered by the model, with predictions from the perturbed dataset suggest that an overall elevation of mean annual temperature by 2°C is likely to cause a marked forest:climate disequilibrium. Upwards migration into montane areas of species currently dominant in the lowlands is indicated throughout New Zealand, with broadleaved species predicted to invade large areas now largely dominated by *Nothofagus* spp. Southwards migration of northern species is also predicted, particularly into the higher solar radiation areas of the eastern South Island. In contrast, the much cloudier environments of the western South Island would appear less likely to be invaded by species currently dominant further north.

7. FUTURE DEVELOPMENTS

Results to date indicate how a small set of environmental variables can be used to successfully predict the distribution of many New Zealand forest tree species. Results also indicate how

predictions can be significantly improved using spatial and competition parameters. The former allows the detection of residual spatial autocorrelation, provides an objective method for partitioning the relative importance of environmental versus other factors, and allows the distribution of climatically ill-adjusted species to be more realistically modelled. The latter gives a substantial refinement in predictions of the distribution of species subject to competitive displacement by species ill-sorted in relation to climate.

Although the correlational approach used here offers considerable advantages in its ability to be applied over wide spatial areas, it can give no indication as to the time scales over which predicted changes will occur, or to the likely successional pathways which will be followed [Lenihan 1993]. Conversely, although mechanistic models can give some insight into these latter questions, at the present time their insights can be scaled up from the individual tree or forest stand to a landscape scale only with difficulty. The challenge we face, in common with researchers elsewhere, is to develop a hybrid approach which brings together the spatial strengths of correlational models with the more explicitly mechanistic insights from dynamic models.

In particular, we need to incorporate the dynamic processes likely in the forest:climate disequilibrium which will occur if temperatures rise as predicted. For example, how will elevated levels of atmospheric CO_2 alter the current environmental relationships of mature trees? Will climatic changes be sufficient to bring about accelerated death of current site occupants, or will new invaders have to await normal senescence? How will differences in dispersal ability filter the mix of new species invading sites as temperatures rise? How effectively will species be able to migrate in landscapes where once extensive tracts of forest are now severely fragmented?

Building these factors in will present a considerable challenge, but by combining recent advances in modelling the spatial nature of invasion [e.g., Hengeveld 1994] with the quantitative understanding of species:environment relationships developed here, further progress seems achievable.

8. ACKNOWLEDGMENTS

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