

## DETERMINANTS OF PLANT EXTINCTION AND RARITY 145 YEARS AFTER EUROPEAN SETTLEMENT OF AUCKLAND, NEW ZEALAND

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**Abstract.** We analyze a 114-year historical record (1871–1985) of the change in abundance of 373 native plant species in Auckland, New Zealand, with the aim of identifying the attributes that predisposed some species to local extinction and rarity following European settlement. The 1871 survey records the relative abundance of native plants in the Auckland area just 31 years after Europeans began clearing the native vegetation for settlement, whereas the 1985 survey records the relative abundance of the same species 114 years later, when the area had been transformed into an urban landscape. Four attributes were significantly and independently related to the probability that a species was locally extinct or rare in 1985: (1) compared with species that were common in 1871, initially rare species were more likely to be extinct or rare in 1985; (2) compared with tall species, short species were more likely to be extinct or rare in 1985; (3) gymnosperms and dicotyledons were more likely to be extinct or rare in 1985 than were pteridophytes or monocotyledons; and (4) species occupying habitats that suffered the greatest loss of area following European settlement were more likely to be extinct or rare in 1985 relative to species occupying less affected habitats. Two additional attributes, long-distance dispersal ability and capacity for clonal spread, failed to independently explain significant variation in 1985 abundance. We discuss the likely causes of these relationships and consider their implications for understanding extinction processes.

**Key words:** *clonal spread; dispersal ability; exotic invasion; extinction processes; habitat destruction; human settlement; New Zealand; phylogenetic effects; plant rarity; population decline.*

### INTRODUCTION

The arrival and settlement of humans in an area is invariably followed by population declines and local extinctions of native species (Wilson 1988, Steadman 1995). These losses can result from various human impacts, including the direct exploitation of native species (Diamond 1984), the destruction and fragmentation of native habitats (Pimm and Askins 1995, Wilcove et al. 1998), the introduction of exotic predators and competitors (Atkinson 1985, Savidge 1987), and the alteration of major biogeochemical and disturbance cycles (Leach and Givinish 1996, Vitousek et al. 1997). Many of these impacts have intensified within the last 200 years because of rapid human population growth and advances in technology. As a consequence, the current rate at which local populations (as opposed to entire species) are disappearing due to human activities is alarming; Hughes et al. (1997) estimate that  $16 \times 10^6$  genetically distinct local populations are destroyed annually in tropical forests alone.

Nevertheless, not all species are equally threatened by human impacts. While some decline rapidly to local extinction, other species are able to persist, and even

increase in abundance, following habitat alteration by humans (Laurance 1994, Angermeier 1995, Bolger et al. 1997, Davies and Margules 1998). Our understanding of the processes driving the current wave of human-induced extinctions, and the final outcome of those processes, would be enhanced if we knew why some species are able to persist while others go extinct. Specifically, do the species most at risk of extinction from the impacts of human settlement share a predictable set of attributes? The answer to this question is central to efforts aimed at conserving biodiversity (Meffe and Carroll 1994). A knowledge of the relative vulnerability of species to extinction would help in making informed decisions about where best to direct scarce conservation resources.

Opportunities to study in detail the patterns of local extinction that accompany human settlement and habitat modification are rare. Many parts of the world were settled and substantially altered by humans a long time ago, so that few records of the biotic responses to those changes exist. For some taxa, notably mammals and birds, the broad pattern of local extinctions can be reconstructed from fossil or historical records (Brash 1987, Newmark 1987, Atkinson and Millener 1991). For most taxa, however, such records do not exist and the extent of even relatively recent species losses is uncertain. Several studies have begun to directly doc-

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ument human impacts on native biota, particularly the effects of habitat fragmentation, using large-scale experiments (Lovejoy et al. 1984, Robinson et al. 1992, Margules 1993). Although the detailed and replicated nature of these experiments should vastly improve our knowledge of extinction processes, the relatively short time that most experiments have been running currently limits our understanding to short-term impacts. At only a few localities do we have accurate, long-term records of the species losses that have resulted from human-caused habitat alteration (e.g., Drayton and Primack 1996, Leach and Givinish 1996, Turner et al. 1996).

New Zealand was the world's last major land mass to be colonized by humans. The first evidence of Maori settlement dates from about AD 1200 (Anderson 1991), with a second wave of European settlers arriving in the mid 1800s. Because of its recent history of colonization, the impact of these two waves of human settlement on New Zealand's native biota can often be clearly discerned. The prehistoric faunal extinctions and vegetation change that accompanied Maori settlement can be broadly reconstructed from subfossil and pollen records (Holdaway 1989, McGlone 1989, Atkinson and Millener 1991). A more detailed record of the impact of European settlement is available at those localities where scientists and naturalists systematically documented the biota shortly after European arrival.

In this paper, we analyze data from one such locality, a 114-year historical record (1871–1985) describing the change in abundance and local extinction of native plants following European settlement and urban expansion in Auckland, New Zealand (Kirk 1871, Esler 1991). The baseline survey of 1871 by Thomas Kirk records the native plant species present in the Auckland area 31 years after Europeans first settled and began clearing the native vegetation. The 1985 survey by Alan Esler records the native plant species present 114 years later, after the area had been transformed into an urban landscape. Because Kirk found no evidence of plant extinctions in the area between initial European settlement in 1840 and his survey of 1871 (Kirk 1871), this record documents all of the local plant extinctions that occurred in the first 145 years of European settlement. The record is also unusually detailed; not only are the species present in 1871 and 1985 carefully documented, but also there are data on the relative abundance of each species at those times. We use this historical record to test five hypotheses about attributes thought to predispose species to local extinction and rarity through impacts associated with human settlement.

1) Rates of extinction should be negatively correlated with abundance in 1871 because initially rare species should be at higher risk of extinction from the direct effects of habitat destruction or because of subsequent demographic, genetic, or environmental stochasticity (Gilpin and Soulé 1986, Johnson 1998).

2) Rates of extinction should be higher among spe-

cies common in vegetation types that suffered the greatest loss of area, because species–area relationships and metapopulation models predict that extinction rate should be proportional to the rate of habitat loss (Simberloff 1992, Tilman et al. 1994).

3) Rates of extinction should be negatively correlated with plant height because, even if populations become nonviable at the same rate, individuals of tall, long-lived species will persist longer in the landscape (Turner et al. 1996).

4) Rates of extinction should be lower in good vs. poor long-distance dispersers because good dispersers can “rescue” populations isolated by habitat fragmentation or can colonize unoccupied habitat fragments (Hanski 1991, Lawton 1995).

5) Rates of extinction should be lower in species with the capacity for clonal spread because clonally spreading species should be less susceptible to population declines resulting from seed or pollination failure (Bond 1995, Fischer and Stocklin 1997). Such failures are predicted to be an important consequence of the local extinction of seed-dispersing or pollinating mutualists (Janzen 1987, Clout and Hay 1989, Bond 1995).

## METHODS

### *The data set*

In 1871, the botanist Thomas Kirk published a description of the vegetation with a list of all the native vascular plant species found in a 174-km<sup>2</sup> area comprising the isthmus and adjacent land on which Auckland city is located (Kirk 1871; see Esler 1987 for descriptions of the climate, geology, and vegetation of the Auckland area). Kirk ranked each species in one of eight “relative abundance” categories that reflected aspects of both the distribution and local abundance of species in the study area (characteristics that are usually correlated; see Brown 1984, Hanski et al. 1993). Kirk stated that “the first three [categories] are restricted to local species, represented by a few individuals [whereas the next two categories] are used for local species, represented by a larger number of individuals;” in an earlier paper using the same categories (Kirk 1870), he stated that the scheme “gives a definite idea of the distribution of each species.”

Auckland city was founded and settled by Europeans in 1840. At that time, Auckland had a near-continuous cover of native vegetation broken by only a few patches of Maori cultivation (Graham 1922, Cranwell 1981). The native vegetation had nevertheless been substantially altered by several centuries of Maori occupation. The area around Auckland was covered in tall forest prior to Maori arrival, but in 1840 it was dominated by fire-induced shrubland and open vegetation, and *Pteridium esculentum* fernland on the more fertile volcanic soils that were previously under Maori cultivation (Kirk 1871, Cranwell 1981, Esler 1991). Maori settle-

ments in the Auckland area were once extensive, but, because of tribal warring, most Maori had abandoned the area in the 150 years prior to European settlement (Graham 1922). When Europeans arrived, those areas previously disturbed by fire or cultivation were succeeding back to tall forest. There were extensive wetlands and coastal vegetation, with patches of tall forest mostly confined to steep-sided gullies that afforded protection from fire (Kirk 1871, Cranwell 1981).

At the time Kirk published his survey in 1871, Auckland was a small town of 23 000 people with much of the surrounding vegetation cleared for agriculture (Kirk 1871). Despite this, large patches of native vegetation remained and Kirk found "no evidence to show that the operations of the settler have entirely eradicated even a single species." His survey nevertheless records the relative abundance of native plants in a landscape already substantially altered by 31 years of European occupation.

Between 1970 and 1985, Alan Esler repeated Kirk's survey and ranked each species into six relative abundance categories, compressing four of Kirk's original categories into two (Esler 1991). We used Esler's scheme in all of the analyses that follow, with relative abundance categories being: very local, local, fairly local, moderately common, common, and very common. We add a seventh category, "extinct," for species recorded in 1871 that had disappeared by 1985. Esler also classified each species by the vegetation type in which it was most commonly found: forest, coastal (under the influence of salt water), wetland, shrubland (dominated by *Leptospermum scoparium* or *Kunzea ericoides*), or open vegetation.

Esler's study area covered all of Kirk's original 174-km<sup>2</sup> area, but included additional land to the north, south, and west, increasing the total area to 308 km<sup>2</sup> (see Esler 1987 for a map and description of the enlarged study area). Esler enlarged the study area to include most of 1985 urban Auckland, and this enlargement has a potential consequence. Estimating the number of species lost between 1871 and 1985 by counting the number of species that Kirk recorded, but that Esler failed to find, may underestimate the true rate of local extinction in Kirk's original study area. A species recorded by Esler in 1985 could be locally extinct in Kirk's study area, but still persist in Esler's enlarged study area.

Between 1871 and 1985, the human population in the enlarged study area increased to ~820 000 and the countryside was transformed into an urban landscape, losing most of its remaining cover of native vegetation (Esler 1991). By 1985, Esler noted that "significant native vegetation remains," but the remnants were small, scattered, and often highly modified fragments that survived as public reserves or in sites unsuited to urban development (Millener 1979, Cranwell 1981, Smale and Gardner 1999). Habitat loss was not uniform across vegetation types. Because it occupied land most

suited to urban development, wetland, shrubland, and open vegetation suffered a disproportionately greater loss of area than forest or coastal vegetation (Esler 1987, 1991). Europeans further altered the composition of the Auckland flora by introducing numerous exotic plants. By 1985, 615 species of exotic plants were naturalized in the Auckland area (Esler and Astridge 1987), several of which pose a threat to native plants because of their aggressive colonizing ability (Esler 1988, 1991, Smale and Gardner 1999).

Esler (1991) listed 399 native plants that Kirk recorded in the study area in 1871, but Esler queried the status of 26 species because subsequent changes in taxonomy made it unclear exactly to which species Kirk referred. We restricted our analysis to the 373 species for which there was no confusion in taxonomy. To test hypotheses 3–5 (see *Introduction*), we collected data on the long-distance dispersal ability, capacity for clonal spread, and height of each species from flora descriptions, herbarium specimens, and our personal observations. We ranked each species as either a "good" or "poor" long-distance disperser on the basis of diaspore morphology. Good dispersers had one or more of: a fleshy diaspore, hooked diaspore, winged or plumed diaspore, dust seeds, or spores (Willson et al. 1990, Thompson and Hodgson 1996). Species with creeping aerial stems or spreading rhizomes were classified as having a capacity for clonal spread, and each species was ranked in one of five height categories (excluding reproductive structures):  $\leq 0.3$ ,  $>0.3$ –1,  $>1$ –3,  $>3$ –10, and  $>10$  m tall.

In summary, our data set contained the following for each of the 373 native plant species present in Auckland in 1871: relative abundance in 1871 (six ordered categories), relative abundance in 1985 (seven ordered categories), vegetation type (five nominal categories), long-distance dispersal ability (two nominal categories), capacity for clonal spread (two nominal categories), and height (five ordered categories).

#### *Statistical methods*

We tested the five hypotheses outlined in the *Introduction* by quantifying the relationships between the response variable abundance in 1985 and the explanatory variables abundance in 1871, vegetation type, long-distance dispersal ability, capacity for clonal spread, and height. Abundance in 1985 is an ordinal variable; hence, its categories can be ranked from lowest to highest (extinct to very common), but the intervals between adjacent categories are unknown. Nevertheless, if certain attributes were to predispose species to population decline and local extinction, then we would expect a greater proportion of the species in progressively lower 1985 abundance categories to possess those attributes.

To test this, we fit a regression model describing the cumulative probability of a response in progressively higher 1985 abundance categories as a function of the

predictor variables, termed a proportional odds model (McCullagh 1980, Agresti 1990, Long 1997). This model is appropriate when an underlying continuous variable,  $Y$ , has been measured as a series of  $J$  ordered categories such that  $Y = j$  ( $j = 1, 2, \dots, J$ ) if  $a_{j-1} < Y \leq a_j$ , where the  $a_j$  are cut points that separate the ordered categories. In this case, the  $J$  categories are the seven 1985 abundance categories ordered from extinct to very common (with the first cut point separating extinct species in 1985 from the rest, the second cut point separating extinct plus very local species in 1985 from the rest, and so on). A model is then fit based on the logits of the cumulative response probabilities,  $p_j = P(Y \leq j | \mathbf{x})$ , such that

$$\text{logit}(p_j(\mathbf{x})) = \ln[p_j(\mathbf{x})/(1 - p_j(\mathbf{x}))] = a_j - \boldsymbol{\beta}\mathbf{x},$$

$$j = 1, \dots, J - 1. \quad (1)$$

The outcome of fitting a proportional odds model is thus a series of  $J - 1$  regression lines on a logit scale. These lines are described by the cut point intercept terms (the  $a_j$ , one for each regression line fit across each cutpoint) and a vector of slope estimates ( $\boldsymbol{\beta}$ , one slope estimate for each explanatory variable in the model). The interpretation is that the odds of observing a response  $\leq j$  (i.e., the odds that a species occurred in the  $j$ th or lower 1985 abundance category) are  $\exp[\boldsymbol{\beta}(\mathbf{x}_1 - \mathbf{x}_2)]$  times higher at  $\mathbf{x} = \mathbf{x}_1$  than at  $\mathbf{x} = \mathbf{x}_2$  (Agresti 1990). We fit proportional odds models using PROC LOGISTIC in SAS (SAS Institute 1990). The significance of a variable in predicting 1985 abundance was assessed using a chi-square test on the resulting change in deviance when that variable was added to a model.

Several of the explanatory variables in our data set were confounded. As an example, consider height and vegetation type: 35% of the species  $< 1$  m tall were most common in forest vegetation, compared with 70% of the species  $\geq 1$  m tall. Such confounding could inflate or obscure relationships in our data because a significant association between 1985 abundance and one variable could arise through an indirect correlation with a second variable. We adjusted for confounding effects by testing whether each variable could significantly predict 1985 abundance when added last to a proportional odds model that already included the other variables as covariates.

Initially, we treated each attribute as a nominal categorical variable, ignoring the order inherent in the categories for abundance in 1871 and height. However, the hypotheses outlined in the *Introduction* make specific predictions about the form of the relationship between categories of the explanatory variables and 1985 abundance. If extinction rate is negatively correlated with initial abundance and with height, then species in progressively higher 1871 abundance and height categories should have correspondingly lower probabilities of local extinction. Similarly, if species common in vegetation types that suffered the greatest loss of

area also suffered higher rates of extinction, then species common in wetland, shrubland, and open vegetation (the most disturbed vegetation types) should be more prone to extinction and rarity than species common in forest and coastal vegetation. We tested these specific predictions by replacing the nominal categorical variables with variables that modeled relationships of the predicted form. Specifically, we replaced the abundance in 1871 and height categories with a linear rank order score (e.g., for each species, the variable "abundance in 1871," which was coded previously as five dummy categories, was coded as a number from 1 to 6 denoting the rank order of the abundance category in which the species occurred), and replaced the categories for vegetation type with a binary variable scored 1 for species most common in forest and coastal vegetation and 0 for species most common in wetland, shrubland, and open vegetation. If replacing the nominal categorical variables with these new variables does not significantly change the model deviance, then we can conclude that these new variables adequately model the form of the relationship with 1985 abundance. We also tested whether including any two-way interaction terms significantly changed the model deviance when added after all main effects.

An assumption of the proportional odds model is that the slope estimates are the same across all of the cut points, i.e., the series of  $J - 1$  regression lines that are fit to the data are parallel (termed the parallel regression assumption; Long 1997). This need not be the case, however, because some variables could significantly predict a response across some cut points but not others. In our study, this would be particularly significant if the effect of a variable across the cut point "extinct or not" differed from its effect across other cut points (those cut points that largely separate the rare from the common survivors), implying that the variable has a different effect on survival or extinction than on being more or less common. We tested the parallel regression assumption using the score test (Peterson and Harrell 1990, SAS Institute 1990, Long 1997).

Ordinal response variables, in which an underlying continuous variable has been measured as a series of ordered categories, occur often in ecology (e.g., Landa and Rabinowitz 1983, Rydin and Borgegård 1991, Kunin and Shmida 1997, Rees 1997). The proportional odds model provides an efficient and robust method for analyzing ordinal data because it takes into account the ordering of categories, but makes no assumption about the intervals between adjacent categories. Although this model has been widely applied in the medical and social sciences, where ordinal outcomes are also common (see examples in Agresti 1990, Long 1997), it deserves wider recognition for its potential application to ecological problems.

#### *Taxonomic effects*

We avoided the problem of confounding by testing whether each variable could predict 1985 abundance,

having adjusted for the influence of other variables in the model. However, a limitation of this approach is that it controls only for the confounding effects of those attributes we measured and included in the model. It is possible that any significant relationship that remains could still be confounded with factors other than those we measured.

Another way of adjusting for confounding factors is to control for the effects of phylogenetic relatedness (Harvey and Pagel 1991). Closely related species tend to share attributes because of their common ancestry. Some of those attributes may influence extinction risk, whereas others may not, but are correlated with the extinction-biasing attributes through their shared evolutionary history. In our data set, several explanatory variables were confounded with high-level taxonomic grouping. Pteridophytes, for example, were overrepresented among good dispersers and were absent among poor dispersers, because all pteridophytes reproduce via small, wind-dispersed spores. Consequently, a spurious relationship between dispersal ability and 1985 abundance could arise indirectly if pteridophytes share some unmeasured attribute that is absent in other taxa, but that strongly influences extinction risk. Other variables were similarly confounded. Pteridophytes were overrepresented among species common in forest compared with other vegetation types, and both pteridophytes and monocotyledons were overrepresented among short plants and plants with a capacity for clonal spread.

Modern approaches to controlling for the effects of phylogenetic relatedness are based on the method of independent contrasts, which partitions the variation in the data in such a way as to provide the appropriate degrees of freedom for testing relationships independent of phylogeny (Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992). Currently, none of the methods available for calculating independent contrasts can deal with an ordinal response variable and a combination of categorical and rank-ordered explanatory variables (e.g., Purvis and Rambaut 1995). An alternative approach is to include a variable in the model that describes taxonomic relatedness at some level. This variable then acts as a surrogate for any attributes that are shared by species within the same taxonomic group. In our study, we grouped species into four high-level taxonomic groups (pteridophyte, gymnosperm, monocotyledon, or dicotyledon) because it was clear that several attributes were confounded with taxonomy at this level. We tested whether taxonomic group was a significant predictor of 1985 abundance when included last in a proportional odds model that already included the other explanatory variables. We then adjusted for the influence of any unmeasured factors that were correlated with high-level taxonomy by testing if each explanatory variable could independently predict 1985 abundance when added last to a proportional odds model

TABLE 1. The change in model deviance resulting from adding the explanatory variables in the left-hand column to a proportional odds models with relative abundance in 1985 as the response variable, for the 373 native plant species present in Auckland, New Zealand, in 1871.

Variable	df†	Alone‡	Last§
Vegetation type	4	15.4**	16.2**
Abundance in 1871	5	92.8***	102.0***
Height	4	35.0***	20.0***
Long-distance dispersal	1	6.0*	5.8*
Clonal spread	1	0.6	10.4**
All variables	15	152.3***	

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

† Change in deviance was tested with a chi-square test using the appropriate degrees of freedom.

‡ The change in model deviance when a variable is included alone in a proportional odds model.

§ The change in model deviance when a variable is included last in a proportional odds model that already includes the other explanatory variables.

el that included the remaining variables and taxonomic group as covariates.

## RESULTS

Of the 373 native plants present in Auckland in 1871, 80 were locally extinct by 1985, an average extinction rate of 0.2% per year. As discussed, this figure may underestimate the true rate of local extinction in Kirk's original study area. Of the 293 surviving species, Esler placed 188 species (64%) in a lower abundance category than Kirk had in 1871, 65 species (22%) in the same abundance category, and 40 species (14%) in a higher abundance category. Although this suggests that most species declined in abundance, a direct comparison of abundance rankings in 1871 with those in 1985 is problematic because the two surveys cover different areas, and Kirk and Esler may have differed in their interpretation of the abundance categories. In our analysis, we used abundance in 1871 to predict abundance in 1985; thus, the two abundance ranking schemes need not be the same.

### Model construction

Four of the five attributes were significant predictors of 1985 abundance when included alone as nominal categorical variables in a proportional odds model (Table 1). Fig. 1 shows the frequencies across the first cut point of the response variable: the proportion of species in the "extinct" relative to all other 1985 abundance categories. Plants with the following attributes had a higher probability of extinction in the period 1871–1985: low abundance in 1871, common in wetland or open vegetation, short-stature, and poor dispersal ability. Nevertheless, the relationships shown in Fig. 1 do not take into account intercorrelations among the explanatory variables. When each variable was added last to a proportional odds model that already included the other variables, then all five attributes were significant predictors of 1985 abundance (Table 1). Capacity for

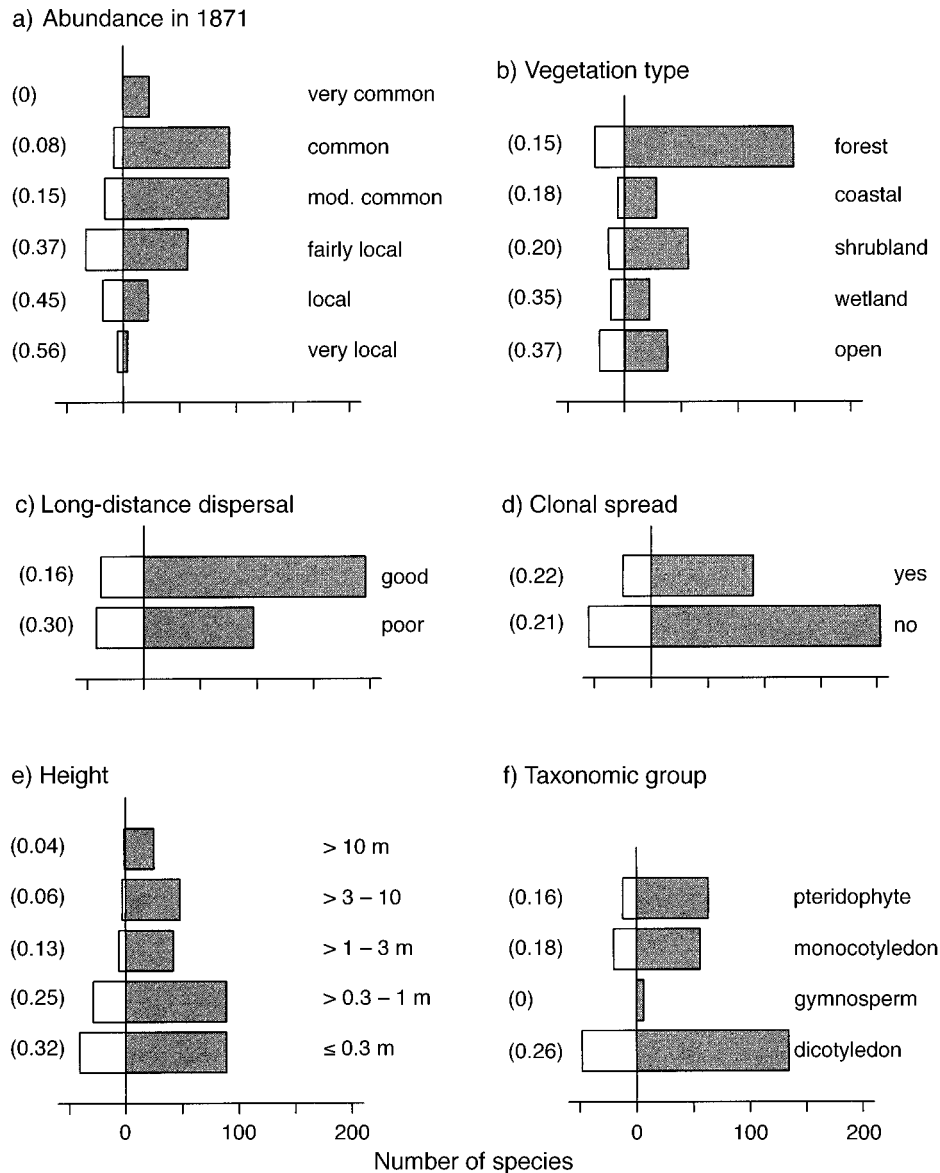


FIG. 1. Numbers of the 373 native plant species present in Auckland in 1871 that were either locally extinct (open bars) or still surviving (shaded bars) in the area by 1985, by attribute categories (a–f). The number in parentheses beside each attribute category is the proportion of locally extinct species in that category.

clonal spread was not a significant predictor when included alone, suggesting that the effect of clonal spread was obscured by the influence of other variables and was evident only after their effects were adjusted for. Having adjusted for these effects, species without the capacity for clonal spread were more likely to be extinct or rare in 1985 than species with this capacity.

Replacing the nominal categorical variables for 1871 abundance and height with linear rank scores, and replacing vegetation type with a binary variable did not significantly change the model deviance (Table 2; change in deviance = 8.7,  $df = 10$ ,  $P = 0.56$ ). This

suggests that the logit of abundance in 1985 varies as a linear function of the rank-order category scores for both abundance in 1871 and height, and that the influence of vegetation type results primarily from differences between species common in forest and coastal vegetation compared with species common in wetland, shrubland, and open vegetation. None of the two-way interaction terms for these main effects was significant ( $P > 0.05$ ). The score test for the parallel regression assumption for this model was highly nonsignificant ( $\chi^2 = 13.4$ ,  $df = 25$ ,  $P = 0.97$ ), indicating that this assumption was reasonable.

TABLE 2. Results of a proportional odds model with relative abundance in 1985 as the response variable and the attributes in the left-hand column as explanatory variables, for the 373 native plant species present in Auckland in 1871.

Variable	df†	Last‡	Slope estimate (1 SE)
Vegetation type	1	13.0***	
Forest and coastal			0.737 (0.204)
Wetland, shrubland, and open			0
Abundance in 1871	1	97.7***	
Rank order category score			0.862 (0.092)
Height	1	17.6***	
Rank order category score			0.349 (0.084)
Long-distance dispersal	1	5.8*	
Good			0.488 (0.203)
Poor			0
Clonal spread	1	10.0**	
Yes			0.684 (0.218)
No			0
All variables	5	143.6***	

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

† Change in deviance was tested with a chi-square test using the appropriate degrees of freedom.

‡ The change in model deviance when each variable is added to the proportional odds model after the other explanatory variables have already been included.

#### Taxonomic effects

The nominal categorical variable for taxonomic group (pteridophyte, gymnosperm, dicotyledon, or monocotyledon) did not significantly predict 1985 abundance when included alone in a proportional odds model (change in deviance = 6.1,  $df = 3$ ,  $P = 0.10$ ), but was a highly significant predictor when added last to the model in Table 2 (change in deviance = 18.0,  $df = 3$ ,  $P < 0.001$ ). The slope estimates for the categories for taxonomic group suggested that pteridophytes and monocotyledons had responded in a similar way, but differed from gymnosperms and dicotyledons. Furthermore, having adjusted for the effects of the other attributes and taxonomic group, long-distance dispersal ability and capacity for clonal spread failed to significantly predict 1985 abundance (change in de-

viance when added to the model last = 1.7 and 2.1, respectively, for dispersal ability and clonal spread;  $P > 0.1$ ). We therefore simplified the model by replacing the nominal categorical variable for taxonomic group with a binary variable scored 1 for pteridophytes and monocotyledons and 0 for gymnosperms and dicotyledons, and dropped the variables for long-distance dispersal and clonal spread. Despite losing a degree of freedom, this simplified model (Table 3) explained more deviance than the model in Table 2.

None of the two-way interaction terms for the main effects in Table 3 was significant ( $P > 0.05$ ), and the score test for the parallel regression assumption for this model was highly nonsignificant ( $\chi^2 = 6.8$ ,  $df = 20$ ,  $P = 1.0$ ), indicating that this assumption was reasonable.

TABLE 3. Results of a proportional odds model with relative abundance in 1985 as the response variable and the attributes in the left-hand column as explanatory variables, for the 373 native plant species present in Auckland in 1871.

Variable	df	Last	Slope estimate (1 SE)
Vegetation type	1	14.7***	
Forest and coastal			0.779 (0.204)
Wetland, shrubland, and open			0
Abundance in 1871	1	98.4***	
Rank-order category score			0.866 (0.092)
Height	1	32.0***	
Rank-order category score			0.498 (0.088)
Taxonomic group	1	27.0***	
Pteridophytes and monocotyledons			1.092 (0.212)
Gymnosperms and dicotyledons			0
All variables	4	156.5***	

Notes: This model is a refinement of that shown in Table 2, with a variable describing taxonomic group included and the variables for long-distance dispersal ability and capacity for clonal spread dropped. Changes in model deviance and tests are as defined in Table 2.

\*\*\*  $P < 0.001$ .

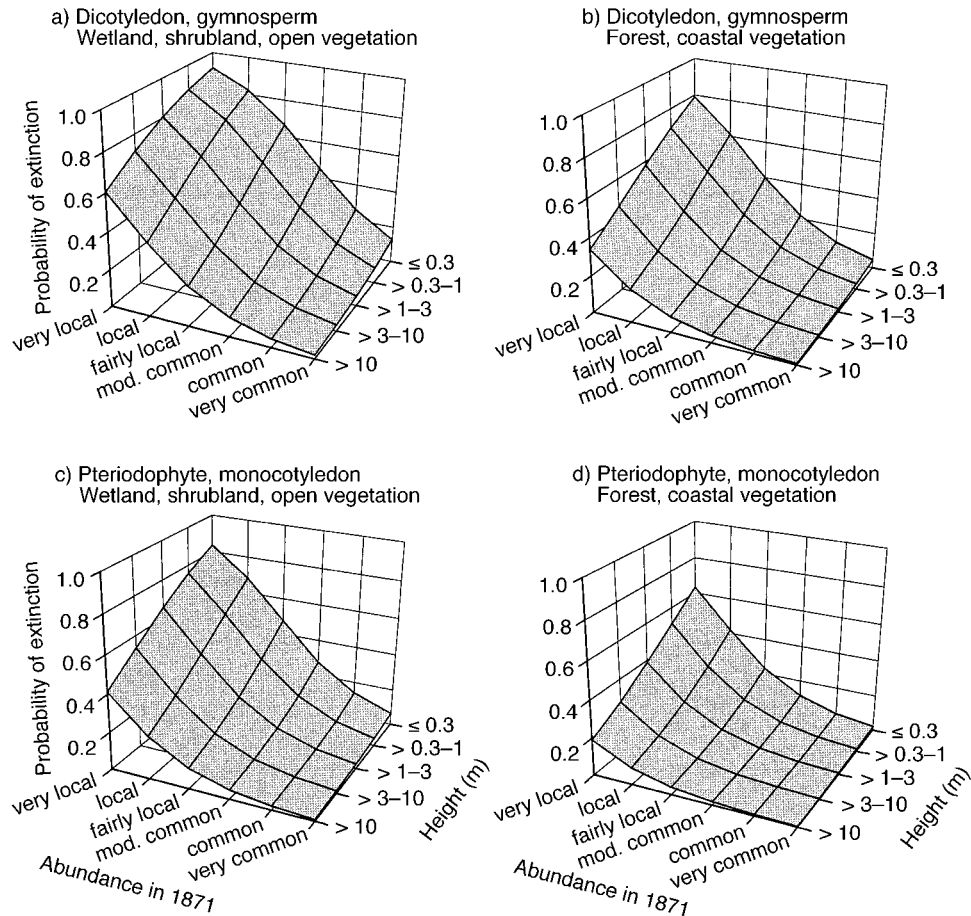


FIG. 2. Predicted probability (from the model in Table 3) that a native plant species present in Auckland in 1871 had become extinct by 1985, as a function of the attribute categories. Note that we have joined adjacent points in each plot to form a surface, making it easier to visualize how extinction probability changes with 1871 abundance and height. Strictly, these attributes are ordered categories and do not form a continuous surface.

#### Model interpretation

The slope estimates (Tables 2 and 3) give the effect of each explanatory variable on 1985 abundance while keeping constant the effect of all other variables in the model. For the rank-scored variables (abundance in 1871 and height), positive slopes indicate that species with higher scores were more likely to be found in higher 1985 abundance categories. This means that both abundance in 1871 and height were negatively related to the probability of local extinction and rarity in 1985.

For the nominal variables, species in the category with a positive slope were more likely to be found in higher 1985 abundance categories relative to species in the category with zero slope. Hence, species common in vegetation types that suffered the greatest loss of area (wetland, shrubland, and open vegetation) were more likely to be extinct or rare in 1985 than species common in less affected habitats. Dicotyledons and gymnosperms were more likely to be extinct or rare in 1985 than pteridophytes or monocotyledons.

The effect of changing each attribute on the probability of extinction is shown in Fig. 2. Extinction probabilities were calculated from the slope estimates in Table 3 and the intercept term for the regression line at the first cut point, separating the extinct from the surviving species. It is clear that attributes interact under this model, not in the logit but in the linear dimension. In particular, species that were abundant in 1871 had a low probability of extinction, regardless of other attributes they possessed, whereas rare species in 1871 had a wider range in extinction probability, with the magnitude of that probability depending on the particular combination of other attributes present.

The slope estimates in Table 3 can be transformed to a more informative measure of the effect of each explanatory variable, termed the odds ratio (Agresti 1990, Long 1997). For the nominal explanatory variables (vegetation type and taxonomic group), species in the category with a positive slope were  $\exp(\beta)$  times more likely to be found in a higher 1985 abundance category than were species in the category with zero



slope (where  $\beta$  is the slope estimate). Hence, species most common in wetland, shrubland, and open vegetation were 2.2 times more likely to be extinct than species most common in forest and coastal vegetation, whereas dicotyledons and gymnosperms were 3.0 times more likely to be extinct than pteridophytes and monocotyledons.

For the rank-scored explanatory variables (abundance in 1871 and height), species with a lower score were  $\exp(\beta(h - l))$  times more likely to be less abundant in 1985 than species with a higher score (where  $h$  and  $l$  are the high and low rank scores, respectively). Hence, a species ranked one height category lower than a second species was 1.6 times more likely to be extinct in 1985. Likewise, a species ranked one 1871 abundance category lower than a second species was 2.4 times more likely to be extinct in 1985.

The odds ratios point to initial abundance as a crucial factor influencing the likelihood of extinction. Lowering 1871 abundance by just one category has a similar effect on the probability of extinction (2.4 times more likely) as shifting from a less to a more disturbed vegetation type (2.2 times), shifting from a less to a more vulnerable taxonomic group (3.0 times), or a quite marked decrease in plant height (dropping two height categories on the relatively coarse height scale that we used increases the probability of extinction by 2.7 times).

#### DISCUSSION

A major difficulty confronts attempts to identify attributes that predispose species to local extinction in the face of human impacts: at most locations, there is no direct record of the species that were once present but have subsequently become extinct. Consequently, many studies that seek to identify the attributes of extinct species rely on indirect evidence to infer local extinctions (e.g., Bolger et al. 1991, Laurance 1994, McIntyre and Lavorel 1994, Grashof-Bokdam 1997, Suarez et al. 1998). Kirk's and Esler's studies provide a direct record of the local plant extinctions that occurred in the Auckland area during the first 145 years of European settlement. This record is remarkable both for its length and because the initial abundance of each species was recorded, allowing us to directly test the hypothesis that locally rare species were predisposed to extinction, and to adjust for the effect of initial abundance before testing whether other attributes were related to extinction risk (Pimm et al. 1988).

Our results support the first three hypotheses that we outlined in the *Introduction*. Initial abundance was a critical determinant of extinction risk such that, relative to common species, rare species in 1871 were much more likely to be locally extinct in 1985. Our results therefore support the widely held view that rarity is a key factor predisposing species to extinction (Gaston 1994). Nevertheless, because there are few records directly documenting local extinctions in which the ini-

tial abundance of each species has been measured, our study is one of few to have directly tested this hypothesis (Diamond 1984, Pimm et al. 1988, Leach and Givnish 1996, Fischer and Stocklin 1997). Our results also show that the relationship between initial abundance and extinction probability varies between species, depending on the combination of other attributes present (Fig. 2). Species become increasingly prone to extinction with declining initial abundance if they possess other attributes that further predispose them to extinction.

The importance of rarity as a factor predisposing species to local extinction has been challenged recently by theoretical models predicting that as habitat is destroyed the most abundant species will disappear first (Tilman et al. 1994), or that the order of extinctions will be independent of initial abundance (Tilman et al. 1997). These outcomes, and those of similar models (Nee and May 1992, Kareiva and Wennergren 1995, Moilanen and Hanski 1995, Loehle and Li 1996), arise because, under the model assumptions, good colonizing ability is the key factor favoring persistence in fragmented landscapes, and the disadvantage of poor colonizing ability outweighs any advantage of high initial abundance. Unless colonizing ability (i.e., the rate of propagule output rather than the distance that propagules are capable of dispersing, Holmes and Wilson 1998) is strongly correlated with initial abundance in the Auckland data set, and we see no compelling reason why it should be, then our results do not support an important prediction of these models: that the order of extinctions should be independent of initial abundance (Tilman et al. 1997).

Those species most common in habitats that suffered the greatest loss of area (wetland, shrubland, and open vegetation) had higher rates of extinction and were more likely to be rare in 1985 relative to species common in less affected habitats (forest and coastal vegetation), confirming our second hypothesis. This outcome is intuitively reasonable; species that lose a greater proportion of their habitat are more likely to suffer population declines and local extinctions. (see Plate 1). Nevertheless, factors other than the degree of habitat loss per se could have caused or contributed to this relationship. Several species of exotic plants aggressively compete with, and are known to exclude, native plants from habitat remnants in the Auckland area (Esler 1988, Smale and Gardner 1999). The higher rates of extinction and rarity in species common to wetland, shrubland, and open vegetation could result from these vegetation types being more extensively invaded by aggressive exotics. Indeed, Esler noted precisely this pattern: fewer exotic species threaten native plants in closed forest and coastal vegetation compared with shrubland, wetland, and open vegetation (Esler 1991). The extents of both habitat loss and exotic invasion are likely to be linked (Suarez et al. 1998). The surviving remnants of vegetation types that were more substan-

PLATE 1. Loss of habitat is almost certainly a cause of local plant extinctions in the Auckland area since Thomas Kirk's survey of 1871. Smith's Bush, a sizeable native forest remnant, was acquired as a reserve in 1943 but much of the forest was destroyed in the 1950s when a motorway cut the reserve in two, and in the 1960s when the motorway was widened. Photograph by Ewen Cameron, Auckland Museum, 1987.



tially reduced in area are likely to have been more highly disturbed and fragmented, and, consequently, more susceptible to exotic invasion (Crawley 1987, Timmins and Williams 1991).

An additional possibility is that variation in the rate of extinction and rarity among vegetation types reflects their contrasting history of modification (Balmford 1996). Prior to European arrival, Maori destroyed most of the forest in the Auckland area and it was replaced by successional shrubland and open vegetation (Esler 1991). The massive reduction in forested area prior to European arrival could have eliminated most of the extinction-prone forest species. The resulting forest flora of the 1800s may have then been relatively resistant to the further changes that accompanied European settlement. Although this could explain the lower rates of extinction and rarity in forest species relative to species common in wetland, shrubland, or open vegetation, it cannot account for the equally low rates of extinction and rarity in coastal species. There is no evidence that coastal vegetation was modified to the same extent as forests before European arrival.

Compared with tall plants, short plants were more likely to be extinct or rare in 1985, confirming our third hypothesis. We can advance four explanations to account for this relationship, all of which could have played a role. First, even if populations become non-viable at the same rate, individuals of tall, long-lived species will persist longer, an explanation used to account for the lower rates of extinction found in tree and shrub species, relative to other life-forms, in a Singapore forest remnant (Turner et al. 1996). This explanation assumes a positive relationship between plant height and longevity, which will certainly hold across the broad height categories that we used. Nevertheless, it could be argued that a more conclusive test would result from explicitly including longevity as a variable in our analysis. At best, however, we could only crudely categorize species by longevity (e.g., annual, biennial, or perennial). Given the low percentage

of annual and biennial species in the Auckland flora (fewer than 10%), plant height is likely to be a more informative measure of longevity (see Rees 1997).

Individual longevity could account for the present persistence of some species in the Auckland area. *Metrosideros robusta*, for example, is a canopy tree that lives for several hundred years. It was ranked "moderately common" in 1871 but only "very local" in 1985, and currently survives in the Auckland area only as adult trees with no juvenile recruitment (Esler 1991). The surviving adults may therefore be relics of an effectively extinct population.

The second explanation is that competition from aggressive exotic plants has selectively eliminated short-statured species from habitat remnants. Taller plants could persist by overtopping a suppressive invader that shades out shorter plants. There is some evidence to support this. Smale and Gardner (1999) describe the vegetation of a small forest remnant in urban Auckland that has been extensively invaded by the exotic trailing herb *Tradescantia fluminensis*. In patches dominated by *T. fluminensis*, they found a reduced abundance of native ground-layer and understory species, a pattern typical of forest remnants elsewhere in New Zealand that have been invaded by this species (Kelly and Skipworth 1984, Whaley et al. 1997).

The third explanation is that tall, long-lived species are more likely to persist through unfavorable periods for regeneration. In the early stages of European settlement, for example, most of the Auckland area was under agriculture, and uncontrolled grazing would have removed understory and ground-tier species and would have limited plant regeneration in habitat remnants on or adjacent to agricultural areas, as evidenced by the impacts of introduced grazing animals elsewhere in New Zealand (Atkinson 1964, Wardle et al. 1973, Mark and Baylis 1975). The reduction in livestock grazing due to urban expansion would have removed this constraint on regeneration in the surviving remnants. However, only species that had survived grazing and lived

long enough to persist through the period of little or no recruitment would have regenerated. Because the seeds of most New Zealand natives are short-lived in the soil (Burrows 1994), the survivors would most likely have been species with tall, long-lived adults.

The fourth explanation is that a change in the disturbance regime has favored taller plants. In the absence of fire, native shrubland and open vegetation in the Auckland area is succeeding back to tall forest, and most of the present forest remnants have regenerated after clearance by European settlers (Millener 1979, Esler 1991). More frequent disturbance in the past may have favored short-statured plants that are now being excluded by taller, later successional species. Leach and Givinish (1996) found that local plant extinctions in prairie remnants in the northern United States were biased toward short-statured species, in part because fire suppression was leading to dominance by tall-statured woody vegetation.

Plants classified as having poor long-distance dispersal ability were more likely to be extinct or rare in 1985, consistent with our fourth hypothesis. However, this relationship was confounded with taxonomy such that the significant cross-species relationship between dispersal ability and 1985 abundance was primarily a consequence of (1) all pteridophytes being good dispersers, and (2) pteridophytes, along with monocotyledons, being less prone to extinction and rarity than other taxa. With pteridophytes excluded from the data, dispersal ability failed to significantly predict 1985 abundance (for gymnosperms, dicotyledons, and monocotyledons only, when dispersal ability was added last to the model in Table 2, the change in deviance was 2.0,  $P = 0.16$ ). These outcomes highlight two points. First, our results provide little support for the hypothesis that variation in dispersal behavior strongly influences extinction risk, despite the emphasis in the theoretical literature on the importance of between-patch dispersal in maintaining populations fragmented by habitat loss (Harrison and Bruna 1999). At best, good dispersal ability could partly explain why pteridophytes fared better than other taxa, but it fails to explain any difference in extinction vulnerability among species in the other taxonomic groups. The significant cross-species relationship between dispersal ability and 1985 abundance could be a spurious consequence of pteridophytes sharing some other, unmeasured attribute that is less common in other taxa, and that significantly lowers extinction risk. Second, we probably would have overstated the importance of dispersal ability had we not examined the effect of taxonomic relatedness, highlighting the importance of considering phylogenetic effects in comparative studies (Harvey and Pagel 1991, Harvey 1996, Silvertown and Dodd 1997).

Similarly, clonally spreading species had lower rates of extinction and rarity as predicted (hypothesis five), but this relationship was likewise confounded with taxonomy. The relationship arose largely because pteri-

dophytes and monocotyledons had both a greater percentage of clonally spreading species (45% compared with 14% for dicotyledons and gymnosperms) and a lower probability of extinction and rarity. Having controlled for differences in extinction vulnerability among these high-level taxonomic groups, there was no evidence that possessing the capacity for clonal spread buffered species from decline and local extinction. Again, the significant cross-species relationship between clonal spread and 1985 abundance could be a spurious consequence of pteridophytes and monocotyledons sharing some unmeasured attribute that is less common in other taxa and that significantly lowers extinction risk.

We found unexpectedly that, having adjusted for the effects of other attributes, dicotyledons and gymnosperms were more prone to local extinction and rarity than pteridophytes and monocotyledons. Other studies have similarly found that rare or extinct species tend to be concentrated in particular taxonomic groups (Hodgson 1986, Schwartz 1993, Bennett and Owens 1997, McKinney 1997, Russell et al. 1998), although ours is the first to show marked variation in extinction vulnerability in high-level plant taxa. It is important to note that taxonomy was a significant predictor in our study only after we adjusted for the influence of other explanatory variables (see *Taxonomic effects*). Hence, similar taxonomic effects could be obscured in other studies in which factors such as initial abundance have not been measured and cannot be controlled for. In our study, the taxonomic effects presumably arise because species with attributes predisposing them to extinction and rarity are overrepresented in the dicotyledon and gymnosperm groups, and underrepresented in the pteridophyte and monocotyledon groups. Whatever these attributes are, they explain variation in 1985 abundance independent of the attributes already measured in this study.

Finally, the parallel regression assumption held for the explanatory variables included in the proportional odds models in Tables 2 and 3. This implies that each explanatory variable had a similar effect across all cut points of the ordered abundance categories, and, therefore, that those variables that distinguished the extinct from the surviving species likewise distinguished the rare from the common survivors. This has an important implication. A common approach to identifying attributes that might predispose species to local extinction is to identify the attributes that distinguish the rare from the common species in a particular area (Green 1996, Goerck 1997, Selvi 1997, Sosa and Platas 1998), the assumption being that the attributes that characterize the rare species contributed to their rarity and will further predispose them to local extinction. However, this need not be the case. Rare species could possess attributes not because they contributed to their rarity, but because rarity in the first place favored the adoption of those attributes (Gaston 1994). Rather than predis-

posing species to further rarity and eventual extinction, such attributes may favor the persistence of rare species. Our results provide empirical evidence that, at least among plants in a highly human-modified habitat, the attributes that distinguish the rare from the common species also predispose those rare species to extinction.

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