

Climate-Change Effects on Alpine Plant Biodiversity: A New Zealand Perspective on Quantifying the Threat

Authors: Halloy, Stephan R. P., and Mark, Alan F.

Source: Arctic, Antarctic, and Alpine Research, 35(2) : 248-254

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2003\)035\[0248:CEOAPB\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0248:CEOAPB]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Climate-Change Effects on Alpine Plant Biodiversity: A New Zealand Perspective on Quantifying the Threat

Stephan R. P. Halloy

New Zealand Institute for Crop & Food
Research Limited, Private Bag 50034,
Mosgiel, New Zealand.
halloys@crop.cri.nz

Alan F. Mark

Botany Department, University of Otago,
P.O. Box 56, Dunedin, New Zealand.

Abstract

New Zealand's alpine region is populated by many (~613) species of vascular plants with a high endemism (~93%). To investigate the potential impact of climate warming, we used species-area relations to estimate current and projected vascular plant floras and tested model sensitivity scaling from the whole world to small alpine regions.

Within their limitations, these models show that if the present mean temperature of ~0.6°C higher than in 1900 were maintained, together with a large pool of exotic species, 40–70 species of native plants could become at risk. With a rise of 3°C, an approximate expectation for the following 100 yr, the total New Zealand alpine vascular flora could reach ~550–685 species and lose 200–300 indigenous alpine species, the rest being exotic. Fragmentation of alpine areas could, over millennia, favor speciation, but in the short term, the loss of ~80% of existing alpine islands will severely increase extinction risks.

These model projections will be modified by downward extension of species through unplanned vegetation destruction, or following deliberate vegetation clearance to create habitats favorable to alpine species, as well as through a number of other as yet unquantified factors. These projections are not predictions of extinctions but rather broad probabilities of risk to a whole flora.

Introduction

Global climate change has affected biotas through the ages, but the present century is predicted to show a rate of temperature rise amongst the highest in the world's history. The 1997 Intergovernmental Panel on Climate Change (IPCC) scenarios of future global warming suggested an increase in temperature of 1 to 3.5°C by the year 2100 (Watson et al., 1997); the 2001 report increased these estimates to 1.4 to 5.8°C (IPCC, 2001). It has been claimed that many species of plants and animals will be at increased risk of extinction due to warming climates and that mountaintop communities are particularly at risk given their isolation and lack of an "escape route" (Grabherr et al., 1995).

New Zealand is unique in being simultaneously one of the most isolated, ancient, and topographically diverse continental islands. Its form and size have fluctuated markedly over millions of years (Lee et al., 2001), significantly affecting the geographic distribution of alpine species (McGlone et al., 2001). Although the land is ancient, the present mountains developed only in the last 5 million to 7 million yr (Walcott, 1998). The high species richness of alpine vascular plants (>600 species; Mark and Adams, 1995) and invertebrates (Watt, 1975) in the alpine region may seem extraordinary in view of an evolutionary time span of only ~2 million yr (Wardle, 1978), although a longer time span may have been available, according to other studies (Fleming, 1963; Wardle, 1968; McGlone, 1985; McGlone et al., 2001). Overall endemism of these plants is around 93%, but many can exist below treeline in a variety of open environments (Mark and Adams, 1995; McGlone et al., 2001).

Climate change and increasing rates of human disturbance will affect the alpine biota concurrently. Human impact since first arrival around 1,000 yr ago has been pervasive. Forest destruction in many areas has allowed alpine and subalpine plants to significantly extend their ranges downslope, while high-alpine plants have extended locally into low-alpine tussock grasslands opened by burning and grazing by

introduced herbivores (e.g., McGlone et al., 1997). To a large degree, these relatively recent changes override potential present climate-change signals for rising vegetation lines.

Several approaches can be used to study the effects of climate change on mountain biodiversity. Long-term monitoring through photo-points or permanent plots has a long history in New Zealand (Evans, 1973; Mark, 1977; Wills and Begg, 1986; Scott et al., 1988; Dickinson et al., 1992; Bellingham et al., 1999; Bellingham et al., 2000, Duncan et al., 2001). A claim for a small recent advance in southern beech treelines (Wardle and Coleman, 1992) was disputed by a later study designed specifically to determine the response to global warming. The latter study found occasional storm disturbances to have obscured any possible climatic response (Cullen et al., 2001). On a wider scale, an alpine vegetation transect on the Southern Alps in south Westland is one of the most detailed such studies in New Zealand (Mark et al., 2000), and its repetition in a number of years should provide key information on change. Although many of the locations and designs of these studies were meant to determine the effects of introduced herbivores, fire, and other more or less direct human impacts on vegetation, some of this information will be of use for assessment of effects of climate change as well. Careful analysis of historical records may also provide valuable insights.

Additional research approaches including spatial explicit modeling and experimental manipulation at a small scale would provide new insights (Gottfried et al., 1998; Guisan et al., 1998). A large scale approach, used here for the first time in New Zealand, is to model nonlinear species-area relations at the appropriate scales to provide scenarios of climate-change effect as vegetation zones migrate. This approach provides hypotheses that can help design more rigorous long-term monitoring as well as developing scenarios to guide management responses. Calculations of species-area relationships have been used to estimate threats from climate change in a detailed study on mammals in isolated mountains of the U.S. Southwest (McDonald and Brown, 1992)

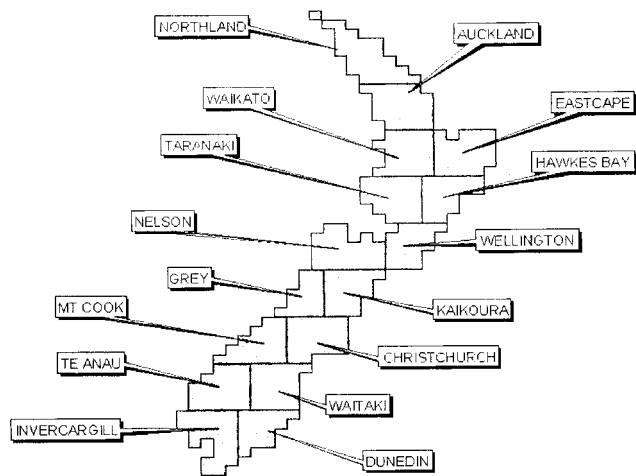


FIGURE 1. Map of the 16 Land Information New Zealand map squares used in this paper.

and have also been used on a very much coarser global scale (Malcolm and Markham, 2000). We used recent 1:50,000 topographic maps with 20-m contour intervals, incorporating latitudinal changes in altitudinal zonation of treeline to provide a credible range of estimates of the risk of vascular plant species loss under various climate-change scenarios.

Methods

New Zealand was divided into 16 rectangular horizontal blocks (Fig. 1) from the Land Information NZ (LINZ, <http://www.linz.govt.nz>) database of 1:50,000 contour maps. We used ArcInfo to create triangular irregular networks (TINs), then calculated areas above each 100-m contour line with ArcView (37 vertical slices). Treeline (or timberline; they are similar in New Zealand and represent the lower limit of the alpine vegetation) was set at 900 m asl for the southernmost regions, gradually increasing to 1400 m for the northernmost mountains. The increase in treeline from coastal to inland mountains was not considered, given the scale of the study.

The species-area relationship was modeled by the nonlinear Arrhenius equation $y = a + bx$, where y is log number of species, x is log of area, and a and b are constants derived from the empirical data (Preston, 1962). Different sets of empirical data will lead to different values of a and b , and hence estimates of species numbers. The model is better known in island biogeography and conservation biology for estimates of species loss with area reduction (MacArthur and Wilson, 1967; Simberloff, 1974; May, 1981; Soulé and Wilcox, 1980). Although such uses have their limitations (Lugo et al., 1993; Brokaw, 1998) they are underpinned by the theoretical basis of lognormal species abundance distributions (Preston, 1962; Halloy, 1998; Hubbell, 2001). The species-area relation is a very general yet simple rule, but if the parameters are not correctly chosen, the calculations are of little value. We address some of these practical limitations by testing the sensitivity of the species-area function with six different data sets (Table 1), scaling down from global estimates to smaller sets increasingly relevant to the New Zealand alpine vascular flora (full list of sites available on request):

- A = 67 areas around the world
- B = 12 islands up to the size of Madagascar
- C = 30 alpine regions around the world
- D = 6 alpine regions in New Zealand + total alpine New Zealand + total New Zealand
- E = 6 alpine regions in New Zealand
- F = 2 points: total alpine New Zealand + total New Zealand

Estimations of actual species numbers tend to increase with time as biotas become better known. However, given the exponential nature of species-area relationships, small changes in estimates will not affect the general shape of the relation based on many sites.

The number of indigenous species at saturation after climate change is estimated parsimoniously as a proportion of the total-saturation flora at the given scenario level equal to the proportion of the original natives to the original total-saturation flora (*saturation* is used here interchangeably with the term *equilibrium* as used in original biogeographic theory from MacArthur and Wilson, 1963 onward). The assumption of neutral species-area models is that “all species are equal” in a statistical sense (e.g., Hubbell, 2001). Hence, as the alpine

TABLE 1

Vascular plant species numbers and species-area constants for different scenarios obtained through different empirical data sets. A = 67 areas around the world; B = 12 islands up to the size of Madagascar; C = 30 alpine regions around the world; D = 6 alpine regions in New Zealand + total alpine New Zealand + total New Zealand; E = 6 alpine regions in New Zealand; F = 2 points: total alpine New Zealand + total New Zealand. Probabilities (*t*-test and *F*-test) for Scenarios A to D < 0.001, for E < 0.05, for F n/a (only 2 points)

	Scenarios					
	A	B	C	D	E	F
Parameters from empirical data sets						
a intercept	1.34	1.13	1.63	1.70	1.90	-0.10
b slope	0.43	0.45	0.29	0.25	0.13	0.64
Number of species expected						
	Actual	Calculated at pre-climate change saturation				
Total NZ	2450	3604	1629	1182	384	2450
Total alpine region	613	1351	862	679	291	600
Remarkables alpine zone	124	129	188	180	150	21
Mt Burns alpine zone total	162	115	174	169	145	18
Mt Burns high-alpine zone	82	18	52	59	86	1
Number of species at saturation after 3°C temperature increase						
Total alpine region	992	685	554	463	240	224
No. native alpine spp remaining	310	304	386	409	240	224
No. exotic spp in alpine zone	682	381	168	54	0	0
% native alpine spp remaining	51.7	50.7	64.3	68.2	40.0	37.3

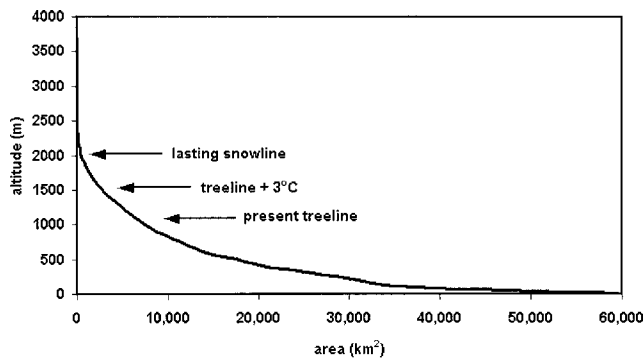


FIGURE 2. Compound topographic profile of New Zealand, representing the sum of areas in every 100-m contour interval of terrain (bold line). Present treeline and summer snowline are shown (median value for around 42°S), together with the equilibrium treeline at a +3°C scenario, to show the resultant reduction in land area.

area contracts, exotic and native species are equally at risk (although see discussion on types of species more at risk).

The reduction in area available is determined assuming a 0.6°C/100-m altitudinal lapse rate (Körner, 1999; Mark et al., 2000; Wardle, 1998). Thus, if, for example, treeline was at 1000 m, in the 3°C warming scenario it will be raised to around 1500 m, and the new area for alpine plants will have been reduced accordingly (Fig. 2). The scenario of rising forests assumes that the New Zealand treeline is determined to a major extent by temperature (Körner, 1999; Tranquillini, 1979; Wardle, 1974). The increase in available area above the present upper limit of alpine plants is insignificant at this scale. Only 0.03% of the total area above treeline is higher than the highest recorded vascular plants.

In addition to area reduction, we studied the effect of a rising treeline on the fragmentation and elimination of alpine “islands” (every separate mountain area emerging above the assumed treeline altitude and separated from other such areas by passes below that altitude) by quantifying the transformation as contour lines are raised from 1000 to 1500 m on a 1:1,000,000 topographic map of New Zealand (Department of Lands and Survey, 1984). Such an analysis is a rough approximation because it disregards the change in altitude of the treeline with latitude as well as the smallest fragments not apparent at the mapping scale.

Results

First we describe the prehuman species levels and how they compare to the species-area models. Then we move to the present situation as affected by habitat degradation, exotic species, and developing climate warming. Finally we examine the effect of expected warming in the coming 100 yr, in terms of both total area reduction and its effects on the loss of alpine islands (fragments).

PREHUMAN BENCHMARK

In the Landcare Research database, 2039 native and 2065 adventive vascular plant species are recorded for the contemporary vascular plant flora of New Zealand (E. Nicol, 1997, in Halloy et al., 2000). Groombridge (1992) estimated the total indigenous vascular flora at 2371 species. To avoid overestimating extinctions, we use a slightly higher estimate of 2450 species for all of New Zealand. The total New Zealand alpine vascular flora has been estimated at about 613 species (Mark and Adams, 1995). Alpine plants are distributed with a maximum species richness around 1250-m elevation, with numbers declining rapidly below treeline elevation and around 50

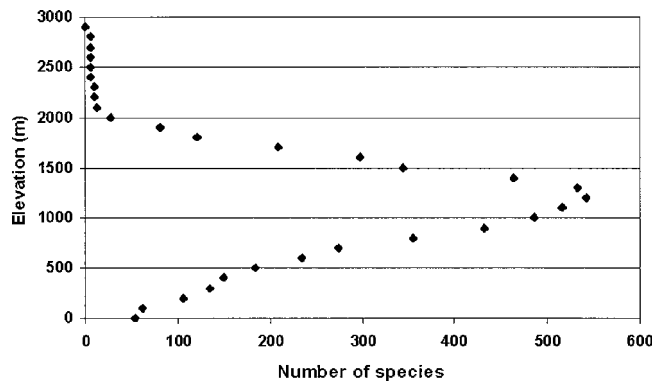


FIGURE 3. Species richness of New Zealand alpine vascular plants in relation to elevation. The values are based on the 655 taxa (613 species) and their altitudinal ranges as described in Mark and Adams (1995).

species when elevation reaches sea level (Fig. 3). Although occasional isolated plants have been recorded up to 2930 m (Mark and Adams, 1995), we used a conservative assumption of 0 plants above 2400 m because extremely few vascular plants grow above this altitude. These numbers of vascular plants are good representations of the prehuman benchmark as only around 3 (Groombridge, 1992) to 5 (de Lange et al., 1999) vascular plant species may have become extinct since human settlement, and none of them are alpine.

As one might expect from an island isolated for 80 million yr, both the total vascular flora and its alpine component are well below species numbers for areas of similar size that are in contact with larger species pools, as shown in Scenarios A (estimates close to 5000 species) and B (~3600 species) for the total flora and Scenario C (~860 species) for the alpine flora (Table 1). Although Scenario C underestimates the total flora (giving ~1630 species), it provides the overall best estimate for the alpine flora at different scales. Scenarios D and E provide the closest estimates to the very small Mt. Burns high-alpine area, but at the cost of strongly underestimating the total New Zealand flora. Scenario F is useful as a comparative benchmark but less so for small-scale alpine regions. Later we discuss only the most likely scenario (C), together with two extremes presented by B and E, to show the range (sensitivity) of potential loss of species. To verify the precision of each model at different scales, Table 1 provides three specific alpine areas differing in size and documented diversity (from Halloy and Mark, 1996).

PRESENT SITUATION—DEGRADATION AND EXOTIC SPECIES

After ~800–1000 years of Polynesian and 160 years of European occupation, around 90% of indigenous vegetation has been degraded to some degree (Halloy et al., 2000). At the same time, a large pool of vascular plant species has been introduced into New Zealand, with estimates ranging from 14,195 counted in the Landcare Research database (E. Nicol, 1997, in Halloy et al., 2000) to 26,000 reported from the Ministry of Agriculture and Fisheries database of plants in New Zealand (M. Dickson, 2001 pers. com.) and 40,000 estimated by an expert (W. Sykes, 2001 pers. com.). Already 2065 exotic vascular plant species, more than the total number of indigenous vascular species recorded, have become established in the wild (E. Nicol, 1997, in Halloy et al., 2000). However, most of these species are only in and around urban areas and farmland. Very few exotic vascular species have become established in alpine regions, many of which regions show a relatively low level of degradation, particularly in the higher-rainfall regions (Mark et al., 2000).

Given the larger pool of exotic vascular species now available in New Zealand, it has been estimated that the total New Zealand vascular

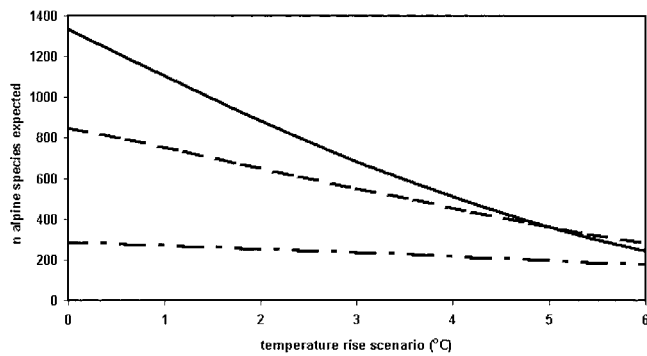


FIGURE 4. Projections of numbers of species of New Zealand alpine vascular plants (native and exotic) at equilibrium after a given temperature rise. Scenarios B (solid line), C (dashes), and E (dashes and dots) calculated from parameters in Table 1, as explained in Methods.

flora could rise from the present ~2450 to ~5000 species (Halloy, 1996). Estimates A and B in Table 1 are in reasonable agreement with this projection, as is the rapid human-mediated establishment of exotic vascular plants up to now. At the same time, as a result of both habitat degradation and exotic competition, the probabilities are that indigenous vascular species could decline to less than half their current number, or close to 1000 species, with the remaining 4000 species being exotic. These changes would occur regardless of climate change in a “biogeographic equilibrium” situation (*sensu* MacArthur and Wilson, 1963).

For the alpine zone the “equilibrium”, or saturated flora, assuming that a large pool of appropriately adapted exotic vascular species remains available for a long time, could rise to around 860 (Scenario C) to 1350 (B) species. As long as habitat degradation remains low, such an equilibrium alpine flora would still include close to the present 600 native vascular plant species. However, present invasion by exotic alpine vascular species into New Zealand’s alpine zone seems to be delayed by the following factors: (1) Exotic species in New Zealand are predominantly of Northern Hemisphere origin. Northern Hemisphere alpine species are from continental climates with short, warm summers [in contrast to Southern Hemisphere alpine longer but cooler summers and milder winters, e.g. Halloy and Mark (1996), Mark et al. (2000), Troll (1948), Troll (1960)], and few seem to adapt to New Zealand’s oceanic alpine climate. (2) The pool of potentially adapted alpine vascular species is small compared to the total number of exotics. (3) Most true alpine species have low dispersal capability, and most are grown in lowland gardens far from the alpine regions.

PRESENT SITUATION—CLIMATE WARMING

If the present mean temperature of around 0.6°C higher than in previous centuries were to be maintained for a long time, the equilibrium vascular flora could still rise to around 800 (Scenario C) to 1200 (Scenario B) species, including some 530 (Scenarios A and B) to 560 (Scenario D) native species. Hence, some 40 to 70 indigenous vascular species are already at risk of extinction as a result of climatic warming alone.

FUTURE PROJECTIONS

Given the range of temperature-change scenarios presented by the IPCC for 2100 (increase of global temperature between 1.4 to 5.8°C, IPCC 2001), we calculated the sensitivity of the different species-area models and show a conservative middle estimate as well as the range

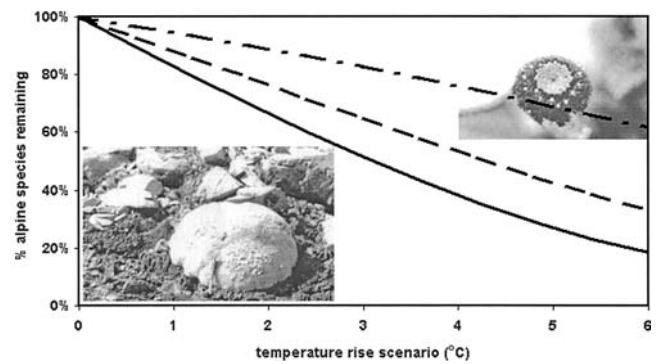


FIGURE 5. Predicted native species decline in relation to air-temperature increases given the species-area Scenarios B (solid line), C (dashes,) and E (dashes and dots) of Table 1. *Leptinella dendyi* flower (upper right) and *Raoulia eximia* cushion (lower left) as examples of alpine species.

of scenarios in Figures 4 and 5. With a midpoint rise of 3°C the total present alpine area estimate of 30,000 km² will reduce to 15,400 km². The total equilibrium New Zealand alpine vascular flora (exotic and indigenous) could drop to around 460 (D) to 685 species (B, Fig. 4), which would include 300 (B) to 410 (D) indigenous species. The number of indigenous alpine species remaining ranges from 37 to 68% of the original flora with all scenarios, with 51 (B) to 64% (C) the more parsimonious values (Fig. 5). Thus, with a 3°C temperature rise, the equilibrium New Zealand alpine vascular flora may lose 200–300 species.

FRAGMENTATION

We counted 441 “alpine islands” above 1000 m and 364 above 1500 m in New Zealand (Table 2). A comparison between the North and South Island’s provides insights on how topographic differences may have a major effect on biogeographic fragmentation and evolution. With its alpine area dominated by relatively smooth volcanic cones, the North Island has 87 separate areas above 1000 m. If vegetation zones rose 500 m (with a 3°C temperature rise), 81 of these islands would be lost (93%, in addition to major area reductions). In turn, the 6 remaining islands would fragment into 20 smaller islands. In contrast, the more rugged South Island has 354 separated areas above 1000 m, and 344 would still exist above 1500 m. However, 77% of the original 354 would have disappeared, the remaining ones being new fragments from the larger remaining blocks.

Discussion

DYNAMIC EXPANSION AND CONTRACTION

Palynological, sedimentological, and other paleovegetation and paleoclimatic evidence shows that New Zealand underwent major vegetation changes during and after the last glaciation (e.g., Fleming, 1963; McGlone, 1985, 1989; Stevens et al., 1988). During the last glaciation, suitable habitat for alpine plants would have been substantially larger than at present. Yet the number of species presently below biogeographic equilibrium, even for the smaller area today, suggests that the former larger area did not persist long enough for the evolution of a saturated flora or that some major extinction event intervened. Major human-induced habitat modification in New Zealand in the last millennium has created a range of situations from rapid recovery to ongoing degradation; changes that in many cases could override potential effects of climate change until the present. However,

as the magnitude of climate change increases, the effects should become increasingly apparent over and above local degradation.

The fragmentation analysis highlights the dynamic fluctuations in area, size distribution of those areas, and distances between them that are fundamentals of the evolutionary biogeography of extinction and speciation. Clearly, the temporal variations in past millennia of fluctuating vegetation lines would have created conditions of fragmentation and refugia formation, followed by fusion and amalgamation, over and over again. Such conditions have been postulated as causes for high diversity and evolutionary dynamics in areas such as the Amazon (Brokaw, 1998) and may relate to the high speciation rate observed in several endemic or mostly endemic alpine vascular genera of New Zealand (e.g., *Celmisia* and *Aciphylla*; see for example Wardle, 1978; Lee et al., 2001; McGlone et al., 2001). Yet, paradoxically given this potential increase in species richness, area reduction alone leads to reduction of species. Total submersion of alpine islands beneath forest would clearly lead to extinction of at least some low-dispersal local endemics. The reason for this paradox is that the time scale of extinction may be decades and centuries, while that for speciation is more like hundreds of thousands to millions of years.

An additional component of threat to population viability occurs through reduction in the number of populations of any one species. For example, a species with a total available area of x , distributed in 50 populations over 50 mountain peaks, could have its total area reduced to $x/2$, but the number of populations could conceivably reduce to only five or even one. Such populations can no longer benefit from meta-population dynamic exchanges and are at increased risk of extinction (Eriksson and Jakobsson, 1998; Tilman, 1996).

MODIFYING FACTORS

Many factors could affect models of extinction predictions:

1. downward extension of alpine plants through forest and shrubland destruction;
2. varying rates of upward invasion of exotic plants, depending on the nature of the species pool;
3. the fact that the flora is below saturation;
4. in addition to temperatures rising, the increase in carbon dioxide partial pressure could enhance growth rates and competitive ability (Halloy, 1981), favoring forests and shrublands in competition with alpine plants;
5. climatic and topographic heterogeneity, including pockets of drier, wetter, windier, cooler, steeper, or other less common conditions, some of which may restrict the advance of more competitive vegetation and allow the survival of alpine species;
6. biotic interactions, including disease and predation, in addition to the competition factor already considered.

Specific examples can be more easily visualized on relatively low peaks such as Mt. Burns (1634 m, 82 high-alpine species) in the high-rainfall Fiordland region or on flat-top mountains such as the Old Man (1695 m, 156 high-alpine species) or the Rock and Pillar Ranges (1450 m, 112 high-alpine species) in the rainshadow region of Central Otago (species numbers from Halloy and Mark, 1996). Here, high-alpine species will have nowhere to go if they need to ascend 500 m. The Mt Burns alpine zone would virtually disappear in the 3°C warming scenario because forest could reach close to the summit. For locally endemic high-alpine species, such as *Myosotis oreophila*, growing close to the crest of the Dunstan Mountains in Central Otago (Stanley et al., 1998), such a scenario would lead to species extinction unless rapid adaptation or other unknown factors occurred. However, the Remarkables area has a higher summit (2324 m) and because of drier conditions and past burning is not surrounded by forest, so it is likely

TABLE 2

Number of alpine islands in New Zealand before and after a 3°C warming

	Current no. alpine islands	With 3°C warming	No. lost (%)
North Island	87	20	81 (93)
South Island	354	344	273 (77)

that some alpine plants could survive there in a warming environment through lack of competition.

RATES OF CHANGE

The calculations of probabilities are based on an achieved equilibrium, possibly after hundreds or thousands of years. However, the conservative scenario of a 3°C mean temperature rise by 2100 implies a rise of isotherms of around 50 m per decade. It is unlikely that most vascular plant species will be able to move at such rates (including the rising forests). A long-term study in the European Alps suggests that the most common alpine species ascended 1–2 m per decade, with a maximum of 4 m during the last half century in which climatic warming equated to an 8–10-m rise or more per decade (Grabherr et al., 1995). Although there is still uncertainty (Cullen et al., 2001), comparable rates of ascent have been noted for the New Zealand treeline (Wardle and Coleman, 1992). The speed of change is thus likely to place pressure on vascular plants near vegetation limits over and above the pressures due to area reduction and fragmentation.

In addition, extinction may be subject to long lag times. A temperature rise of 3°C may place a certain number of species at risk, but extinction may not follow for many decades, and the species may linger on as an “extinction debt” (Tilman, 1996) or “living dead” (Revkin, 2000). It is possible to attempt to identify the species most at risk through a combination of ecological and biogeographic information (e.g., dispersal capability, habitat specialization, population sizes and distribution, recruitment rates). For example, McGlone et al. (2001) estimated that out of 571 New Zealand alpine vascular plants, 244 (43%) had low dispersal capabilities. These species (which are also mostly specialists with smaller altitudinal ranges) are at the highest risk from climate change. In contrast, some widespread species with good dispersal mechanisms may not suffer such a fate because they may be able to disperse from one mountain to a higher one.

UNCERTAINTY AND GENERALITY

Because the total number of New Zealand alpine vascular plant species after warming could be above 600 (Scenarios A and B), there may be no extinction pressure from reductions in area per se for the ~600 existing indigenous species. In other words, because the alpine flora is below saturation, it could conceivably tolerate considerable compression without extinctions. However, regardless of area, the main pressures in those scenarios would be due to invading species, total loss of endemics on alpine islands, and the relative rapidity of change requiring upward migration into areas where suitable soils may not be available.

The range of uncertainty of extinction predictions for alpine vascular plants at the scale of New Zealand should not detract from the basic statistical generality and certainty of the message formalized in species-area models: if climatic warming leads to species of taller vegetation establishing at higher elevations on mountains, the consequent reductions in available habitat area for alpine species (often to zero) may lead to the extinction of a considerable number of species unless countermeasures are taken.

Given the generality of the species-area relationship, other large biotic groups, such as insects, could suffer similar proportional degrees of threat. However, these generalizations may not hold for smaller taxonomic groups where specific taxonomic-ecological-scaling relations may apply, potentially leading to higher or lower risks.

Other vegetation types and ecosystems at lower altitudes will also be forced upward by rising temperatures, reducing their available area, with similar degrees of threat applicable in accordance with Figures 4 and 5. At sea level, the areas vacated by these rising ecosystem boundaries is likely to be filled by generalist, high-dispersal species, both indigenous and exotic, with a high degree of plasticity.

Conclusion

Long-term monitoring sites in New Zealand were mostly set up to follow recovery from grazing and burning within representative sites (Dickinson et al., 1992). Even in relatively undisturbed sites, workers have concluded that large-scale, occasional disturbances were overriding climate-change signals in relation to treeline dynamics (Cullen et al., 2001). Monitoring to interpret climate-change signals in New Zealand will require focused research approaches and experimental designs that are aimed at distinguishing such signals from the background noise (e.g., Mark et al., 2000; Pauli et al., 2001). Such an approach has recently been initiated at the Mt. Burns site in Fiordland.

Species-area models suggest that a 3°C rise in temperature could lead to a loss of 33–50% of indigenous alpine vascular taxa in the longterm. Additional losses would occur from the submersion of alpine islands, with ~80% of those potentially disappearing. At the same time, the resulting flora could be enriched by over 100 exotic vascular species. The resulting flora would include a much larger proportion of high-dispersal, genetically plastic species. Local endemics and low-dispersal and specialist species will be the first at-risk species to disappear.

As climate changes, rainfall, wind patterns, snow-lie, human disturbance, and invasive species behavior will also change in interdependent ways. Temperature rise is only one aspect of a multifaceted changing environment. Alpine plant species generally require open habitats and many have ruderal, colonizing abilities. Some are able to extend downward when forest cover below treeline is removed. Such species could actually enlarge their ranges due to extensive deforestation, irrespective of climate change. The scenarios presented here must be seen within these contexts. The value of these scenarios is that they are based on transparent assumptions and explore the sensitivity of the empirical datasets used to calculate the equation parameters.

Species-area, fragmentation, and metapopulation models can help suggest testable hypotheses and guide the design of large-scale monitoring projects as well as quantify potential threats particularly to smaller-scale mountains and low-dispersal endemic species. Overall, the present models suggest that maintaining all existing alpine species can be done only at a cost. Mitigating measures could include reducing the effect of competition from taller plants (trees and shrubs), as is already done today to maintain some areas of low-elevation induced tall-tussock grasslands (Calder et al., 1992), and the transfer of species trapped on mountaintops to higher summits in the same region, if available. Such decisions run into ethical dilemmas regarding how much society is willing to “engineer” species conservation as well as society’s will to constrain the unequal resource distribution that drives the excessive production of greenhouse gases (e.g., Costanza et al., 1997).

This study also identifies important knowledge gaps. Our level of ignorance, even in a relatively well-studied country such as New Zealand, is sobering. Out of the 441 alpine islands counted here (which may be much less than the real number), how many have biological inventories? How many have even been visited? Without inventories,

we have no knowledge of regional endemisms, and our taxonomic information is patchy at best. Accurate predictions of biotic impacts require this information.

Acknowledgments

We would like to thank all the people who contributed information on long-term monitoring sites, particularly Louise Cullen, Malcolm Douglas, Peter Espie, Alan Nordmeyer, and Greg Byron, who also provided access and guidance for using the Land Information New Zealand database. Matt Scott summarized the data for Figure 3. We are grateful to Katharine Dickinson, Bill Lee, Peter Wardle, Tracy Williams, two anonymous referees and the journal editor for commenting on earlier versions of the text.

References Cited

- Bellingham, P. J., Stewart, G. H., and Allen, R. B., 1999: Tree species richness and turnover throughout New Zealand forests. *Journal of Vegetation Science*, 10: 825–832.
- Bellingham, P. J., Wiser, S., Coomes, D., and Dunningham, A., 2000: Review of permanent plots for long-term monitoring of New Zealand’s indigenous forests. *Science for Conservation*, 151: 1–75.
- Brokaw, N., 1998: Fragments past, present and future. *Trends in Ecology and Evolution*, 13: 382–383.
- Calder, J. A., Wilson, J. B., Mark, A. F., and Ward, G., 1992: Fire, succession and reserve management in a New Zealand snow tussock grassland. *Biological Conservation*, 62: 35–45.
- Costanza, R., Cumberland, J., Daly, H., Goodland, R., and Norgaard, R., 1997: *An Introduction to Ecological Economics*. Boca Raton, Florida: St. Lucie Press. 275 pp.
- Cullen, L. E., Stewart, G. H., Duncan, R. P., and Palmer, J. G., 2001: Disturbance and climate warming influences on New Zealand *Nothofagus* tree-line population dynamics. *Journal of Ecology*, 89: 1061–1071.
- de Lange, P. J., Heenan, P. B., Given, D. R., Norton, D. A., Ogle, C. C., Johnson, P. N., and Cameron, E. K., 1999: Threatened and uncommon plants of New Zealand. *New Zealand Journal of Botany*, 37: 603–628.
- Department of Lands and Survey, 1984: Map of New Zealand—North Island, South Island—NZMS 265. Department of Lands and Survey.
- Dickinson, K. J. M., Mark, A. F., and Lee, W. G., 1992: Long-term monitoring of non-forest communities for biological conservation. *New Zealand Journal of Botany*, 30: 163–179.
- Duncan, R. P., Webster, R. J., and Jensen, C. A., 2001: Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand. *New Zealand Journal of Ecology*, 25: 35–47.
- Eriksson, O., and Jakobsson, A., 1998: Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. *Journal of Ecology*, 86: 922–933.
- Evans, G. R., 1973: *The Alpine and Upper Montane Grasslands of the Eyre Mountains*. Rangiora, N.Z.: Forest Research Institute. 19 pp.
- Fleming, C. A., 1963: Age of the alpine biota. *Proceedings New Zealand Ecological Society*, 10: 15–18.
- Gottfried, M., Pauli, H., and Grabherr, G., 1998: Prediction of Vegetation Patterns at the Limits of Plant Life—a New View of the Alpine-Nival Ecotone. *Arctic & Alpine Research*, 30: 207–221.
- Grabherr, G., Gottfried, M., Gruber, A., and Pauli, H., 1995: Patterns and current changes in alpine plant diversity. In Chapin, F. S. and Körner, C. (eds.), *Arctic and Alpine Biodiversity*: Berlin, Heidelberg: Springer Verlag, 167–181.
- Groombridge, B., 1992: *Global Biodiversity: Status of the Earth’s Living Resources*. London: WCMC, Chapman and Hall. 585 pp.
- Guisan, A., Theurillat, J. P., and Kienast, F., 1998: Predicting the Potential Distribution of Plant Species in an Alpine Environment. *Journal of Vegetation Science*, 9: 65–74.
- Halloy, S. R. P., 1981: La presión de anhídrido carbónico como limitante altitudinal de las plantas. *Lilloa*, 35: 159–167.

- Halloy, S. R. P., 1996: Native and managed diversity. *Agricultural Science*, 9: 31–36.
- Halloy, S. R. P., 1998: A theoretical framework for abundance distributions in complex systems. *Complexity International*, 6: 12.
- Halloy, S. R. P., and Mark, A. F., 1996: Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the Alps. *Journal of the Royal Society of New Zealand*, 26: 41–78.
- Halloy, S. R. P., Mark, A. F., and Dickinson, K. J. M., 2000: Management of New Zealand's terrestrial biodiversity as a complex adaptive system. In Halloy, S. R. P. and Williams, T. (eds.), *Applied Complexity—from Neural Nets to Managed Landscapes*: Christchurch, New Zealand: New Zealand Institute for Crop & Food Research, 104–123.
- Hubbell, S. P., 2001: *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, New Jersey: Princeton University Press. 375 pp.
- IPCC, 2001: *Summary for Policymakers: A Report of Working Group I of the Intergovernmental Panel on Climate Change*. Intergovernmental Panel on Climate Change, <http://www.ipcc.ch/pub/reports.htm>. 20 pp.
- Körner, C., 1999: *Alpine Plant Life—Functional Plant Ecology of High Mountain Ecosystems*. Berlin: Springer. 338 pp.
- Lee, D. E., Lee, W. G., and Mortimer, N., 2001: Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany*, 49: 341–356.
- Lugo, A. E., Parrotta, J. A., and Brown, S., 1993: Loss in species caused by tropical deforestation and their recovery through management. *Ambio*, 22: 106–109.
- MacArthur, R. H., and Wilson, E. O., 1963: An equilibrium theory of insular biogeography. *Evolution*, 17: 373–387.
- MacArthur, R. H., and Wilson, E. O., 1967: *The Theory of Island Biogeography*. Princeton: Princeton University Press. 224 pp.
- Malcolm, J. R., and Markham, A., 2000: *Global Warming and Terrestrial Biodiversity Decline*. Gland: WWF, 23 pp.
- Mark, A. F., 1977: Vegetation of Mount Aspiring National Park, New Zealand. *National Park Scientific Series, Department of Lands and Survey, Wellington*, 2: 1–79.
- Mark, A. F., and Adams, N. M., 1995: *New Zealand Alpine Plants*. Auckland: Godwit Publishing Ltd. 269 pp.
- Mark, A. F., Dickinson, K. J. M., and Hofstede, R. G. M., 2000: Alpine vegetation, plant distribution, life forms, and environments in a perhumid New Zealand region: Oceanic and tropical high mountain affinities. *Arctic, Antarctic, and Alpine Research*, 32: 240–254.
- May, R. M., 1981: Patterns in multi-species communities. In May, R. M. (ed.), *Theoretical Ecology, Principles and Applications*: London: Blackwell Scientific Publications, 197–227.
- McDonald, K. A., and Brown, J. H., 1992: Using montane mammals to model extinctions due to global change. *Conservation Biology*, 6: 409–415.
- McGlone, M. S., 1985: Plant biogeography and the late Cenozoic history of New Zealand. *New Zealand Journal of Botany*, 23: 723–749.
- McGlone, M. S., 1989: The Polynesian settlement of New Zealand in relation to environmental and biotic changes. In Rudge, M. R. (ed.), *Moas, mammals and climate in the geological history of New Zealand*: New Zealand Journal of Ecology, 115–129.
- McGlone, M. S., Duncan, R. P., and Heenan, P. B., 2001: Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *Journal of Biogeography*, 28: 199–216.
- McGlone, M. S., Moar, N. T., and Meurk, C. D., 1997: Growth and vegetation history of alpine mires on the Old Man Range, Central Otago, New Zealand. *Arctic and Alpine Research*, 29: 32–44.
- Pauli, H., Gottfried, M., Hohenwallner, D., Hülber, K., Reiter, K., and Grabherr, G., 2001: *The Multi-Summit Approach—Field Manual*. Vienna: Global Observation Research Initiative in Alpine Environments. 43 pp.
- Preston, F. W., 1962: The canonical distribution of commonness and rarity. *Ecology*, 43: 185–215, 410–432.
- Revkin, A. C., 2000: Extinction Turns Out to Be a Slow, Slow Process. New York: New York Times, Late Edition, 24 October 2000, Section F, Page 1.
- Scott, D., Dick, R. D., and Hunter, G. G., 1988: Changes in the tussock grasslands in the central Waimakariri River Basin, Canterbury, New Zealand, 1947–1981. *New Zealand Journal of Botany*, 26: 197–222.
- Simberloff, D. S., 1974: Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics*, 5: 161–182.
- Soulé, M. E., and Wilcox, B. A., 1980: *Conservation Biology. An evolutionary-ecological perspective*. Sunderland, Mass.: Sinauer Associates, Inc. 395 pp.
- Stanley, R. J., Dickinson, K. J. M., and Mark, A. F., 1998: Demography of a rare endemic *Myosotis*: boom and bust in the high-alpine zone of southern New Zealand. *Arctic and Alpine Research*, 30: 227–240.
- Stevens, G., McGlone, M. S., and McCulloch, B., 1988: *Prehistoric New Zealand*. Auckland: Heinemann Reed. 128 pp.
- Tilman, D., 1996: Competition and biodiversity in spatially structured habitats. *Ecology*, 75: 2–16.
- Tranquillini, W., 1979: *Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps*. Berlin: Springer Verlag. 137 pp.
- Troll, C., 1948: Der Asymmetrische. Aufbau der Vegetationszonen und Vegetations Stufen Auf der Nord-und Südhalbkugel. *Ber. Geobot. Forschungsinst. Rübel, Zürich*, 1947: 46–83.
- Troll, C., 1960: The relationship between the climates, ecology and plant geography of the southern cold temperate zone and of the tropical high mountains. *Proceedings of the Royal Society (Biological Science)*, 152: 529–532.
- Walcott, R. L., 1998: Modes of oblique compression—Late Cenozoic tectonics of the South Island of New Zealand. *Review of Geophysics*, 36: 1–26.
- Wardle, P., 1974: Alpine Timberlines. In Ives, J. D. and Barry, R. G. (eds.), *Arctic and Alpine Environments*: London: Methuen, 371–402.
- Wardle, P., 1978: Origin of the New Zealand mountain flora, with special reference to trans-Tasman relationships. *New Zealand Journal of Botany*, 16: 535–550.
- Wardle, P., 1998: Comparison of alpine timberlines in New Zealand and the Southern Andes. *Royal Society of New Zealand Miscellaneous Publications*, 48: 69–90.
- Wardle, P., and Coleman, M. C., 1992: Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany*, 30: 303–314.
- Watson, R. T., Zinyowera, M. C., Moss, R. H., and Dokken, D. J., 1997: *The Regional Impacts of Climate Change: An Assessment of Vulnerability—Summary for Policymakers, A special Report of IPCC Working Group II: Intergovernmental Panel on Climate Change*, <http://www.ipcc.ch/pub/reports.htm>.
- Watt, J. C., 1975: The terrestrial insects. In Kuschell, G. (ed.), *Biogeography and Ecology in New Zealand*: The Hague: W. Junk, 507–535.
- Wills, B. J., and Begg, J. S. C., 1986: The Cockayne plots of Central Otago—a 1985 evaluation. *New Zealand Journal of Ecology*, 9: 41–55.

Ms submitted June 2002