

Introduction: Themes and
Concepts in the Ecology of
Nothofagus Forests

**The Ecology
and Biogeography
of *Nothofagus* Forests**

millions of years: geological history, climatic change, evolutionary processes
decades to millennia: climate change, natural & anthropogenic disturbances.

short-term } history of vegetation change ⇒ ↑ ability to "Envision" possible
long-term } future scenarios

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Introduction: Themes and Concepts in the Study of *Nothofagus* Forests

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Southern Hemisphere temperate forests are dominated by *Nothofagus*

The unifying theme of this book is its focus on change in Southern Hemisphere *Nothofagus* forests. Forests characterized by *Nothofagus* species range from highland New Guinea at the equator to the southeastern tip of Tierra del Fuego at 56° S (fig. 1.1). At a timescale of millions of years we are concerned with how this distribution has developed in response to geological history, climatic change, and evolutionary processes. At a timescale of decades to millennia we seek to explain changes in the structure and composition of these forests that may be related to climate variation as well as to natural and anthropogenic disturbances. An important motive for our study of the long-term and short-term history of vegetation change is a desire to improve our ability to predict future vegetation change in relation to possible anthropogenic climate change. In this chapter we review some of the major themes and concepts in the study of vegetation change and comment on their relevance to *Nothofagus* forests. We raise a number of questions regarding the ecology and biogeography of *Nothofagus*. For some questions the data presented in subsequent chapters permit tentative answers, whereas for others insufficiency of data leaves them largely unanswered, but they remain useful guides for future research.

Traditionally ecologists, who study the dynamics of modern plant communities, and paleoecologists, who study vegetation change over

longer time spans, have worked independently, and in many cases largely unaware of each other (Davis 1989). They have tended to be isolated by their differences in data and methodologies, research questions, and theoretical frameworks. Recently, however, these artificial barriers to communication have been breached, and increasingly ecologists and paleoecologists are collaborating to explain the patterns and processes of vegetation change across a broad range of spatial and temporal scales (Davis 1989; Glenn-Lewin et al. 1992). The organization of this book strongly reflects this positive trend toward greater integration of ecological and historical perspectives on vegetation change.

The arrangement of chapters in this book is intended to promote this integration of perspectives. Following a discussion of the long-term and broadscale patterns of origin and differentiation in the genus (Chapter 2), each major *Nothofagus* region is treated first in a chapter discussing contemporary ecological patterns and subsequently in a chapter on the history and paleoecology of the region. The temperate zone of the southwest Pacific region is treated in Chapters 3 and 4 (on New Zealand), and in Chapters 5 and 6 (on Australia). The adjacent tropical zone of the southwest Pacific is the subject of Chapters 7 and 8. Chapters 9 through 11 deal with South American *Nothofagus* regions ranging from the Mediterranean-type cli-

*Land changes in land-use!
we can not forget this much more rapid & widespread change!

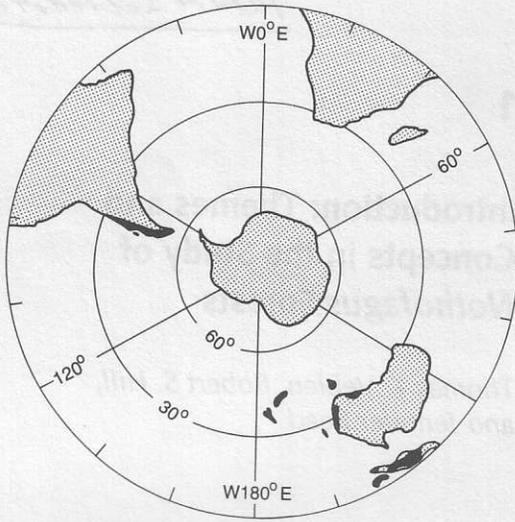


Figure 1.1. Map showing the current distribution of *Nothofagus* (after Humphries 1981).

mate region of central Chile to the subantarctic latitudes of Tierra del Fuego. In the Epilogue we review the most important themes in the study of the biogeography and ecology of *Nothofagus* and highlight some potentially fruitful topics for further research.

Temporal and Spatial Scales of Vegetation Dynamics

We use the term *vegetation dynamics* to refer to a broad array of changes in vegetation composition and structure (Miles 1979; Glenn-Lewin and van der Maarel 1992). The study of vegetation dynamics includes the traditional concept of plant succession, in which one assemblage of species is replaced by another. It also includes regeneration dynamics, or maintenance dynamics, in which there are no major trends in the species composition of a community but in which structural changes inevitably occur as a consequence of the reproduction, growth to maturity, and death of long-lived plants. Thus, ecologists have been concerned primarily with changes occurring at temporal scales of a few years to a millennium and at spatial scales of a few square meters to a few square kilometers (that is, microscale *sensu* Delcourt et al.

1983). In contrast, paleoecologists have examined vegetation change primarily in the sense of compositional and physiognomic change rather than population structure. They have been concerned mostly with change at the macroscale level (one to many millennia) and occasionally at the megascale level (periods of millions of years). They tend to describe vegetation change at spatial scales greater than tens of square kilometers (Foster et al. 1990).

The data and the methods that ecologists and paleoecologists use are distinct. At the temporal microscale the ecologist may study change through the direct observation of permanent plots or draw inferences from population structures or historical documentation (including historical photographs) or by substituting space for time in identifying chronosequences (Miles 1979; Glenn-Lewin and van der Maarel 1992). Thus, direct testing of predictions and experimental manipulations are theoretically available to the ecologist, although these methods are not utilized frequently for long-lived trees, for which obtaining significant results often requires many decades. Choosing between experimenting with ecophysiological responses to environmental variation and conducting at least short-term demographic experiments has been an important strategy for understanding the microscale processes of vegetation dynamics. The paleoecologist, in contrast, is dependent on the incomplete record of micro- and macrofossils and on inference from data on environmental history. High-resolution palynological techniques (Bradshaw and Zackrisson 1990) and annual-resolution dendroecological techniques (Ogden 1985b) have helped to link the temporal scales of the ecologist and the paleoecologist.

Imprecise usage of temporal and spatial-scale concepts has led to substantial confusion and debate among vegetation scientists. For the ecologist, changes in population structures and in compositions of communities dominated by annual and other short-lived plants that are related to annual environmental variation are regarded as short-term fluctuations. Such changes are seen as impermanent and may be incorporated into the

vegetation dynamics → changes in vegetation → composition
 → P (ecological processes) → structure

concept of an equilibrium state involving fluctuation around a mean composition (Miles 1979; Glenn-Lewin and van der Maarel 1992). In contrast, succession is usually evident only over time periods of a decade or more and is regarded as directional rather than fluctuating change in comparison with the life spans of the longest-lived plants in the community (Miles 1979, 1987). The boundaries between fluctuation and succession, however, are arbitrary. Spatially, this arbitrariness is evident in the case of a forest-shifting mosaic where species' abundances change in small patches (for example, $<100 \text{ m}^2$) while remaining near the average over larger areas. Temporally, the arbitrariness is also evident when we adopt a long time perspective according to which vegetation composition is changing slowly but directionally. In addition to the recognition of vegetation change as being scale-dependent, the adoption of different timescales also leads to different interpretations of vegetation change. First, we review some of the explanations of vegetation change at the microscale of the ecologist and then some themes are discussed at the macroscale of the paleoecologist.

Paradigm Shifts in Successional Theory

Interpretations of the dynamics of *Nothofagus* forests have changed fundamentally as different ecological paradigms have gone out of fashion. For example, in New Zealand the same patterns of stand structure that were once interpreted as evidence of climate-induced change toward a new type of climax vegetation (Cockayne 1928; Holloway 1954; Robbins 1962) have subsequently been interpreted as the consequences of stand dynamic processes without invoking climatic change (Veblen and Stewart 1982; Ogden 1985a, 1985b; Stewart 1986; Stewart and Rose 1989, 1990). Whether acknowledged or not, shifts in ecological paradigms have significantly influenced interpretations of ecological patterns in *Nothofagus* forests.

Frederick Clements (1904, 1916) offered a comprehensive theory of plant succession that dominated the field for the first half of the twen-

tieth century (Pickett et al. 1987; Glenn-Lewin et al. 1992). Clements believed that from environmentally distinct starting points, communities converged through succession toward a climax vegetation, the characteristics of which were controlled solely by the regional climate. He developed a scheme of succession-driving processes (1904, 1916) that has been an enduring framework for the study of successional processes (Pickett et al. 1987). The equilibrial and deterministic nature of his theory, however, was soon attacked by other ecologists (Gleason 1917, 1926; Raup 1957), and today these aspects of his theory are no longer accepted (Glenn-Lewin et al. 1992). Although most modern vegetation scientists accept the importance of autogenic factors that may lead toward a hypothetical equilibrium, they believe that attainment of equilibrium is relatively rare.

Two major conceptual trends have dominated research on vegetation dynamics since the mid-1970s (Glenn-Lewin et al. 1992): (1) a shift away from holistic explanations of successional phenomena (for example, Margalef 1963 and Odum 1969) toward reductionist and mechanistic approaches emphasizing proximate causes of vegetation change; and (2) a shift away from paradigms that emphasize equilibrium and toward viewpoints that accept continued change as the norm. Thus, in contrast with the predictions derived from deterministic driving forces of earlier successional theories, the tendency today is to predict vegetation change from an empirical knowledge of the mechanisms of vegetation change that apply to a particular local habitat (Pickett et al. 1987). In contrast to older views of succession that stressed the role of plant-controlled environmental modification (that is, reaction, or autogenic change) as the dominant mechanism of successional change, modern viewpoints emphasize a multiplicity of causal mechanisms (Pickett et al. 1987; Glenn-Lewin et al. 1992). Modern views of succession also stress the importance of repeated disturbance in contrast to the emphasis in Clementsian theory on a long disturbance-free period (Pickett and White 1985; Glenn-Lewin et al. 1992). Thus, they accept the importance of both autogenic and allogenic changes.

Disturbance and the Patch Dynamics Perspective

Disturbance, or "the mechanisms which limit the plant biomass by causing its partial or total destruction" (Grime 1979), is now viewed as a major influence on the structure and composition of plant communities. At a landscape scale, spatial discontinuities in plant communities often result in a mosaic of patches that differ in composition or structure (Pickett and Thompson 1978; Sousa 1984). This patchwork mosaic may result from the influences of disturbances on the intensity of biological interactions and resource availability. This point of view, known as the patch dynamics perspective (Pickett and Thompson 1978; Veblen 1992), has frequently been applied to the study of both fine-scale gap dynamics and stand-level dynamics of *Nothofagus* forests (Veblen 1985; Veblen et al. 1981; Ogden 1985b; Read and Hill 1985, 1988; Stewart 1986; Stewart et al. 1991; and see Chapters 3, 5, 7, 9, and 10).

Even in a forest stand in compositional equilibrium, at a particular point the canopy composition may be continually changing due to fine-scale treefalls. However, over the entire stand the pattern of gap-phase replacement may maintain similar relative abundances of dominant species. This focus on the gap phase has provided an appropriate framework for much research on the dynamics of *Nothofagus* forests (Veblen 1985; Stewart et al. 1991; Rebertus and Veblen 1993). In forests characterized by fine-scale treefall gap dynamics it is often useful to examine tree responses to a range of gap characteristics (Veblen 1992). Also, in this context, Grubb's (1977) concept of the regeneration niche has proved useful. The regeneration niche concept emphasizes the importance of niche differences during the early stages of life histories in relation to fine-scale environmental heterogeneity.

In many forested landscapes coarse-scale exogenous disturbances such as fire, mass movements, insect outbreaks, and extensive blowdown are widespread and sometimes frequent enough to have a controlling influence on forest structure

and composition at a landscape scale (White 1979; Pickett and White 1985). For the conceptualization of stand development patterns in forests characterized by coarse-scale disturbances, and therefore by "whole stand replacement," Oliver's (1981) general model of stand development has proved useful. According to this model, after stand-destroying disturbances the following developmental stages can be expected (Oliver and Larson 1990): (1) stand initiation; (2) stem exclusion; (3) understory reinitiation; and (4) old growth. The model applies best to disturbances that kill an entire stand and result in the establishment of a new tree cohort of one or several species and has frequently been applied to *Nothofagus* forests (for example, Veblen et al. 1981; Wardle 1984; Wardle and Allen 1983; Stewart 1986; Veblen and Lorenz 1987; Ogden 1988; Read et al. 1990; and see Chapters 3, 5, 7, 9, and 10). Since in most landscapes disturbances of a variety of scales and intensities occur, this type of whole-stand-replacement model is best combined with the paradigm of fine-scale treefall gap dynamics.

An intriguing aspect of the dynamics of *Nothofagus* forests is the occurrence of conspicuous stand-level dieback or partial crown mortality throughout the distribution of the genus. Such diebacks have been attributed to a variety of complex interactions among predisposing factors and triggering and accelerating factors (see Chapters 3, 5, 7, and 10). Predisposing factors include climatic conditions, site conditions (soil fertility, soil moisture availability), and stand-age structure, whereas triggering and accelerating factors include insect attacks, fungal pathogens, and windthrow and other physical disturbances. Although in many cases the etiologies of these diebacks are not fully understood, the even-aged character of postdisturbance *Nothofagus* populations is a common predisposing factor in most cases.

In the context of describing tree population responses to disturbance of varying types and scale, the concept of regeneration mode is useful (Veblen 1992). *Regeneration mode* refers to the spatial scale at which regeneration occurs in relation to disturbance; it usually can be inferred from

the age structure and spatial patterns of tree populations. The regeneration mode concept complements the regeneration niche by providing a coarser-scale perspective on regeneration patterns in relation to disturbance. A continuum of regeneration modes may be segregated arbitrarily into three types: catastrophic, fine-scale gap-phase, and continuous (Veblen 1992). A particular regeneration mode may be characteristic of a species in only a general way, and may vary with forest type, abiotic site factors, or stage of stand development.

The concept of disturbance regime is a useful way of describing the spatial and temporal characteristics of disturbances that affect a particular landscape (Sousa 1984; White and Pickett 1985). For each type of disturbance (fire, blowdown, snow avalanche, and so on), the key descriptors of a disturbance regime are (1) spatial distribution of occurrence, particularly in relation to environmental gradients; (2) frequency of occurrence; (3) size of the area disturbed; (4) mean return interval (that is, the inverse of frequency); (5) predictability; (6) rotation period (the time required to disturb an area equivalent in size to the study area); (7) magnitude of the disturbance, measured either directly as the intensity of the disturbing agent or indirectly as the severity of its impact on the vegetation; and (8) the synergistic interactions of different kinds of disturbances. Application of the disturbance regime concept has proved useful in interpreting the dynamics of *Nothofagus* forests (Stewart et al. 1991; Veblen et al. 1992; Rebertus and Veblen 1993).

Microscale Climatic Variability and Vegetation Change

Climatic variability is an important exogenous factor in regeneration dynamics and successional processes in forest communities (Davis 1986; Prentice 1992). Recent concern over the ecological effects of anthropogenic climate change has accelerated efforts to understand and quantify climate-induced vegetation change (COHMAP members 1988; Davis 1989; Graham et al. 1990;

Clark 1990; Overpeck et al. 1990). Both modeling and paleoecological approaches have proved useful in elucidating the effects of climate change on vegetation dynamics. Current capability to predict climate-induced vegetation change is limited, however, by spatial and temporal scale problems (Overpeck et al. 1990; Graham et al. 1990). In particular, at timescales of a few decades to a century it is often difficult to determine the effects of climatic variation on population dynamics of long-lived trees. Nevertheless, climatic variability at annual-to-decadal timescales undoubtedly affects tree demographic processes, especially in areas near the climatic limits of their distributions.

Current capabilities to predict the influences of climatic variation on vegetation dynamics at decadal timescales are also limited by inadequate knowledge of how disturbance regimes will be affected. It is likely that the most immediate manifestation of climatic influences on vegetation dynamics will be mediated through altered disturbance regimes (Johnson and Larsen 1991; Sirois and Payette 1991). The effects of climatic warming may, however, have uncertain consequences for disturbance regimes. For example, climatic warming may result in a greater number of fire ignitions in presently mesic environments, but in more xeric environments reduced productivity could result in a decrease in the amount of fuel for fires. Similarly, climatic variability affects both the population dynamics of forest insect pests and the resistances of trees to insect attack. There is a glaring need for studies of the effects of climatic variation on disturbance regimes in different habitat types in order to predict the effects of climatic variation on vegetation dynamics. Given the importance of climatically related disturbances such as fire, blowdown, and insect outbreaks in many *Nothofagus* forest types, these forests are likely to be particularly susceptible to climatically induced change in disturbance regimes. Similarly, the distribution of many *Nothofagus* forest types in ecotonal areas where temperature and/or moisture level limit forest distribution also suggests that these forest types would be particularly sensitive to climate change.

36 mill. AP → corriente circumpolar antártica ⇒ ↓ t° en lat. altas

↑ genero
separación de → Australia
→ Sudamérica
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Antártica

Hb. ↓ la humedad q' antes provenia de las corrientes tropicales ⇒ ↓ lluvia
↑ t° → lat. tropical
↓ células

Macro- and Megascale Vegetation Change

Over the last sixty million years there have been at least four major and interacting sources of environmental change that have had important effects on plant species and species interactions at high southern latitudes: climate change, changes in photoperiod, changes in carbon dioxide levels, and changes in the positions of the southern landmasses.

CLIMATE CHANGE

The broad aspects of climatic change during the Cenozoic (fig. 1.2) are well documented (for example, Quilty 1994) and consist of substantial changes in both temperature and rainfall. In particular, temperature has decreased throughout this time, especially at high southern latitudes, although not at a steady rate. There was a major temperature drop at about the Eocene-Oligocene boundary, possibly associated with the initiation of the circum-Antarctic current. Prior to this time ocean currents circulated water from the warm tropics to high latitudes, thus introducing a vast mass of warm water to the region. This had the effect of lessening the temperature gradient between the equator and the pole and producing warm conditions with little diurnal or seasonal variation at very high latitudes. The separation of Australia and South America from Antarctica caused a major redistribution of oceanic currents, with the circum-Antarctic current predominating and thus confining a large mass of water at high latitudes. This caused a steep increase in the equator-to-pole temperature gradient and a rapid cooling at high latitudes.

Changing circulation patterns also affected rainfall. The early Tertiary equator-to-pole currents caused high atmospheric humidity and year-round moist conditions. The change of oceanic circulation and movement of the subtropical high-pressure cell later in the Tertiary caused a decline in rainfall, a shift to more seasonal rainfall, and finally, in southeastern Australia, a change from summer-dominant to winter-dominant rainfall (Bowler 1982).

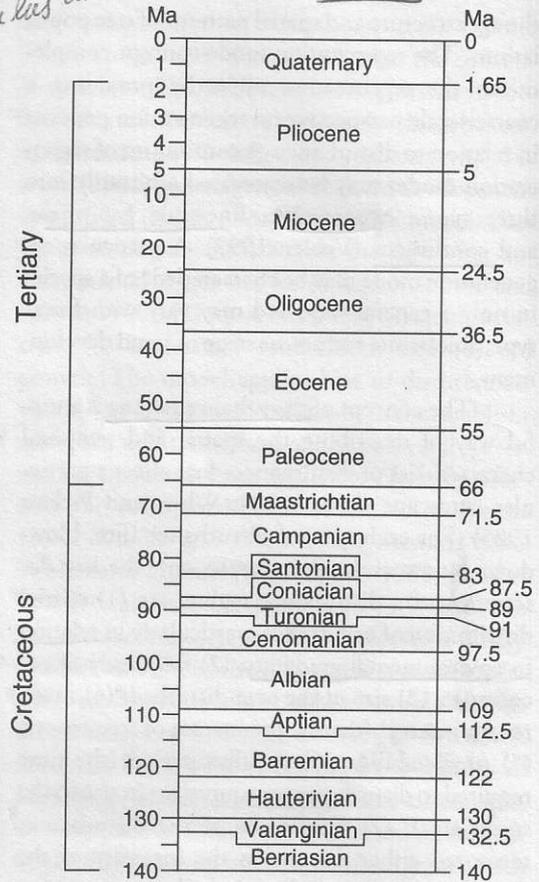


Figure 1.2. Geological timetable for post-Jurassic time (after Haq and Eysinga 1987).

Thus, during the Cenozoic there were major climatic changes, and, equally important, there have been climates in the past that no longer occur today, especially at high southern latitudes. This must have had a major impact on species distributions and interactions at the community level in the areas encompassed by the present and past range of *Nothofagus*. These changes can be assessed at a gross level by examining such aspects of ecophysiology as the response of species to frost. In the early Tertiary, frost at high latitudes was probably a rare phenomenon, much as is the case today in highland New Guinea. There are, however, records of the devastating effects of rare frost on *Nothofagus* in New Guinea, and this frost is likely to have been an important factor in plant

t°

lluvia

⇒ ∴ plantas empiezan a responder a ↓ T° = heladas
↓ lluvia

Movim. de continentes ⇒ 4 lat. ⇒ 4 fotoperiodo ⇒ respuestas de plantas

evolution and species extinction as temperatures dropped at high southern latitudes. Finer-level effects are difficult to reconstruct for such remote times, but the apparently conservative morphology of *Nothofagus* is useful here, since it implies a conservative physiology and thus information gained from living species can be applied to the past with some confidence. Research on water use and photosynthetic performance on extant *Nothofagus* species will be increasingly useful as our understanding of the fossil record is refined. The effects of these climatic changes are discussed for each region in Chapters 4, 6, 8, and 11.

PHOTOPERIOD

During the Cenozoic much of the dry land at high southern latitudes has been drifting from high into lower latitudes. For example, Australia has moved approximately 30° north over the last sixty million years (Veevers et al. 1991). This means that southern Australia has shifted from essentially polar photoperiods, with ever-light summers, low sun angles, and ever-dark winters, to its current mid-latitude photoperiod. Such a dramatic change in photoperiod would have required major evolutionary changes in the photoperiodic responses of high-latitude plants, including *Nothofagus*. It also implies significant changes in the life-form composition of the vegetation and in faunal assemblages characteristic of the southern landmasses over the last sixty million years. Among the more obvious responses here is the switch from the evergreen to the deciduous habit, which seems to have taken place several times (Hill and Jordan, 1993) and which must have been heavily influenced by photoperiod. It is clear that a very high proportion of fossil *Nothofagus* leaves from Antarctica were from deciduous plants, and, given that the climate seems to have been relatively mild at the time, photoperiod was probably the main reason. Photoperiod effects on evergreen leaves were more subtle, and it is too early to determine any recognizable patterns.

CARBON DIOXIDE LEVELS

Changes in CO₂ levels during the Cenozoic are uncertain, and their method of calculation may

involve circularity. There are, however, accumulating data to suggest that CO₂ levels were substantially higher than present levels during the early Tertiary (about 450 ppm, Caldeira and Rampino 1991) and subsequently declined. Detailed analysis of the Vostok Ice Core (Barrett 1991) shows rapid fluctuation between extremes of just under 200 to just under 300 ppm CO₂ during the last 160,000 years. There is a wide-ranging literature on the effects of elevated CO₂ levels on living plants, but it is difficult to extrapolate these results backward in time. Plants have the capacity to adapt to changing conditions; millions of years' worth of adaptation may lead to a much different result than that obtained from instantaneous experiments that subject extant plants to suddenly changed levels of CO₂. Thus the effect of variations in past CO₂ levels is still uncertain and will require more directed research in the future.

Nothofagus and other plants that have grown in high southern latitudes during this sixty-million-year period have had to survive these long-term, and, more recently, short-term fluctuations. The combination of extinct climatic conditions, unusual photoperiod, and alternating high and low CO₂ levels gives rise to a variety of conditions that plants encountered in the past but that have no modern analogue. The response of plants to these conditions is critical to understanding present species distributions and interactions in communities.

CHANGES IN LANDMASS POSITION

Far southern landmasses offer an interesting biogeographical problem in that their position shifted dramatically during the Cenozoic, when the living flora was establishing. Thus, past events loom large in explaining present distributions. In recent decades the theory of plate tectonics has played a large role in explaining land-based dispersal as the major force in living plant distribution, and there is no doubt that this is true at the broad scale. However, evidence is accumulating to suggest that long-distance dispersal, though rare, has been important even for taxa that have traditionally been considered to be particularly land-

deciduos o siempreverdes

60.000 d.u. = 01

⇒ hábito deciduo de los *Nothofagus* de la Antártica se relaciona con el fotoperíodo.

plate tectonics
long-distance dispersal

locked (for example, *Nothofagus*). Macphail et al. (1994) have demonstrated the likely long-distance dispersal of several *Nothofagus* species from Australia to New Zealand during the Cenozoic, long after the Tasman Sea was in place. As discussed in Chapter 2, as more data accumulate on past distribution of taxa in high southern landmasses the history of the region becomes more complex.

Biodiversity and Conservation

An important goal of this book is to integrate perspectives from historical biogeography and contemporary ecology to show how the present patterns of biodiversity in *Nothofagus* forests have developed over time. The timing and environmental conditions under which the differentiation of the genus has occurred are of interest not only to the historical biogeographer but also to those interested in preserving the present biodiversity of these forests.

Nothofagus forests range in type from pure stands dominated by a single tree species to species-rich temperate and tropical rain forests.

The historical and modern factors that account for broad- and local-scale variations in the floristic composition of these forests are extensively treated in each of the regional chapters. From the point of view of preserving biodiversity (including intraspecific genetic diversity), such knowledge is vitally important.

Over most of the distribution of the genus, *Nothofagus* forests have been significantly influenced by humans through logging, the use of fire, and introduction of livestock and other exotic herbivores. Thus, the degree to which *Nothofagus* forests in each region have been altered by humans is an important subtheme of this book. Similarly, the current state of ecological knowledge for the silvicultural management of these forests is discussed for each region.

Summary

The dominant theme of this book is change in *Nothofagus* forests—change ranging across

timescales of decades to many thousands and even millions of years. Over the relatively short timescale of the ecologist, change in the structure and composition of forest stands has frequently been related to both natural and anthropogenic disturbance. Over the multimillennial timescale of the paleoecologist, climate change and broad-scale human impacts have typically been invoked as the causes. Increasingly, however, the arbitrary nature of the distinction between these timescales and causes has been recognized. In this book we strive to provide an integrated perspective that cuts across the whole hierarchy of spatial and temporal scales at which the processes of vegetation change occur.

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