Climatic change: ecology’s big question

Science is driven by substantive questions that organize and focus the intellectual efforts of researchers. In Astronomy, how did the Universe begin? In Physics, what comprises matter? In Biology, how are genes duplicated over generations? In Ecology, how do ecosystems change when climate changes? Answering this substantive ecological question, particularly when climate alteration includes an increase in the amount of carbon dioxide in the atmosphere, requires a synthesis of all we think we know – from the physiology of plants and animals to population and community ecology to ecosystem productivity and element cycling – and we still do...
not have a complete answer. Answering this climate–ecosystem question is given urgency by the implications of global climate change for life on Earth.

The climate–ecosystem question is in today’s news but it springs from deep roots in Ecology’s history. Relationships between climate and vegetation are among the earliest ecological observations and most relevant to our big question. As early as the 3rd century BC, Theophrastus, a Greek philosopher sometimes called the ‘Father of Ecology,’ conducted experiments by transplanting species to areas outside their natural range to determine if they would grow (or flower). He documented systematic changes in patterns of deciduousness and evergreenness with different climate conditions. Theophrastus also observed the positive relationship between altitude and latitude with respect to their climates and vegetation. Two millennia later, these early observations and the long history of others were codified by the great exploratory biologists of the 18th and 19th centuries. Alexander von Humboldt stands out as the most conspicuous example. He was a holistic thinker with a unique capacity to record biological and cultural details coupled with a fascination with diverse environmental data.

Alexander von Humboldt was the intellectual giant of the early 18th century. He developed an observation-based, detail-rich approach to scientific inquiry that fuelled his remarkable capacity to synthesize the underlying generality from details. His ‘Humboldtian Science’, the detailed measurement of the planet with the goal of understanding how physical and biological processes shape and sustain the world, was the guide to a scientific great-generation to follow. Certainly, Alexander von Humboldt’s life and work make him the pathfinder in the scaling-up of the consequences of finer scale observations of processes and patterns to larger consequences – the essential challenge in predicting climate change effects on ecosystems. He saw as one of his principal accomplishments the understanding of how the environment influences ecosystems. Today, two centuries later, ‘scaling-up’ and quantifying vegetation–climate relations remain as the kernel needed to understand the ecological workings of Earth, a planet that we are actively changing.

In 1804, when he returned from his extended travel to the Americas, Alexander von Humboldt had laid the foundation that would make him the most celebrated intellect of his time. He had performed dramatic deeds. By a dangerous boat journey, particularly so as he could not swim, von Humboldt first demonstrated that, uniquely among the major rivers of the world, the Orinoco drainage exchanged waters with the Amazon basin. Along with Aimé Bonpland and Carlos Montúfar, he climbed to 5875 m on the tallest mountain in Ecuador, Mount Chimborazo. Blocked by a
crevice, they could not reach the 6268 m summit. At that time, Chimborazo was thought to be the tallest mountain on Earth. Theirs was the highest altitude reached by any European mountaineer, a record that would stand for decades.

He brought new and novel observations of the new world tropics. In New Granada (now Colombia), he observed mud volcanoes in Turbaco and inspected mastodon fossils on the Campo be Gigantes. Through all of this and much more, he withstood pestilence, disease, and the rigours of travel in unexplored regions. He collected notes on plants, animals, geology, the environment and the human condition. While returning to Europe in 1804, he met with President Jefferson at the White House and later was his guest at Monticello. Jefferson wrote in a letter to Casper Wistar on 7 June 1804. ‘I have omitted to state above the extreme satisfaction I have received from Baron Humboldt’s communications. The treasures of information which he possesses are inestimable …’ The two men corresponded for years hence.

Returning to Paris in 1804 with crates of notes on geological, astronomical and biological ‘treasures’, he began his life work of writing and synthesizing this knowledge. Humboldt was Prussian, but he lived in Paris for the next 23 years and spent his fortune publishing maps and reports. One of these publications is shown in Fig. 1.1, part of von Humboldt’s Tableau des Régions équinoxiales published in 1807. It shows the distributions of plants with elevation on a cross-section through the Andes. On the original diagram to the left and right of this cross-section, there are two tables (not shown in order to enhance the detail in Fig. 1.1). These flanking tables were arranged by elevation and listed (as a function of elevation): the heights of Andean mountains as well as the distance these mountains should be visible at sea, bending of light by the atmosphere, the appearance of electrical phenomena, vegetation, loss of weight as evidenced by change in pendulum swing in a vacuum, blueness of the sky, humidity of the atmosphere and atmospheric pressure, minimum and maximum temperatures, the chemical composition of the atmosphere, the height of the lower snow line, the animals found at different altitudes, boiling points of water with altitude, geological notes and the amount of the weakening of sunrays while passing through the atmosphere. This is but an indication of the breadth of his observations and his capacity for synthesis of large volumes of data.

Over his life time, von Humboldt produced 44 books and reports, several with multiple volumes, including the five volume Kosmos with its fifth volume published in the year of his death at age 90 in 1859. Luminaries of his time – Honoré de Balzac, Lord Byron; Victor Hugo, Gustave Flaubert – praised him and his remarkable intellect. His friend,
Johann Wolfgang von Goethe, stated, ‘One can truly say that he has no equal in information and lively knowledge’, and Simón Bolívar, ‘Alexander von Humboldt is the true discoverer of South America’. Ralph Waldo Emerson likened him to Aristotle and provided the excellent summary that, ‘Humboldt was one of those wonders of the world ... who appear from time to time as if to show us the possibilities of the human mind, the force and range of the faculties, – a universal man.’

Von Humboldt saw his own accomplishments more modestly. As an octogenarian in 1854 in a letter to his publisher Georg von Cotta dated 31 October 1854\textsuperscript{12}, he listed his ‘only’ three accomplishments as: (i) observations concerning geomagnetism that resulted in the establishment of magnetic stations throughout the planet; (ii) the geography of plants,
particularly of the tropical world; (iii) the theory of isothermal lines. The magnetic stations were the consequence of a direct appeal by Humboldt to the Royal Academy and to the British Society for the Advancement Science. The station observations eventually tied changes in the Earth’s magnetic field with sunspot activity. His work on the biogeography of plants and his vivid description of tropical ecosystems lead Darwin to sail to the tropics on *HMS Beagle* and was a principal influence on the development of Darwin’s theory of natural selection. The accomplishment that is most immediately germane to this chapter is the ‘theory of isothermal lines’ (Fig. 1.2).

Isothermal lines are those that connect locations with the same annual average temperature. As calculated by von Humboldt, this temperature is obtained by averaging of two daily observations, the temperature at sunrise and at 2 p.m., over a year. Isothermal lines captured the regular variations in the height of snow on mountains (the higher in latitude the lower the line of permanent snow) and vegetation features (tree lines, transitions from evergreen to deciduous forests, etc.) as they changed with elevation and latitude (Fig. 1.2). Earlier discussion of Figure 1.1 listed the variety of measurements von Humboldt made with a diverse kit of instruments. He
was a dedicated empiricist who collected measurements of the state of the environment all the time. From this myriad of observations on the state of the environment, he found isothermal lines provided a general summary of the global pattern of environment and vegetation. Von Humboldt probably would not have viewed isotherms as the ‘limiting factor’ for vegetation interacting with climate. Von Humboldt saw the world as full of strong interconnections – ‘Alles ist Wechselwirkung’ [Everything is interconnected]. Isotherms were measurements bringing along all of the interconnected physical, chemical and biological interactions.

Nevertheless, the perfection of how best to represent the environment and its interaction with the planet’s vegetation was to occupy biogeographers for the next two centuries right up to the present day. There are two interdependent, fundamental issues that must be dealt with to evaluate the effect of climate change on natural systems.

1 How is the system resolved in time, space or complexity? To understand climate change effects on vegetation, must we understand leaf response, whole plant response, population response, etc., or somehow all of the above? This is the topic of this chapter and this will be revisited in Chapters 3 and 4. The development of increasingly more aggregated, more holistic representations of ecological systems is part of the historical development of the vegetation–climate challenge.

2 What in the environment dominates the response to ecological systems? What are the controlling factors? Most importantly, will the importance of these environmental factors change under novel conditions? In particular, will the importance of factors change with an increase in the CO₂ levels of the atmosphere – which has already happened to a degree from human actions and should continue to do so? Or, under novel climatic conditions will new factors control natural system response?

The importance of this understanding has been sharpened greatly by our concerns on the effects of climate change on the Earth’s ecosystems. These two issues and the questions they imply derive from ecology’s historical roots. They are brought into a fresh immediacy by our present-day concerns with global environmental change.

1.1 Early environmental biogeography: from mapping plant species distributions to mapping vegetation

The earliest mapping of vegetation over large areas touched upon the same issues that are in the current problem of evaluating the effects of climate change on vegetation. One of the issues involves identifying the factors in
the environment that seem to control the vegetation. In past maps, environmental controlling factors in one region might not work so well in another region (the analogous current problem is that the rules that seem to work well in today’s climate might not work in a future climate). Another important issue is the level of ecological organization that allow one to best understand patterns and changes in patterns. Von Humboldt in the discussion above focused on species as the unit of interest. Other units of organization might be fundamental processes such as photosynthesis or respiration and how they respond to climate. Alternatively, groupings of species into functional groups may better reveal climate–vegetation relationships. Perhaps amalgamating whole assemblages of species into recognizable plant communities is the key? These issues are topics of research in global change today and they are part of the deeper history of vegetation–climate relations.

European maps with indications of plants and vegetation date at least to the 15th century, when maps indicating forest vegetation with groups of small symbols of trees appeared. In the 16th century, as the importance of forests increased in designing military campaigns and the value of forests for timber and hunting in a deforested Europe became apparent, greater detail in the representation of forests and other vegetation on maps followed. However, our focus here is not on the history of maps but on maps as formal expressions of relationships between climate and vegetation. To do so we will discuss a pair of important early maps.

First, von Humboldt’s diagram (Fig. 1.1) is what is called a ‘transverse view’ map of vegetation. It shows the elevational distribution of hundreds of plant genera and species as well as zones with some specific assemblages of plants (Zone of Palms; Region of Chaquiraga, the Gentinians and Frailexon from 2000 to 4100 m, etc.) on an idealized cross-section through Mount Chimborazo. It is not the oldest such map but it is certainly an important one. Twenty-three years earlier in 1784, Giraud-Soulavie had made the first transverse vegetation map of the changes in Mediterranean flora with latitudinal climate gradients. These transverse-view maps idealize the manner that vegetation is arranged under the control of altitude – they are abstract models of climate–vegetation organization intended to be interpreted based on knowledge of the topography of a region.

Second, the Swiss botanist Augustin-Pyramus de Candolle and fellow naturalist Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck printed the map shown as Fig. 1.3 in 1805. Lamarck’s remarkable contribution as a naturalist is historically eclipsed by his development of a now-rejected theory of the evolution of species, namely the idea that acquired traits in an individual’s life time would be inherited by its offspring. Ironically, de Candolle’s son (also a Swiss botanist), Alphonse Louis
Pierre Pyramus de Candolle also is attributed as the first biogeographical map maker for his map made in 1855. The inspiration of the father can certainly be seen in the work of the son. The Lamarck and elder Candolle map (Fig. 1.3) is discussed by Ebach and Goujet in their history of what they call ‘biogeographical maps’, which they define using C.H. Merriam’s.
statement that biogeography is the study of geographical differences, namely the change ‘that takes place in the flora and fauna of a region in passing from one region to another, or from low valleys or plains to high mountains – geographic differences’ [p. 3].

Lamarck and de Candolle’s map (Fig. 1.3) differs from von Humboldt’s transverse map because it is a conventional map. It is drawn from an overhead view of the mapped surface. The 1805 map encoded the degree to which different parts of France had been surveyed by botanists by using different styles and sizes of type to indentify towns in regions with more or less botanical reconnaissance. Primarily, their map provided the distribution of regions of plants in France (its legend is translated by Ebach and Goujet). Their map also shows the northern range for the cultivation of olive, grapes and maize as a set of parallel lines. In their notes to the map, Lamarck and de Candolle give an opinion on the environmental controlling factors. ‘From the preceding considerations, I [A.P. de Candolle] believe that in a given country, such as France, the causes that determine the plant region [habitation] could be reduced to three: 1. Temperature, as determined by distance from the equator, height above sea level and southern or northerly exposure. 2. The mode of watering, which is more or less the quantity of water that reaches the plant. The manner by which water is filtered through the soil and the matter that is dissolved in the water which may or may not be harmful to the growth of the plant. 3. The degree of soil tenacity or mobility.’ [p. 768]

The two historical maps (Figs 1.1 and 1.3) display different biological units. Von Humboldt mostly mapped genera and species; Lamarck and de Candolle mapped floristic provinces and discussed (in accompanying text) a methodology for classifying these provinces. Lamarck and de Candolle produced a map of where in France their floristic provinces are found; von Humboldt produced a more cartographically idealized mountain profile in his transverse diagram. In both cases, the maps include a considerable amount of information on the species of plants comprising the vegetation – this is hardly surprising for maps from the early 1800s produced in the wake of the Swedish scientist Carl von Linné’s (‘Linneaus’) development of the genus/species scientific-binomial 50 years before.

The maps, particularly von Humboldt’s map (Fig. 1.1), disagree substantially with Linnaeus’ ideas on the chorology of species. Heackel in 1866 invented the term, chorology, as ‘the science of the geographic spread of organisms’ or the study of the rules of distribution of living organisms across the Earth’s surface. Linnaeus thought that unchanging species had spread across the Earth from the landing point of the biblical Noah’s Ark on Mount Ararat in Turkey. Dispersal after landfall generated the flora and faunas of the world. If this were true, then species in similar environmental
conditions but in different locations should be the same. Scientific exploration soon showed this not to be the case. In 1762, Comte Georges Louis Leclerc de Buffon observed that the large mammals of the tropical parts of the Old and New Worlds are quite different taxonomically. Von Humboldt expanded Buffon’s observation that unrelated species are found in separated but environmentally similar locations (sometimes called Buffon’s Law) to flowering plants, birds, reptiles, insects and spiders. The two maps (Fig. 1.1 and 1.3) are at the beginning of the systematic biogeography tradition.

1.2 Global distributions of vegetation

Studies in this biogeographic tradition involved climate from their inception (Figs 1.1 and 1.3). This led to an interest in how climate and other environmental factors controlled the distributions of species, of types of vegetation and of what we would today call biomes. In this section, we will provide examples of different systems that interrelating climate with different conceptual models of vegetation organization produced:

1. vegetation characterized by the physiognomy of the dominant plants;
2. vegetation as a collection of types of plants based on form sorted by climate conditions;
3. biome or formation organizations in response to climate conditions.

These are all holistic attempts to understand the patterns of vegetation at a level that goes beyond taxonomy to understanding larger patterns and eventually the functioning of vegetation.

In 1872, Grisebach developed the first world-scale vegetation map (Fig. 1.4). In his two-volume book with over 1300 pages in total, he described the vegetation of each of the zones mapped in Fig. 1.4. The initial section of each of these descriptions was ‘Klima’ or the climate of the region. Grisebach’s early map showed several biomes with similar physical appearance (such as tropical rainforest, prairies, etc.) even though their taxonomical make-ups were different. Mixed with these were also taxonomic categories that revealed less about the character of the vegetation and more about their taxonomic origins (e.g., the Australian flora, the New Zealand flora, etc.). In formulating his map, Grisebach used detailed accounts of species in different regions but he also designated some 54 forms of vegetation for his appearance-based vegetation categories. Many of these forms have a strongly ecological focus (Bamboo, Banyan, Liana, Steppe Grass, Annual Grass, etc.) while others are more taxonomic (Cactus, Cactus,
Palm, Ferns, Bromeliads, etc.). Schimper developed the first vegetation map (Fig. 1.4) with modern biomes, namely:

Tropical Rainforest, Subtropical Rainforest, Monsoon Forest, Temperate Rainforest, Summergreen Broadleaf Forest, Needleleaf Forest, Sclerophyll
Woods, Savanna Forests, Thorn Forests and Scrub, Savannas, Steppes and Transitions between Steppes and Deserts (Semi Deserts), Heaths, Dry Deserts, Tundra, Cold Deserts.

These vegetation categories (or something close to them) continue today to categorize world vegetation at the highest level of interaction. Explaining these patterns inspired the early plant geographers to postulate relationships between climate and plant structure as the conceptual basis for mapping the global pattern of vegetation.

Reciprocally, early and many modern-day maps of climates are based strongly on the tight relationship between climate and vegetation. These maps reinforce the importance of the climate–vegetation connection. In the Köppen climate system, climate is initially divided into main climate zones (equatorial, arid, warm temperate, etc.) that also relate strongly to broad categories of vegetation. Subordinate categories in some cases have embedded vegetation formations (e.g., desert, tundra). Different climates are delineated by temperature, precipitation and the seasonality of precipitation.

This seasonality component is important because it separates areas in which the rain does not occur in the most favourable season for growth from those in which it does. For example, savannas receive their precipitation in summer and are raingreen; mediterranean shrublands in winter and are mostly evergreen. Detailed climate maps often show climates for locations where there are no weather stations recording data (e.g. tops of mountains in remote locations). In these cases, the climate maps are often based on knowledge of vegetation pattern converted to the expected climate pattern.

1.2.1 Vegetation maps and climate–vegetation interactions

Later chapters will deal with the use of ecological models as tools for predicting the effects of climate change on ecosystems. Maps are ecological models, just as much as the mathematical models that will be discussed later. Maps and these other models share some fundamental issues. For example, the issue of scale (discussed in more detail in Chapter 3) has always been important in the development of vegetation maps and is a central issue in ecological modelling. For maps, it was realized from the beginning that patterns in vegetation appear (and disappear) or become enlightening (or confusing) at different spatial resolutions.

Because of this, plant geographers developed formal systematic methods of abstracting the vegetation into maps. Narratives of von Humboldt (Fig. 1.1) and Lamarck and de Candolle (Fig. 1.3) detailed their procedures to
develop their early maps. Thankfully, this tradition has persisted since. In these procedures, there are important assumptions concerning the fundamental nature of vegetation seen at different scales. At what level of resolution is the structure of the vegetation the essential feature to map? At what level of resolution does one need to include the important species? Do the rules for appropriate resolutions change in different continents? In different regions? These theoretical implications involved in making maps of vegetation were well understood by the early plant geographers, although there was an understandable variation in the solutions that they developed for these and similar questions.

In the sections below, we will discuss approaches at exploring different levels of organization as bases for relating plant attributes with climate: form determined by plant tissues in terms of locations of buds; life forms based on sets of attributes of tissues (leaves, branches, etc.) and the shape of the entire plant; unique assemblages of plant species (associations); formations of different species of plants forming biomes of similar appearance in different locations.

Vegetation maps can show the actual vegetation or the potential vegetation at a given location. Formerly, actual vegetation maps were for small areas. Potential vegetation maps are based on often complex theories as to what vegetation should occur at what location. The application of vegetation maps in modern assessments of the effects of climate change raises issues of what should be mapped – in these issues the century-old problem of relating vegetation to climate persists to the present day in climate-change assessments.

Maps are limited by their medium. A printed map with a high degree of spatial detail must be for a small area or it becomes too large to be inspected. A map of the world’s vegetation greatly simplifies the spatial variability in vegetation pattern or it becomes an unreadable clutter of notes, symbols and colours. Modern geographical information systems (GIS) use digital computers to store and display vast amounts of information in a map-form at different resolutions. The GIS maps eliminate the ‘map clutter’ problem and display details over large areas. Satellite images display the attributes of the Earth’s vegetation along with an array of other physical information and specialized products such as daily global distribution of wildfires.

Printed maps cannot simultaneously describe the detailed locations of all the species in a region. There are simply too many species and the resultant ‘map clutter’ renders the map difficult to use. Von Humboldt’s map (Fig. 1.1) displays the altitudinal range of about 700 plant species and is difficult to read in anything other than in an elephant-folio book format. To avoid map-clutter and map a region of any size, one must develop basic concepts as to how to classify the vegetation.
Plants compose vegetation. These plants can be classified either by their taxonomy or morphology (based on the physiognomy or form of the plants). Traditionally, the vegetation names in different classifications show this difference in taxonomy versus physiognomy. Taxonomic classifications have ‘associations’ as units and emphasize the dominant taxa; physiognomic classifications have ‘formations’ as units and emphasize the general appearance of the vegetation. Both terms are old.

The basic idea of a vegetation association is attributed to Humboldt’s early work. Danish botanist, Joachim Frederik Schouw in 1823 developed another early biogeographical map (sometimes attributed as the earliest such map) in 1823. Schow used the suffix -etum to indicate association names in vegetation. For example, Quercetum, would be used to describe a woodland where Oaks (genus Quercus) were the principal plants – a convention of naming plant associations that continues into the present. By 1832, Grisebach, who would later develop the first world vegetation map (Fig. 1.4), introduced the word ‘formation’ for vegetation types based on the structure of the vegetation, such as tundra, or prairie. Over the years, different schools of vegetation scientists have embellished the formation and association concepts to an elaborate but sometimes confusing degree. In general, vegetation formations (such as forest formations dominated by trees or steppe formations dominated by grasses) have been most frequently associated with climate – mostly over large regions.

1.2.2 Plant form and climate–vegetation interactions

Buffon’s Law indicates that while vegetation classifications based on the dominant species or genera might work regionally, they should fail when comparing similar vegetation units on different continents (because the taxonomy of the plants would be different). The concept of defining vegetation formations based on the dominant plants’ physiognomy has an appeal in that it is straightforward – and the taxonomic complications are avoided. Von Humboldt discussed the issue with, ‘... sixteen forms of vegetation are principally concerned in determining the aspect or physiognomy of nature.’ The idea that a forest is vegetation that is mostly made of trees has a basic appeal to reason. In addition, many of the non-technical words used to describe either vegetation (forests, woodland and prairie) or plants (trees, grasses, shrubs) designate the structure.

Physiognomic categories may be more complex than they initially seem (Fig. 1.5). Must a tree have branches? Must it have leaves? Does it have only one trunk or can it have several? The same sorts of questions arise if one considers ways to subdivide trees. Forest formations differ based on the
Figure 1.5 Strange Trees. Top: Banyan life-form *Ficus* sp. tree with multiple trunks produced by roots dropping from branches and then consolidating to form trunks. Bottom left: Boojum (*Fouquieria columnaris*) tree with enlarged water-storing trunk but no branches. Bottom centre: Baobab (*Adansonia digitata*) with enlarged water-storing trunk and branches. Bottom right: Saguaro (*Carnegiea gigantea*) with enlarged water-storing trunk and branches but no leaves. (Photographs by H.H. Shugart.)
dominance of evergreen trees versus deciduous trees. Deciduous trees might lose their leaves when it is cold (summer-green trees) or when it is dry (rain-green trees). Other classifications would see trees as subcategorized by being needle-leaved or broad-leaved.

Over time, ecologists have moved beyond description to consider dimensions of plant form in ways that corresponded to underlying environmental factors. In 1934, Raunkiaer developed a categorization of plant form based on the height of ‘perennating tissue’ (Table 1.1). Perennating tissue remains inactive during a cold or dry period and then grows to produce new plant structure when conditions are favourable. The buds on the ends of branches of trees and shrubs produce leaves and twigs in the springtime or at the onset of a wet season and are familiar examples of perennating tissue. Such plants with buds in the end of the branch position, Raunkiaer called ‘phanerophytes’ (Table 1.1).

The position of perennating tissue relates to a plant’s adaptation to climate. Plants surviving in harsh environments protect their perennating tissue. The proportion of Raunkiaer life forms in a local plant community responds over time to experimental manipulation of shelter. For example, building stone walls to increase the protection of alpine vegetation in Italy produces changes in the abundances on the life forms making up the vegetation. At the global scale in tropical rainforests, phanerophytes with exposed perennating tissue at the end of branches (trees or vines) comprise virtually all of the plants. In moist tundra vegetation, hemicryptophytes with their perennating tissues protected near the ground surface predominate.

One sees in the Raunkiaer classification an important initial attempt to relate the form of the plants with conditions in the environment. In this case the environment is treated qualitatively – ‘harsh’ environments versus ‘less-harsh’ environments. More quantitative evaluations of adaptation to environmental conditions have also been developed and have been incorporated into present-day evaluations of the effects of climate change. For example, plants in different climates have a regular spectrum of physiological adaptations to minimum temperatures. The freezing point of pure water (0°C) and the point at which supercooled water will freeze (−40°C) are major divisions for cardinal minimum temperatures (Table 1.2). When the temperature is below 0°C, the water in plants can potentially freeze and thus damage plant tissues. To withstand this, plants demonstrate such adaptations as increasing cryoprotectants (Table 1.2). At temperatures of −40°C, supercooled liquid water (water below the freezing point but still in liquid form) will spontaneously form ice, regardless of how much anti-freeze/cryoprotectant there is in the plant, and extensive adaptations in the physical features of the cell structure are required.
Table 1.1 A Comparison of Plant Life Systems developed by Raunkiaer\textsuperscript{41} and part of the system developed by Box\textsuperscript{46}.

<table>
<thead>
<tr>
<th>Plant life-forms of Raunkiaer</th>
<th>The Box life form system</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perennating tissues are shown in black, woody tissues are in grey, and deciduous tissues are unshaded\textsuperscript{34}</td>
<td>Numbers indicate the life forms listed in table 2 (pp. 21–23) of Box\textsuperscript{46}. Note that while some of Box’s categories differ from Raunkiaer’s categories, the Box system largely elaborates in greater detail the Raunkiaer system. Broad-leaved Trees (1), Narrow-leaved Trees (2), Small and Dwarf Trees (3), Rosette (tuft) Trees (4) and Rosette Treelets (5), Arborescents (6), Krummholz (7), Shrubs (8), Stem Succulents (12), Arborescent Grasses – Bamboo (13), Various Forbs (14) and Rosette Shrubs (11)</td>
</tr>
<tr>
<td><img src="image1" alt="Phanerophyte" /></td>
<td><strong>Phanerophyte</strong>, a tree or tall shrub, with buds more than 25 cm above the ground</td>
</tr>
<tr>
<td><img src="image2" alt="Chamaephyte" /></td>
<td><strong>Chamaephyte</strong>, a semi-shrub with buds less than 25 cm above the ground or a sub-shrub with buds less than 25 cm above the ground</td>
</tr>
<tr>
<td>25 cm</td>
<td>25 cm</td>
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<tr>
<td>Dwarf Shrubs (9), Cushion Shrubs (10), Grasses (13) and Forbs (14)</td>
<td></td>
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<tr>
<td>Plant life-forms of Raunkiaer</td>
<td>The Box life form system</td>
</tr>
<tr>
<td>------------------------------</td>
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</tr>
<tr>
<td><em>Hemi-cryptophyte</em>, a perennial herb with its buds at the ground surface</td>
<td>Grasses (13), Forbs (14), Small Herbs (15) and Fems (17)</td>
</tr>
<tr>
<td><em>Geophyte</em>, a perennial herb with a bulb or other perennating organ below the ground surface</td>
<td>Not recognized separately in the Box system</td>
</tr>
<tr>
<td><em>Therophyte</em>, an annual plant surviving unfavourable periods only as a seed</td>
<td>Not recognized separately in the Box system – except for some Ephemeral Desert Herbs (15)</td>
</tr>
<tr>
<td>Other life forms not originally mentioned in Raunkiaer</td>
<td>Vines and Lianas (16), Epiphytes (18) and Thallophytes – Lichens and Mosses (19)</td>
</tr>
</tbody>
</table>
Table 1.2  Expected dominant plant adaptations to cardinal minimum temperatures\textsuperscript{45}.

<table>
<thead>
<tr>
<th>Minimum temperature (°C)</th>
<th>Phenomenon</th>
<th>Comments(s)</th>
<th>Expected physiognomy</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;15</td>
<td>Temperature not limiting</td>
<td>The most productive types of vegetation are broad-leaved evergreen\textsuperscript{74} under these conditions if there is adequate water. Under inadequate rainfall, one would expect drought-deciduous vegetation\textsuperscript{75,76}</td>
<td>Broad-leaved evergreen when rainfall is adequate</td>
</tr>
<tr>
<td>1 to 15</td>
<td>Chilling</td>
<td>To tolerate cool but not freezing temperatures, plants show changes in their physiology involving plant membranes. These changes have a cost in terms of energy required and there is an associated loss in physiological efficiency\textsuperscript{77,78}.</td>
<td>Broad-leaved evergreen</td>
</tr>
<tr>
<td>−15 to 0</td>
<td>Freezing and supercooling</td>
<td>Ability to withstand these temperatures often associated with tolerance of frost drought and summer drought\textsuperscript{79}. There are structural changes in the cell membranes, increase in protective cryoprotectants, increase thickness in cell walls and in leaves\textsuperscript{80}.</td>
<td>Broad-leaved evergreen</td>
</tr>
<tr>
<td>−15 to −40</td>
<td>Freezing and supercooling</td>
<td>Dormant buds, xylem and cambium of deciduous trees can have survival limits\textsuperscript{81} between −15 to −40. While frost- tolerant needle-leaved evergreen trees may make some photosynthetic gains in the winter\textsuperscript{82}, the high photosynthesis rate of deciduous vegetation confers an advantage even though they are photosynthetically active over a shorter interval</td>
<td>Broad-leaved deciduous</td>
</tr>
<tr>
<td>Below −40</td>
<td>Freezing and supercooling</td>
<td>Extensive adaptations in chloroplasts\textsuperscript{83}, cell membranes\textsuperscript{84} and cell osmotic properties\textsuperscript{85}.</td>
<td>Evergreen and deciduous needle-leaved (coniferous)</td>
</tr>
</tbody>
</table>
Within the 0° to −40°C temperature range, other adaptations (such as using supercooling to prevent freezing at low temperatures) allow plants to tolerate lower temperatures. Plants, through the process known as hardening, can tolerate a lower temperature if they are previously exposed to lower temperatures over a period of time. If two plants of the same species, one protected in a greenhouse and the other exposed to outside conditions for increasing intervals, are exposed to a low temperature, then the greenhouse plant will show damage in cases where the ‘hardened’ plant does not.

1.2.3 Plant life form: connecting climate and the physiognomy of plants

Many plant geographers have related the shapes and sizes of leaves, plant sizes and other aspects of plant physiognomy to systems of vegetation classification. Probably the most highly elaborated coupling of climate conditions with plant attributes is found in the system developed by E.O. Box to predict global and regional vegetation. Box’s system is simultaneously remarkable and cumbersome in its detail. It provides a list of different physiognomic types that might occur at a location along with a ranking of the importance of these types. One can also map the expected occurrence of different life forms over large areas or even globally and use a particular life form as an indicator of the other associated life forms. In a sense, the Box scheme combines the often remarkable convergence of physiognomy seen in unrelated plants in equivalent environments (Fig. 1.6) with the ‘association concept’ often used to map vegetation according to combinations of dominant taxa.

Box started with the premise that features of the plant that are involved in its water and energy balances are the key linkage between plant form and function. This is a premise strongly indicated by the convergence in the form of unrelated plants in similar environments. The similarity of the physiognomy of unrelated plants in separate but similar environments is striking and strongly implies environmental control on plant form (Fig. 1.6). An elaboration of the details of the physiognomy of the plant forms that make up a vegetation (such as in the Box life form systems) provides for possible connections between aspects of plant form and environmental factors.

Box used this fundamental premise to synthesize the findings of earlier plant geographers in a creative synthesis. He first identified what he took to be the main adaptive characters in plants.

1 Structural type. Box identified 19 structural types primarily having to do with size and pattern of branching of the plants. Whether the plants
were woody, herbaceous or succulent was also an important consideration. Table 1.1 summarizes Box’s structural types and compares them to the categories in the Raunkiaer41 life form system. Many of the Box structural types are elaborations of types in the Raunkiaer system, but certainly not entirely so. Box also categorized some structural types not considered by Raunkiaer.

2 Relative plant size. Life forms vary in the height of a particular plant with respect to others of the same structural type. Four types designated were tall (large), normal, short and dwarf.

3 Leaf type (including photosynthetic stems and other photosynthetic organs). Four recognized types were broad, narrow, graminoid (grass-like) and absent of leaves.
4 *Relative leaf size.* Leaves were categorized as large, normal, small and very small.

5 *Leaf structure.* Leaves can be categorized by referring to the ‘hardness’ of the leaves. Box’s categories were malacophyllous (herbaceous), coriaceous (leathery), sclerophyllous (both hard and stiff), succulent, ligneous (with woody photosynthetic parts) and pubescent (with a covering of fine hairs).

6 *Photosynthetic habit.* The seven categories include evergreen plants, semi-evergreen plants (usually evergreen when conditions permit but losing their leaves during unfavourable times), raingreen plants, sumergreen plants and suffrutescent plants (having perennial woody bases that produce shoots). The shoots are lost at the end of the growing period), marcescent plants (grasses and erect herbs) and ephemeral plants (capable of rapidly producing leaves or shoots from seeds or bulbs).

The Box system combines the categorical plant attributes to produce life forms. The 19 structural types × 4 plant sizes × 4 leaf types × 4 leaf sizes × 6 leaf structures × 7 photosynthetic habits imply over 50,000 plant life forms. However, some of these combinations are illogical, such as leafless trees with large leaves. Other combinations either do not occur in nature or are very rare. The life forms that are considered in the Box system are on the order of 100 of the many combinations of attributes listed above (76 life forms are tabulated in the original Box description in 1981). The Box life form classification produces descriptive, almost poetic, names for the different elements of the vegetation (e.g. raingreen broad-leaved trees, xeric tuft-treelets, leaf-succulent evergreen shrubs).

To predict vegetation, Box associates each of the approximately 100 life forms with ranges of macroclimatic variables assumed to limit each life form. In this as well as other climatic-envelope-based schemes for locating species, functional types, life forms or vegetation types across the Earth, it is very difficult to actually test these assumed relationships experimentally. This issue will be taken up in Chapter 3 in discussing the difficulties of expressing species niches at different scales. These macroclimatic variables are:

1 the highest monthly mean temperature;
2 the lowest monthly mean temperature;
3 the annual range of mean monthly temperatures;
4 the annual precipitation;
5 an annual moisture index based on the ratio of total annual precipitation to annual evapotranspiration and measured by the method devised by Thornthwaite and Mather.47;
the highest average monthly precipitation;
the lowest average monthly precipitation;
the precipitation of the warmest month.

Given the climate of a location expressed as these variables, one can sort through the life forms to see which could possibly occur there. The list that results from this procedure is then subjected to an additional set of criteria to determine which types would dominate the others. For example in moist situations, forest trees dominate small trees, which in turn dominate large shrubs, then small shrubs, then forbs and ferns. The moisture index is also used to determine the total vegetative cover, the layering of the vegetation and other descriptive terms for the vegetation.

Significantly, climate–vegetation systems without indicators of seasonality have some difficulty in application in more variable climates. This tendency is seen in the need to represent the seasonality in precipitation and temperature. For example, savannas and Mediterranean scrublands receive similar amounts of rainfall and have similar average temperatures. In savannas the rain comes during the growing season and the vegetation is often deciduous (‘raingreen’); in Mediterranean vegetation the rainfall is in the winter and the vegetation is often evergreen with leathery leaves.

While elaborate, the Box system produces descriptions of the vegetation that can be tested against actual vegetation from known locations. With climatic and vegetation data from a large number of sites, one can generate and test the classification of vegetation world-wide. Box used 1225 such sites in his original development of the model. The Box system predicts a complex list of vegetation attributes and allows for rich comparisons with actual vegetation. It also allows for interregional comparisons.

How much does the evolutionary history of a region affect the life forms found there? For example, parts of the Northern and Southern Hemispheres have had relatively separate evolutionary histories and consequent differences in patterns of plant taxonomy. Box compared the occurrence of life forms between the Southern and Northern Hemispheres and found several life forms that were found in only one hemisphere. An interesting example was for temperate giant trees. Temperate giant conifer trees of the genera *Sequoia* and *Sequoiadendron* (Redwoods) have no analogue in the Southern Hemisphere; the temperate giant broad-sclerophyll trees of Australia (*Eucalyptus regnans* and *E. diversicolor*) are unique to Australia in the Southern Hemisphere. With the exception of one species in the Philippines, the *Eucalyptus* trees that dominate Australia’s forest and woodlands have no Northern Hemisphere analogue (but they are certainly effective introduced species throughout the world). Box found several abundant tree life-forms unique to the Northern Hemisphere: boreal
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evergreen conifer trees – *Picea* (spruces) and *Abies* (firs); deciduous conifer trees – *Larix* (larches) and *Taxodium* (bald cypress); boreal deciduous broad-leaved trees – *Betula* (birches), *Salix* (willows) and *Populus* (poplars). The vast boreal forests of the Northern Hemisphere, the most extensive forests on Earth, are dominated by genera manifesting these life forms. Their analogue does not occur in the Southern Hemisphere. Box⁵¹ also cites several other Southern Hemisphere life forms, mostly smaller Australian woody plants, without an equivalent in the Northern Hemisphere.

Box’s detailed life-form categorization holds the promise for a mechanistic joining of plant form and environmental conditions. For example, one might develop a process-based understanding of what in the environment might control plant heights or leaf sizes⁵²,⁵³. But are the complex vegetation types described in the Box system functionally different from one another? For example, using the Box life form system, one finds sclerophyll (hard-and-stiff-leaved) shrub-dominated vegetation in all of the Earth’s five regions of Mediterranean climate. However, the Northern Hemisphere Mediterranean shrublands have deciduous trees and shrubs (summer-green – losing their leaves in the dry summers) that are not found in the Southern Hemisphere⁵³. Does this imply Mediterranean shrubland functions the same way in France and California but in some other way in Chile? This is not a question unique to a Box life form map. It remains to determine what structural differences in vegetation mean in terms of the function of the vegetation and its response to climate change.

The last large-scale research programme to compare and contrast the function of different biomes in different parts of the world was the International Biological Programme (IBP, 1964–74) now over three decades past. The IBP studies compared different ecosystems with respect to underlying processes⁵⁴ and overall ecosystem performance⁵⁵,⁵⁶. The warm-desert-biome project focused on convergent evolution⁵⁷. The Mediterranean-biome project specifically compared California and central Chile⁵⁸ and focused on the important role of nutrients in structuring ecosystems⁵⁹. In the 30 or 40 years since the IBP, ecologists have developed a remarkable array of insights, techniques and instruments that can be deployed to increase greatly our knowledge of ecosystem response to change. The need to implement a new global research programme to address our new questions on the consequences of large-scale environmental change is obvious. The ideas behind such a programme have been vetted in numerous publications of the International Geosphere Biosphere Programme⁶⁰ and its subdivisions. The need for synthesis from an understanding of processes and an appreciation of change in the planet are clear to many global scientists. The support of such projects in the fashion seen in the earlier IBP projects seems a necessary ingredient.
1.3 Formation or biome interactions with climate

Large-scale boundaries of vegetation follow mapped patterns of climatic variables, particularly for temperature- or moisture-related variables. Just as climate classification systems draw from the vegetation/climate relationship, global vegetation classifications use climate variables, temperature and moisture indices to predict patterns in vegetation.

1.3.1 An early regional system to relate climate and vegetation

C. Hart Merriam worked in the western USA at the turn of the 20th century on the distribution of the plants and animals. He initially focused on the altitudinal gradients in the San Francisco Peaks in northern Arizona and, as von Humboldt, emphasized the importance of temperature as the focal variable controlling the distribution of the biota. Indeed, Merriam’s work shows many parallels with the concepts embodied in Alexander von Humboldt’s isotherms (Fig. 1.2). Merriam had a holistic view of nature as did Humboldt. They saw temperature, albeit using different measurements, as synthesizing the interaction between natural systems and the environment. In the latter parts of the careers of both men, there was an increasing emphasis on humans as a part of nature: von Humboldt with his sweeping multivolume book, Kosmos, and Merriam with a remarkable compilation of basic anthropological data on American Indian culture.

Merriam’s paper in 1892 emphasized the factors controlling the distribution of mammals, which he pointed out were indicative of their entire ecological system. By 1894 he had perfected his system for plants and animals, and by 1898 he had developed a large regional analysis for natural systems and crops. His depiction of life zones (including plants and animals) incorporated a sense of ‘wholeness’ with ecological systems of plants, birds and mammals all responding with some degree of synchrony to the environment, as indicated by measurements of temperature. Merriam’s stated his basic position of the working of the environment on the biota as indicated by warmth, ‘… apart from obvious mechanical barriers such as oceans, temperature is the most important single factor in fixing the limits beyond which particular species of animals and plants cannot go. Investigations conducted by the Biological Survey have shown that the northward distribution of terrestrial animals and plants is governed by the sum of positive mean daily “temperatures,” using $6^\circ$C as the threshold value, for the entire season of growth and reproduction, and that the southward distribution is governed by the mean temperature of a brief period [using the mean normal temperature of the six hottest consecutive weeks] during the hottest part of the year.’
indicators coincide with one another so that in Merriam’s transverse maps (e.g. Fig. 1.7), the southern boundary of one system of plants and animals (determined by maximum temperature over 6 weeks) smoothly joins the northern boundary of the system below it (determined by a heat sum).

Merriam (Fig. 1.7) made direct analogies between the zonation of vegetation that he saw in the San Francisco Mountains with continental distributions of ‘equivalent’ vegetation types as controlled by temperature (or indices of temperature). Von Humbolt in his applications of isotherms (Fig. 1.2) had the same objective. So did Theophrastus, except he did not have a thermometer at his disposal in the 3rd century BC. Merriam’s system has been used in the western National Parks in the western USA for over a century now to educate the public about the patterns of vegetation, the organization of animal habitats and the relation to the vegetation of a given park to those of nearby locations.

Figure 1.7 Life zones for the Francisco Peaks altitudinal gradient in Arizona. (From: http://www.geo.arizona.edu/Anteys/biomes/azlifzon.html)
1.3.2 Global biome-scale relations between vegetation and climate

The Holdridge Life Zone system\(^68,69\) relates climate and vegetation zones (called ‘Life Zones’) using indices of temperature and the moisture available for plants and serves as a global scale example. The Life Zone system has been used to evaluate regional and global vegetation patterns in several tropical countries, particularly in the New World Tropics, and it was used in the first global assessment of carbon-dioxide-related climate change effects on vegetation\(^70,71,72\). The Holdridge approach relates the response of the vegetation to four interdependent environmental variables.

1. **Biotemperature.** A heat summation index based on calculating the average of temperatures over time intervals with the substitution of zero for all intervals when the temperature is below 0°C or above 30°C. The 0°C and 30°C limits are felt to demarcate the range in which most plants typically are physiologically active.

2. **Precipitation.** The mean annual precipitation in millimetres of water.

3. **Potential evapotranspiration.** Calculated by multiplying the biotemperature by 58.93, a constant derived by Holdridge. Result of the calculation is in millimetres of water evaporated or transpired from the system.

4. **Potential evapotranspiration ratio.** The ratio of average annual potential evapotranspiration to average total annual precipitation. A value of 1.00 indicates that the precipitated moisture equals potential evapotranspiration. Larger values imply an abundance of water; smaller values are associated with more arid climates.

Holdridge\(^68\) developed a geometrical model of his Life Zones (Fig. 1.8) that classifies vegetation in terms of climate variables. Trained scientists working in the field can also interpret the vegetation to apply the Life Zone classification based on vegetation physiognomy without direct reference to climatic data or even in the absence of climatic data.

The Holdridge system is quantitative with measures of climatic condition being derived from meteorological data. For the climatic indices recommended by Holdridge, the geometrical model (Fig. 1.8) can be used to generate the expected Life Zone. Applied to all the points of a map (often obtained by using a meteorological observation network spread over a map according to topography), one can generate a Holdridge Life Zone Map (Fig. 3.3 is an example).

This painting of vegetation maps onto climate maps has been used (almost always to produce potential vegetation maps) for other different formal vegetation–climate classifications. Von Humboldt’s\(^10\) transverse map could be painted across the Andes using this methodology and the
same could be done for vegetations based on Box’s model of life forms or on Merriam’s life zones. Many of the early approaches to evaluating the effects of climate change used precisely this approach. Dynamic global vegetation models (which will be discussed in later chapters) that have been developed to predict change on the Earth’s vegetation and to interface with models of the Earth’s climate often have an explicit biogeographical-mapping component. All of these methods use summary indices of climate to express the manner that climate influences vegetation. The more modern vegetation–climate algorithms feature measures of temperatures, precipitation balanced against evapotranspiration, severe events (e.g. maximum and minimum temperatures) and the seasonality of precipitation and warmth.

Deriving future vegetation distributions on maps based on current vegetation–climate relations is appealing. The procedures may be cumbersome and require computers but they are straightforward: determine which variables will be used to quantify climate; determine at what level (individual plant, life form, life zone) vegetation interacts with these climate variables; resolve the expected rules for change. Wise practice would be

**Figure 1.8** Diagram for the classification of world life zones based on climate variables developed by Holdridge.

The diagram shows a classification of world life zones based on climate variables developed by Holdridge. The classification is based on mean annual biotemperature and potential evapotranspiration ratio. The diagram includes latitudinal belts and altitudinal belts, with different vegetation types represented at various points. The key life zones include Polar, Subpolar, Boreal, Cool Temperate, Subtropical, Tropical, Cool Temperate, Subpolar, Boreal, Cool Temperate, Subtropical, Tropical, and others, each associated with specific climate conditions and vegetation types.
to compare several different methods to see what predictions are consistent over different methods. Predicting past vegetations under different past climates is another logical test on the strength of this approach. However, as we will discuss below, increased understanding of the change in vegetation in past climates creates a substantial challenge. A further problem is that a mapping procedure may predict accurately the present-day vegetation but one can never be sure if future predictions are correct. Predicting the past, when climates were different, tests the capability to predict conditions different from those today. Even then climate differences in the past often involve cooler conditions; our concern for future conditions at present is for a warmer planet than today.

1.4 Concluding comments

In a sense this introductory chapter deals with two histories. The first is in our human history of the science of ecology and the conceptual roots of our science. With Theophratus, von Humboldt and others from the very origins of ecology and ecosystem studies, one finds an appreciation of the importance of climate and its interaction with natural systems at a range of ecological scales (individual organisms, species, communities, ecosystems, biomes and the biosphere as a whole). Our field is rooted in understanding the interaction of climate with the Earth’s biological systems.

A second, deeper history is that of the systems we study. We are studying the biology of a living planet at a time that seems particularly dynamic. The 2 million years of the Pleistocene epoch featured waxing and waning of dozens of intervals with extensive continental glaciers. The past 12,000 years, within the latest Pleistocene and the Holocene epochs, has seen the development of human civilization and an increasing human effect on planetary systems. When we inspect this natural ecosystem over this history, we see change – change in the biota at locations over time, in the range of species, in the nature of ecosystems and biomes, in climate, change produced by humans, changes from astronomical cycles, and changes from sources we have only begun to understand. The progress in revealing these changes has been a remarkable interdisciplinary fusion of ecology with the physical sciences. The discovery process is still well underway and we have much to learn. These topics will be taken up in more detail in the next chapter.

These two histories come together in the form of the scientific challenge of predicting the nature of our planet under the influence of future change. We have ample reason to suspect that we are changing the planet’s climate; we have ample reason to expect it would change without our influence.
Regardless of the source of climate change, how well can we predict ecological changes in the future? How can we understand the reliability of these predictions? These questions join our historical interests in climate and ecosystem from the tradition of our science with the modern appreciation of the history of Earth’s ecosystems change. They are the great questions for our field made immediate by the fact we live and depend on the ecosystems we wish to better understand and predict.

The same issues confronted by the early biogeographers continue to arise in modern attempts to understand the consequences of global environmental change. Today, conditions never before seen in the environment in human history present us with similar novelty. The ecological pathfinders of the 19th century had their concepts tested by the results of exploration. For scientific rigour, we also need equivalent tests as to whether we can answer these questions correctly.

References and notes

6. Helferich, G. 2004. *Humboldt’s Cosmos: Alexander von Humboldt and the Latin American journey that changed the way we see the world*. Gotham, New York, 358 pp. Interestingly, Chimborazo is probably the tallest mountain on Earth if distance from the centre of the Earth (and not altitude above sea level) is used as an elevation indicator.
9. Aimé Bonpland, who accompanied Humboldt on his expedition, became disengaged from the writing in Paris and took a position in charge of the Empress Josephine’s gardens at Malmaison. On the death of Josephine in 1814, he married and took a professorship in natural history in Buenos Aires. He never returned to Europe. While on a field expedition near the Argentine border, he was wounded and placed under house arrest in a remote location in Paraguay until 1830. Deserted by his wife, he eventually ended up owning a ranch in Uruguay where he fathered several children with an Indian woman and died in 1858. The other
mountaineer on Chimborazo, Carlos Montúfar, accompanied Humboldt to Paris but returned to Ecuador in 1811 to die there as a member in a revolutionary army against the Spanish colonials.


