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BIOCLIMATIC ZONES FOR THE ANTIPODES
- AND BEYOND?

Summary: A bioclimatic zone system is proposed that defines a set of biogeographical cells so as to facilitate valid global comparisons of ecological data. These zones are primarily defined on grounds of temperature and secondarily on moisture balance. They roughly correspond with potential vegetation boundaries, but extant vegetation is not necessarily a biogeographically useful index of a site.

Keywords: Biogeography, zones, bioclimate, temperature, moisture, continentality, vegetation, growth-form.

Introduction

Bioclimatic zone systems aim to define reproducible sets of named biogeographical cells that facilitate global comparisons of ecological data. Zones based on extant vegetation loosely reflect contemporary climate, but are vitiated by climate history, chance establishment, genetic potential of local species, terrain instability, intrazonal soils, and biotic disturbance. The system of zones presented here derives its basic format from both northern hemisphere tradition (Merriam, 1894; Love, 1970) and the New Zealand applications of Zotov (1938), Wardle (1964) and Burrows (1967). Inspiration is drawn from the concepts employed by Holdridge (1967) and Ahti, Hamet-Ahti and Jalas (1968). One recent contribution to southern biogeography (Bliss, 1979) pinpoints many of the difficulties associated with boreal-austral comparisons. I would support several aspects of Bliss í system, although I believe he relies too heavily on current vegetation (formation) limits which reflect heterogeneous historical accidents. My austral-centred scheme is ordered firstly by available energy and secondly by the hydrological balance - which is variously related to continentality - all in relation to potential plant life-form on non-limiting soils.

A Bioclimatic Zone System

The primary, energy factor is reflected in the thermal regime. For hygrophytic, continental to semi-oceanic situations (Fig. 1) the latitudinal and thermally equivalent altitudinal zones are defined thus (Fig. 2).

Tropic: mean warmest-month-temperature (MWMT) = c. 32.5-27.5°C, always frost-free; thermal potential, vegetation structure-emergent and canopy strata of numerous giant dicot. trees, with characteristic morphology (Eyre, 1968: pp. 200-202), 30-<40 m tall.

Subtropic (≡ Colline): c. 27.5-22.5 °C, mean coldest-month-temperature > 0 °C; emergent and canopy strata of several giant dicot. trees, 30-50 m

Warm Temperate (≡ Lower Montane): c. 22.5-17.5°C; emergent or canopy strata of several giant coniferous and/or some dicot. trees, 100-40 m

Cool Temperate (≡ Upper Montane): c. 17.5-12.5°C; few emergent giant coniferous and/or dicot. trees> 40 m, over a c. monoculture canopy, 40-10 m

Subantarctic (≡ Subarctic ≡ Subalpine): c. 12.5-10°C; simple canopy of dwarf conifer, fagaceous, myrtaceous, heath or daisy trees, 10-2.5 m

Low Antarctic/Arctic (≡ Low Alpine): c. 10-5°C; shrubs 2.5-0.16 m

High Antarctic! Arctic (≡ High Alpine): c. 5-0°C; dwarf shrubs 0.16-0 m
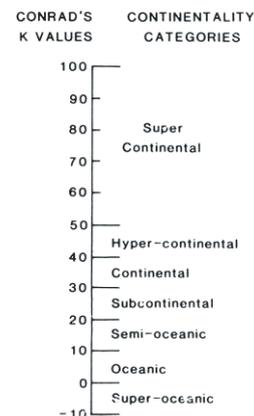

Figure 1: *Continentality categories in relation to Conradís (1946) index (k) values - originally based on a zero (extreme oceanic) to 100 (extreme continental) scale. It is suggested that whichever is the greater, of maximum range of monthly mean temperatures or mean diurnal range, should be substituted for A in Conradís k formula (see text).*

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Low Polar ($\equiv$ Low Nival): c. 0–5 °C; bryophytes and fruticose lichens
High Polar ($\equiv$ High Nival): c. < – 5 °C; crustose cryptogams.
Equivalent oceanic and equatorial alpine boundary temperatures may be 1–2 °C less than

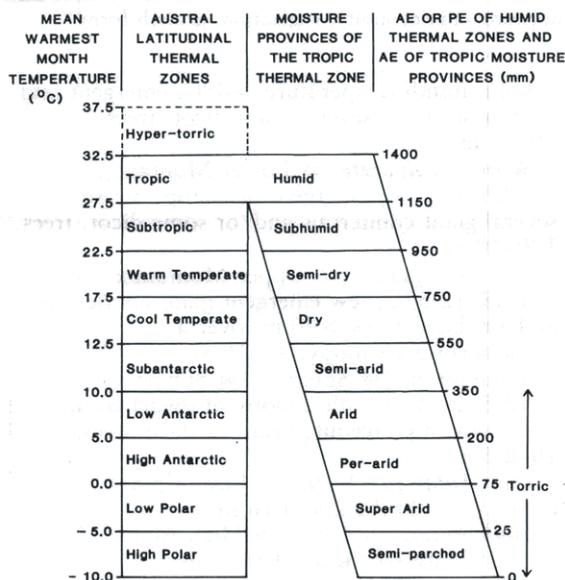| MEAN WARMEST MONTH TEMPERATURE (°C)	AUSTRAL LATITUDINAL THERMAL ZONES	MOISTURE PROVINCES OF THE TROPIC THERMAL ZONE	AE OR PE OF HUMID THERMAL ZONES AND AE OF TROPIC MOISTURE PROVINCES (mm)
37.5	Hyper-torric		
32.5	Tropic	Humid	1400
27.5	Subtropic	Subhumid	1150
22.5	Warm Temperate	Semi-dry	950
17.5	Cool Temperate	Dry	750
12.5	Subantarctic	Semi-arid	550
10.0	Low Antarctic	Arid	350
5.0	High Antarctic	Per-arid	200
0.0	Low Polar	Super Arid	75 Torric
– 5.0	High Polar	Semi-parched	25
– 10.0			0

Figure 2: *Postulated annual potential* or *actual evapotranspiration (PE or AE) for Humid thermal zones (i.e. where effective Precipitation $\geq$ PE); and moisture provinces for the Tropic life zone. Humid thermal zones are potentially represented by zonal tessera (the "climatic associations" of Holdridge, 1967) as defined in the text. Within a thermal zone, each reduction of AE to that of an adjacent cooler thermal zone results in a corresponding lowering of biological capacity (e.g. woodland to scrubland when transferring from Subantarctic Humid to either Subhumid or Low Antarctic Humid) and warrants assignment to a drier category. Thus the Cool Temperate is Humid when an AE of 750-550 mm can be realised, Subhumid where AE is 550-350 mm, Semi-dry when 350-200 mm, and so on.*
   Note that a full description of the bioclimatic cell would now demand three prefixes, e.g. Warm Temperate, Semi-oceanic, Subhumid, Subalpine (i.e. an elevated zone with MWMT of 10-12.5^{o}C from text, an AE of 200-350 mm from this Fig. 2, a k value of 10-20 from Fig. 1, and a basal life zone with MWMT of 17.5-22.5^{o}C). Where the basal zone is being described the altitudinal name can be assumed, hence Semi-oceanic, Subhumid, Subantarctic ("Subalpine" being implicit).

these values because of their extended growing season and large heat sums for spring and autumn (Fig. 3, but see below).

In continental sectors, beyond the Tropics of Cancer and Capricorn, where warm to hot summers are followed by cool to cold winters and aridity prevents the growth of thermally potential vegetation, the terms "Tropic" and "Temperate" as popularly understood seem inappropriate. The seasonally hot deserts, steppes and prairie regions fall into this category. "Boreal" may be an adequate term for northern hemisphere, continental, "temperate" climates, however "Cool Summer Continental" and "Warm Summer Continental" are possible alternatives. The predominant deserts of the subtropics might be termed "Subtorric" and the arid tropics would be "Torric". For those local, very hot and dry areas with MWMT >32.5ºC, "Hypertorric" could be used.

This nomenclature is symmetrical between hemispheres and emphasises unity rather than contrast between latitudinal and altitudinal zonations. Moreover, the information concerning the peculiarities of high and low latitudes is retained by indicating the basal latitudinal zone. Thus Low Arctic environments have many similarities with, but also differences from Warm Temperate, Low Alpine environments.

It is emphasised that, whereas the temperature criteria are intended to be definitive, actual vegetation boundaries will only more or less correspond depending on the historical vicissitudes of the site and biota as outlined in the opening paragraph. The precise temperatures for the higher/distal zones may need to be adjusted if a vegetation height characterisation of zones is valued.

The system applied to New Zealand
For New Zealand (Fig. 3) the boundaries chosen coincide well with traditional attitudes - namely that Raoul Island is Subtropical, the northern, warmth-demanding or cold-avoiding (Warm Temperate) element of the New Zealand flora is restricted to coastal North Island and northern South Island (Cockayne, 1921), and Auckland and Campbell Islands are Subantarctic (although see legend to Fig. 3). In the well-developed alpine terrain of South Island the upper limits of *Dracophyllum* and *Cassinia* shrubs, thus of the Low Alpine Zone, more or less correspond with the 5ºC MWMT level (e.g. The Remarkables and Old Man Range, Otago; Meurk, 1982) and also
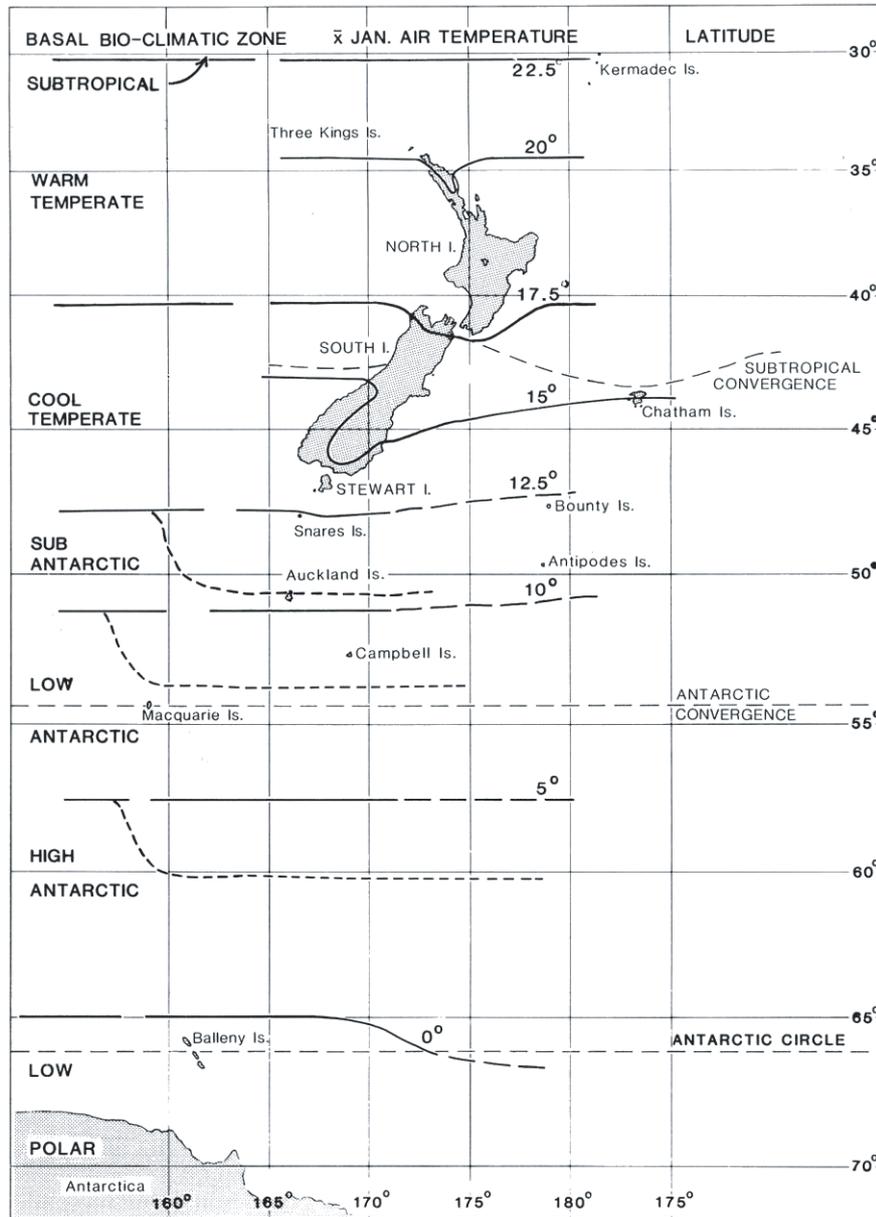
Figure 3: *Map of New Zealand and outlying islands showing the approximate positions of mean January ($\overline{x}$ JAN.) air isotherms, marine convergences and sea-level (basal) bioclimatic zones. The isotherms are derived from interpolations between land-based meteorological stations; however there is less than one degree of latitude difference between these and equivalent surface sea temperature isotherms. Basal bioclimatic zones denote potential growth form (see text) for a hypothetical continental situation (continuous lines corresponding to diagnostic isotherms) and for actual super-oceanic island conditions (short-dashed lines curving below isotherms). Where there is adequate shelter from wind the very long growing seasons and dampened temperature ranges of oceanic . conditions compensate vegetation for the cool mean summer temperatures to the extent of about 2.5° of latitude.*

the extreme upper limits of *Chionochloa rigida* or
C. flavescens (loc. cit., Wardle, 1977).
Chionochloa macra and *C. pallens* are regarded
as High Alpine Zone species as they each have the
propensity, in their respective humidity provinces,
to exceed the altitudinal limits of *C. rigida* in the
southeast and of *C. flavescens* in the north and
west. The ultimate limits in a region appear to be
set more by instability of terrain (especially in
Canterbury), depressed permanent snow-line in
the west (Wilson, 1976: Figs 1, 2), or simply
local absence of sufficiently elevated mountains,
rather than direct temperature considerations.

Continentality

Radiation balance and wind

One of the biggest problems in equating oceanic
and continental climates using a single MWMT
value is that oceanic, temperate, thermal regimes,
like those of equatorial mountains (Troll, 1960),
have very extended snow-free seasons - c. eight
months at natural timberline compared to as little
as three months in boreal regions. For example,
in the year-round growing seasons of the
equatorial New Guinea mountains, forest limit
occurs at a MWMT (or annual biotemperature)
of c. 6°C (Smith, 1975). And in New Zealand
the ability of *Pinus contorta* (but few other
northern tree species) to grow as trees 100-200 m
above native tree limits (Benecke and Havranek,
1980) suggests that ecologically equivalent
MWMT thresholds in oceanic climates are lower
by 1-2 °C compared to continental climates. The
fact that such a minor adjustment is necessary
when there appears to be such a marked
discrepancy in the degree-day sums (c. 2200 in
New Guinea, 2000 in New Zealand, 1500 for
Scotland, and 1200-800 for continental
timberlines) may be explained by several factors
which influence plant-sensible heat, but not
meteorological air temperature and heat sums etc.
Firstly, the greater humidity and cloudiness of
oceanic environments reduces the time during
which plants can benefit from direct sunlight,
which, if unobstructed, brings about substantial
elevation of leaf temperatures above that of
ambient air. In the extreme case of perpetual
cloud, day-time plant temperature will only be a
few degrees above ambient, whereas in a
perpetually sunny, calm, though cool
environment, leaf temperature will be 10- > 15°C
above ambient (Korner and Cochrane, 1983).

Even with equally sunny conditions part of the
time, the oceanic mountain vegetation has to
contend with a second cooling influence - wind.
Oceanic regions are generally windier than
continents by several m s^{-1}, at least during
summer (excluding ridges and summits). At an
irradiance of 1.03 I min.$^{-1}$ and ambient air
temperature of 10 °C, leaf (1 cm diameter)
temperature will be 14, 10, 8.7, 6.7 and 5.1 °C
above ambient at near-surface wind speeds of 0.1,
0.5,1,2 and 4 m s^{-1} respectively (Gates, 1965:
from Fig. 4). Thus, when conditions are not
cloudy, and other factors are equal, temperatures
of fully irradiated leaves in cool, oceanic climates
will, on average, still be at least 1°C less than
those in continental mountains (i.e. 30 degree-
days a month based on 1 and 0.5 m s^{-1} surface
wind speed respectively).

Biological equivalence of zonal boundaries,
between continental and oceanic sectors, will
undoubtedly be enhanced by using temperature
sums, but only after the data have been
appropriately transformed to plant-sensible
temperature by some function of the type:
Plant Temperature =
f(Air Temperature, Net Radiation, Relative
Humidity, Wind Speed).

Hydrological balance

Although it plays a comparatively muted role in
an oceanic environment such as New Zealand,
the second major coordinate in this biogeographic
scheme is the moisture regime. A simple index of
this parameter has been difficult to derive (see the
review by Tukhanen, 1980) because of
insufficient, empirical evapotranspiration data and
the changing significance to plants to absolute
moisture deficits or surpluses with changing
thermal regime. However, the following
generalisations are offered with the aim of
defining longitudinal humidity provinces
compatible with the continentality sections
proposed for northern Europe by Ahti et. al.
(1968) and the potential evapotranspiration (PE)
ratio of Holdridge (1967).
Conrad's (1946) continentality index,
$$k = 1.7A/(\sin(\Phi + 10) - 14)$$
where A = average annual range of temperature
and Φ = latitude, may provide a satisfactory
interim scale (Fig. 1) roughly correlated with
moisture status. All New Zealand stations fall
within the superoceanic (Subantarctic islands) to
semi-oceanic categories with a maximum value of
15 for Central Otago.

Actual evapotranspiration (AE) is probably the most desirable index because it is a real or concrete quantity and correlates precisely with growth and growth form (Rosenzweig, 1968; Lieth and Whittaker, 1975:p. 256): c. < 150 mm per annum for desert, 250 mm for shrubs, c. 300 mm for trees, c. 700 mm for mixed Temperate forests, > 1100 mm for Tropical forests (d. Major, 1977). Values reported or inferred for New Zealand are < 50 mm per annum in the Nival Zone, < 200 mm for a rocky mountain catchment (Hayward, 1976), c. 400-500 mm for Subalpine tussock grassland with shrubs (Mark, Rowley and Holdsworth, 1980) and pasture, c. 600-700 mm for Upper Montane forest (Pearce, Rowe and O'Loughlin, 1982) and c. 1000 mm in humid forested areas (i.e. equal to PE) (Pearce, O'Loughlin and Rowe, 1976). Note that about one half of this last total is interception or direct evaporative loss.

A scheme for integrating these AE data with the thermal provinces is outlined in Figure 2. Those humidity sectors which permit maximum potential vegetation stature for a given thermal zone may be regarded as potentially supporting the "zonal" vegetation/soil complex. These tessera are the equivalents of Holdridge's "Humid Province (PE/Precipitation ratio = 1-0.5) Climatic Associations" which here are equated with "Zonal" bioclimatic cells.

An alternative "Precipitation minus PE" scale would have the advantage of encompassing and quantifying superhumid or leaching as well as subhumid environments. Furthermore, isolines of this index could be directly mapped from readily available data as humidity province boundaries. But these provinces would exaggerate the aridity in cold and under-estimate it in hot climates because of the changing evaporative significance of deficits or surpluses along this thermal gradient. The quantity is also too abstract. The same criticism applies to Holdridge's PE ratio.

Conclusions

Northern, continental biomes which dominate geographically and in the literature are seen as the norm. They differ from oceanic (New Zealand) biomes in three important respects:

1. In tundra, the snow regime is quite different. Total precipitation is relatively low in continental mountains, but the intense winter cold may produce a very deep snowpack of low density which is slow to melt - especially in the absence of warm spring rains. This tundra environment has the aspect of a giant snowbank, as exemplified in the American Pacific Northwest, or that of a wind desiccated fellfield, as in much of the Colorado Rockies. Consequently continental, high mountain vegetation either receives much less energy than would be expected from the normal, regular temperature lapse rate and the period of above-freezing air temperatures, or is subjected to very exposed and arid conditions. That is, many northern alpine tundra are intrazonal habitats which are truncated by either depressed permanent snowlines or "summit effects". The shrub belts, which are diagnostic of the Low Alpine Zone as proposed here, are thus restricted. Such shrubs as do occur in this zone in the Rockies cling to tenuous transitional sites at the upper margins of deep snowbanks (Scott Burns, pers. comm.) which provide just enough winter protection and summer moisture for the shrubs' survival. On the other hand the shrubs are spared the extreme, persistent burden of snow that would restrict the summer energy input. Perhaps the well developed shrublands beyond timberline, reminiscent of New Zealand's rainshadow mountains, the equatorial alpine, some Arctic areas, the European Alps, The Himalayas, together with the microhabitats along those snowbank margins of the Rockies, are truly "normal" (or zonal in the sense of Tedrow and Cantlon (1958) and as used here) in that their vegetation limits are governed by the usual steady thermal lapse, and less by other (intrazonal) factors such as excessive snow accumulation, bogginess or winter and summer drying!

2. The effective growing season and temperature sum appears more limited in continental situations. This disparity concerning thermal regimes was considered earlier. The long growing seasons of oceanic tundra are, to some extent, compromised by greater cloud cover, humidity, windiness and summer frostiness. There is also noteworthy evidence that extant North American timberlines are relics of a former more hospitable era, out of phase with present climates (Ives and Hansen-Bristow, 1983). The steady state may thus be even less at odds with the New Zealand situation where, if anything, the vegetation is readjusting from a "Little Ice Age".

3. A third contrast between continental and oceanic biomes relates to the greater stature attained by forest trees in Continental, Subalpine and Cool Temperate zones compared to the gradual tapering of the subalpine forest and Low

Alpine scrub communities in New Zealand. If American timberlines are relict (loc. *cit.)* this may explain the very abrupt reduction in tree height in the Sierra Nevada at the timberline and the decadent nature of the trees. Interaction of wind, snow and cloudiness are also implied causes of dwarfed woody vegetation at timberline in New Zealand (Wardle, 1973).

This scheme has so far presupposed that no factors other than firstly temperature, then moisture, are significantly limiting. Clearly the third important gradient of variation in phytogeography is soil fertility (Scott and Groves, 1982a) and the potentials described above are only realised given an adequate nutrient supply. Although individual species, because of physiological intolerance and competition, may have quite narrow preferences on a fertility gradient, growth forms tend to have wider amplitudes - at least in undisturbed or uncropped situations. A promising approach to integrating the complexity of soil nutrition is through the bioassay technique (d. Scott and Groves, 1982b; Foggo and Meurk, 1983) although there are problems with interpretation of some results from disturbed soils.

There is nothing absolute about the order - temperature, moisture, nutrition - all are essential to life on this planet; however my choice is a fairly traditional perspective in the business of ordering the world, and it is as well to provide something familiar for the reader's sense of security in an admittedly speculative arena such as this.

Acknowledgements

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