

Explain why the biome concept is useful in understanding the geography of the biosphere and identify the extent to which the identity of named biomes have survived rapid and extensive climate change.

Biomes are global-scale biogeographic regions - such as tundra, tropical grasslands and savanna - shaped by climate and distinguished from one another by the unique collections of ecosystems and species assemblages that have evolved there. The biome concept as such charts a cartography of the structure and composition of vegetation and the functioning of terrestrial ecosystems, which at a local scale are shaped by environmental factors (constraints/gradients) - such as temperature and moisture - and at a global scale, by climatic patterns and the uneven latitudinal receipt of insolation. The geographic distribution of biomes is thus closely correlated with measures of temperature, precipitation, evapotranspiration and net primary productivity/decomposition rates (Bonan, 2011). From this the several well-established biomes (e.g. tropics, savannah, tundra) emerge; the currency lining a quantitative framework through which planetary ecology and the role of global climate-vegetation dynamics are conceptualised. The established, global 'biome map' has nevertheless undergone several revisions/adaptations throughout the years (Walter, 1976; Olson et. al 2001) , problematised by scale and the divergent discourses of mechanistic/correlative modelling. In latter sections I approach these ambiguities.

Primarily, this paper reproduces a global biome map of hierarchical organisation (Walter, 1976) in which terrestrial biomes are delineated then further subdivided into finer-scale ecoregions. Nested within biomes, these ecoregions reflect finer regional-scale patterns of ecological organisation created under abiotic (local geology/climate) and biotic (competition/disturbance) regimes. (Olson et. al, 2001). The main body of this paper then explores the generalised relationships among major plant formations, annual mean temperature and annual precipitation. Temperature is important because sufficient warmth, but not excessive heat, is a prerequisite for the biochemical reactions that support life. Water is important because 80-90% of the mass of a plant is water. The latitudinal gradient from tropical forest to temperate, boreal and then arctic tundra pervades this logic and further reifies the relationship between evapotranspiration (temperature/precipitation) and plant distributions (Thornthwaite, 1948 cited in Bonan, 2011).

The latter sections of this paper readdress the problematic areas of the biome concept and the responsive/adaptive capacities/thresholds expressed by terrestrial biomes. The problematic of scale arises primarily because landscapes are dynamic, successional mosaics wherein conditions (temperature, salinity) and resources (competition) are in a continual, effervescent state of flux. The tundra/taiga biome is one such: uniform from the Apollonian eye yet deeply heterogenous and clustered when observed at the local. The problematic of biome modelling/methodology emerges at the nexus between intensive (mechanistic) and extensive (correlative) modes of observation. Mechanistic models as such require rigorous field observation - 'a degree of realism' - and incorporate physiologically limiting mechanisms in a species' tolerance to environmental conditions. Conversely, correlative models aim to estimate the environmental conditions (using algorithms for photosynthesis, respiration, allocation) that are suitable for a species by associating known species' occurrence records with suites of environmental variables that can reasonably be expected to affect the species' physiology and probability of persistence (Yates et. al, 2000). Fundamentally, this paper identifies with a mechanistic, 'Gleasonian' model wherein biomes are not taken as pre-given, static entities but as emergent and dynamic through the interaction of constituent plants. The Quaternary record is here conceptualised as the unequivocal demonstration that plants react to climate change as individual taxa; entire biomes forming, dissolving and re-forming

within a single Milankovitch cycle (Prentice et. al, 1992). Such individualistic behaviour of vegetation - to respond/adapt to climate with flexibility - has enabled biomes to survive, albeit sporadically, several glacial/interglacial periods. A more recent study (Campos et. al, 2013) on biome-scale resilience (through altering water-use efficiency) to drought and increased rainfall variability/aridity of the last three decades will be referenced. Finally, this paper suggests that whilst there is plasticity in biome response, there remain critical thresholds (Scheffer et. al, 2012) which, once crossed, may lead to non-linear and abrupt transitions from one biome type to another. It is predicted that anthropic pressures - particularly fuel combustion and land use change - will lead to a spatial shift in tropical and boreal vegetation northwards and to the formation of novel 'no-analog communities', particularly in the transition zones ('ecozones') at the interstices between biomes.

The global map envisioned by Walter (1976) recognises nine climatic zones and corresponding vegetation zones/biomes (Figure 1). As Addison et. al (2002) posit: the equatorial zone lies between about 10° N and 10° S [with] daily variation in temperature greater than the annual variation, in the range of 25°-27°. Generally annual rainfall is high, with the maximum occurring at times of the equinoxes. Vegetation is classed as the tropical evergreen rain forest zone (1). Tropical rainforests are the dominant vegetations in hot, wet equatorial regions of South America, Africa, South East Asia and Indonesia. Plants here grow rapidly and continuously. Within this equatorial region of maximum insolation, Thornthwaite (1948) observed - and extrapolated for the globe - a strong correlation between evapotranspiration and plant distribution. The tropical rainforest climate as such is warm throughout the year, has a large positive net radiation balance, and a high rate of potential evaporation. A large annual rate of precipitation is required to maintain a positive water balance. In contrast, the tundra or subarctic climates have a short warm season, receive less radiation, and have a lower evaporative potential (Bonan, 2011). Correspondingly, annual net primary production increases with warmer climate, such that sites with low annual evapotranspiration have low productivity because temperatures are cold (tundra) or water is limiting (desert). However as evapotranspiration increases, temperature/water no longer limits production, permitting a floristic flourish. Walter's classification (I - IX) of climatic zones essentially continues to zonally map the transition of vegetation types (Figure 3) from tropical evergreen rainforest to the sparse tundra that encircles the North Pole in the Arctic and the southern-most tips of South America and many small southern ocean islands. Although fundamentally zonal, 'variations will occur [within biomes] caused by factors such as proximity to oceans, the influence of trade winds and monsoons, and the presence of major mountain range, as well as local micro-environmental differences caused by topography and soil types' (Addison et. al, 2002).

The close correspondence between climate zones and biomes is readily apparent as climate zones such as tropical savanna, tropical rainforest and tundra are named after vegetation (Bonan, 2011). Moving polewards from the tropical evergreen equator, grasses become prominent, within the dry tropical and temperate regions. Collatz et. al (1998) make the distinction between photosynthetic pathways, such that in cool climates grasses tend to utilise the C3 pathway, whilst in warmer climates, C4 plants dominate. To the north of tropical rainforest, the savanna biome (II) thus emerges with widely spaced trees interspersed among tall grasses. Here, growth forms often reflect frequent fire disturbances, high temperatures and lack of moisture. These grasslands are transitional between forest and desert vegetation. Desert (III) might be viewed as grassland that has exceeded a critical threshold associated with water stress. As such, the arid climate of deserts is hot and dry, populated by specially-adapted vegetation such as the cacti that minimises water loss in transpiration through the CAM photosynthetic pathway, or drought-deciduous plant that lose their leaves during dry

| Climatic zone | Vegetation zone | Vegetation zone |
|---------------------------------|-----------------|--|
| I Equatorial | 1 | Tropical evergreen rain forest |
| II Tropical | 2 | Tropical moist forest |
| | 2a | Dry deciduous forest and savanna |
| III Subtropical dry | 3 | Subtropical desert and semi-desert |
| IV Transitional and winter rain | 4 | Sclerophyllous forests of winter rain region |
| V Warm temperate | 5 | Temperate wet – evergreen forest |
| VI Typical temperate | 6 | Deciduous forest |
| VII Arid temperate | 7 | Steppe |
| | 7a | Semi-desert and deserts with cold winters |
| VIII Boreal cold temperate | 8 | Boreal coniferous |
| IX Arctic | 9 | Tundra |
| X Montane | 10 | Mountain |

Figure 1. Climatic & Vegetation Zones of Earth (adapted from Addison et. al, 2002)

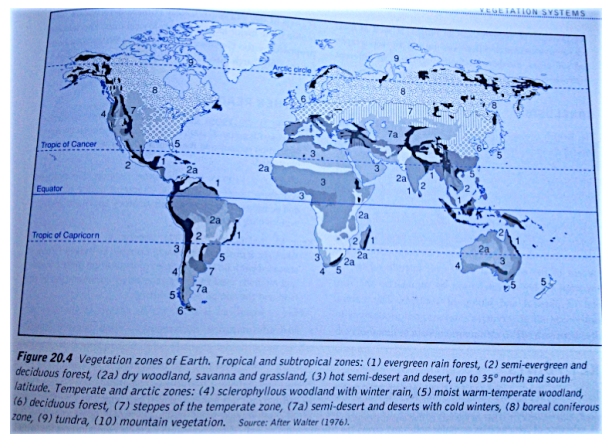


Figure 2. A global 'biome map' adapted from Walter's I-IX zonal classification (Walter, 1976 cited from Addison et. al, 2002)

spells to conserve energy/water. Beyond this subtropical, dry climatic zone, productive temperate deciduous and evergreen forests (V/VI) exist, buoyed by abundant annual precipitation (+1000mm per year) and moderate to pronounced seasonality. Bonan (2011) elicits the thick, luxurious forests in the Pacific Northwest region of North America supported by mild temperatures and high annual precipitation that support growth. Further north however, in Alaska, northern Canada, northern Europe and Russia the biome classification shifts towards boreal forest and tundra/taiga. Here, annual production and decomposition are low and trees are predominantly shorter, needleleaf evergreens that are more open than their temperate counterparts. At very high latitudes (65°N - 70°N) this boreal forest gives way to the treeless tundra, sparsely populated by grass-like sedges, dwarf shrubs, lichens and mosses. Here, the cold wet soil restricts tree root growth, decomposition and plant productivity (Bonan, 2011).

The conciseness of the biome map - partitioning seemingly unconnected/unrelated landmasses into latitudinal categories - occurs precisely because the biome concept is not a map of species distribution but of the distribution of vegetation zones with shared characteristics of plant structure, forms and physiology. As Townsend et. al (2009) posit, 'biomes are defined by factors such as plant structures (trees, shrubs, grasses); leaf types (broad-, needle-leaf) and spacing (forest, woodland, savanna). For example, root profiles and the ratio of belowground-to-aboveground biomass (root-to-shoot ratio) reveal how vegetation structure changes in different environments. In general, rooting depth varies with climate and increases with higher annual evapotranspiration, higher annual precipitation, and longer warm season. Thus tundra, boreal and temperate grassland have the shallowest root profiles (Schenk & Jackson, 2002; Bonan, 2011). Similarly, whilst the rainforest of Brazil and South-East Asia contain different species, they are structurally twinned, both dominated by a tiered, assemblage of tall ever-green and broad-leaved trees. There are further evolutionary symbioses exhibited by fauna such as pollination performed predominantly by small bird species. Changes in net primary production and allocation in response to climate are thus reflected in the structure of vegetation, such that, as a climatic parameter shifts - increased annual precipitation - floristic species respond by becoming taller and gaining a dense canopy with large leaf area index. Such changes are a manifestations of the dynamic balance among precipitation, soil water and leaf area (Woodward, 1993, cited in Bonan, 2011).

These relations - between plants and their environment - underlie the study of autoecology pressed by the German soil chemist, Liebig, in the 19th Century. His formulation of the 'law of the minimum' expresses the influence of an environmental factors on plant growth such that 'growth is governed by the factor which operates at a minimum.' Environmental conditions in this sense exist as gradients, wherein there will be upper (upper limit of tolerance) and

lower threshold (lower limit of tolerance) values beyond which the species cannot survive. The fundamental niche then occurs within these thresholds as: 'the maximum theoretically inhabited hyper-volume where a species, free from any sort of interference (competition), can occupy the full range of variables within the community to which it is adapted' (Addison et. al, 2002). The 'niche' is deeply embedded in the individualistic, physiological mode of classifying/interpreting biomes. As such, the global latitudinal zonation of biomes might be seen as a microcosm of individual-plant-community dynamics, specifically concerning those functional and physiological traits that enable one plant to survive and utilise local resources/conditions better than another. Cox et. al (2000) observe this global-local dichotomy within the Himalayan belt, positing that the altitudinal transition there from one biome (savanna) to the next (temperate deciduous forest) is essentially a reproduction at the local of latitude transitions:

Ascending from the northern indian savanna and thorn scrub, we move up through subtropical monsoon forest, largely occupied by drought-deciduous tree species. A zone of scrub follows, which owes its existence to the impact of human activity (italics my own) and domesticated animal grazing. Above this is temperate deciduous forest...its general form and appearance similar to that of Western Europe. Coniferous forest lies above the 'oak zone'...alpine birch that lead on up to the tundra and the permanent snows of the high mountains (Cox et. al 2000).

Global terrestrial biome models have been developed to simulate net primary production, biomass accumulation, litterfall, carbon storage and surface energy flux. These numerical models are fundamentally underlain by the relationships between annual temperature, precipitation and evapotranspiration with bioclimatic vegetation (Figure 4). Further conceptualisations of the biome have been proposed, such as Budyko's (Figure 5). His diagrammatic analysis posits a relationship between biome geography and the radiative dryness index, defined as the ratio of

net radiation to the amount of energy required to evaporate the annual precipitation. As such, values of the dryness index less than 0.3 correspond with tundra; forest vegetation, 0.3-1; grassland, 1-2; semi-desert vegetation > 2 and desert, greater than 3. (Budyko, 1974). The problematics of scale and modelling methodology have long been

- A – Humid tropical. No thermal winter, with all months having a mean temperature above 18°C.
- B – Dry climates, in which evapotranspiration substantially exceeds precipitation over the year, and there are constant water deficit conditions.
- C – Humid middle latitude climates with mild winters. These are defined as having a coldest month with an average temperature below 18°C, but above -3°C.
- D – Humid middle latitude climates with cold winters. These are defined as having a coldest month with an average temperature below -3°C, but the average of the warmest month is > 10°C.
- E – climates with no thermal summer. These are defined as having an average temperature in the warmest month < 10°C.

Figure 3. The Köppen Climatic Classification (Kottek, 2006) - A system based on the identification of a series of average climatic parameters, which are thresholds for support of large-scale vegetation units.

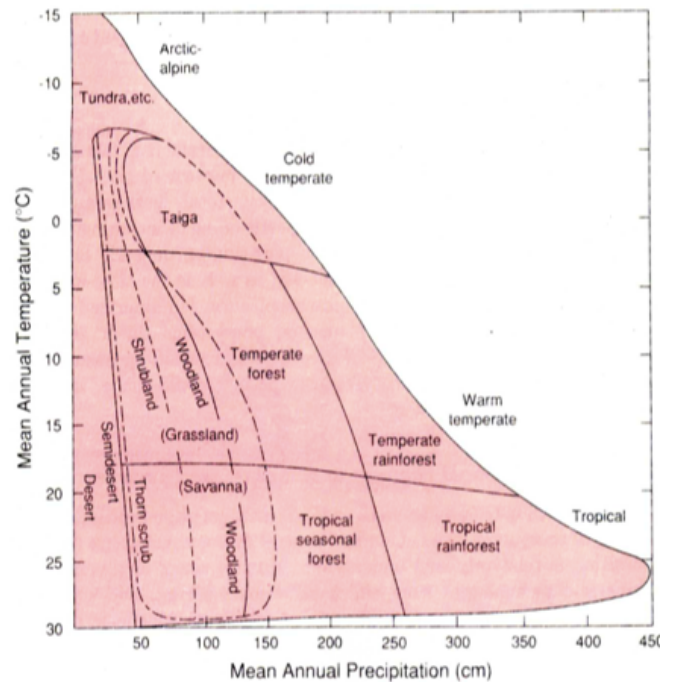
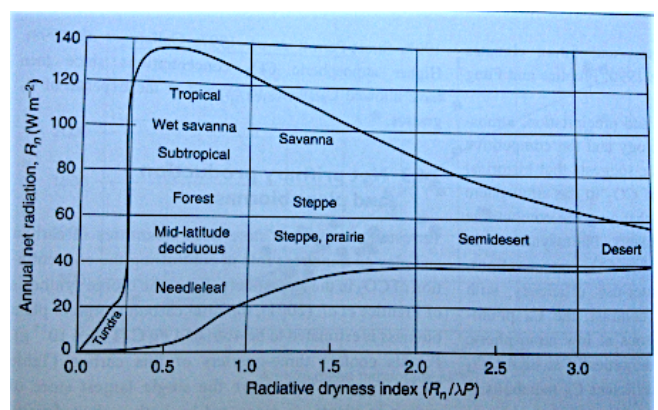


Figure 4. Generalised relationships among major plant formations, annual mean temperature and annual precipitation. (Whittaker, 1975) Note that within the area bounded by the dotted lines, various local/regional factors - such as geographical location, seasonality (drought/disturbance) and human pressures (land use, atmospheric alteration) - subtly determine the biome type which develops.



established in biome discourses. As Bonan (2011) writes:

[the] models of planetary ecology span a range of approaches from simple empirically based models to mechanistic process models of plant physiology and biogeochemical cycles... [models] differ greatly in how they calculate environmental conditions such as soil water and temperature, how these conditions affect physiological processes, and how multiple resource limitations collectively affect net primary production and carbon allocation. Simulated 'results' can thus often differ greatly among models. Nonetheless, Bonan suggests this multiplicity, rather than a disillusioning process, actually facilitates the future mapping and prediction of biomes. As such, mechanistic representation of net primary productivity - when coupled with more correlative, Clementsian traditions - poses the opportunity for greater insight/validation upon existent, biome behaviour models. The problematic of scale might be reduced by integrating biogeochemical models (correlative) - that simulate the carbon cycle given a prescribed biome dataset as input to the model - with vegetation dynamics models (mechanistic) that simulate changes in population structure and community composition in response to disturbance. The result is a detailed physiological and demographic map of the biome in all its spatial and temporal complexities. In a study of carbon flux at several needleleaf evergreen forest sites in Oregon, Thornton et. al (2002) were able to capture monthly dynamics of evapotranspiration and gross primary production succinctly by such method across a wide gradient in climate and stand age.

There have been several attempts to model and predict future biome shifts, such as in Europe (de Groot, 1987) and the Swiss Alpine foothills (Leadley & Stocklin, 1996). The former, de Groot's study predicted the changes that would occur given a rise in temperature and precipitation of 5°C and 10% respectively. His study effectively proposed the retreat of Scandinavian boreal forests and replacement by deciduous forest. Furthermore, the current deciduous forest would see its spatial extent enveloped by a Mediterranean, chapparral type vegetation. The latter study - of the Alpine foothills - posited that a rise in atmospheric CO₂ concentration from 330ppm to 660ppm would constitute a renaissance of certain tolerant species at the demise of others. This raises a significant point about the individualistic model, species show a wide range of responses to climate such that natural communities (biomes/ecozones) are likely to disassemble and reform in a transient, fragmentary, non-equilibrium manner (Huggett, 2004). As Zavaleta et, al (2009) posit, 'species populations respond to changes in climate through changes in abundance, distribution and, in some cases, rapid evolutionary change.'

Biomes - particularly during periods of rapid and extensive climate change - might thus be conceptualised as entities embedded in a fluid, spatial mosaic of discrete 'change' and 'no-change' zones. Furthermore under water stress, the fragmentation of these zones might be more pronounced as 'every variation in topography and soil become important to site water-balances and the survivorship of different organisms. With reference to the ecotone (biome boundary) specifically, Neilsen proposes that under such stress it 'disappears a while [then] reappears at a new location...disassembly and reestablishment.' (Neilson, 1993 cited in Huggett, 2004). Thus, whilst it is common for species to move in the same general direction, this does not necessarily engender entire communities move together. Rather, species behave individualistically, an ecological axiom that complicates the mapping/prediction of biome change.

Climate change, over periods of centuries to millennia, alters the biogeography and functioning of Earth's vegetation. One of the longest timescales at which climate changes is the recurring waxing and waning of glaciers. Bonan (2011)

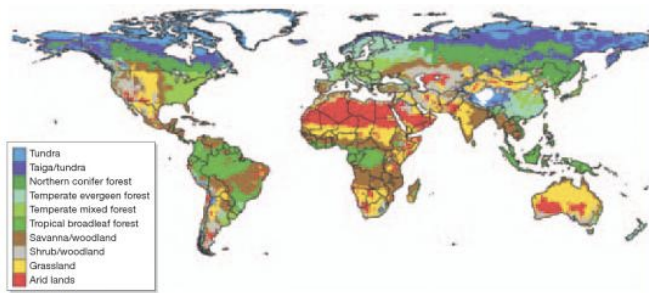


Figure 4.12
The distribution of major biome types under the current climate, as simulated by the MAPSS biogeography model.

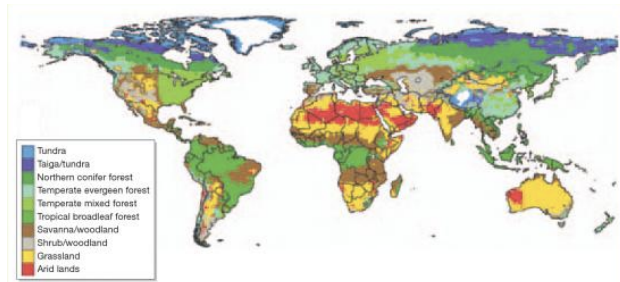


Figure 4.13
The potential distribution of major biomes resulting from climate changes associated with an effective doubling of carbon dioxide concentration, as simulated by the MAPSS biogeography model.

Figure 8. The potential change in biome geography associated with an effective doubling of CO₂ concentration. Note Top - current map; Bottom - future predictions (Neilson, 1998)

reproduces the biome coverage of the Earth some 18,000 years ago at the height of the last ice age when much of the Northern hemisphere high latitudes were covered in glaciers. Models, based upon preserved pollen in lake and bog sediments, simulate the changing geographic distribution of biomes as climate warmed and atmospheric CO₂ concentration increased. Vegetation adapted to cold climates shifted northwards to be replaced by warm vegetation types. Again, some 6,000 years when the Earth was in a period of intense warming (brought about by a Milankovitch ‘eccentricity’ cycle) the middle and high latitudes of the Northern hemisphere experienced bioclimatic shifts, such that vegetation extended northward beyond modern range limits. Furthermore the effects upon biome/vegetation zones during this period were accentuated in Northern Africa and Asia by changing the moisture and atmospheric circulation profile of the region: ‘Increased summer solar radiation created a warmer, wetter climate in North Africa compared with today. Stronger than present solar radiation heated the African continent and increased the land-sea temperature contrast. Surface pressure dropped over land, enhancing air flow onto the continent and increasing the African summer monsoon. As a result of the wetter conditions, grasses and shrubs covered much of the modern Sahara Desert.’ (Bonan, 2011).

Climate models that aim to map and predict future biome shifts take into account these palaeo-climatic occurrences. Broadly, both equilibrium and dynamic vegetation models show major poleward shifts in cold-limited biomes as a result of recent climate change. For instance, tundra is predicted to decline in distribution as it will largely be ‘purged’ from the North American and Eurasian continents with the northward expansion of boreal forest. Furthermore, arid lands are expected to shrink, as is boreal forest as temperate forests expand northward. Dynamic models (Neilson et al. 1998) predict these vegetation changes will result in large productivity increases in northern latitudes. Hoekstra et. al (2005) conceptualise the current global situation as that of a biome crisis, ‘threaten[ing] with biodiversity loss, ecological dysfunction and [the] consequent impacts to human lives and economies.’ The biome and its survival is placed at the simple binary between habitat conversion and habitat protection. Using this, Hoekstra et. al suggest that ‘habitat conversion exceeds habitat protection by a ratio of 8 : 1 in temperate grasslands and Mediterranean biomes, and 10 : 1 in more than 140 ecoregions.

Conversely to the existential pessimism of Hoekstra et. al, empirical research suggests that biomes are far more resilient/adaptable to climatic change. As such, observations of ‘aridifying’ regions (Campos et. al, 2013) in the subtropical-temperate latitudes gleaned a common ecosystem water-use efficiency (WUE: above-ground net primary production/evapotranspiration) across biomes ranging from grassland to forest that indicated an intrinsic system sensitivity to water availability across rainfall regimes, regardless of hydroclimatic conditions. The results found higher

WUEe in drier years that increased significantly with drought to a maximum WUEe across all biomes; and a minimum native state in wetter years that was common across hydroclimatic periods. As Campos (2013) concludes: 'this indicates biome-scale resilience to the interannual variability associated with the early twenty-first century drought—that is, the capacity to tolerate low, annual precipitation and to respond to subsequent periods of favourable water balance.'

The complexity of biome response/capacity to survive rapid and extensive climate change is further problematised by the non-linearity and successional complexity of 'individualistic' vegetation communities. It has been postulated that the the tundra communities of the high Arctic (Wookey & Robinson, 1997) might exhibit continued resilience - a 'refugia of tundra fragments' - to the encroachment/shift of temperate forest northwards. Wookey et. al posit several reasons for this inertia: (i) soils are very nitrogen and phosphorus poor complicating the immigration of temperate flora; (ii) physical barriers, the presence of tundra on remote, fragmented islands (Greenland, Faroe Islands) and (iii) the genetic diversity and evolutionary, physiological traits of Arctic tundra are resistant/resilient to change. As such the tundra biome exhibits properties that extend its critical threshold, allowing it to potentially survive extensive (anthropic) climate change . Such empirical modelling remains however deeply ambiguous/chancing. As corollary research undertaken in the boreal forest (Scheffer et. al, 2012) suggests:

Rapid warming has already caused extensive thawing of permafrost, accompanied with changes in hydrology, which are likely driving changes in vegetation, wildfires, and insect outbreaks. [However] despite these major changes, the potential response of boreal systems to further climate change is poorly understood. One of the big questions is whether boreal biomes will change gradually, as assumed by most dynamic vegetation models, or might have tipping points where changing conditions can invoke critical transitions. Such uncertainty reifies the problematic of scale, in that landscapes are dynamic, successional mosaics wherein conditions (temperature, salinity) and resources (competition) are in a continual, effervescent state of flux. Thus whilst the tundra/taiga biome might appear uniform and thus predictable from afar, in actuality it is deeply heterogenous, underlain by feedback effects, intrinsic and extrinsic thresholds.

The biome concept charts a cartography of the structure and composition of vegetation and the functioning of terrestrial ecosystems, which at a local scale are shaped by environmental factors (constraints/gradients) - such as temperature and moisture - and at a global scale, by climatic patterns and the uneven latitudinal receipt of insolation. The geographic distribution of biomes is closely correlated with measures of temperature, precipitation, evapotranspiration and net primary productivity/decomposition rates (Bonan, 2011). The biome concept have nevertheless stoked controversy and undergone several problematic revision/adaptations over the decades. Primarily, this paper has shown the generalised relationships among major plant formations, annual mean temperature and annual precipitation. Temperature is important because sufficient warmth, but not excessive heat, is a prerequisite for the biochemical reactions that support life. Water is important because 80-90% of the mass of a plant is water. The latitudinal gradient from tropical forest to temperate, boreal and then arctic tundra pervades this logic and further reifies the relationship between evapotranspiration (temperature/precipitation) and plant distributions (Thornthwaite, 1948 cited in Bonan, 2011). Finally, this paper has revealed that biomes are themselves inherently resilient, adaptive and fluid. The biome as such might be conceptualised as a macrocosm of the community-wide successional mosaic. Biomes - rather than the static entities that cartographic representations might allude to - are dynamic, in a continual state of flux.

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