Identify the various sources of disturbance which can lead to changes in community composition and structure, and explain how individuals or ecosystems may respond

Ecosystems, rather than being static entities, are in a state of continual flux. Communities exist in diverse composition and structure. This diversity is maintained by the stochastic nature of disturbance and the dynamic responses of biota that occur subsequently. Disturbance - the episodic destruction of ecosystem components - is thus an integral part in the functioning of many ecosystems. The 'continual flux' of the system occurs when such disturbance initiates vegetation dynamics (relay floristics) that vary according to life history patterns and competition among plants for light, water and nutrients (Bonan, 2011). Integral to these dynamics is the concept of the ecological threshold and its dual sub-parameters, resistance and resilience. Resistance refers to the ecosystem's capacity to absorb stress without change, termed the inertia. If a disturbance is large/catastrophic enough to overcome this inertia however, the system changes/ crosses a threshold from metastable to unstable condition. Resilience refers to the ability of this disturbed system to subsequently recover from such cross-threshold change. Species and community response to disturbance - resilience - depend upon: (i) external factors, such as the magnitude of the event, spatial extent, return interval, resource availability and environmental constraints after the event; and (ii) internal factors, such as biodiversity of the regional species pool, preadaptation to the type of disturbance, and any internal functional strategies. Throughout, post-disturbance (secondary) succession is recognised as the primary mechanism through which resilient individuals and communities respond in attempting to restore order/stability to the system.

Exploring the ecological dynamics that occur between the moments of disturbance, threshold-crossing and response lie at the crux of this paper. Primarily, I produce a geography of disturbance, delineating its spatial and temporal aspects within the ecosystem. The focus then shifts to describe the various sources of stress as generally exogenous/physical or endogenous/biological in origin. In particular, fire and wind disturbance within boreal forest ecosystems will be observed. The main body of this paper then explores post-disturbance succession and the interactions of early and late successional species. Using the theories of succession - facilitation, inhibition and tolerance - I describe how the landscape maintains its diversity through the ecological rhythms set by disturbance regimes. These 'natural' regimes serve to continually renew and facilitate the coexistence of r- and K-selected species in their respective temporal niches. In this sense the landscape emerges as a 'mosaic of successional communities whose composition and structure
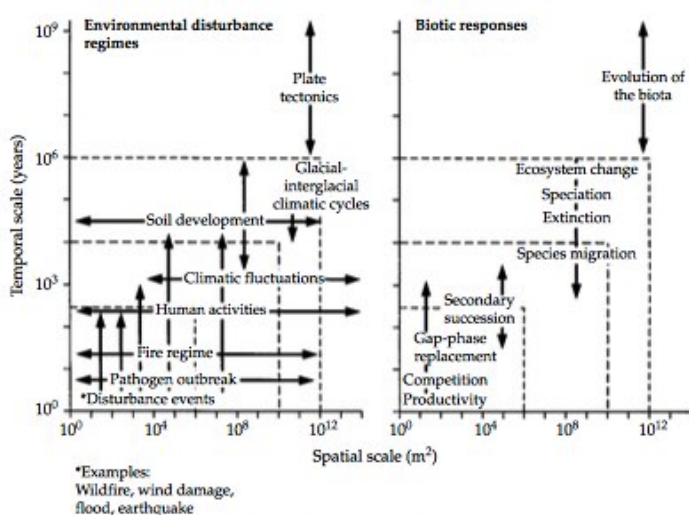

Fig. 1 The Spatial & Temporal Aspects of Disturbance-Response Regimes (Delcourt & Delcourt, 1977)

Figure 2.20 Environmental disturbance regimes and biotic responses, viewed in the context of four space–time domains (shown here bounded by dashed lines), named micro-, meso-, macro-, and mega-scales by the scheme's authors. (Redrawn from Delcourt and Delcourt 1991, Fig. 1.6; from an original in Delcourt and Delcourt 1988, with kind permission from Kluwer Academic Publishers.)

is determined by the type and severity of disturbance' (Whittaker, 1977). The complexity of these mosaic ecosystems are explored in a case study of dispersal-led succession upon a remote volcanic island - Krakatau - in the Pacific. Finally, this paper suggests that in some disturbance events - such as catastrophic volcanic eruption or incremental global cooling - the successional response is not possible. In such scenarios, non-linearity and chaos predominate with modes of ecological response manifest in extinctions and mass migration. As human activities increasingly disrupt and exacerbate 'natural' disturbance regimes, these modes of ecological response will plume perhaps ever more so.

Disturbances occur at various spatial and temporal scales. As Delcourt et. al observe 'environmental forcing functions, biotic responses, and patterns of organisation of communities on terrestrial landscapes vary on all scales in space and time' (Delcourt et al. 1983a). High mountain ecosystems for example are characterised by geomorphological and cyrospheric processes such as cryoturbation, solifluction, mass movement and erosion (glacial/fluvial/soil). Huggett makes a distinction between what he calls random and point disturbance. The former refers to disturbances such as strong winds or foraging animals which act randomly within a landscape to produce a patchy network. Eroded soils created by grizzly bears excavating dens or searching for food is an example. The latter - that of point disturbance - refers to the common behaviour of disturbances such as fire, pathogens and pests, to begin at a point within a landscape and then gradually diffuse outwards to other areas. In both cases, disturbance operates in a 'heterogenous manner because some sites within landscapes will be more susceptible to disturbing agencies than other sites' (Huggett, 2004). Such sources of stress furthermore affect landscapes at all scales. At the micro-scale (1-500 years; 1m2-1km2) - affecting individual plants and forest stands - wind damage, wildfires, clearcut, floods and earthquakes are the dominant disturbances. These local stresses of relatively short duration can have quite immediate effects on community composition.

At the mesoscale (defined as half a millennium to 10 millennia and 1km2-10,000km2) - a scale which encompasses the Quaternary glacial-interglacial periods - a patchy, landscape mosaic is created through the interactions of frequent disturbance regimes such as climatically-driven wildfires and pathogenic events. Species migrations and displacements occur on this scale in response to the changes in environmental gradients inherent during periods of disturbance. Disturbance at the macroscale (continents, hemispheres) are driven by plate tectonics which alter climate and influence biotic evolution through processes of vicariance and dispersal. Human activity, volcanism and meteorite impacts further disturb the composition and structure of global biota. Such was the case in the Cretaceous-Tertiary extinction event (K/T) which rendered the dinosaur extinct 65 million years ago. At the meso- and macro- scales, disturbance processes create heterogenous patches of varying sizes, shapes, distributions and biotic legacies. These disturbance regimes, when coupled with the ecological attributes of habitat complexity, susceptibility, stability, persistence and resilience serve to partition the globe into the biogeographic regions observable today.

There are various sources of physical and biological stress that affect community composition and structure. Physical disturbance relates to wind, fire and geomorphic processes. Tree-throw by strong winds is the primary means by which species richness is maintained in many forest ecosystems. Fallen trees create gaps in the forest canopy and thus initiate successional pathways and vegetation dynamics. As Huggett (2004) writes, these gaps provide 'niches with much sunlight for pioneer species', encouraging the release of suppressed, shade-tolerant saplings and the recruitment of new individuals. Such gap dynamics are cyclical and self-perpetuating. In a study of Far East tropical rainforest, Whitmore

observes how of the seedlings that initially colonise the gap, many die. Of the few survivors, some grow into saplings, which thin over time into a mature stand of a few large trees. This then initiates a new cycle of growth when these mature trees eventually succumb to biotic or abiotic disturbance (Whitmore, 1975). The forest landscape thus exists as a mosaic of individual patches in different stages of development - the processes of establishment, thinning and gap formation occurring in a cycle. Gap dynamics influence community composition and often facilitate complex patterns of species abundance in the landscape. One such theory of forest dynamics suggests that treefall gaps promote coexistence of species with different resource-use patterns, dispersal, and competitive abilities. As Bonan elicits, 'shade intolerant species require a canopy gap for successful regeneration, but many are small and do not achieve sufficient size to create a large opening in the canopy.' Conversely, shade tolerant trees tend to be longer lived, grow to large size, and produce large gaps in the canopy. The presence of the small, gap-requiring species is thus maintained by the gaps and temporal niches created by the larger trees (Bonan, 2011).

Disturbance by fire dominates many biogeographical regions of the globe. Indeed, fire commands its own field of study in ecology as Whelan's seminal, The Ecology of Fire, would suggest. Recurring fires, both natural and human, are common to grasslands, Mediterranean vegetation, savanna, and many temperate and boreal forests (Whelan, 1995). In similar vein to wind disturbance, fire initiates the successional dynamics that form a mosaic landscape. Wildfires within terrestrial ecosystems create a mixture of totally burned, partially burned, and unburned sections called a burn mosaic. These varying degrees of burn are a result of multiple factors such as wind shifts, daily temperature changes, moisture levels, and chemical composition of the various vegetational outcrops. Another determining factor of the burn mosaic is the stand age of species. Mature trees with thick, fire resistant bark often exhibit fewer gap phase dynamics and thus there are fewer early-age successional species in its canopy than a young forest. Huggett suggests that the fire disturbance regime has both detrimental and beneficial effects upon an ecosystem. Of the detrimental, (i) many organisms suffer mortality and are lost from the community; (ii) the ground after severe fire is left vulnerable to soil erosion and thus the loss of nutrients to aeolian/ fluvial process and (iii) minerals are lost in smoke and through volatilisation which releases large quantities of nitrogen and sulphur (Huggett, 2004). There are however beneficial effects that often counterbalance the loss of nutrients from erosion such as the reduction of burnt, dead litter to ash and the appearance of nitrogen-fixing legumes that commonly thrive in the high-stress, burn mosaic, environment.

| Observation	Possible explanations
Increased productivity	Increased nutrient availability
	Removal of suppressive dead leaves
	Increased average soil temperature
	Extended period of high temperatures
	Earlier start to growing season
	Removal of competing vegetation
Increased flowering	Increased nutrient availability
	Increase in numbers of shoots sprouting
	Removal of competing vegetation
Increased seed-dispersal distances	Removal of canopy from around fruits improves wind-flow
	Removal of ground vegetation and litter
	Greater foraging distances by seed-dispersal agents
Synchronous release of canopy-stored seeds	Heat treatment of sealed follicles or scales
Synchronous germination of soil-stored seeds	Heat treatment of impermeable seeds coats
	Charcoal residues break dormancy
Alteration of surface light and/or temperature regime	
Improved establishment of seedlings	Increased nutrient availability
	Decreased herbivore activity
	Satiation of populations of seed predators
	Removal of competing vegetation
	Degradation of allelopathic chemicals
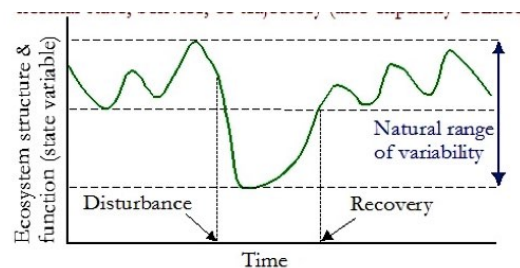
Figure 3. A Chronology of Succession: Disturbance - Cross threshold - Response (McGarigal, 2001)

A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment, including both destructive, catastrophic events as well as less notable, natural environmental fluctuations. Typically, a disturbance causes a significant change in the system under consideration (White & Pickett) 1985)

Fire regimes strongly influence the structure and function of some plant species and communities. As Liu et. al (2005; cited in Bonan, 2011) observed in their study of surface energy flux in Alaska, 'fires act[ed] as a rapid decomposer, consuming all or portions of the forest floor and replenishing the supply of nutrients'. Furthermore, in the Chiricahua Mountains of Arizona and the Central Himalayas, the elevational distribution of pine species is determined chiefly by relative exposures/disturbance by fire and not the common determinants of differing light levels, shade tolerances or drought resistances. The Arizonan mountains might thus be regarded as a system of biotic and abiotic individuals moulded and structured by frequent, fire disturbance. In similar vein, communities actively alter these regimes of disturbance through response mechanisms (Fig. 2). Evolutionary adaptations of resistance (pre-threshold) and resilience (post-threshold) exist in many tree species within regions prone to frequent terrestrial wildfires. Van Wilgen et. al (1992) document how many mountain fynbos plants in Cape Province, South Africa possess a wide range of regeneration strategies and fire-survival mechanisms. He posits, 'many species sprout rapidly' after a fire - a universal mode of resilient, successional response. Furthermore, several species, particularly the fire lily and rosy watsonia have adapted their flowering regimes to coincide with the changes in soil temperature associated with fire disturbance.

Biotic disturbances relate to diseases, pests and human activity that serve to alter the species composition and structure of ecosystems. Biotic disturbance agents - among which pathogens and outbreak species of insects predominate - have historically accounted for several major episodes of tree loss in the hardwood forests of the eastern USA and the Canadian boreal forests. Some biotic disturbance agents, such as the aggressive bark beetle species, cause widespread boreal mortality. Other disturbance agents -such as defoliators, root insects, and root pathogens - injure trees and thus predispose them to mortality from secondary stressors. These modes of biotic disturbance are often sensitive to climatic change; periods of warmer than average temperatures are often associated with increased insect activity and thus tree mortality. In a paper commissioned by the Canadian forest service, Hall & Moody calculated that in Canada the annual forest volume loss, due to mortality and reductions in 'normal' growth caused by insects and pathogens, averaged 102.8 million cubic metres between 1982 and 1987. Such a loss was almost three times the volume lost to fire, accounting for 70% of the volume harvested nationwide (Hall & Moody 1994). The plight of the American chestnut, decimated by a parasitic sac fungus, similarly reveals the adverse effects wrought by biotic disturbance upon an ecosystem's structure and composition. In particular, Davelos (2004; cited in Bonan, 2011) observed how the differing capacities for successional recovery (individual resilience) between the American species reconstituted the hardwood forest mosaic anew; 'in the wake of the chestnut blight, several oak species, beech, hickories and red maple became co-dominants...oak-chestnut forest rapidly turned to oak-hickory.'
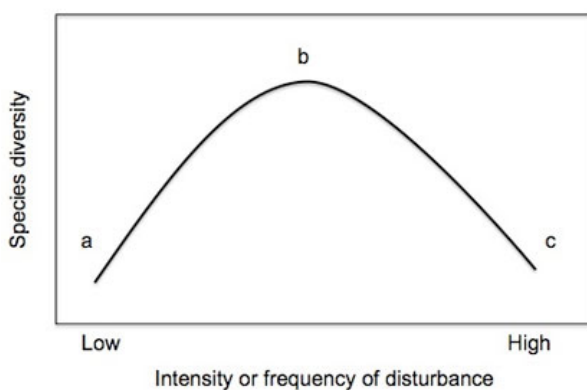

Figure 4 The Intermediate Disturbance Hypothesis (IDH)
(a) Species diversity is low at low disturbance frequency because of competitive exclusion (b) Species diversity is higher at intermediate disturbance frequency due to a mix of goof coloniser and good competitor species (c) Species diversity is low at high disturbance frequency because only good colonisers or highly tolerant species can persist Hughes, 2012).

Rapid ecological change, which happens as critical ecological thresholds are crossed, may be the result of subtle, natural processes related to the disturbances of herbivory and grazing. In a multivariate regression analysis, Milchunas & Lauenroth (1993) observed the differences in species composition, aboveground net primary production, root biomass, and soil nutrients in grazed versus protected, ungrazed plots. Their research posited that 'changes in species composition with grazing depended primarily on aboveground net primary production and the evolutionary history of the site' (Milchunas & Lauenroth, cited in Huggett, 2004). Nevertheless, the effects of herbivory and grazing are often difficult to observe and quantify, given that they often occur in tandem with other disturbance regimes such as fire. Cumberland Island in Georgia, USA was the site of important ecological research in the 1980's, when Turner & Stratton (1987) observed the dynamic interactions between biotic/abiotic disturbance regimes (grazing and fire/ 'consumers' of biomass) with the physiological modes of resilience and resistance exhibited by the Island's vegetation.

Grazing, performed predominantly by the populous, native white-tailed deer serves to deplete the forest understorey of Cumberland reducing interdune and high marsh vegetation to a plateau. Such grazing behaviour determines the sources of energy for subsequent fire disturbance, in line with the logic that, grazed regions with less consumable plant material will be more resistant to fire than an abundant plant, high-fuel understorey. Grazing thus altercates the physical path along which an abiotic, disturbance agent such as fire or disease might diffuse. Furthermore, Tu rner & Stratton observed how highly resistant species (strong pre-threshold response) were often poorly resilient (weak post-threshold response) to fire disturbance. Specifically, the oak forests of Cumberland exhibited high resistance (fire-retardant bark) yet low resilience (slow recovery after burning), whilst the salt marshes and grassland had low resistance (episodically destroyed) yet high resilience (rapid recovery/recolonisation). These differences arise from the internal, physiological traits of allocation, such that oak trees partition greater energy sources to fire defence/resistance whereas marsh vegetation allocates more towards rapid growth/reproduction (seed dispersal). These individual responses to disturbance will be explored later as analogous with the differing life history characteristics and functional traits of r- and k-selected species. As Huggett (2004) concludes on behalf of Turner and Stratton, 'fire and grazing disturbances on Cumberland Island seem to be driven by resilient patches within the landscape, yet influence resistant patches from which little energy is obtained.'

Ecosystems respond to disturbance through the initiation of vegetation and species dynamics that gradually serve to recolonise and repopulate the disturbed area. Bonan (2011) conceptualises the landscape as 'a mosaic of successional communities whose composition and structure is determined by the types and severity of disturbance.' The actual successional mechanism begins wherein,

disturbance removes existing vegetation and creates an environment with high sunlight and reduced competition for resources. These conditions favour the germination, establishment and growth of early successional species. [These] early successional plants are maintained in the landscape by a fugitive life history and recurring disturbance...In contrast, the abundance of late successional species is promotes by long intervals between disturbances. (Bonan, 2011)

These differing physiological and behavioural traits of r- and K-selected species account for the strong Gaussian distribution observed between the level of disturbance (frequency/intensity) and species diversity within the
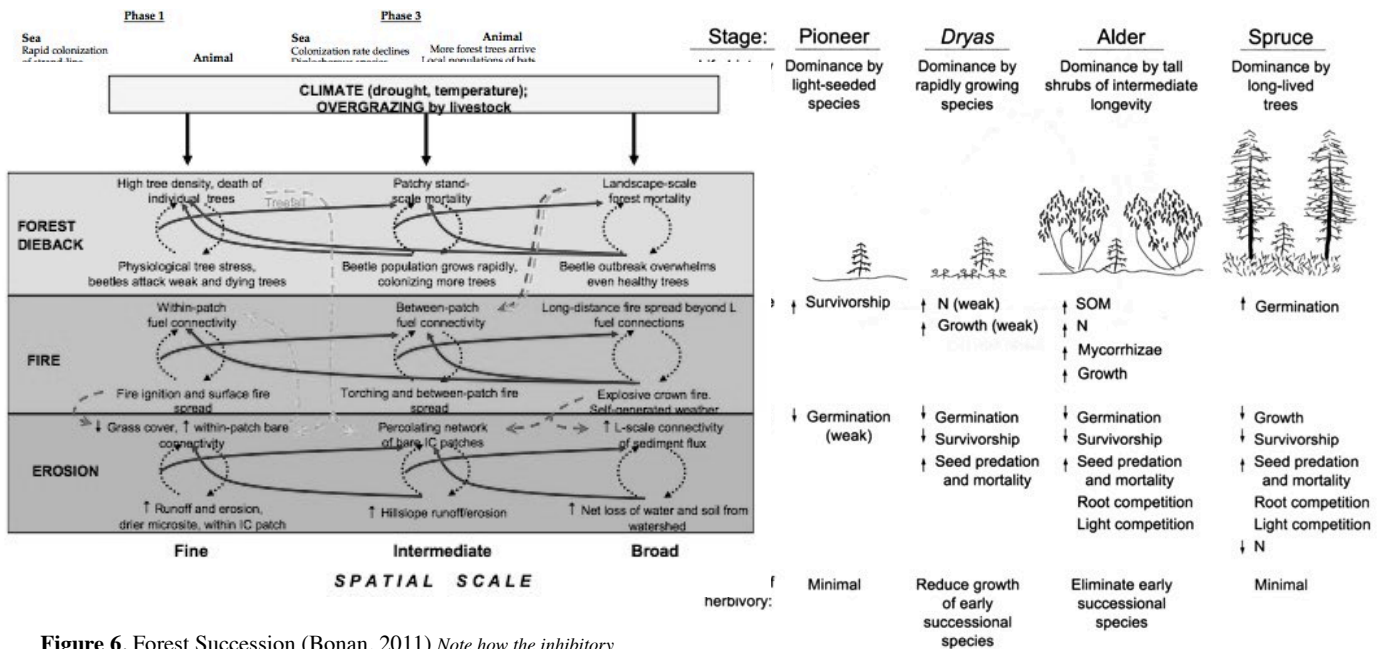
Figure 6. Forest Succession (Bonan, 2011) *Note how the inhibitory and facilitative models of succession describe the physical alteration of the*

Intermediate Disturbance Hypothesis model (Figure 4). The differing temporal niches and life history patterns of early and late successional species underlie the IDH model. In contrast to the traditional Clementsian view - of succession as 'orderly, predictable change that culminates in a stable, climax ecosystem [and thus] an equilibrium balance of functions' - the IDH model implicitly relies on a non-equilibrium, chaotic/chancing system wherein succession is regarded as a 'population process' deeply enmeshed in the differential growth, survival, and colonising abilities of species adapted to different points in an environmental gradient (Bonan, 2011).

 Such life history patterns are related to a tradeoff between an ability to rapidly colonise and dominate a site (r- selected species) versus slow growth and ability to compete in a resource limited environment (K- selected species). These behavioural traits/capacities, coupled with a knowledge   of individual species' modes of immediate disturbance response and resource utilisation give way to the universal concept of vital attributes. Succession and the dynamics of relay floristics are enshrined in these attributes and the numerous life histories they produce: (i) method of arrival or persistence at a site during and after a disturbance; (ii) ability to establish and grow to maturity in the developing community and (iii) time required for an individual to reach critical life stages such as seed production. Species may either facilitate, inhibit, or tolerate other species (Figure 5).

Disturbance regimes strongly determine vegetation patterns and succession in the boreal landscape; as Viereck et. al posit (1986) fire and biotic agents - such as pathogens and invasive bark beetle species - create the distinctive 'spatial patterns of vegetation types, age-structure and successional stage of mosaic patches' that then affect the 'ecological properties of Boreal forest, such as albedo and carbon storage.' Even so, there remains an element of stochasticity in the Boreal mosaic due to chance, and the presence of widely dispersed, finite aeolian seeds that might colonise an area long distant from its original source. Furthermore gap dynamics - randomised tree mortality rather than age-related - create complex patterns of species abundance and community composition. Bonan & Van Cleve's research (1992) of the Boreal forests of Interior Alaska posited the existence of a successional forest mosaic of broadleaf deciduous and needleleaf evergreen trees that reflected recovery from recurring floods and fires. Topography as such was key in determining the disturbance-threshold-response complex of certain areas of the forest. For instance, the facilitative model of successional response is observable along river floodplains, [wherein] recurring floods initiate succession. For

the first one or two years, large floods deposit sediments and form terraces along river banks. As the terraces rise, flooding is less frequent and willow, alder, and balsam poplar invade the exposed sites...with the rise of a closed poplar canopy, the pioneer shrubs decline (Bonan & Van Cleve, 1992).

Whittaker et. al noted a similar mosaic-ed, heterogenous response from vegetation in their dispersal-structured model of island recolonisation within the Krakatau islands of the Pacific: 'the interior forests of the Krakatau islands continue to accrue new species of higher plants' - due to aeolian, frugivorous and coastal processes (Figure 7) - 'and the balance of species in the canopy is undoubtedly in a state of flux, with strong directional shifts in the importance of particular species being evident over the period since 1979.' (Whittaker et. al 1998). Both studies - of Alaskan Boreal forest and Krakatau - suggest that post-disturbance recovery/response can follow multiple trajectories; that rather than being the orderly, predictable, Clementsian climax model, succession is inherently disorderly and random, dependent upon the myriad species and life patterns/behaviours involved. Nevertheless, both Bonan and Whittaker portray systems that might reach a state from which little further change occurs - an alternative stable state. In such a scenario, the ecosystem has developed a relatively stable structure/composition (resilience effects) that is different from what was present before the disturbance. Furthermore, the stability of the new system often occurs due to the crossing of an extrinsic or intrinsic threshold - a non-linear change in response to a stress/disturbance. This 'threshold approach' to ecological disturbance-response models is becoming more important, given the potentially catastrophic effects of global warming and associated wild climatic fluctuations on global ecosystems' composition and structure.

As the U.S Climate Change Science Programme posited in their collaborative report Thresholds of Climate Change in Ecosystems (2009): 'an ecological threshold is the point at which there is an abrupt change in an ecosystem quality, property, or phenomenon, or where small changes in one or more external conditions produce large and persistent responses in an ecosystem...[such] non-linear instabilities - and subsequent irreversible change (extinction/mass tropical refugia migration) may proliferate... particularly as disturbance mechanisms, such as fire and insect outbreaks predispose many landscapes to threshold change when the stress of climate change is added' (U.S CCSP, 2009). Ecosystems, rather than being static entities, are in a state of continual flux. As much existing literature/research suggests, this diversity is maintained by the stochastic nature of disturbance and the dynamic responses of biota that occur subsequently. Disturbance as such is integral to the creation of a landscape mosaic of successional communities. This continual, disorderly state of flux perpetuates in space and time due to the disturbance-threshold-response complex wherein species - early (r-selected) and late (K-selected) - with differing vital attributes and thus behaviours of resistance and resilience collide and interact to produce a diverse and heterogenous ecosystem, both in composition and

structure.

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