Emerging ecosystems:

theoretical and management aspects of the new ecological world order

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Abstract

As more of the Earth becomes transformed by human actions, novel ecosystems increase in importance, but are relatively little studied. An emerging ecosystem can be defined as "An ecosystem whose species composition and relative abundance have not previously occurred within a given biome." The key characteristics of emerging ecosystems are novelty, in the form of new species combinations and the potential for changes in ecosystem functioning, and human agency, in that emerging ecosystems are the result of deliberate or inadvertent human action. Either the degradation or invasion of native or "wild" ecosystems or the abandonment of intensively-managed systems can result in the formation of these novel systems. Important considerations are whether these new systems are transient or persistent and what values they may have. A series of case studies illustrate the different types of emerging ecosystem which deserve further consideration in both a theoretical and practical context.

Key Words

Emerging ecosystem, biotic invasion, ecosystem transformation, degradation, land abandonment

"Synthetic ecosystems include conditions and combinations of organisms never before in existence." (Odum 1962)

Introduction

For thousands of years organisms have lived only where they had a natural distribution, limited by characteristics of the environment and their genetically determined attributes. Responding to modifications and disturbances of the environment, ecosystems have developed and have evolved into the variety of biodiversity and landscapes that amaze us today.

In evolution's play of interactions, humans have taken an increasingly important role, to the extent that now most ecosystems are impacted by humans to a greater or lesser extent [Sanderson, 2002 #12881;Vitousek, 1997 #6737]. Odum (1962) observed that "With vast flows of energy man now begins to possess the ecosystems that spawned him." Global trading has breached biogeographical boundaries and facilitated the spread of species into regions that they would probably never have reached under normal conditions (French 2000, Jenkins 1996, McNeely 2000). Pollution, including the emission of greenhouse gases, has steadily increased; free flowing waters have been dammed and diverted, poor land planning has caused habitat fragmentation, and in the meantime we have continued making use of the ecosystem services and goods, without necessarily valuing these goods and services effectively (Daily 1997, Daily and Ellison 2002, Heal 2000a,). As a result, many ecosystems have already irreversibly changed and others will follow.

Efforts have been made for some time to maintain and restore ecosystems and their related services and goods. Deforested areas have been reforested, and never-forested lands afforested; introduced tree species have been planted to prevent soil erosion; insects or predators have been introduced into ecosystems as biological pest control agents, waterways have been modified and restored. Some interventions have had adverse effects on biodiversity and ecosystem functioning, sometimes even causing irreversible changes, while in others, functioning has been maintained or improved (Bridgewater 1988, 1997).

Issues like loss of biodiversity, species introduction, and habitat alteration arising from global change have already affected most ecosystems of the earth and provide major challenges for our efforts to maintain productive systems and to conserve nature. Nowadays, we have an earth system that is changing rapidly from the one present prior to the Industrial Revolution; in other words, we are dealing with new ecological systems. It therefore seems timely to deepen our understanding of local, regional and global ecosystem processes arising from irreversible changes and think about appropriate management strategies.

This paper aims to initiate discussion of a novel ecological concept of ecosystems emerging from new combinations of species and altered ecosystem processes that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species from other parts of the world. It explores the meaning and scope of the term "emerging ecosystems," provides some examples, discusses the implications of embracing this idea in terms of ecological theory and ecosystem management, and points to directions for future research.

What are emerging ecosystems?

An emerging ecosystem can be defined as "An ecosystem whose species composition and relative abundance have not previously occurred within a given biome." This definition does not attach any judgement on the value of the emerging ecosystem relative to "natural" or other ecosystems. The key characteristics of emerging ecosystems are the following:

1. Novelty: new species combinations, with the potential for changes in ecosystem functioning.

2. Human agency: emerging ecosystems are the result of deliberate or inadvertent human action.

Emerging ecosystems result from biotic response to human-induced abiotic conditions and/or novel biotic elements (e.g., land degradation, enrichment of soil fertility, introduction of invasive species). This includes the cessation of management of systems that have been managed or created by humans (e.g. agroforestry systems, pastoral land).

Traditionally, distinctions have been made among different types of ecosystems, landscapes and vegetation (Westhoff 1971) – *natural* (spontaneous species assemblages in natural conditions); *subnatural* (spontaneous species assemblages in slightly changed conditions); *seminatural* (spontaneous assemblages in managed conditions) and *cultivated* (species assemblages and conditions both managed). Most potentially natural ecosystems, like forests, are subject to human-induced disturbances (clear-cutting, fires, etc.) and are thus in the subnatural stage, but could recover given sufficient time. Seminatural ecosystems persist only due to human influence – for example, temperate European grasslands remain open so long as humans use them as pastures or hayfields. When management ceases, succession towards the natural ecosystem (e.g., shrublands, forests) will begin. In cultivated ecosystems, animal and plant communities are largely controlled by humans. Emerging ecosystems represent 'unusual species combinations' that are typically not found in regional natural, subnatural, seminatural and cultivated ecosystems. Such unusual assemblages may arise in conditions of strong direct or indirect human impact. In particular, there are three main reasons for their existence:

a. Human impact has resulted in local extinction of most of the original animal, plant and microbial populations and/or the introduction of a suite of species not previously present in that biogeographic region.
b. Predominating urban, cultivated or degraded landscapes around target ecosystems create dispersal barriers for many natural animal, plant and microbial species to persist.
c. Direct (e.g., removal of natural soil, dam construction, harvesting, pollution, etc.) and indirect (e.g., erosion due to lack of vegetation or overgrazing, etc.) human impact has resulted in major changes in the abiotic environment accompanied by a decrease or lack of the original propagule species pool, which prevents the re-establishment of original species assemblages.

Emerging ecosystems can be thought of as occupying a zone somewhere in the middle of the gradient between "natural" or "wild" ecosystems on one hand and intensively managed systems on the other (Fig. 1; see Sanderson et al. [2002] for a discussion of this gradient). Clearly, the proportion of each broad type of ecosystem will vary from place to place. However, it could be argued that the proportion of the gradient in Fig. 1 that is occupied by emerging ecosystems is increasing as more wildlands become degraded and areas of intensive agriculture are abandoned around the world. We suggest that, while considerable ecological research has been conducted in “natural” ecosystems and equivalently large amounts of research have gone into agricultural and other intensively managed systems, relatively little consideration has been given to the middle ground inhabited by emerging ecosystems. Given their increasing importance in our increasingly modified world, we consider that this situation needs to be redressed.

Under what sort of conditions will emerging ecosystems become important? Clearly, there are many different biomes in the world, the distribution of which is determined primarily by climate, and categorizations of climates and life zones are available (e.g., Holdridge 1947; 1967). Environmental harshness will vary across life zones, depending on temperature, fertility and moisture availability. Ewel (1999) suggested that abiotic stress was likely to display a non-linear relationship with environmental harshness (Fig 2a); similarly, as environmental harshness declines, the opportunity for more kinds of organisms to grow and thrive increases, leading to increased competition and predation, which Ewel aggregated into “biotic stress”.

If abiotic and biotic stresses are combined, total stress is greatest at either end of the gradient: in harsh environments the constraints to establishment and/or growth are primarily abiotic, while in more benign environments the constraints are mostly biotic, arising from the pre-existing mix of species present. The inverse image of this graph (Fig 2b) can be considered to describe the ease with which an ecosystem will redevelop following disturbance or human modification. Redevelopment to a pre-existing composition can be expected to be limited by abiotic conditions at one end of the graph and biotic conditions at the other. Human activities increasingly either degrade ecosystems, leading to harsher abiotic conditions and/or more limited dispersal of the species originally present, or introduce new species which alter the biotic environment and potentially reduce the potential for system re-development. In both of these situations, emerging ecosystems can be expected.

System thresholds

A further consideration is whether emerging ecosystems can be considered to have crossed a threshold to a new or different state, which could either be transient or stable. This question requires further consideration, perhaps in the light of current discussions of thresholds in a restoration- ecology context (Hobbs and Harris 2001, Hobbs and Norton 1996, Whisenant 1999).

In principle, there are two thresholds that ecosystems have to 'cross' before reaching the stage called 'emerging ecosystem'. The "*soft"* or *biotic threshold* is created by dispersal barriers. Because of that, unusual combinations of species and functional groups arise. For example, an ecosystem in human-dominated landscapes may be dominated by soil-born pathogenic microbes and by invasive plants that are pathogen-resistant (Klironomos 2002) and do not depend on symbiotic fungi, while other functional groups are relatively underrepresented. This will probably also affect the functioning of the whole ecosystem. In principle, such ecosystems may develop towards the natural state in conditions of enhanced dispersal. The succession, however, may take a very long time since many natural species may need special conditions for establishment. For example, many plant species require the presence of gaps with the appropriate community of symbiotic microbes and the absence of pathogens. Due to the absence of such conditions in the emerging ecosystem, the establishment of diaspores of many plant species may fail for decades.

The "*hard"* or *abiotic threshold* is created when dispersal limitation is combined with severely changed abiotic conditions. For example, soil erosion on clearcut or overgrazed slopes, or different hydrological conditions due to changed evapotranspiration, or the conversion of flowing waters in rivers to slow moving reservoirs will result in novel abiotic conditions where species from the original natural ecosystem cannot establish even when dispersal barriers are crossed (Dukes and Mooney 2003; Levine et al 2003; see Boxes 5 and 7). Species assemblages of such ecosystems remain novel compared to natural and seminatural ecosystems of the same region.

In special cases, major changes in the local environment may also arise due to the invasion of new keystone species. These species will prevent the growth and regeneration of many 'original' species due to competition or predation by the invaders and/or because the invading species causes changes in ecosystem functioning, including disturbance regime (See Box 1). In such cases, changes in abiotic environment are not irreversible in principle, but, as there is no force eliminating the invader, they are irreversible *de facto*. Nevertheless, even if eradication or control of the invaders could be effective, it can have unwanted or unexpected impacts on native ecosystems of larger magnitude than the invasion itself. There are also cases that with the removal of the target invaders, other invaders take advantage and alter the ecosystem even more (Zavaleta et al. 2001).

A further consideration regarding thresholds is in relation to the gradient of human impact ranging from wild ecosystems without appreciable human impact to extremely modified systems which only persist due to human inputs. This gradient is probably not smooth and continuous, and thresholds may be present in some parts of the gradient. These thresholds may represent sharp discontinuities in major biophysical process, such as biotic dispersal, changes in community composition and/or dominance, or abiotic changes in energy and matter flux. If such thresholds exist, their identification may help in identifying new transient or stable states.

Temporal and spatial scales

Questions of thresholds and transient and stable states depend heavily on the timeframe being considered. Indeed what is and is not an emergent ecosystem to a certain extent depends on the temporal and spatial scale being considered. All ecosystems are naturally dynamic, and the primary differences between "normal" ecosystem dynamics and those prevailing in an emerging ecosystem are the increased importance of human modification and the availability of new species to form new assemblages. Clark (2000) has recently pointed out that the processes of human modification of ecosystems and the transport of species across the world has been happening for centuries, and hence that the opportunity for novel ecosystems to develop has been available for a long time. For instance, in areas such as the Mediterranean Basin, most ecosystems are heavily transformed and are composed of species with mixed biogeographic origins (Blondel and Aronson 1995). Our current concern with emerging ecosystems must thus be set in a longer timeframe, and questions of relative value of emerging versus natural ecosystems should perhaps focus on the services either provided by or lost from particular types of ecosystem. It is, however, clear that rates of change are much faster in modern times and that new technologies help overcome biogeographic and biophysical barriers to establishment.

Spatial scale is also an important consideration, and emerging ecosystems need to be considered within a landscape context. Many parts of the world are now a patchwork of different land uses and ecosystems ranging across the "natural"- "intensively managed" gradient. A particular ecosystem or patch within this patchwork has both intrinsic and contextual characteristics. The dynamics of an emerging ecosystem are to some extent determined by the transport of propagules and movement of organisms across the landscape, and in turn the ecosystem may act as a source of propagules that move into less modified areas.

What can case studies tell us?

The case studies (see boxes) illustrate the range of situations in which emerging ecosystems can occur. These range from cases where the biotic composition of an ecosystem has undergone either drastic or more subtle but has become established and relatively stable, through to cases where managed ecosystems have undergone change either through proximate changes in management or because of broader scale environmental changes. Changes in plant-animal interactions, biogeochemistry, and disturbance frequencies can all be important. The development of emerging ecosystems has occurred in similar ways in different parts of the world – this probably represents some sort of "convergence" through homogenization of biotas and parallel activities of humans aimed at shaping ecosystems to their own purposes. The case studies also highlight the prevalent role of biological invasions in the new species assemblages, and the strong interaction between successful invasions and environmental change.

The rate at to which emerging ecosystems appear is very variable: e.g., centuries in the case of New Zealand tussock grasslands (Box 4) to decades in the Brazilian cerrado (Box 3). Some emerging ecosystems appeared a long time ago and remnants of the "pristine" ecosystems do not exist, making it difficult to know the magnitude of the change. However, in other cases, they do exist, providing unique opportunities to compare natural and seminatural ecosystems to emerging systems.

As illustrated by the tussock grasslands in New Zealand and the cerrado in Brazil, emerging ecosystems can be the product of culturally induced ecosystem change across thresholds that are very difficult to reverse. Emerging ecosystems are neither "good" nor "bad" compared with historic ecosystems; they are different and have different values.

As illustrated by the example of Mediterranean forest ecosystems (Box 6), climatic unpredictability and global change act in a synergistic way with other biotic drivers (loss of biodiversity and homogenization of afforested woodlands), reinforcing the processes of degradation and favouring ecosystem instability. It also illustrates that human-induced changes in the nature and strength of key plant-herbivore interactions deeply affect terrestrial ecosystems. An interesting point to consider is whether many emerging ecosystems are likely to possess a component of “living dead” elements – species whose regeneration requirements can no longer be met in the changed biophysical settings, or whose mutualists have moved away; or, indeed whether whole ecosystems are in effect “living dead” and will be replaced by a different, emergent, ecosystem as a result of a particular environmental cue.

New biotic assemblages affect the fabric of key interactions and processes, such as plant-animal interactions, microbial communities breaking down organic matter in soils, and the impacts and reaction to increasing soil salinity. Key questions for the future are how we develop management schemes that maximise beneficial changes and reduce the less beneficial aspects. Management goals for emergent ecosystems present special problems (cf. traditional nature conservation or agricultural goals), reflecting their history and instability.

Because emerging ecosystems result from human actions, management is required guide their development. How we manage these new ecosystems effectively is a point for debate: what should the goals be and how should these emerging systems fit with other systems along the wild – intensively managed gradient? If the emerging system is transient, how do we guide it along a particular trajectory? If it is stable, can we manage it effectively to gain benefit from its current state or devise effective methods of directing it to a new, more preferable, state? It is certainly clear that these emerging systems will be very difficult if not impossible to return to some "more natural" state in terms of time, effort and money. This is a very important point since it simultaneously argues for (1) conserving less impacted places now so they do not "emerge" in some new form, and (2) not wasting precious resources on what may be hopeless quest to "fix" these systems. Rather we should perhaps appreciate them for what they are and what benefits they provide. As Redford and Richter (1999) discuss, there are a variety of ways in which humans and ecosystems interact, and emerging ecosystems are likely to have some useful kinds of functions, while not others. We should perhaps move away from the one-dimensional dichotomy between natural and wild, towards a more complicated but more effective depiction of how human beings interact with nature.

Also, because ecosystems are "emerging" due to human impact, an explicit incorporation of human activities in ecological research programs is needed. In other words, natural and social scientists must work together in order to understand these altered systems. The study of emerging ecosystems will benefit from the developing links among ecology, restoration ecology, conservation biology, and ecological economics.

What needs to be done?

In this paper we have attempted to synthesise current thought on the subject of emerging ecosystems. There remain significant differences of opinion over everything from which words to use, whether to define terms strictly, and whether terms used are value laden or not, to the more detailed questions on thresholds, timescales and the place of emerging ecosystems within the bigger picture of ecosystem dynamics. These debates need to continue, and the process has only started.

Many questions remain to be explored more fully. For instance,

1. Are emerging ecosystems on the increase? Will emerging ecosystems predominate at the end of the present century? What does this mean for our attempts to conserve “wild” or “natural” ecosystems?
2. Do we need special concepts and methods to approach today's emerging ecosystems or do they just represent one quite typical example of ecosystem dynamics that has always occurred?
3. What do emerging ecosystems mean from the evolutionary point of view? Which traits will be selected for in changed landscapes with novel species combinations and in new abiotic conditions? Will selection favour certain life-history types like well-dispersed pathogen-resistant nonmycorrhizal plants?
4. Are new species combinations provoking “new” ecosystem functions or properties? To what extent will a new combination of species maintain a similar function with respect to the old species pool (i.e., is there functional redundancy or are new properties added)?

5. To what extent do these new species combinations alter the original network of mutualistic and antagonistic interactions, and what are the consequences for community organization?
6. Can we recognise thresholds in ecosystems and landscapes?
7. How do emerging ecosystems affect the relative values of “natural” and managed systems?
8. How does the concept of emerging ecosystems relate to the marine environment?
9. What are the important socio-economic aspects to be considered in relation to emerging ecosystems?

Regardless of the details of the debate on emerging ecosystems, it is clear that we are assisting with the development of new ecosystems, all over the planet. Emerging ecosystems are not emerging de novo. Instead they are emerging from 'within' pre-existing systems that have already undergone profound changes and may pass from one state to a new one upon the arrival of one more exotic species, or the removal of a native one. Just as in organismic biology we know that most mutations 'fail' in reproductive terms, so many emerging ecosystems may prove to be transitory. Others, however, will persist.

Over 40 years ago, H.T. Odum proposed and defined a new field of ecological engineering, used the concept of self-organization to explain how ecosystems respond to human effects, used the term “emerging ecosystem” and viewed these synthetic or emerging systems as a natural outcome of the way the world was evolving with humans. Odum paved the way for a modern interpretation of emerging ecosystems. It is clear that emerging ecosystems are real phenomena, and given that they exist we need to consider how best to manage and utilize them for benefit to society. We hope that we can move forward and embrace the idea of emerging ecosystems as a valid and urgent topic for research, management and policy consideration.

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We dedicate this paper to Howard T. Odum. This paper developed from discussions at a workshop in Granada in September 2002, during which news came through of

H.T.'s death on 11 September 2002. Several workshop participants were Odum's students, it is also, perhaps, appropriate to recognise that H.T. Odum was thinking about emerging ecosystems 40 years ago (Odum 1962). In March of 1962, H.T. Odum and nine other ecologists participated in the Lockwood Conference on the Suburban Forest and Ecology. This conference dealt with the new forests forming on suburban lands and in a sense, anticipated the emerging ecosystem workshop in Granada, and several quotes from Odum's chapter appear in this paper.
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Figure headings

Figure 1. Emerging ecosystems arise either from the degradation and invasion of “wild” or natural/semi-natural systems or from the abandonment of intensively managed systems.

Figure 2. (a) Stress on an ecosystem is related to environmental harshness and biotic complexity: in harsh environments the constraints to establishment and/or growth are primarily abiotic, while in more benign environments the constraints are mostly biotic, arising from the pre-existing mix of species present. Total stress is greatest at either end of the gradient. The inverse image of this graph (Fig 2b) portrays the ease with which an ecosystem will redevelop following disturbance or human modification, Ecosystem degradation leads to more abiotic stress, while the addition of new species leads to more biotic stress, and ecosystem redevelopment is less likely in both cases.

Figure 3. Alternative pathways of ecosystem development in Puerto Rico: see text for details.

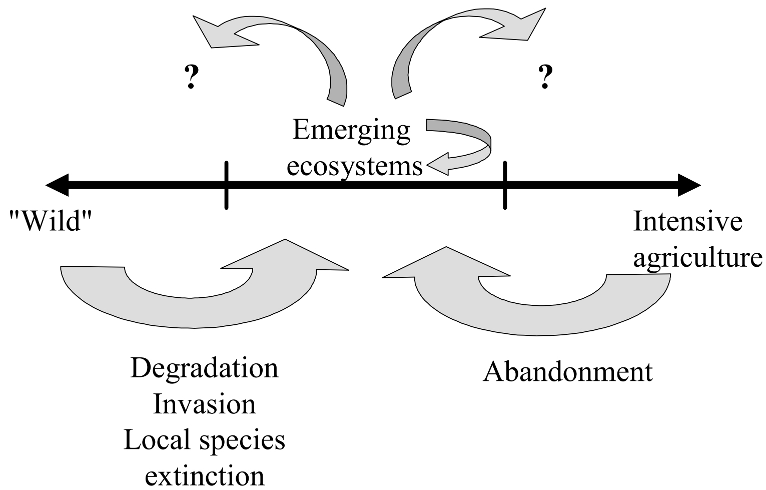
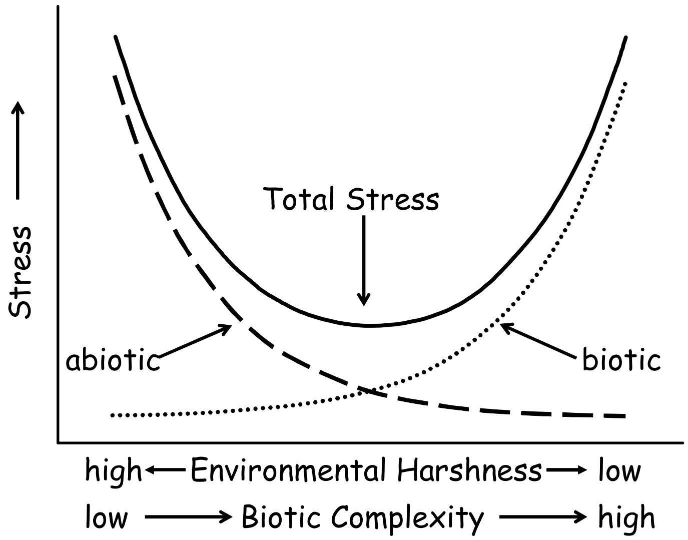

?
?
Emerging
ecosystems
"Wild"
Intensive
agriculture
Degradation
Invasion
Local species
extinction
Abandonment

Figure 1.

(a)


Total Stress
Stress
abiotic
biotic
high
Environmental Harshness
low
low
Biotic Complexity
high

(b)

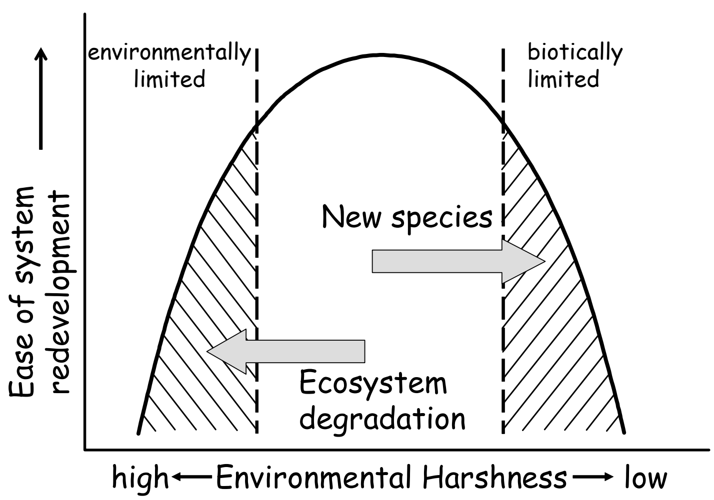

environmentally limited
biotically limited
Ease of system redevelopment
New species
Ecosystem degradation
high
Environmental Harshness
low

Figure 2

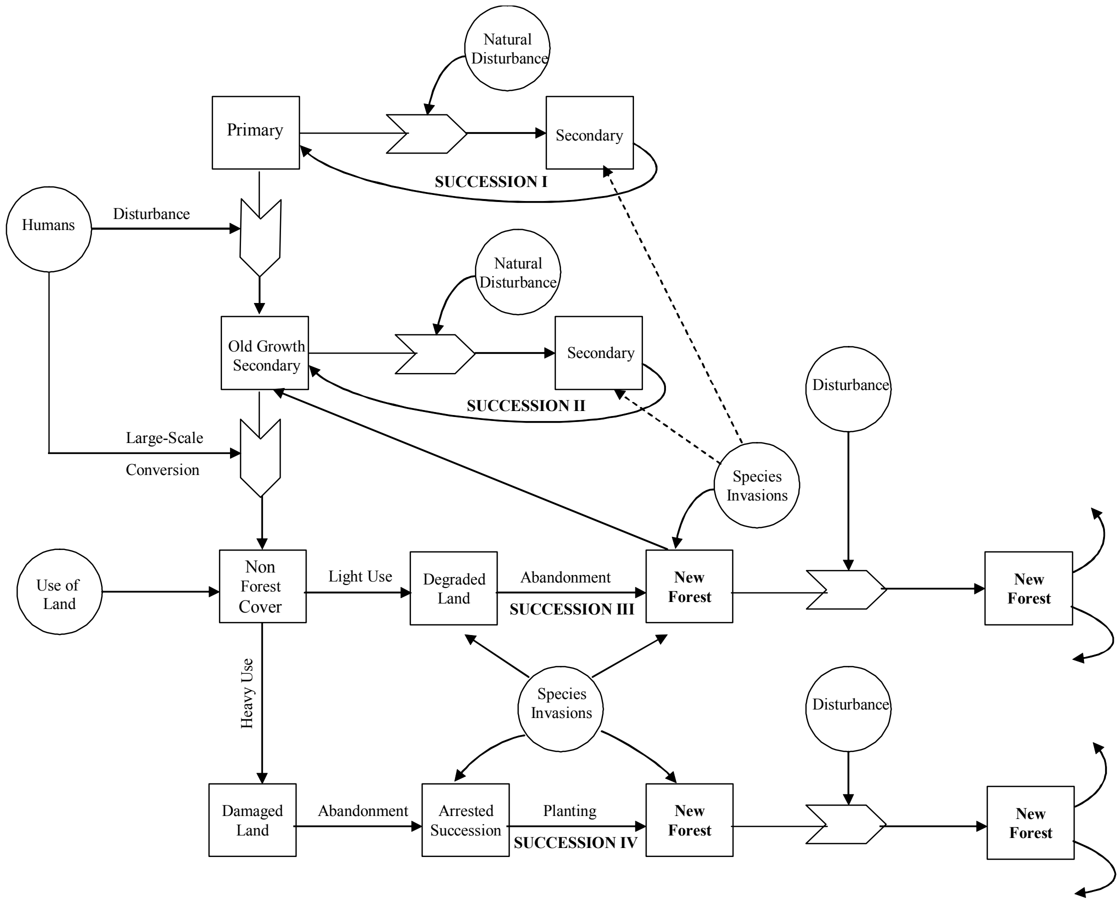

Natural Disturbance
Primary
Secondary
SUCCESSION I
Humans
Disturbance
Natural Disturbance
Old Growth Secondary
Secondary
SUCCESSION II
Disturbance
Large-Scale
Conversion
Species Invasions
Use of Land
Non Forest Cover
Light Use
Degraded Land
Abandonment
SUCCESSION III
New Forest
New Forest
Heavy Use
Species Invasions
Disturbance
Damaged Land
Abandonment
Arrested Succession
Planting
SUCCESSION IV
New Forest
New Forest

Figure 3

Boxes

Box 1. South African fynbos invaded by pines

There are many examples of invasive alien plants acting as keystone species and radically altering ecosystem processes, often very rapidly, to the extent that native species are suppressed or eliminated.   One of the most intriguing cases is where alien pine species (*Pinus halepensis*, *P. pinaster* and *P. radiata*) invade and transform the species-rich fire-prone fynbos shrublands in South Africa's Cape Floristic Region.

Much of the famous floristic diversity and complexity of fynbos results from differential post-fire recruitment of coexisting species. Overstorey shrubs in particular show highly variable recruitment after fires of different intensities, frequencies, and at different times of the year. The resulting non-equilibrium dynamics drive "shifting clouds of species abundance" across the landscape, creating conditions that promote community-wide floristic patchiness which is an important agent of diversification in the understorey flora. Local extinction and recolonization over short distances appear to be key processes in the maintenance of biodiversity in these systems.

Serotinous alien trees such as pines colonize fynbos after fires. The aliens initially behave much like the native shrubs, but their short juvenile periods and large reserves of highly mobile seeds buffer them against fire-induced population crashes. The natural non-equilibrium system is disrupted, and cyclical replacement of native overstorey shrubs is prevented. As the invaders proliferate after each fire, competition with fynbos elements is intensified, eventually leading to their local extinction as residual seed stores are depleted. There is no cyclical replacement without abnormal conditions (such as felling of pines by humans), and a depauperate steady-state results (Richardson & Cowling 1992). Emerging ecosystems such as these are frequently much more susceptible to further invasions of alien species than the ecosystems they replaced. The process whereby alien species facilitate invasion of other alien species has been termed "invasional meltdown" (Simberloff & von Holle 1999).

Box 2. Puerto Rico's "new forests"

In Puerto Rico, regenerating forest stands on degraded lands are highly fragmented (60 percent were < 1 ha in 1991), function as refugia for organisms, and at 60 to 80 yr old have similar species richness and structural features as native stands of similar age. However, they exhibit important differences from native forests. New forests in Puerto Rico are young (<100 yr). They have fewer endemic species and large trees (≥ 35 cm dbh) than native forests; they have higher soil bulk density and lower soil carbon and litter stocks; and they accumulate aboveground biomass, basal area, and soil carbon more slowly than forests of similar age that native species dominate. New forests also exhibit high dominance by a few species, including alien tree species, during forest establishment. These alien tree species play an important role in establishing and maintaining forest cover. Furthermore, some alien species form canopies that facilitate forest regeneration. We suggest that, as a response to novel environmental conditions that humans introduce to the planet, new forests will become increasingly prevalent in the biosphere.

Fig 3 illustrates the different types of vegetation succession that can occur on Puerto Rico. Type I succession occurs after natural disturbances, e.g., hurricanes, in primary forests of the Luquillo Mountains. Type II occurs after natural disturbances in mature native secondary forests where the size of clearings relative to the forest matrix is small. The native pioneer *Cecropia schreberiana* dominates the early stages of this succession in wet forests, and there are few if any alien or naturalized alien species in the various forest seres (A naturalized alien species is an alien species with self-sufficient populations that no longer depend on humans for their establishment and survival). Type III succession occurs after abandonment of forestlands that have experienced the cycle of deforestation, agricultural use, and abandonment. The succession on these lands is a natural succession, but native pioneer species are uncommon. Alien and naturalized alien species dominate the early stages of Type III succession. Alien and naturalized alien species also dominate Type IV succession, which occurs on lands that are in a state of arrested succession or are so degraded after human use, that trees must be planted to jump-start succession. Mature forest stands develop under all four types of succession. However, they can have different species composition, because they developed under different conditions, including different levels of propagule availability. Mature stands are those whose rate of change of structural state variables approach steady state, irrespective of species composition.

Type III and IV successions lead to new or emerging ecosystems, which occur after a change in land cover from forest to non-forest and back to forest after abandonment. Type I and II successions do not result in emerging ecosystems.

Box 3. Brazil´s tropical savannas (the "Cerrado")

The Cerrado is the second largest biome of Brazil, after the Amazon rain forest, representing 22% of the country, or approximately 2 million km^2. It is a tropical seasonal savanna, with a continuous layer of herbaceous species (mainly C4 grasses) at the peak of the vegetation growth, scattered with shrubs and trees that sometimes form a continuous canopy. Generally four physiognomic types of savanna are recognized in the Cerrado: "campo limpo" (grassland), "campo sujo" (wood savanna), "cerrado *sensu strictu*" (savanna), and "cerradão" (woodland), which differ from each other by the relative abundance of woody and herbaceous species. During the rainy season grasses are active and produce a large amount of green biomass that dries out during the dry season. The accumulation of dead material facilitates the occurrence of fire, especially at the end of the dry season. The Cerrado has the richest flora among tropical savannas and is one of the world´s "biodiversity hotspots".

Two main factors were responsible for the modern occupation of Cerrado (Klink & Moreira 2002); the construction of Brasilia, Brazil's new capital, in the late 50's, and the adoption of development policies and investments in infrastructure between 1968 and 1980. The construction of highways allowed occupation and the expansion of commercial agriculture in the Cerrado. Until 40 years ago the region was used primarily for extensive cattle ranching. Today it is estimated that 47% of its natural vegetation has been transformed into cultivated pastures, crop fields, dams, urban settlements, and degraded areas. The most significant forms of land use are cultivated pastures and commercial crops - mainly soybeans, corn, rice, cotton, coffee, and beans. It is estimated that the total area of transformed land in the Cerrado today is around 90 million hectares (1.8 times the size of Spain), up from 50 million ha in

1985.

Agricultural expansion has led to an increase in burning, and areas still covered with natural vegetation are now burned almost every year. Fire controls the proportion of woody and herbaceous plants, because it has a negative effect on tree and shrub seedlings; protection against fire for sufficiently long periods of time favours the appearance of more wooded savannas.

Extensive cultivation of African grasses has occurred, and these proliferate, spread, and persist in new areas. One of the most widespread African species is the molassa or fat grass (*Melinis minutiflora*), which is known for its impacts on biodiversity and ecosystem functioning in other parts of the world. Although it has been superseded by more productive African species it is extensively found in disturbed areas, roadsides, abandoned plantations, and nature reserves. The high biomass produced during the rainy season dries out during the dry season and becomes a highly combustible fuel; that initiates a grass-fire interaction capable of preventing the regrowth of natural vegetation. In places where *M. minutiflora* reaches high cover, the diversity of the local flora is considerably lower than native areas. Compared to natural savanna fires, fires in *M. minutiflora* are far more intense and have a much longer residence time.

Overall, large expanses of natural savanna have been transformed from a mixture of trees and grasses into planted pastures and crops. Many trees and shrubs are deep-rooted and take up soil water at 8 meters depth or more. Simulations of the effects of the conversion of natural savannas into open grasslands on regional climate have shown a reduction in precipitation of approximately 10%, an increase in the frequency of dry periods within the wet season, changes in albedo, and increased mean surface air temperature by 0.5^{o}C (Hoffmann & Jackson 2000). Also, considerable amounts of carbon are stored in roots and soil organic matter: up to 70% of the live biomass in the vegetation is underground, and up to 640 tones of soil organic carbon has been found to a depth of 620 cm under natural vegetation (Abdalla et al.1998). Given the extension of Cerrado vegetation already transformed into planted pastures and agriculture, it is probable that a significant change in both root biomass and the regional carbon cycle has already occurred.

Box 4. New Zealand rain-shadow tussock grasslands

Prior to human settlement, New Zealand was almost totally forested below the alpine timberline. With Polynesian settlement around 1200-1300 AD, extensive areas of forest were burnt, especially in the rain-shadow areas of the eastern South Island. While some regeneration towards forest occurred, the almost complete removal of forest coupled with the difficult climate (cold and dry) and ongoing fire maintained tussock grassland and shrubland communities in most areas. European settlement (1850s onwards), brought extensive pastoralism to these grasslands, with more frequent fire and heavy grazing (especially by sheep, but also rabbits) leading to a compositional shift in many areas from tall tussocks (*Chionochloa* species) to short tussocks (*Festuca* and *Poa* species). More recently, invasive plants (herbaceous and woody) have become increasing dominant and compositional change appears to be ongoing irrespective of management practices.

These tussock grasslands are an example of an emerging ecosystem in that they are novel ecosystems that have been induced and sustained by cultural activities. Furthermore, they have almost certainly crossed ecological thresholds that in most cases will be difficult to reverse. While the rain-shadow tussock grasslands are the product of cultural activities, they are highly valued for both their biological and landscape attributes, with conservation groups arguing strongly for their protection through the removal of pastoralism and inclusion within the public conservation estate. Some areas would obviously benefit from the exclusion of pastoral activities (e.g., wetlands), but for much of this area the exclusion of pastoral activities will not necessarily result in the outcomes that conservation groups desire. The dilemma for conservation is that by protecting these grasslands from pastoralism, they are likely to shift in composition towards woody vegetation. Furthermore, in many cases the original native woody species have been removed, and alien species such as *Pinus* and *Betula* species are the most likely to dominate. Thus removal of pastoralism will result in the loss of the very values that the removal of pastoralism was trying to protect.

Box 5. Australian Salinizing Landscapes

Secondary salinity is arguably the most important natural resource management issue in Australian at present, and along with land clearing, it presents the greatest broad-scale threat to terrestrial ecosystems. By 2050, up to 17 M ha of the Australian landscape will be at high risk from salinity, including over 2 M ha of remnant or planted native vegetation. Over 40,000 km of streams and lake perimeters are at risk, as are 130 important wetlands. The Australian landscape is ancient and geologically stable, consisting of deeply weathered soil profiles that contain considerable stores of salt. The broad-scale clearing of deep-rooted, perennial native vegetation, and its replacement with shallow-rooted, annual crop plants has greatly reduced the amount of precipitation intercepted by vegetation and subsequently lost to the atmosphere by evapotranspiration. Excess soil water not used by crop plants drains down to the groundwater table. Once the capacity of the system to discharge the additional groundwater laterally to creeks and streams is exceeded, groundwater levels rise upwards, mobilizing the salt stored within the soil profile and carrying it towards the soil surface. As water evaporates from the soil surface, or is used by plant roots, salt gradually accumulates within the soil profile unless leaching by rainfall or flooding occurs.

Secondary salinity has serious implications for ecosystem health and function. The hydrological cycle is a primary ecosystem process: the breakdown of the natural hydrological equilibrium and the subsequent salinization of the soil profile, combined with the extended periods of waterlogging frequently associated with shallow water tables, generally forces remnant vegetation across a transitional threshold to a new stable state. This new stable state is characterized by severe reductions in biodiversity and ecosystem function, which further reduces the hydrological integrity of the system. While it was initially thought that more salt-tolerant species would colonize newly saline areas, there has been little evidence of this. Instead, rich and structurally diverse vegetation assemblages are replaced by a small number of native chenopods and salt-tolerant alien species, while localized specialist fauna are replaced by ‘weedy’ generalist species. The extreme abiotic stress posed by the combination of soil salinity and waterlogging prevents the recruitment and survival of all but the most stress-tolerant of plant species; even many salt-tolerant species require periods of non-saline conditions for seed germination and establishment. Further, the highly fragmented nature of native vegetation in the agricultural districts where secondary salinity is a problem provides further barriers to propagule dispersal into areas affected by salinity.

Our knowledge of salinizing landscapes as emerging ecosystems in Australia is very much in its infancy. While extensive hydrological modelling has been undertaken to elucidate how much of the landscape will be affected by secondary salinity, we have little knowledge of how ecosystems will respond once a new hydrological equilibrium is reached. It is fairly clear, however, that remnant vegetation in areas at high risk from salinity will require direct management, either in the form of restoration or by facilitating the development of novel, salt- and waterlogging-tolerant ecosystems. Restoring the hydrology that existed prior to clearing is not possible - to reduce even the *rate* of hydrological change in these systems, broad-scale modification of the physical environment is required. Within this context, restoring the original vegetation of remnants becomes extremely problematic – restoration of the vegetation requires that the underlying primary ecosystem processes (hydrology) are also restored. There is little doubt that, in geological time, new and diverse ecosystems will emerge in Australian salinized landscapes. However, within human timeframes, we are currently facing a period of difficult and costly (both ecologically and economically) decision-making as how to manage these landscapes so that they maintain some elements of ecological integrity.

Box 6. Altered trophic interactions in the Mediterranean Region: responses to local and global human impacts

The Mediterranean basin has historically been shaped by human intervention. Native forests have virtually disappeared from most habitats, whereas planted stands spread everywhere. The result is a change in the plant-herbivore nature and strength of interactions, from remnant, native fragments to large, homogeneous pine stands. These changes are occurring under a regional scenario characterized by high disturbance and in the context of strong temporal climatic variability (Rodó and Comín, 2001). Two complementary examples are:

a) Ungulate herbivory strength and the regeneration of woody vegetation under a variable climate

The biomass of herbivores supported per unit of primary productivity is about one order of magnitude greater in humanized than in natural ecosystems, for a given level of primary productivity (Oesterheld *et al*. 1992). This fact is especially evident in Mediterranean and arid habitats, browsed by domestic livestock over thousands of years (Noy-Meir *et al*. 1989). Overbrowsing severely affects forest regeneration, especially among non-resprouting species. due to the selective consumption of saplings and resprouts. The increase in wild and domestic herbivores eliminates the most palatable species, resulting in a plant community shaped by herbivores at different levels (species diversity, spatial structure, ecological succession). From the standpoint of a trophic web, overbrowsing creates the conditions of top-down regulation. On the contrary, natural terrestrial ecosystems with low impact are traditionally bottom-up regulated (Jefferies *et al*. 1994). Constant browsing overexploits the plant community, especially when primary production fluctuates strongly due to temporal climatic variability (Zamora *et al*. 2001).

b) Global warming favours emerging interactions: Effects of insect pest on afforested woodlands

Climatic change can wreak changes in many plant-animal interactions by shifting the phenology and geographical ranges of interactive species (Peñuelas and Filella, 2001; Parmesan and Yohe 2003). Altitudinal gradients in mountains may mimic, on a narrower spatial and temporal scale, changes taking place in latitudinal gradients, thus providing a good framework to analyse the biological consequences of global change. With temperatures steadily warming, insects can easily change altitudes in just a generation, while the original host plants must remain in the unfavourable climatic belt. In fact, warmer winter temperatures are currently triggering an uphill displacement of *Thaumetopoea pityocampa*, a Mediterranean caterpillar pest of most Mediterranean pine woodlands (Hódar *et al*. 2003; Hodar and Zamora *in press*). The consequences are the establishment of new interactions throughout the range where there are suitable new hosts (Whittaker 2001, Peñuelas *et al*. 2002). The potential deleterious consequences of these new, emerging interactions are thus due to climatic warming, which favours altitudinal displacements, and humanized, homogeneous structure of the afforested pine woodlands. This represents a 'culture medium' that promotes the capacity of the newcomer to increase dramatically in abundance.

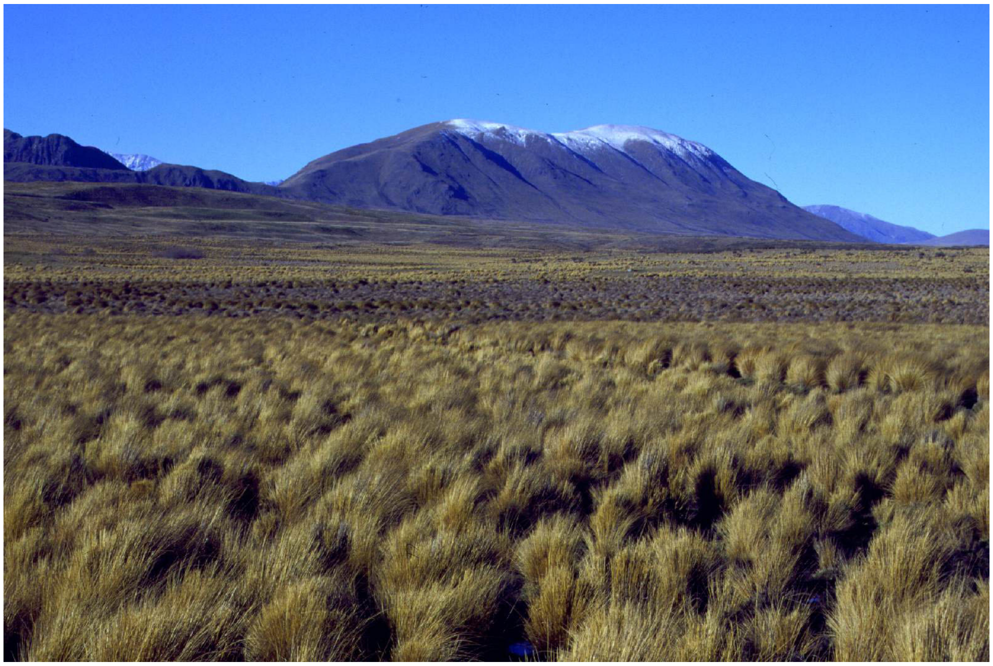
From these two examples, we can conclude that climatic variability and global warming act in concert with human-induced changes (increase of wild and domestic ungulates, fragmentation of remnant forests and homogenization of afforested woodlands), inducing major changes in the nature and in the strength of key plant-herbivore interactions, thereby determining the diversity and organization of terrestrial trophic webs in Mediterranean ecosystems. The current situation where key trophic interactions have been changed is not stable, and, consequently, ecosystems must be managed by humans in order to increase resistance to major disturbances. Furthermore, management has both global and local dimensions: global, in order to mitigate global warming, and local, in order to avert overpopulation of herbivores and to restore the natural structure and diverse composition of the Mediterranean vegetation.

Box 7. Freshwaters worldwide

Freshwater is vital to human life and enterprise, so it is no surprise that freshwater ecosystems worldwide have been highly modified. More than 50% of the world's freshwater is already appropriated for human use through the construction of dams and reservoirs, diversions for irrigation, and pumping of groundwaters (Postel et al. 1996). Collectively the alteration of freshwaters is occurring far faster than at any other time in human history, and constitutes a global-scale change in aquatic ecosystems. The permanent alteration of rivers, lakes and wetlands by channelization, damming, polluting, and dewatering, creates novel habitats and species assemblages. These are clear examples of emerging ecosystems.

Freshwater ecosystems are regionally unique in their species and community assemblages, and physical modification of each one creates an "emerging ecosystem," by altering flow regimes, water quality, thermal and light characteristics, and sediment and organic matter inputs. Freshwater ecosystems are dynamic, and require a range of natural variation or disturbance to maintain viability, or resilience (Holling 1986). Both seasonal and interannual variability in flow are needed to support production and persistence of species (Poff et al. 1997). The sizes of native plant and animal populations and their age structures, the presence of rare or highly specialized species, the interactions of other species with each other and their environments, and many ecosystem processes are influenced by the temporally varying hydrologic regimes that characterize these ecosystems (Baron et al. 2002). Freshwater ecosystems are also tightly linked to their watersheds; both water and species move in three spatial dimensions: longitudinal (upstream-downstream), lateral (channel-floodplain), and vertical (surface water-groundwater). Physical barriers encourage alteration of food webs and functional groups. Increasingly, invasive generalist species with rapid reproductive and dispersal rates are able to successfully colonize modified freshwater aquatic ecosystems (Kolar and Lodge 2002).

Western rivers of the United States serve as examples of how flow manipulation altered the structure and function of riverine, and riparian ecosystems. Closure of large dams on rivers such as the Colorado, the Arkansas, the Rio Grande, and the Missouri have contributed to widespread loss of native species that cannot survive in clear, cold waters below dams (Moyle and Light 1996). These are replaced by non-native species, such as trout. Warm water invertebrate species with specific thermal tolerances are replaced by nearctic and alpine species whose nearest natural neighbors may be hundreds or thousands of kilometers away (Ward and Stanford 1979). Western North American rivers were sediment laden prior to disturbance, but sediment is now stored behind dams. This has caused widespread failure of native cottonwood regeneration, since they require periodic influx of coarse sediments to germinate. Cottonwoods that supported a diverse community have been replaced by other species and communities, often composed of non-native species (Scott et al. 1999). Dewatering of western rivers has increased salinity, deprived downstream wetlands of freshwaters, and contributed to extreme alteration of food webs at their coastal mouths (Postel et al. 1998, Kowalewski et al. 2000).



New Zealand tussock grasslands (Photo by David Norton)

Woodland affected by secondary salinity, Western Australia (photograph by Richard Hobbs)