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GUEST EDITORIAL

The parable of Green Mountain: Ascension Island, ecosystem construction and ecological fitting

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ABSTRACT

Aims To use the ecosystem on Green Mountain, Ascension Island, to illustrate aspects of ecosystem construction and function as well as possible mitigation of human caused global environmental change.

Location Ascension Island, tropical south Atlantic.

Main conclusions The cloud forest on Green Mountain is a man-made system that has produced a tropical forest without any coevolution between its constituent species. This has implications for the way we think about ecosystems and provides a striking example of Janzen's idea of 'ecological fitting'. This system provides ecosystem services, such as carbon sequestration, and illustrates the possible role of man-made ecosystems in the mitigation of global warming.

Keywords

Ascension Island, ecosystem, ecological fitting, Darwin, Hooker, greenhouse effect, global change, terraforming.

> The small-scale studies that can be attempted on islands often provide valuable information that can be used to interpret community and population structure on the larger continents (Schofield & George, 1997, p. 9).

In July 1836, Charles Darwin, homeward bound on H.M.S. Beagle, arrived at Ascension Island in the tropical south Atlantic. He was not impressed by what he saw, writing that: 'The island is entirely destitute of trees, in which, and in every other respect, it is very far inferior to St. Helena. Mr Dring tells me, that the witty people of the latter place say "we know we live on a rock, but the poor people of Ascension live on a cinder" the distinction in truth is very just' (Darwin, 1839, p. 587). Almost 90 years later, in November 1925, the marine biologist Alistair Hardy visited the island. His response was very different, writing enthusiastically that: 'The colours are fantastic. The island which is about $7\frac{1}{2}$ miles in length and 6 in breadth consists of a large number of extinct volcanic cones and craters. The highest of these raises far above the others to a height of 2280 feet [*sic*: actually 2817 ft approx 845 m], and, on account of the clouds which gather about it and give it rain, it alone supports a rich vegetation and is known as Green Mountain. The rest, which vary much in height, are arid cinder heaps; although barren they present a great variety of colour: raw sienna, reds, browns, dark and light greys and yellows, while some are almost crimson – all changing tone with the light and shade from passing clouds' (Hardy, 1967, p. 121).

These contrasting responses were no doubt partly due to the different aesthetic tastes of the two men. Hardy was a good amateur watercolourist and clearly attracted to the range of colours in this volcanic landscape. However, during the nineteenth century, the vegetation of Green Mountain had undergone major changes leading to the 'rich vegetation' described by Hardy rather than the landscape 'destitute of trees' of Darwin's visit.

TERRAFORMING ASCENSION

Ascension is a very recent island, being only about 1 million years old compared with St Helena's 14 million (Ashmole & Ashmole, 2000). Prior to its discovery by humans at the start of the sixteenth century, it appears to have had a limited flora comprising 25–30 vascular plant species, of which about 10 were endemic (Cronk, 1980; Ashmole & Ashmole, 2000). This was the sparse flora that failed to impress Darwin. Even high on Green Mountain the largest plants were ferns and a single species of endemic shrub, *Oldenlandia adscensionis*, that was probably never common – indeed Darwin failed to notice it, and it is now almost certainly extinct (Cronk, 1980).

With the settlement of the island in the early nineteenth century, more plants started to be introduced; however, the key event in the transformation of the Green Mountain ecosystem appears to have been a brief visit by the botanist Joseph Hooker in 1843, 7 years after Darwin. He was on his way back from James Clark Ross's expedition to the Antarctic, and, at the request of the British Admiralty, made recommendations to 'improve' the Ascension environment. Hooker presented four main suggestions (Duffey, 1964):

1. Planting trees on the mountain which he considered 'of the first importance as thereby the fall of rain will be directly increased' (cited by Duffey, 1964, p. 227).

2. Developing the formation of deeper soils by encouraging more vegetation to grow on the steeper slopes.

3. Planting the more promising areas in the lower valleys with drought adapted trees and shrubs.

4. Introducing suitable crops into gardens on Green Mountain.

The thinking behind this scheme is strikingly similar to much more recent ideas for creating life-friendly conditions on Mars (so-called *terraforming*), where the idea 'should not just be about creating a new environment for life through *force majeure*, but about finding ways to allow life to create a new environment for itself' (Morton, 2002, p. 298). The idea that trees promote rainfall, and so improve their own environment, dates from measurements of transpiration rates at the start of the eighteenth century and became an influential idea amongst many administrators of the British Empire (Grove & Rackham, 2001). However, on Green Mountain, the trees probably mainly increase occult precipitation by trapping moisture from the regular mists.

For several years after Hooker's visit, consignments of plants were sent to Ascension every month and, after 1850, twice a year, from England each November and from the Cape of Good Hope each May (Duffey, 1964). Such was the success of this scheme that Alistair Hardy could describe the vegetation of Green Mountain in the 1920s as 'good and hearty', writing that 'tall eucalyptus trees now lined the road, flowering shrubs, conifers and palms of many kinds appeared, and sheep grazed on the slopes of grass in between patches of almost dense jungle' (Hardy, 1967, p. 124).

Today, much of the higher parts of Green Mountain are best described as cloud forest, contrasting strikingly with Darwin's complaint of a landscape 'entirely devoid of trees' (see cover of this Issue). Indeed the mountain is dominated by introduced plant species. Hooker later had second thoughts about the conservation implications of his 'terraforming' scheme, writing: 'The consequences to the native vegetation of the Peak will, I fear, be fatal, and especially to the rich carpet of ferns that clothed the top of the mountain when I visited it' (cited by Desmond, 1999, p. 84).

GREEN MOUNTAIN AND THE NATURE OF ECOSYSTEMS

Most of the ecological interest in Ascension Island has focused on the sea birds, Green Turtles (*Chelonia mydes*), and the surviving native plants and invertebrates. These studies have concentrated on the coast and the arid lowlands (reviewed by Ashmole & Ashmole, 1997, 2000). Indeed, in their recent book on the natural history of Ascension and St Helena, Ashmole & Ashmole (2000, p. 250) wrote of Green Mountain that they had 'spent little time here, since although it is attractive and pleasantly cool after the desert lowlands, it represents a wholly artificial ecosystem'. However, for anyone wanting to understand the nature and functioning of ecosystems, Green Mountain provides an extraordinary experiment. It is a luxuriant tropical ecosystem constructed with almost no role for coevolution, producing the most dramatic example of what Janzen (1985) called 'ecological fitting'.

An important ecological question is: 'How are complex species-rich ecosystems, such as cloud forest, constructed?' One obvious possibility is to appeal to evolutionary processes, the organisms evolving together to fill the potential niches in the system. For example, insects could evolve biochemical counter measures to plant-defence compounds, and, in an arms race, the plants evolve new defences. Plants coevolve with their pollinators and seed dispersers, while the microbes in the soil evolve to deal with the peculiarities of the biochemistry of the leaf litter. Indeed, in their classic 1960s paper on coevolution, Ehrlich & Raven (1964, p. 605) wrote: 'it seems to us that studies of coevolution provide an excellent starting point for considering community evolution'. This view of ecosystems is similar to what Hubbell (2001) called the 'niche-assembly perspective' and is clearly wrong for Green Mountain.

An alternative view is the process Janzen (1985) referred to as 'ecological fitting'. Here the emphasis is not on coevolution but on the chance accidents of history and dispersal, referred to as the 'dispersal assembly perspective' by Hubell (2001). Consider a plant-feeding insect arriving in a new location: it will survive if there are suitable food plants, even if there is no history of coevolution between itself and the plants – by chance it fits into the local ecology. As Janzen (1985, p. 309), suggested of his South American study site: 'Almost all the complex interactions now at Santa Rosa may be nothing more than the consequences of a long series of ecological fittings'.

The Green Mountain system is a spectacular example of ecological fitting. It shows that coevolution is *not necessary* to the development of a complex ecosystem, although it should be noted that this does not necessarily mean that it is *never* important. It should also make us more sceptical of arguments based on long histories of coevolution that are sometimes used to explain high levels of tropical biodiversity. On Green Mountain, where humans have solved the plant-dispersal problems, the system has gone from species poor fern-dominated hillsides to species-rich cloud forest in around

150 years. This extraordinary system could be used to address many important questions in ecosystem ecology (see Box 1).

CARBON SEQUESTRATION AND GLOBAL CHANGE

The parable of Green Mountain may also tell us much of applied interest about how we can respond to the changes we may be inflicting on global ecology. Lovelock (2000) has suggested that the most serious of these changes is the damage we are doing to natural ecosystems aggravated by increases in greenhouse gases. Green Mountain shows that it is possible, in some cases, to turn largely barren areas into tropical forest in around 100 years, not thousands of years. Other evidence suggests that this result is not exceptional. For example, palaeoecological data suggest that tropical forest in Panama recovered in just 350 years after 4000 years of agriculture as a result of depopulation following the Spanish conquest (Bush & Colinvaux, 1994). There is also evidence that, following the mass extinction event at the Cretaceous–Tertiary boundary, terrestrial biomass (but not biodiversity) could have largely recovered on a time-scale of decades (Beerling *et al.*, 2001).

Given the current widespread destruction of natural and semi-natural vegetation, it is thus encouraging that on a 100-year time-scale it appears possible to regenerate functioning tropical forest ecosystems. However, while these ecosystems are capable of maintaining many *ecological processes* (e.g. carbon sequestration, as discussed above and below), they are likely to be disappointing from a nature conservation perspective, lacking many of the rare species of particular conservation interest.

Is it possible to generalize from Green Mountain to suggest, for example, that large deforested areas of Amazonia could be returned to functioning forest on a 100-year time-scale? The reason that Green Mountain was able to support such vegetation was because the trade winds blow large amounts of cloud onto the mountain and hence supply moisture for forest development. Large areas of continental forest (such as the Amazon) would be more problematic, as, once extensive areas of forest have been removed, the lack of transpiration reduces rainfall and can lead to a climate unsuitable for tree growth (Betts, 1999). However with adequate rainfall, forests can sometimes be created on relatively short time-scales. Such systems will be able to provide ecosystem services, but are likely to be dominated by commoner species rather than those of prime biodiversity concern.

Some of the most pressing concerns in environmental science are the climatic changes predicted as a response to human-induced increases in carbon dioxide and other greenhouse gases. In this context, the effect of 'terraforming' on carbon sequestration in the Green Mountain system is of especial interest. I have previously argued that carbon sequestration is a fundamental ecological process, which would tend to be common to the ecologies of any planet with carbon-based life (Wilkinson, 2003). On Green Mountain, the change from a fern-dominated system to cloud forest, with many trees of a trunk diameter at breast height (1.5 m) of >0.75 m, will have greatly increased the carbon stored in the vegetation. In addition, as predicted by Hooker himself, these changes have almost certainly created deeper soils thus forming greater carbon reserves (Box 2). The construction of systems, such as Green Mountain, on areas which are devoid of forest for either natural or human-induced reasons, could help mitigate the effects of global warming in the short term by reducing the *rate* of climate change through carbon sequestration. Nevertheless, the ultimate amount of warming will depend on the amount of carbon dioxide emitted (Lenton & Cannell, 2002).

THE MESSAGE OF THE PARABLE

Green Mountain can teach us much of theoretical interest about how ecosystems are constructed and function. It also gives us some limited optimism that we can create systems capable of delivering ecosystem services, such as carbon sequestration, and

Box 1 Potential research questions for Green Mountain and other similar systems.

Testing ecological fitting (or lack of coevolution)
Do plant-eating invertebrates have geographical ranges that naturally overlap with the plants they eat on Green Mountain (i.e. have they changed host plants)? Similar questions could be asked of pollinators, seed dispersers or mycorrhizal fungi

Ecosystems as equilibrium systems?
Is the composition of the system changing over time? This is a test of the 'dispersal assembly perspective' (Hubbell, 2001) and requires regular surveys of the system over decades

Quantifying ecological processes
Do processes such as primary production and decomposition occur at rates similar to comparable 'natural' ecosystems? That is can a fully functioning tropical forest be created in 150 years?

Niche width
Has reduced competition lead to an increase in niche width? For example, Green Mountain has only three passerine bird species; the waxbill *Estrilda astrild*, canary *Serinus flavemtuii* and myna *Acridotheres tristis*, are their niches wider than in more crowded bird communities?

Studying ecosystems by removal experiments
How does the system respond to the removal of important species (e.g. keystone species or ecosystem engineers)? Such experiments would present fewer ethical problems on Green Mountain compared with more natural systems. For example, rats *Rattus rattus* are abundant on the mountain and probably play an important role in its ecology. What would be the effect of their removal (some limited rat control is already underway)?

Box 2 Organic matter in Ascension Island soils.

The original fern-dominated vegetation of Green Mountain may well have produced soils rich in organic matter. However, the tree-dominated systems now found on much of the mountain are likely to have deeper soils containing a greater total amount (if not a greater percentage) of organic matter, this may also be true of the grassland systems on the windward side of the mountain. Currently the soils on Green Mountain contain much higher percentages of organic matter (estimated by loss on ignition at 550 °C) than those from other more arid parts of the island

Indicative percentage organic matter	
Green Mountain sites	
Bamboo *Bambusa* sp. cloud forest, summit of Green Mountain	36.4
Fern-rich site with large shrubs of Elliot's path	29.2
Other sites	
Hummock Point	0.8
Base of Sisters Peak	2.2

so help to maintain important ecological processes in a human-dominated world. However, such artificially constructed systems will be missing some of the diversity and regional peculiarities that so fascinate the naturalist.

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BIOSKETCH

David Wilkinson has wide interests within biology and the environmental sciences. His theoretical work has concentrated on aspects of evolutionary ecology, biogeography and the Earth system (Gaia). Within biogeography his main contributions have been on protozoan distributions and biodiversity, plant migrations in relation to climate change and using population ecology models in historical biogeography. His more empirical work has focused on Quaternary palaeoecology, environmental archaeology (especially of the Lake District of North West England) and the ecology of protozoa. He has also published on the history of biology and geology.