

Ecosystem Function and the Prediction of Tree Resistance to Defoliators

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Abstract - The utilization of natural tree resistance to insect pests is an acceptable strategy for the sustainable management of forests. However, the identification of predictors or patterns in the natural occurrence of resistance has thwarted the exploitation of this strategy. An explanation of ecosystem function is presented which argues that the lower trophic complexity associated with geographically constrained ecosystems results in an allocation of plant resources to bottom-up defenses against herbivores. Within the meta-population of a plant species, small isolated populations should be the most resistant to insect herbivores.

would approximate the evolutionary center of the plant and its co-evolved phytophage load and that the exposure to a larger array of herbivores would result in a greater suite of plant defenses. Southwood had shown that the numbers of invertebrate herbivores associated with trees increased with the geographic range of the tree species and Levin's hypothesis received some support from an assessment of the palatability of a number of European tree species with differing phytophage loads [7][8]. However, the argument ignores the tritrophic element of ecosystem function and the accepted plurality that both top-down and bottom-up processes assist in the regulation of herbivores [9].

I. Introduction

In the current eco-political environment the options for integrated pest management are declining as the emphasis on sustainable forestry grows. Even the traditional stalwart of biological control of forest pests is increasingly difficult to apply, as risk-averse legislation endeavors to maintain an environmental status quo, supported in part, by the poorly understood concept of biodiversity. The role of biodiversity in ecosystem stability is the great ecological debate of the moment and understanding how ecosystems function will not only enhance conservation programs, but may also generate new paradigms for effective forest pest management.

II. Patterns of Resistance

Natural plant resistance to insect pests offers an acceptable method of pest management for sustainable forestry. However the identification of tree resistance is often fortuitous [1]. Numerous attempts have been made to identify patterns in the distribution of tree resistance to insects but these attempts were thwarted to a large degree by the complexity of ecosystems and the knowledge that the biotic interactions of any particular species vary throughout its range [2][3][4]. However, this geographic variability in itself offers an opportunity to identify patterns.

Plant attributes, such as geographic range, may be regarded as components of 'apparency', as defined by Feeny [5]. Plants which are more apparent in time and space than rare species, should be exposed to a greater range of pests and presumably they should be selected to counter or adapt to the losses incurred. This reasoning lead Levin to predict that plant resistance to invertebrate herbivores would best be sort in the center of a plant's geographic range [6]. He argued that this

III. Recent Research

The gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae) is a major polyphagous defoliator, principally of Northern Hemisphere oak, *Quercus*, (Fagales: Fagaceae) forests. The eggs of this moth are continually intercepted at Australasian ports and over the last decade New Zealand has suffered the establishment of a number of invasive polyphagous invertebrate forest defoliators. These insects, principally Lymantriids, are unrepresented in the New Zealand indigenous invertebrate fauna and would be expected to devastate a 'naive' insular flora. However, they have failed to establish in the indigenous forest and a risk assessment, using gypsy moth bioassays, of key Australasian forest tree species found that New Zealand forest tree species, including the *Nothofagus* (Fagales: Nothofagaceae) taxa, were largely unpalatable, or resistant, to this defoliator [10].

Nothofagus species are the climax dominants, of the endemic forests of the Southern Hemisphere and typically occur as monospecific forests. The fragmentation of the Gondwanan *Nothofagus* community offers an evolutionary view of macroecological dimension. The islands of New Zealand have effectively been isolated for about 65 million years and in that time have themselves undergone fragmentation that, at times, reduced New Zealand to an archipelago of biotic refugia. The South American portion of Gondwana, that is latitudinally equivalent to New Zealand, is considerably larger than New Zealand and has remained in contact with the greater biodiversity of that continent.

An incursion of the painted apple moth, *Teia anartoides*, a polyphagous Australian Lymantriid, into New Zealand, allowed the reciprocal testing of the *Nothofagus* genus with a Southern Hemisphere defoliator [11]. The results, using *T.*

anartoides bioassays, showed the same relative palatabilities of New Zealand species as the bioassays undertaken with *L. dispar*, but that the *Nothofagus* species from South America were significantly more palatable than the New Zealand representatives of the genus and in some instances more palatable than the insect's primary host, *Acacia*.

These results would seem at odds with the accepted paradigm of the vulnerability of island ecosystems to invasion [12]. However, they could be explained through a differential of top-down and bottom-up processes within ecosystems of different spatial magnitude.

IV. An Explanation

The species-area relationship is possibly the strongest empirical generalization in community ecology [13] i.e., biodiversity can be expected to increase with habitat area. A corollary of the species-area effect is that food web complexity will also increase with area. However, habitat fragmentation studies and trophic level patterns in spatially distinct ecosystems, show that the trophic components of invertebrate communities do not change uniformly with area [14][15][16][17][18]. Rather, during habitat fragmentation, the higher trophic levels are lost prematurely or disproportionately, or cannot be maintained in small habitats. These higher trophic levels are the top-down regulators of lower levels and when the lower level comprises the herbivores, they are the key explanation for the maintenance of the 'green world' [19]. The contrasting argument that has fuelled the top-down/bottom-up debate, is that not all plant material is, directly or indirectly, available to herbivores. Herbivore populations may well be constrained by a 'bottom-up' inaccessibility of resources [20][21][22][23]. The existence of a top-down/bottom-up plurality has been generally accepted, but it is empirically difficult to apply. Although both processes have been individually demonstrated in particular insect/plant systems the empirical evaluation of the relative importance of both in one ecosystem remains rare or non-existent [24][25]. However, despite the paucity of data, the fact that top-down *and* bottom-up processes are likely to occur in all ecosystems, suggests that when robust top-down regulation of herbivore populations by natural enemies is reduced or absent over evolutionary time, plants should be selected to allocate resources to 'bottom-up' defense. If food web complexity equates with ecosystem stability (hotly debated [26][27][28][29][30][31]), then in spatially restricted habitats, which do not support complex food webs, herbivore populations must be relatively more regulated by bottom-up forces, to maintain a 'green world' stability.

V. The IRA hypothesis

The Island Resource Allocation (*IRA*) hypothesis presented here, offers the thesis that for plant species that do not escape

herbivory by dispersal or precocious seeding etc, **the susceptibility of a plant species to invertebrate herbivores is proportional to its geographic range.** That is, geographically constrained plant populations will support lower biodiversity, with fewer trophic levels, and be less protected by the top-down regulation of herbivore populations. If top-down regulation of herbivores is weak, because of the lack of trophic complexity, then plants will be selected to allocate resources to a bottom-up defense.

Islands are constantly bombarded by herbivores, which probably arrive without their associated natural enemies, or have founding populations too small to accommodate their associated natural enemies. To survive island plants must be selected for herbivore defense and the necessity of an innate defense must increase as island area decreases. The high rate of endemism on islands is proof of long-term stability. Presumably the stability of these insular systems is reached by some mechanism other than trophic complexity. How else could such ecosystems possibly persist under a constant threat of extinction from unregulated populations of immigrant herbivores?

VI. Summary and Conclusions

That plants from small geographic areas will be relatively resistant to invertebrate herbivores appears to be counter-intuitive because of the long-held view that islands are inherently invadible - through the availability of empty niches. This paradigm assumes that community simplicity negates a requirement for metabolically-costly defenses because of the low numbers of consumer species in the community. This assumption was implicit in the work of Levin in which he suggested that higher levels of plant defense would be expected in plant species with wide geographical ranges. The opposing view offered here is that plant resistance should be sort in smaller, isolated populations within the meta-population of a plant species. There is supporting evidence for both views and more research would not only benefit foresters but also the aid in the development of reliable ecological predictors.

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