SOME ECOLOGICAL PRINCIPLES FOR RE-ASSEMBLING FOREST ECOSYSTEMS AT DEGRADED TROPICAL SITES.

David Lamb[1]

INTRODUCTION

I have been asked to discuss some ecological principles that might be relevant to restoration ecology in the seasonal tropics. I will attempt this, although practice has advanced far more rapidly than theory. That is, in many parts of the world people have:

- Identified plant species that once grew in landscapes that are now degraded.
- Studied the timing and the extent of seed production of these species.
- Developed methods of raising these species in nurseries.
- Planted these species out in the field in mixed communities with the objective of eventually re-establishing the original ecosystem or, at least, something resembling that ecosystem.

The results of these efforts have ranged from “very promising” to “poor”. At “very promising” sites, the planted trees have all survived and are growing rapidly. With time their canopies have merged and closed and additional species have begun to be introduced by seed dispersers such as birds. Poorer results have been experienced:

- where species have been planted at sites outside their original range;
- where sites are no longer suitable for the original species because they have been too severely degraded;
- where insufficient weed control has been carried out and the planted trees have become swamped by grasses or vines and/or
- where (exotic) animals have grazed or disrupted the new successions.

Through a process of trial and error, these common problems have become well known and there is now every chance that the success rate of restoration projects will improve in the future. What, then, is a listing of ecological principles likely to add to this process? Isn’t the task now one of simply extending these operations to a larger scale. That is, haven’t the major problems become socio-economic in nature rather than ecological problems?

---

[1] Botany Department and Cooperative Research Centre for Tropical Rainforest Ecology and Management, University of Queensland, Brisbane 4072, Australia
Email: D.Lamb@botany.uq.edu.au

In response I pose two questions. Firstly, are these approaches really working? We are now in the position of being able to predict the likely future height, cover and biomass of many of these new communities. However, we are still not able to clearly say just what the total species richness of the new community will be in, say, 10 or 20 years time. Nor can we usually say just which plant species (including those planted) will be present at that time. Will the new community have been colonised by the most common species in nearby intact forests or by those species that fruit most prolifically? We can usually only speculate about the range of life forms or functional groups that might be present and can rarely say much at all about the wildlife component of these new ecosystems.

Secondly, are these new communities sustainable? Although the new communities appear to be growing well, are all the species they contain reproducing and replacing themselves? Or is only a sub-set of those planted doing so? Might the newly established community quickly degrade once the populations of the various planted species senesce? Might the site eventually become dominated by a relatively small number of dominant species, rather than develop a diverse mix of species.

In a situation where detailed local ecological information is limited, trial and error is a necessary and a valuable approach. But we also need to:

- learn lessons from these trials. That is, develop generalisations that might be applied elsewhere (“theory”) and
- test existing theory learned in other situations when designing new trials and while waiting for results from our own field work.

SOME RELEVANT ECOLOGICAL THEORY?

Some theory relevant to restoration:

Niches: every species occupies a multi-dimensional ecological space, referred to as the niche of that species. This is the habitat of that species and that area of the landscape in which it is normally found. It is necessary, however, to distinguish between the potential niche a species might theoretically occupy and the actual niche it does occupy. Part of the theoretical space may be unoccupied because not enough time has elapsed to allow a particular species to disperse and colonise all parts of a landscape potentially open to it. Part may also be excluded because of competition or predation.

Consequence for restoration: knowledge of the resource requirements and tolerances of species is necessary before attempting to re-introduce these to degraded landscapes.

Successions: the ways in which ecosystems change over time, as new species enter and some existing species are replaced, has been a topic of ecological research for more than 100 years. Despite this, we are still unable to predict the outcome of successional change over time in any particular ecosystem, because successional theory is still poorly developed. What does seem clear, however, is that several processes may occur during successions. These include facilitation (in which one species facilitates the entry of another into the successional community), inhibition (in which a species inhibits the entry of one or more species to the successional community) and tolerance (where a particular species is able to enter a successional community despite the presence of other species already present).

Consequence for restoration: the benefits of facilitators e.g. nitrogen-fixing trees such as *Acacia*, or bird-attracting species, such as figs, are well-known. Sometimes, however, the same species can act as a facilitator to some species, whilst simultaneously inhibiting others. For example, a dense stand of *Acacia* may slow forest succession for many years, despite enriching the soil with nitrogen. Conversely, species such as grasses, normally regarded as inhibitors of forest succession, may sometimes benefit seedlings of tree species, normally found only in mature successional stages, by providing shade. This means that ecological theory is still poorly developed in areas most relevant to restoration. It is unable to provide much more than broad generalisations to guide practice and is unable to offer much predictive capacity.

Disturbance and change: The environments in which plant communities are found are always changing and, as a consequence, all ecosystems are invariably in a state of flux. Ecosystems are subject to a disturbance regime defined by differences in disturbance frequency, intensity and scale. Species in any particular ecosystem are adapted to these disturbance regimes and many are dependent upon them for reproduction and survival.

Consequence for restoration: a prime need in any restoration work is to exclude disturbances (especially those that may have led to degradation in the first place) to allow restoration to proceed. But, at some time, disturbances must be allowed again if the restored ecosystem is to function as before. The question is when might this be desirable and what sort of disturbances (e.g. fire?) might be allowed or even fostered?

Species interactions: ecosystems are made up of food webs spread over 3-4 trophic levels. A variety of interactions occur between species in these webs. These include herbivory or predation as well as competition and mutualistic relationships (e.g. pollination, seed dispersal) or commensal relationships (e.g. epiphytes on trees).

Consequence for restoration: species forming obligatory mutualistic relationships will need both partners to survive and reproduce in the newly restored ecosystem. This may mean both must be re-established at the site or that they can access the site from intact forest remnants nearby. Herbivory, predation and competition have the capacity to exclude certain species from a community and may need to be managed to prevent this.

Predicting successional outcomes from theory

If we knew the niche requirements and attributes of various species, as well as how these species interact with one another and with the abiotic environment, we might be able to predict long-term consequences of various approaches to restoration. Managers could then fine-tune their management inputs to achieve desired outcomes and we could predict these outcomes with some degree of success. Unfortunately ecological theory is nowhere near developed enough to do this.

Three possible outcomes of initiating a restoration project in a particular environment are shown in Fig 1. The first alternative (A) indicates that a large number of future states are possible and the identity or nature of these depends entirely on the species used to initiate the community. In this situation the environment itself exerts little influence. By contrast, alternative C indicates that in that particular environment only one outcome is likely over the longer term irrespective of what species are used to initiate the succession. The third alternative (B) falls between these two and shows that the initial species composition is influential but that environmental conditions and chance still play a role and that it is difficult to predict the outcome over time.

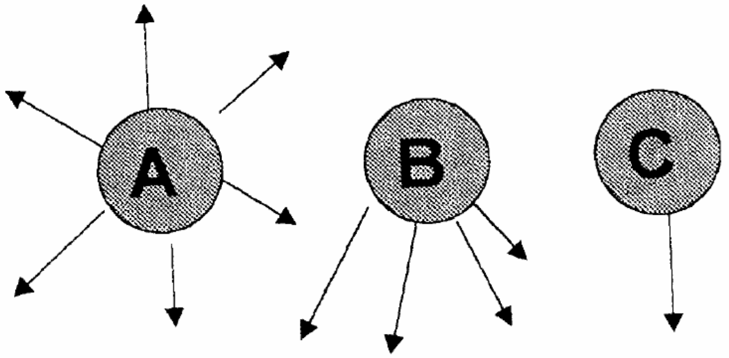

Figure 1. Possible successional trajectories

Present evidence suggests alternative A is most likely in complex, species-rich systems not subject to stress. In these situations, chance historical events such as the sequence in which various species arrive influence the assembly trajectory. Alternative C is more likely in simple systems subject to predictable stresses such as a severe annual dry or cold season that limits the number of potential community members. Alternative B is probably more common than A or C in the seasonal tropics. It these areas, environmental constraints apply but the species themselves and their manner of entry into the new community are also important.

SOME DRAFT "PROPOSITIONS" GUIDING COMMUNITY ASSEMBLY

In 1975, Diamond coined the expression "rules of assembly" to describe how bird communities developed in a series of New Guinea offshore islands. There has been considerable interest since then in widening the idea to describe how other and more complex ecosystems might be assembled. So far the work has mostly been undertaken by theoreticians and no one has attempted anything as complex as developing assembly rules for tropical forests. Our understanding of these ecosystems is still far too rudimentary to attempt formulating rules of the type envisaged by Diamond. However, I outline below a series of "propositions" and some corollaries as a first step in this process on the assumption that these can be tested, modified and expanded in the light of further field experience.

Proposition 1.

The future state of any restored forest heavily depends on the current state (i.e. the species initially sown or planted at the site).

Corollary: small differences in initial conditions (e.g. rainfall, soil fertility) can cause successional trajectories to diverge rapidly, making it difficult to predict outcomes.

Corollary: disturbances are capable of changing successional trajectories (e.g. fires or grazing animals can remove particular plant species from a site).

Corollary: feedback loops can be very significant (e.g. canopy closure occurs enabling seed-dispersing birds to enter the succession, thereby accelerating the rate at which new plant species enter the community).

Proposition 2.

The more plant species that can initially be re-introduced, the faster the subsequent succession.

Corollary: the more species the greater the structural complexity at a site and hence the more likely it is to be attractive to a wider range of wildlife species.

Proposition 3.

Some plant species combinations are unlikely to be successful. Fast growing species with dense crowns may exclude some slower growing species unless these latter are especially shade tolerant or canopy gaps are present or are frequently created.

Proposition 4.

An initial (planted) community of pioneer and early secondary species will be short-lived and is unlikely to be self-sustaining. It is not necessary or desirable to attempt to simulate natural successional patterns by only initiating restoration projects using pioneer species. In many (though not all) cases, species from the functional groups usually found in later stages of successions can also be grown in the open in early stages of community development. In many natural successions their delayed colonisation may be as much a consequence of their limited dispersal as their physiological tolerances. This means many species from mature successional phases can often be planted in relatively open, old-field situations.

Corollary: plantings of species from functional groups represented by fast-growing pioneer and early secondary species may be useful as a means of quickly eradicating weeds. Ideally there should be forest remnants nearby from which species from more mature successional stages and other functional groups will colonise. If not, such species can be subsequently sown or under-planted beneath this initial canopy.

Proposition 5.

The sequence in which species are re-introduced to a site are important in determining the assembly trajectory. At a trivial level this is obvious. For example trees are necessary before epiphytes can colonise a site. But at a more fundamental level, we may need some important “structuring” species early in a successional sequence rather than at a later stage. If these species are not present then some introduced species may fail and disappear. This is not to argue that all primary forest species must only be planted beneath a canopy of early secondary forest species. Rather, this principle re-affirms that facilitation and inhibition can occur during succession and can influence successional trajectories.

Corollary: the most influential species able to “structure” a succession are likely to be those that rapidly modify the physical environment or those with large numbers of mutualistic relationships with other plant or animal species.

Proposition 6.

The rates at which restoration occurs depends on the extent of the environmental stresses present. Sites with strongly seasonal climates or with low soil fertility are likely to be more difficult to restore than those with more benign climates or with more fertile soils. Frequent but unpredictable stress (e.g. fires, droughts) make it particularly difficult to re-assemble new communities. Once restored however, such communities may buffer some of the stresses (e.g. the more humid microclimate within a new forest may limit the rate of spread of fires)

Corollary: it may be necessary to use some non-native species on highly degraded sites that are no longer suitable for some of the original species. Non-native species can ameliorate site conditions (e.g. nitrogen fixers that improve soil fertility) and facilitate the subsequent re-entry of native species.

Proposition 7.

Most new tree species reaching a restored site will be carried there by animal dispersers.

Corollary: the diaspores of these species will have attributes that make them attractive to animals (e.g. fleshy fruit, arils, mostly small to medium fruit size).

Corollary: certain plant species will be unlikely to colonise restored sites and will always need to be introduced. These include poorly dispersed species (e.g. with diaspores lacking animal-attracting features, those with large fruit or those that fruit infrequently) as well as rare species usually present in small numbers.

Corollary: few wind-dispersed species will reach and colonise a site once canopy closure occurs.

Proposition 8.

The rate at which additional plant species enter a site, once restoration has been initiated, depends on the distance to sizeable intact forest remnants. The rate also depends on the extent to which populations of animals capable of dispersing seed from these remnants remain in the landscape.

Corollary: little colonisation is likely at isolated sites or in landscapes where only small forest fragments remain and so restoration of tropical forests is rarely feasible at such sites (although it may still be possible to re-establish species-rich forest communities).

Corollary: the nature of the vegetation matrix separating the restored site and intact forest will influence the rate at which seed dispersal and colonisation occur. A matrix, containing shrubs and scattered trees, is likely to foster faster seed dispersal than a grassland.

Proposition 9.

The attractiveness of a site to animal seed-dispersers affects the rate at which they bring in seeds of new species. Structurally complex sites are likely to be more attractive than simple ones and animals are likely to begin to enter the new community in significant numbers after canopy closure. Sites with tall trees are likely to be more attractive than those with only short trees or shrubs; large restored areas are likely to be more attractive than small areas.

Proposition 10.

Species colonising a restored site, after canopy closure has occurred, must have some degree of shade tolerance, enabling them to persist as understorey species (or to eventually grow up and join the canopy layer). It is difficult for secondary species to enter a restored site once canopy closure has occurred. Even primary forest species that colonise after canopy closure may take many years to grow up and join the canopy layer. This means the rate of successional change and progress towards a fully restored state will be slow after canopy closure.

Corollary: Rapid canopy closure reduces the likelihood (but will not necessarily prevent) weed colonisation. Some weed species may still be able to persist under moderate levels of canopy cover, particularly when that canopy cover is uneven. Alternatively weeds may arrive at a site and persist in a soil seedbank.

CONCLUSIONS

The task of restoring the most complex ecosystems on Earth will be difficult. Ecological theory is still in a comparatively early stage of development and has not yet reached the stage at which prediction of successional trajectories is possible or assembly rules can be declared. On the other hand, enough experience has now accumulated in various tropical forest ecosystems to establish a set of propositions or generalisations defining how newly established forest communities are likely to develop. What needs to be done now is to test these. Are they useful generalisations or are they restricted in their applicability? Have they any predictive value for restorationists? More particularly, can they be improved?

Any improvement is only likely to come if those engaged in restoration learn much more from their trials than has been the case so far. Some suggested details that should be recorded are listed in Table 1. Forest restoration is a long-term task and those doing the evaluation will not necessarily be those establishing the trials. Meticulous documentation is needed, to allow restoration trajectories to be monitored and evaluated. In addition, more varied approaches to restoration should be tested. For example, perhaps sets of adjacent trials might be established in which different species introduction sequences are used. Do these lead to different outcomes? Might these sets of trials collectively hold more species than would be the case if the same area were reforested using just one approach?

Table 1: Objective setting and monitoring tasks for restoration trials.

Task	Details
Define objective	Set quantifiable objectives such that the degree of success can be evaluated in the future (e.g. the objective is to increase site species richness to a particular level by a certain time).
Specify methods used	What species were planted or sown? What proportions of each were used? What functional groups were represented? What was the sequence of species introduction? What form of management has been applied? When did this cease?
Specify the prevailing environmental conditions	What levels of soil fertility? What weather conditions at the time of establishment and subsequently?
Monitor community development	Have all introduced species survived? Have these reproduced and have seedlings become established? What new colonists have regenerated? What wildlife species are now using (for reproduction?) these new ecosystems? Under what circumstances did plant and animal colonisation occur (e.g. timing)? What are the attributes and habitat requirements of these plant and animal colonists?

QUESTIONS AND COMMENTS

Ulfah Siregar

I think that ecological theory alone is not enough to predict the likely success of various approaches to forest restoration. We must include consideration of genetics as well as environmental factors.

David Lamb

I agree

David Young

Formal ecological research has been going on for over 100 years, but it is still unable to provide us with definitive answers. Is it better to be 70% correct and carry out forest restoration now or wait another 100 years to be 100% correct? I refer specifically to the use of indigenous knowledge for forest restoration.

David Lamb

I think we need to implement forest restoration projects now on the basis of the best knowledge currently available, including both ecological research and current traditional practices.