Spatial ecology of regeneration in secondary rainforests: seed dispersal and ecological traits of plant species

Jessie Wells — The Ecology Centre, University of Queensland
jwells@zen.uq.edu.au — CSIRO Sustainable Ecosystems & the Rainforest CRC

Overview

In view of extensive loss, fragmentation and disturbance of rainforests over the past century (Goosem et al. 1999), further understanding of 'secondary' rainforests and their regeneration is now vital for the conservation of rainforest species and ecosystems in many parts of the world.

This project combines aspects of spatial ecology and plant functional ecology, to relate patterns of plant regeneration in primary and secondary rainforests to:
1) spatial distributions of rainforest cover and source plants
2) ecological traits of plant species, for example dispersal, age of reproduction, life-span, and attributes of seeds, stems, and leaves.

Research Components

'Comprehensive' studies of all species, and 'Focal' studies of individual species, link plant species attributes with spatial studies of regeneration in secondary rainforests on abandoned pastures, and in adjacent, intact rainforests in Australia's Wet Tropics and at La Selva Biological Station, Costa Rica.

1) Comprehensive studies — *Site 1, Wet Tropics*

Studies of species composition and the diversity and representation of plant attributes, to quantify changes over distance from the primary forest, and through strata from seedlings to canopy trees.

Surveys of two transects that extend from primary into secondary rainforest recorded 7900 plants of 196 species, 149 genera and 67 families. A set of six 'principal traits' were measured for seedlings and adults of each species, and assigned to individual plants on the transects to quantify changes in the diversity and representation of these traits on the basis of species, stems, and basal area.

2) Focal Species studies — *Sites 1 – 12, 0.84 – 9 ha*

Intensive studies of 3 sets of focal species, to enable analysis of a more-extensive set of functional traits and their inter-relations, and spatial modelling of seed dispersal and early seedling regeneration for individual species. 'Regeneration Shadow' models for two size-classes of seedlings per species are based on 1) observed distributions of source-plants and seedlings, and 2) estimation of source fecundities and probability density functions for dispersal distances, via Likelihood and Bayesian statistical methods.

Focal species set 1 – Atherton Tablelands

– new field studies of 2 tree species at Site 1 (Comprehensive site), and 17 species at Site 2, selected to represent a diverse range of plant, seed and dispersal traits. At Site 1, seedlings were recorded along three 180m transects, and adults over the surrounding 8.6 ha. At Site 2, seedlings were mapped over a continuous area of 60x140m, and adults over the surrounding 5 ha. Site 2 receives relatively low rainfall (1600mm p.a), and is located on nutrient-deficient metamorphic soils.

Focal species set 2 – La Selva, Costa Rica

– Studies of seedling and adult plant attributes for 11 species of Neotropical subcanopy and canopy trees at 4 secondary rainforest sites at La Selva Biological Station, Costa Rica, in collaboration with Prof Robin Chazdon, and El Proyecto Bosques.
– Spatial studies of regeneration for one subcanopy palm species, *Welfia regia*, over 3.64 ha (*site 3*).

Focal species set 3 – CSIRO surveys, Atherton Tablelands

– 10 species of large-seeded trees, based on past surveys at 8 sites on the Atherton Tablelands – 4 sites in rainforest fragments (*sites 4-7,* 2-4 ha) and 4 matched sites within continuous rainforest (*sites 8-11*). Two further canopy tree species were recorded at one primary rainforest site of 0.5 ha (*site 12,* 'Curtain Fig', CMVF 5B 'mabi' forest), by Marion Pfeifer, Institute of Ecology, Jena.

Plant Functional Attributes – trade-offs and interdependencies

A key area of research in plant ecology concerns inter-relations among observable features of plant form and function, and how they reflect aspects of ecological behaviour and evolution.

An objective is to quantify traits that give the most direct indication of ecological mechanisms of dispersal, establishment and persistence, as these processes are central to the regeneration of any plant, and form the basis of plant strategy theories.

The axis of inter-specific variation most often emphasized in rainforest ecology is a spectrum of relative 'shade-tolerance' – from light-demanders to many species that can regenerate in understorey environments. This spectrum is thought to be based on trade-offs between *i)* maximum potential growth rates in environments of higher resource levels, reflecting rapid uptake and utilisation of resources for growth, *versus ii)* survival & realized growth rates in low-resource environments, depending more on efficiency and conservation.

However, shade tolerance does not represent a single, static, spectrum, as relative shade tolerances often change during plant development, and secondly, the abilities to regenerate, grow and/or reproduce in shaded environments often depend on responses to factors other than light – for example water, nutrients, and physical damage.

Principal Traits – considered in comprehensive studies:

1) Seed mass – reflects a trade-off between reproductive allocation to seed size *vs* seed number, and affects seedling establishment in relation to litter cover and hazards of drought, herbivory and damage

2) Dispersal modes

– likelihoods of dispersal by wind, bird species, bats, rodents

3) Age & Light environment at 1st Reproduction

– Age of reproduction affects the length of time for which regeneration is dependent on external sources of seeds, and hence possible forms & rates of colonisation.

– Light requirements for maturity range from direct illumination to understorey shade.

Polyscias australiana, site 2

The remaining traits reflect resource dynamics, and indicate relative allocations to processes of growth and activity *versus* structure, defence, and longevity.

4) Leaf Specific area, Water content, Leaf Strength

5) Maximum *Height*

6) Stem-tissue *Density* (dry mass per unit volume)

This selection concurs with recent proposals for key sets of traits for studies of plant functional ecology (Weiher et al. 1999, Westoby et al. 2002). A more extensive set of traits will be considered for focal species, including lifespan, growth rates, mortality, leaf-lifespan and fruiting phenology.

Research Questions

This study employs Likelihood and Bayesian statistical methods, implemented via Monte Carlo Markov Chain algorithms (MCMC), to *1)* develop and compare alternative model forms and parameterisations (Gilks et al. 1996, Hilborn and Mangel 1997, Burnham and Anderson 2001), *2)* incorporate uncertainties in all variates, and *3)* to model spatial dependencies (Legendre and Fortin 1989, Dale 1999).

Key Questions – Comprehensive studies

1) Inter-relations of plant functional traits for seedling and adult lifestages

– What are the main dimensions of variation among species ?
– To what extent are traits co-ordinated to form alternative sets or strategies ?
– What are the key trade-offs and inter-dependencies underlying the co-ordination of traits ?

The inter-relations and phylogenetic distributions of plant traits will be analysed using linear and non-linear bivariate models, and multivariate analysis of Principal Components.
Bivariate analyses will incorporate uncertainties in both variates, by employing *i)* Standard Major Axis regression for linear models and *ii)* an extension to non-linear models, based on MCMC algorithms.

2) Changes in trait distributions with distance from intact forest & through height strata

– Are there changes in the diversity or representation of functional traits with distance from primary forest ? For example, declines in the diversity of seed sizes present, or declines in the densities or relative representation of species with dispersers such as musky rat-kangaroos ?

– How do trait distributions change when comparing 3 height strata, from seedlings to canopy?

Site1 Brooks Valley, Millaa Millaa: annual rainfall > 4000mm, volcanic basalt soils, 390m a.s.l. Two transects, 10x180m, run 40m through intact rainforest and140m into adjacent secondary rainforest, and contain sub-transects for saplings (5x180m), and seedlings from a minimum of 4th leaf stage (1x180m).

Spatial analyses will quantify changes in means, relative frequencies, and the diversity of values present at each distance along the transects. 'Representation' will be assessed on the basis of absolute and relative numbers of stems, species, or basal area. Geostatistical methods will be used to analyse spatial auto-correlation and changes in local means and variances (Rossi et al. 1992). Three different height strata will be compared, to see how the trait distributions of plants currently regenerating in the understorey differ from those of the earlier canopy, as an insight into temporal changes.

3) Species composition and diversity

Changes over distance and canopy strata in species composition, levels of phylogenetic diversity, species richness, dominance and rarity, and spatial inter-dispersion of different species.

– Are changes similar to those observed for subtropical secondary regeneration within settings of continuous forest ? Predicted changes are: *1)* lower dominance, *2)* higher rarity, and *3)* greater inter-dispersion of species, reflecting a temporal shift from regeneration of several light-demanding species, to more probabilistic and continuous regeneration of many other species (Williams et al. 1969, Hopkins 1975).
– Is it possible to detect centres of past 'nucleation' by trees or copses acting as foci of avian seed deposition and seedling establishment –as suggested by short-term studies in subtropical and neotropical sites? (Guevara and Laborde 1993, Toh et al. 1999, Harvey 2000)

Analyses: Detrended Correspondence analysis of species composition; and analysis of richness (S) and evenness (E) as components of diversity, using SHE Diversity analysis (Hayek and Buzas 1998) and rarefaction methods for analysis of species accumulation curves on per-stem and per-area bases (Olszewski 2004).

Key Questions – Focal Species studies

1) Point patterns of Focal Species – intensities of conspecific aggregation or dispersion

'Relative neighbourhood density' statistics quantify changes in the relative densities of plants as a function of distance from individual plants (Condit et al. 2000, Wiegand and Moloney 2004), for example revealing species-specific rates of decline in the intensity of conspecific aggregation with distance, or the existence of critical scales at which aggregation or repulsion are observed.

This study will consider spatial patterns of conspecifics within each of 3 lifestages.

The O-ring statistic $O(r)$ is calculated for a distance-series of annuli around individual plants (radial distance r to '$r+\Delta r$'), and gives the expected number of points in each annulus. It is calculated as the mean conspecific density in the annulus, multiplied by the 'intensity' of the point pattern, λ. This 'intensity' is either the mean site-level density, or a local density estimated by a 'moving window' to account for heterogenous densities across a site. Estimated O-functions will be compared to those generated from Monte Carlo simulations of a set of stochastic point processes, for example heterogeneous Poisson and Poisson clustering processes (Wiegand and Moloney 2004).

2) Spatial models of regeneration

Regeneration Shadow models will be developed for 1–3 seedling size-classes within each focal species, to enable inference on processes of regeneration from spatio-temporal patterns.

Regeneration Shadow (RS) models are based on *1)* observed spatial distributions of source-plants (possible parents) and of seeds or seedlings, and *2)* 'inverse' statistical estimation of source-plant fecundities *'Q'* (recruits yr^{-1}) and probability functions for dispersal distances $f(r)$, via Likelihood and Bayesian statistical methods.

This form of analysis was developed for closed forests, where regeneration shadows from two or more source plants will often overlap, and so an individual seed or seedling could represent several possible combinations of source and dispersal-distance (Clark et al. 1999). The aim of statistical modelling is to find the probability densities for source strengths and dispersal distances that are most likely to have generated the observed patterns of seedlings.

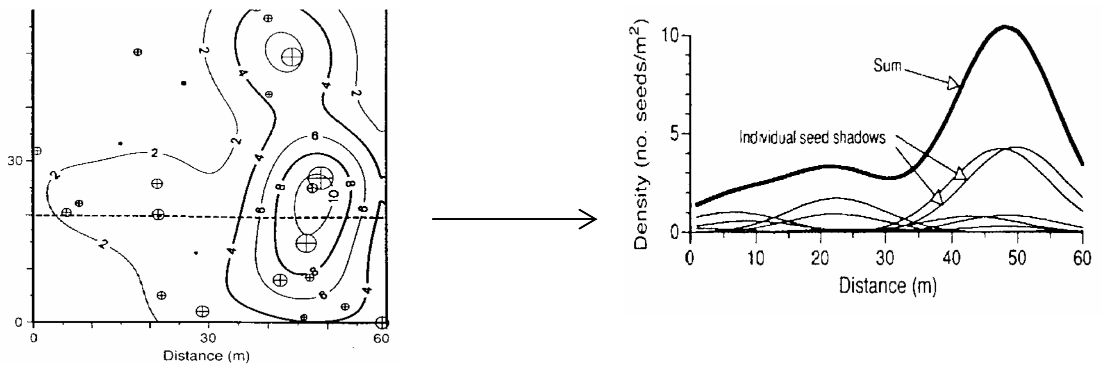


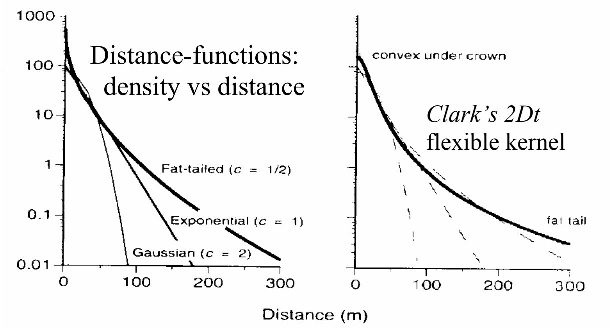
Figure: Example of source & seed distributions from a Temperate deciduous forest

Left – Site map, showing the 2-dimensional distribution of sources (circles, scaled by tree diameters), and contours of seed density. (Clark *et al.*1999, fig 2 p.1479)

Right – Line-transect, showing seed densities from several overlapping seed shadows.

Summed Regeneration Shadow = $\sum^{sources}$ *Source strength* x *Distance function*

$$\hat{s}_j(\mathbf{b},\mathbf{r}_j \mid \beta,\theta) = \sum_{i=1}^{m \text{ trees}} \beta\, b_i \; f(r_{ij} \mid \theta)$$



Where $\hat{s}_j$ is the predicted seedling density at point-location *j* quantified as *seedlings* m^{-2} yr^{-1} ;

βb_i gives the source strength for tree *i*, assumed to be directly proportional to basal area or canopy area b_i ; and

θ is a vector of parameters for the 'distance' probability function

Estimation of source strengths and dispersal functions depends on sampling sufficient quantities of regeneration (as seeds or seedlings), and on mapping adult plants over an area sufficient to include almost all sources adults contributing to the observed regeneration. For example, it can be difficult to resolve parameters for species that occur at low densities, in relatively even distributions, or disperse over long distances.

So far, Regeneration Shadow models have been applied only in settings of primary forest, either to canopy trees of temperate forests, or to rainforest species in the neotropics (Clark et al. 1999, Dalling et al. 2002). For example, a study of seed rain over four years for 13 gap-dependent species in Panama demonstrated clear dispersal limitation on seed arrival for 9 of 13 species (d = 0.68 – 0.97), including species with seeds dispersed by many bird species (Dalling et al. 2002). However, the methods for modelling regeneration shadows require further development to assess model adequacy, and to relate the results to ecological mechanisms of dispersal in more depth than contrasting wide classes of wind and animal dispersers, and finally to relate the results to post-dispersal seedling dynamics.

Four extensions to Regeneration Shadow methods:

1) Analyses will employ Bayesian statistical methods implemented via Monte Carlo Markov Chain algorithms, as an efficient method to search over the parameter spaces of alternative models. Motivations for this extension are to enable estimation of full probability distributions for the parameters of interest, rather than point estimates, and to give a natural means to incorporate further sources of information, for example ecological and genetic data as informative priors.

2) Spatial data on regeneration consist of point co-ordinates for individual seedlings of several developmental stages, mapped over a continuous area. This contrasts with earlier studies based on counts or densities of seeds in a set of spatially-distributed seed traps, or a single class of seedlings in 1m^2 seedling plots.

3) Several alternative forms for the distance function will be considered, including continuous and finite mixture-models to enable representation of seed dispersal via a combination of mechanisms – for example dispersal by gravity, short-distance movements by *Hypsiprymnodon* (musky rat-kangaroo), and longer-distance dispersal by cassowary.

4) Two further sources of information will be utilised for validation and further development of the models: *1*– ecological data on frugivory and seed movement by animal dispersers, and *2*– genetic data from 6 microsatellite loci, to identify parent-progeny relations. Both sources can be used as datasets for comparison and validation of spatial models, or alternatively, can be incorporated into the modelling process as prior information.

Observation of Patterns and Inference on Processes

The distributions of plant regeneration observed in this study result from the combined processes of seed-production, dispersal, germination, and seedling survival. As the observations are from a single point in time, it is not possible to analyse these transitions directly.

However, hypotheses on processes that filter the dispersal template can be explored via:
1) Comparisons between *1–* RS models for early seedlings and *2–* Process models of seed deposition and seed predation, based on studies of frugivore activity, gut passage times, and movement patterns, and developed by D.Westcott and A.Dennis, CSIRO Tropical Landscapes Ecology & Conservation.
2) Comparison of RS models developed for seedlings of two or more age classes
3) Monitoring of seedling growth, damage and survival over 1-2 yrs for 4 of the focal species.

Finally, genetic parentage analysis to identify parent-progeny relationships will be performed for four focal species, based on 6 microsatellite loci. This will give direct estimates of fecundities and distances for the seed dispersal events that have given rise to individual seedlings, and secondly, gives the percentage of seedlings that must have dispersed from more-distant, unmapped adults. This data offers a strong test of both the inverse- and process-modelling methods, for example exploring the consequences of finite sampling of regeneration and source plants. (Collaboration with molecular ecologist Dr. Andrew Lowe, University of Queensland)

In combination, these studies offer insight into source distributions, seed dispersal and seedling establishment as factors in the regeneration of plant species, across a diverse range of dispersal mechanisms and seedling and adult traits.

Research Contributions

– From a theoretical perspective, this study examines how the quantifiable attributes and spatial patterns of plants relate to concepts of their functional ecology and regeneration strategies.

– From the perspective of restoration ecology, this study considers the possibilities and limitations of natural regeneration for rainforest conservation, and how management efforts directed to limiting factors such as seed dispersal could assist the regeneration of species and functional diversity in secondary rainforests.

Brooks Valley, site 1

References

Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research **28**:111-119.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: Patterns across temperate and tropical forests. Ecology **80**:1475-1494.

Condit, R., P. S. Ashton, P. Baker, S. Bunyavejchewin, S. Gunatilleke, N. Gunatilleke, S. P. Hubbell, R. B. Foster, A. Itoh, J. V. LaFrankie, H. S. Lee, E. Losos, N. Manokaran, R. Sukumar, and T. Yamakura. 2000. Spatial patterns in the distribution of tropical tree species. Science **288**:1414-1418.

Dale, M. R. T. 1999. Spatial Pattern Analysis in Plant Ecology. Cambridge University Press, New York.

Dalling, J. W., H. C. Muller-Landau, S. J. Wright, and S. P. Hubbell. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. Journal Of Ecology **90**:714-727.

Gilks, W. R., S. Richardson, and D. J. Spiegelhalter, editors. 1996. Markov Chain Monte Carlo In Practice. Chapman & Hall, London.

Goosem, S., G. Morgan, and J. E. Kemp. 1999. Wet Tropics. Pages 7/1 - 7/74 *in* P. S. Sattler and R. D. Williams, editors. Conservation Status of Queensland's Bioregional Ecosystems. Environmental Protection Agency, Brisbane.

Guevara, S., and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures - Consequences for local species availability. Vegetatio **108**:319-338.

Harvey, C. A. 2000. Colonization of agricultural windbreaks by forest trees: Effects of connectivity and remnant trees. Ecological Applications **10**:1762-1773.

Hayek, L. C., and M. A. Buzas. 1998. SHE Analysis: An integrated approach to the analysis of forest biodiversity. *in* F. Dallmeier and J. A. Comiskey, editors. Forest Biodiversity Research, Monitoring and Modelling. UNESCO, Paris.

Hilborn, R., and M. Mangel. 1997. The Ecological Detective - Confronting models with data. Princeton University Press, Princeton, NJ.

Hopkins, M. S. 1975. Species Patterns and Diversity in the Subtropical Rain Forest. PhD. University of Queensland, Brisbane.

Legendre, P., and M. J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio **80**:107-138.

Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos **104**:377-387.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs **62**:277-314.

Toh, I., M. Gillespie, and D. Lamb. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. Restoration Ecology **7**:288-297.

Weiher, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science **10**:609-620.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics **33**:125-159.

Wiegand, T., and K. A. Moloney. 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos **104**:209-229.

Williams, W. T., G. N. Lance, L. J. Webb, J. G. Tracey, and M. B. Dale. 1969. Studies in the numerical analysis of complex rain-forest communities. III. The analysis of successional data. Journal Of Ecology **57**.