



FORUM

Using biomass to model disturbance

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Whereas ecosystems are products of biotic and abiotic responses to fundamental gradients (Holdridge 1967, Whittaker 1975), they are also often disturbed by a variety of agents that structure them (DeAngelis et al. 1985). Although disturbance has been described (1) by its characteristics or regime (Clark 1996, Pickett and White 1985, Waide and Lugo 1992, Karlson and Hurd 1993), i.e., severity, frequency, size and spatial distribution, and (2) by the responses of the ecosystem after the disturbance is over (Clark 1996, van der Maarel 1993), at the most basic level a disturbance disrupts (DeAngelis et al. 1985) an ecosystem's functions, processes and states, as compared to stress which merely reduces functional performance. This disruption is the effect of the disturbance and defining disturbance this way allows better comparison both among and within disturbance types, without resorting to overly simplified disturbance dichotomies of the past (e.g., natural/human, primary succession/secondary succession, endogenous/exogenous, DeAngelis et al. 1985, Pickett and White 1985).

I argue here that the dynamics of the biomass and those functions associated with those dynamics are the key processes and states of ecosystems. Biomass is, therefore, the currency of both disturbance effects (i.e., loss of biomass) and disturbance responses (e.g., recovery of biomass). Consequently the best model of disturbance has those cycles of loss and recovery at its center, with potential translation to other spatial scales and organizational levels. Disturbance is best characterized by its effect on biomass dynamics, so that the dynamic model which I will define and develop contrasts with those that try to relate either biomass, or any of the functional correlates of biomass, to what has been called "equilibrium" or "normal" levels. The objective and purpose of the following model will be to: first, conceptualize disturbance effects,

second make predictions about responses after disturbances, and third help to understand how ecosystems function and how this function relates to structure.

The conceptual model

As a first attempt to quantify basic disturbance effects, I define an effect space having an axis upon which all disturbances can be placed and differentiated (Figure 1). That axis is percent total biomass remaining (equal to 100% initial biomass - biomass loss or translocated, where live biomass becoming dead is an example) at the time of the disturbance compared to the initial biomass present in the entire patch before any disturbances. One must first estimate initial live biomass in the patch by, for example, (a) direct measurement before the disturbance using nondestructive methods (e.g., allometric equations; Myster 2002), (b) use of productivity models, or (c) measurement of similar patches at the time of the disturbance. I have sampled in a Puerto Rican pasture and found above-ground biomass of $0.5 \text{ kg/m}^2/\text{yr}^{-1}$ in the first few years after abandonment, compared to the bordering forest's (initial) productivity of $10 \text{ kg/m}^2/\text{yr}^{-1}$ (Myster 2002, Fred Scatena pers. comm.). It has been suggested that some disturbances, such as grazing, may lead to an increase in biomass (Milchunas et al. 1992), but this is a response not an effect.

Care must be taken not to confuse amount of biomass with type (e.g., leaves vs. woody stems), but correlations between biomass and type should help to minimize these concerns. For example large biomass loss implies that wood is being removed or translocated rather than just leaves, suggesting that the canopy not just the understory has been affected. This model best applies to terrestrial systems.

This axis is justified for a number of reasons: (1) disturbance can reasonably be defined as loss of biomass (Grime 1979, Pearlt 1989, Pickett and White 1985, Tilman 1988), (2) disturbances differ fundamentally in the amount of biomass they remove; for example hurricanes remove less biomass than clearing for agriculture which in turn removes less than landslides per unit area disturbed (see Figure 1 for an example using these disturbance types from the Luquillo Experimental Forest (LEF) of Puerto Rico: Brokaw and Walker 1991, Myster 1993, Myster and Fernandez 1995, author unpub. data), (3) biomass loss fundamentally changes ecosystem structure (Pickett and White 1985), and (4) changes in availability of many important abiotic resources (an alternative definition for this axis because plant responses are often resource-mediated) are significantly correlated with biomass loss (Burton and Bazzaz 1995, Cooper 1926, Pickett and White 1985, Sousa 1984, Watt 1947). Examples of those changes in resource availability include light increasing in patches (Fernández and Fetcher 1991, Fernández and Myster 1995, Myster and Fernández 1995) as disturbances remove more biomass, and soil nutrient availability first increasing (e.g., a pulse of litter decomposition after a hurricane, Lodge et al. 1991) and then decreasing (e.g., after a more severe landslide, Myster and

Fernández 1995) as more biomass is lost by more severe disturbances.

Alternatively, this axis could have been defined as the presence through human activity of invasive, exotic species persisting more than one generation (Pyle 1995), which can alter ecosystems to a great extent (Denslow 1985, Huenneke et al. 1990, Myster and Pickett 1992, Rejmánek 1996, Tremmel and Peterson 1983) by changing biomass dynamics. However, exotics were not chosen because they are not key in all ecosystems. Some prime examples of the effects of exotics are: (1) chestnut blight, gypsy moths and Dutch elm disease reducing tree biomass in North American ecosystems (Sharples 1983), (2) "weeds" of post-agricultural old fields in the eastern United States reducing herbaceous biomass (Myster and Pickett 1992), (3) additions of ornamental and fruit-bearing plants to roadsides and around human dwellings (García-Montiel and Scatena 1994), and (4) non-native crop plants persisting after agriculture (Myster and Pickett 1990, 1994). In addition, exotics may have long lasting, or even permanent effects, because they often persist and are very competitive (Myster and Pickett 1992), causing both local extinction of natives and the subsequent take-over of their ecosystem functions. Also it should be kept in mind that the importance of exotics to ecosystems worldwide will most probably increase in the future

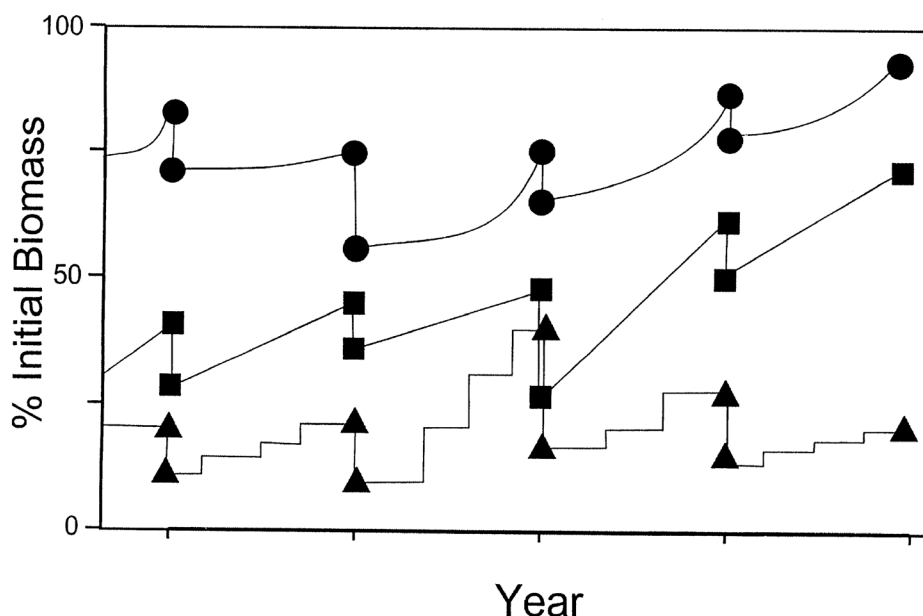


Figure 1. The disturbance and biomass recovery history, i.e., biomass dynamics, of three hypothetical patches (represented as circle, square and triangle) over a period of years. All biomass measurements are relative to an initial biomass in the patch before any disturbances occurred. A timeline is given for each patch where past disturbance events for a given patch are connected chronologically. Recovery trajectories can be linear, exponential or step-wise depending on patch and species characteristics. The entire figure could represent a forested area containing a mosaic of many patches of different disturbance histories. In the LEF, for example, the triangle could represent a patch that recurrently suffers a high-severity disturbance like a landslide, the square may represent a patch that recurrently suffers a medium-severity disturbance like agriculture and the circle may represent a patch that recurrently suffers a low-severity disturbance like a hurricane.

(D'Antonio and Vitousek 1992). Finally other possible axes, such as species loss or changes in local hydrology, are often correlated with the proposed axis of biomass loss.

Use of the model

Using this new effect space one may focus on all disturbances that affect a patch or a set of patches, placing the patch(es) on the defined axis representing fundamental disturbance effects on the ecosystem (Figure 1). This is one important use of the model and encompasses both spatial and temporal disturbance variation of patches (Myster et al. 1997). However, no matter what ecosystem is under consideration we must be careful to make clear which patch or patches were disturbed because patches may be defined in a variety of ways, even hierarchically (Pickett et al. 1987). For example, landslides have patch structure both within them (Myster and Fernández 1995), and among them, where the entire landslide is a patch on the landscape (Myster et al. 1997). We must first delineate the disturbed area and for this purpose it may be helpful to use this working definition of a patch: an area where the internal homogeneity of percent biomass remaining after the disturbance statistically exceeds the homogeneity of the biomass levels of the surrounding matrix. Also, within similar spatial scales, the model implicitly assumes that within-patch processes dominate over between-patch processes in affecting recovery.

Another important use of the model is that it realizes all of the four characteristics that make up the disturbance regime: (1) severity, (2) frequency, (3) size and (4) spatial distribution. First, the effect space recasts severity as biomass remaining (Figure 1). Second, the effect space shows how a patch has been affected by different disturbances in the past so that its disturbance history and land use is the timeline connecting past disturbances chronologically (Figure 1). The effect space also gives the placement of the disturbances in that timeline and the length of time or duration between disturbances, capturing the frequency characteristic in a more complete way than before (see Pickett and White 1985). For example, a common timeline or disturbance history for a patch in the Brazilian rainforest is logging followed by fire and then by agriculture and pasture (Uhl et al. 1990). Third, the effect space may allow investigation of both size and shape variation of patches individually, by placing patches which differ in size and not shape (e.g., a square 1 m² area, a square 2 m² area, a square 3 m² area) or in shape and not size (e.g., a round 1 m² area, a square 1 m² area, a rectangular 1 m² area) on Figure 1 (the scale-dependency of disturbance; van der Maarel 1993). And finally, fourth, the spatial dis-

tribution of patches is realized by placing patches from different locations on Figure 1.

Ecosystem responses, function and structure

Assuming biomass is the currency of disturbance effects and because plants both comprise the vast majority of the biomass in ecosystems and are their major energy, matter and chemical conduits, biomass recovery can be seen as the sum of individual plant responses (e.g., germination, growth, allocation; Myster and Pickett 1988). In that case, an important direction for future research is the investigation of how plant responses combine and interact after disturbance (i.e., the successional mechanisms, see Myster [1993] for old field trees). Indeed, the successional mechanisms of particular interest may be those which control replacements of individual plants (e.g., plant A → plant B → plant C) that can combine to produce species compositional changes over time (i.e., succession; Myster and Pickett 1990, Myster and Pickett 1992). Further, because patches are often defined by their plant composition and abundance, plant replacement processes also show how patches change (as seen in their dynamics on Figure 1).

This focus on biomass dynamics and plant responses leads to a plant-based definition of ecosystem function using Watts' (1947) key functions of *productivity*, with plant organ accumulation of nutrients (reflected in biomass recovery), and *decomposition* (a result of biomass loss or translocation; Myster 2002). Further, I suggest we identify and measure those plant structures that largely determine these key plant functions, and use them, as a first approximation, to define ecosystem structure. These structures could be, for example, leaf chemistry for decomposition and specific leaf area (leaf area/leaf dry mass), gas exchange characteristics (Burton and Bazzaz 1995), root to shoot ratio and leaf/stem architecture for productivity (N. Fetcher pers. comm., Bazzaz 1979). Mapping responses onto the disturbance effect space and evaluating function and structure are also important uses of the model, and I give a concrete example of patches and their disturbance regimes from a forested ecosystem in Figure 1.

Hypotheses and conclusions

I propose that development of disturbance theory proceed along the lines outlined by the causal framework of disturbance effect → plant response (Johnson 1984) → plant function → plant structure. To help in that development, I present hypotheses using this framework that are either (A) generally accepted by ecologists or (B) need to be tested. The second kind of hypotheses may be tested

by within-patch measurement of: (1) the basic disturbance effect of axis 1, (2) plant function (e.g., productivity, decay rate of Carbon, Phosphorus, Nitrogen) and the proposed plant structures, and (3) computation of response data over time.

Generally accepted hypotheses

1. Disturbances structure ecosystems as seen in the high degree of convergence of patches in the effect space of axis 1, especially within the same gradients. A low degree of convergence would suggest dominance of other factors, such as soil heterogeneity.

2. Biomass recovery reflects plant regeneration patterns. For example: recovery in the most severely-disturbed patches will contain fast-growing, small-seeded species and depend on seed processes (e.g., dispersal, seed predation, germination; Myster 1997) for regeneration and recovery after less-severe disturbances will be dominated by advanced regeneration/ resprouting or on the growth of already established saplings and seedlings (Oliver and Larson 1990).

3. Areas which undergo the most severe disturbances will show the greatest convergence and the highest similarity in ecosystem function and structure compared to other areas that undergo less severe disturbances, due to reduced historical effects and smaller differences in available species after the disturbance (i.e., a reduced biological legacy).

4. Patches that have been severely disturbed erase the historical effects (Myster and Pickett 1990; Myster and Pickett 1994) of other less severe disturbances and need an extended period of time (ecological hysteresis), or even restoration (Brown and Lugo 1994), for recovery.

Hypotheses that need to be tested

1. Biomass changes will depend on plant dominance; areas with high richness will show a linear response trajectory of increase in biomass, and those with a low diversity will show more of a step-wise response (see Figure 1). Step-wise response will again be seen when yearly variation in rainfall is great, but a sigmoid biomass recovery pattern may also be common (Kimmins 1997). Responses after severe disturbance will be slow at first but increase later on.

2. Response data will show synergistic effects between sequential disturbances in the same patch, by having similar response timelines among patches with different disturbance histories. Response data will also show species clumping in ordination space, suggesting species are

often interchangeable (sensu Grime 1995) and highly redundant (Gitay et al. 1996, Myster 2002).

3. The degree of convergence among trajectories will be an indication of the degree of functional equivalence of a given type of disturbance.

In summary then, this model and its framework add to disturbance theory by: (1) combining measurement and quantification of disturbance effects with testing of relationships both among disturbances and between effects and responses, (2) incorporating past dichotomies and various disturbance characteristics into a useful synthesis where the entire disturbance history of either a single patch or a set of patches can be examined, (3) using biomass to connect effect and response with ecosystem function and structure, showing how to measure each, (4) helping to illuminate the uniqueness of a disturbance to an ecosystem and (5) allowing us to examine the degree to which responses to disturbance structure ecosystems.

References

- Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10: 351-371.
- Brokaw, N.V.L. and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* 23:442-447.
- Brown, S. and A. E. Lugo. 1994. Rehabilitation of tropical lands: A key to sustaining development. *Restoration Ecol.* 2: 97-111.
- Burton, P.J. and F. A. Bazzaz. 1995. Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. *J. Ecol.* 83:99-112.
- Clark, J.S. 1996. Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *Amer. Nat.* 148:976-996.
- Cooper, W.S. 1926. The fundamentals of vegetation change. *Ecology* 7:391-413.
- D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annu. Rev. Ecol. Syst.* 23: 63-87.
- DeAngelis, D.L., J. C. Waterhouse, W. M. Post and R. V. O'Neill. 1985. Ecological modeling and disturbance evaluation. *Ecol. Model.* 29:399-419.
- Denslow, J.S. 1985. Disturbance-mediated coexistence of species. In: S. T. A. Pickett and P. S. White (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic, Orlando, pp. 307-324.
- Fernández, D.S. and N. Fetcher. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica* 23:393-399.
- Fernández, D.S. and R. W. Myster. 1995. Temporal variation and frequency distribution of photosynthetic photon flux densities on landslides in Puerto Rico. *Trop. Ecol.* 36:73-87.
- García-Montiel, D.C. and F. N. Scatena. 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. *For. Ecol. Manag.* 63:57-78.
- Gitay, H.J., J. B. Wilson and W. G. Lee. 1996. Species redundancy: a redundant concept? *J. Ecol.* 84: 121-124.

- Grime, J.P. 1979. *Plant Strategies and Vegetation Processes*. Wiley, New York.
- Grime, J.P. 1995. Functional types: a comment on Steneck and Dethier 1994. *Oikos* 73:120-121.
- Holdridge, L. R. 1967. *Life-zone Ecology*. Tropical Science Center, San Jose, Costa Rica.
- Huenneke, L.F., S. P. Hamburg, R. Koide, H. A. Mooney P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71: 478-491.
- Johnson, E. A. 1984. Disturbance: the process and the response. An epilogue. *Can. J. For. Res.* 15: 292-293.
- Karlson, R. H and L. E. Hurd. 1993. Disturbance, coral reef communities and changing ecological paradigms. *Coral Reefs* 12:117-125.
- Kimmins, J. P. 1997. Predicting sustainability of forest bioenergy production in the face of changing paradigms. *Bio. Bioe.* 13:201-212.
- Lodge, D.J, Scatena, F. N., Asbury, C. E. and M. J. Sanchez. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rainforests of Puerto Rico. *Biotropica* 23: 336-342.
- Milchunas, D. G., W. K. Lauenroth and P. L. Chapman. 1992. Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia* 92:520-531.
- Myster, R.W. 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. *Bot. Rev.* 59:259-272.
- Myster, R. W. 2002. The use of productivity and decomposition to address functional redundancy in the Neotropics. *Community Ecol.* 3:51-57.
- Myster, R.W and D. S. Fernández. 1995. Spatial gradients and patch structure on two Puerto Rican landslides. *Biotropica* 27:149-159.
- Myster, R.W. and S. T. A. Pickett. 1988. Individualistic patterns of annuals and biennials in early successional old fields. *Vegetatio* 78:53-60.
- Myster, R.W. and S. T. A. Pickett. 1990. Initial conditions, history and successional pathways in ten contrasting old fields. *Amer. Mid. Nat.* 124:125-133.
- Myster, R.W. and S. T. A. Pickett. 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. *J. Ecol.* 80:291-302.
- Myster, R.W and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology* 75: 387-392.
- Myster, R.W., J. R. Thomlinson and M. C. Larsen. 1997. Predicting landslide vegetation in patches on landscape gradients in Puerto Rico. *Landscape Ecol.* 12:299-307.
- Oliver, C.D. and B. C. Larson. 1990. *Forest Stand Dynamics*. McGraw-Hill, Inc. New York, New York.
- Peart, D.R. 1989. Species interactions in a successional grassland. II. Colonization of vegetated sites. *J. Ecol.* 77:752-766.
- Pickett, S.T.A. and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic, New York.
- Pickett, S. T. A., Collins, S. L. and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *Bot. Rev.* 53: 335-371.
- Pielou, E.C. 1984. *The Interpretation of Ecological Data: A Primer on Classification and Ordination*. Wiley, New York.
- Pyle, L. L. 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac river. *Amer. Mid. Nat.* 134:244-253.
- Rejmánek, M. 1996. Species richness and resistance to invasions. In: G. Orians, R. Dirzo and J. H. Cushman (eds), *Biodiversity and Ecosystem Process in Tropical Forests*. Springer-Verlag, New York. pp.
- Sharples, F. G. 1983. Spread of organisms with novel genotypes: thoughts from an ecological perspective. Publ. no. 2040. Oak Ridge, Tenn.: Oak Ridge National Laboratory.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15: 353-391.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Tremmel, D.C. and K. M. Peterson. 1983. Competitive subordination of a Piedmont old field successional dominant by an introduced species. *Amer. J. Bot.* 70:1125-1132.
- Uhl, C., D. Nepstad, R. Buschbacher, K. Clark, B. Kauffman and S. Subler. 1990. Studies of ecosystem response to natural and anthropogenic disturbances provide guidelines for designing sustainable land-use systems in Amazonia. In: A. B. Anderson (ed.), *Alternatives to Deforestation: Steps toward Sustainable Use of the Amazon Rainforest*. Columbia University Press, New York, pp. 24-42.
- van der Maarel, E. 1993. Some remarks on disturbance and its relations to diversity and stability. *J. Veg. Sci.* 4:733-736.
- Waide, R.B. and A. E. Lugo. 1992. A research perspective on disturbance and recovery of a tropical montane forest. In: J. G. Goldammer (ed.), *Tropical Forests in Transition*. Birkhauser Verlag, Basel, Switzerland, pp. 173-190.
- Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- Whittaker, R.H. 1975. *Communities and Ecosystems*. Macmillan, New York.