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Cleary, D.F.R.

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Chapter 1

Introduction

Humans have likely always been interested in how assemblages of plants and animals are distributed through space and time. Although originally, this was due to a need to know the location of the next meal, it is probably fair to say that humans have also regarded such natural phenomena as simply fascinating.

In more recent history, the study of animal and plant communities has continued to captivate many scientific minds. Wallace and Darwin, for example, both collected specimens of sometimes-outlandish species in exotic locations. The marvels that they documented during their voyages sparked one of the greatest of scientific revolutions, the theory of evolution.

Few studies in the tropics, however, have examined biodiversity across landscapes, especially human-dominated landscapes (Ellingsen, 2002; Ricketts et al., 2001). This includes diversity patterns of well-known taxa such as birds (Pearman, 2002). We are mostly wholly ignorant of the diversity patterns of lesser-known taxa.

The lack of empirical work in the field is problematic since models of spatial phenomena, including the arrangement of suitable habitats in space, have been shown to influence dispersal and thereby affect colonisation and extinction of species (Boughton, 2000; Casagrandi and Gatto, 1999; Molofsky, 1994). Recently, Harte et al. (1999) and Hubbell (2001) have provided a theoretical null model for the relationship between species turnover and distance. This in turn has led to some polarisation between adherents of niche-based and neutral-based theories of community dynamics. As I hope to show in this thesis, both deterministic and stochastic processes are important in determining patterns of community similarity in natural environments (see also Robinson et al., 2000). To begin, I sketch the outlines and some relevant dynamics associated with the two approaches. I then describe the main players mediating the interplay between deterministic and indeterministic factors affecting community structure in the tropics: logging, fire and El Niño. Finally, I turn to the structure of my thesis proper.

Niche-based studies and the natural environment

Niche based theories of community structure have a long history in ecological research (Grinnell, 1917; Levin, 1970; MacArthur, 1970; Diamond, 1975). Essentially, these theories are based on trade-off among species. These trade-offs include the competition-colonisation trade-off whereby dominant tree species should be seed-limited; the palatability-growth trade-off in which plant species that grow fastest when herbivores are excluded do so because they invest more in growth than defence. Here, Herbivores are predicted to alter ecosystem functioning by grazing away fast growing but palatable species and allowing unpalatable species to become dominant (Rees et al., 2001). Experimental assessments of trade-offs among plant species have, however, revealed some surprising results.

Under the competition-colonisation trade-off scenario, for example, removal of seeds by herbivores should affect dominant species more than subordinate species. Experimental results in England, however, showed the reverse (Edwards and Crawley, 1999). Subordinate species were more seed limited than dominant species, suggesting that the competition-
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Colonisation trade-off could not promote community diversity. Another study of annual plants (Turnbull et al., 1999), however, showed that even when assumed dispersal limitation of the dominant species was mitigated by very high sowing densities, inferior competitors were not lost from experimental plots. This suggests that there are species-specific life history traits in the system (e.g., growth rate, seasonal phenology and rooting depth) that allows these species to coexist (Rees et al., 2001 and refs therein).

Both the competition-colonisation trade-off and the palatability-growth trade-off are important components of successional dynamics, especially forest gap-phase dynamics (Hill et al., 2001). Successional dynamics have been shown to be highly predictable in plant communities. Early successional or pioneer plant species tend to have a series of related traits including high fecundity and rapid growth under optimal conditions and low survivorship and growth under suboptimal conditions. Early successional species also tend to have good dispersal abilities and can arrive at recently disturbed sites before climax species, reflecting the competition-colonisation trade-off. However, when disturbances are at small enough scale, the competition-colonisation trade-off should be unimportant because of the prevalence of propagules from the competitive dominants. Under initial resource-rich conditions early successional species may still, however, be dominant because the of their performance in optimal conditions. This 'successional niche' mechanism may then be more important for sustaining early successional species than the competition-colonisation trade-off (Rees et al., 2001).

Besides successional differences, tree species are able to coexist because of environmental heterogeneity in their habitat caused by a spatially variable climate, topography, and geological parent material. At larger spatial scales the response to differential water availability is particularly important, and this is obviously also linked to topography. Spatial variation in soil fertility may, however, itself be regulated by tree community composition in addition to physical processes. Tree species differ, for example, in the ratio of nitrogen to lignin in their leaf litter so that nitrogen release can vary from one tree to another by more than a factor two. This variation can be important in nitrogen limiting environments. In studying the mechanisms of species coexistence it is important to differentiate between environmental causes and successional causes of species coexistence (Rees et al., 2001).

The mobility of pollinators and seed dispersers would seem to preclude any small-scale spatial heterogeneity in plant communities. This is in sharp contrast to abiotic resources, most of which are fixed by the immediate topography. The topography, for example, can influence drainage, moisture, and nutrients (Wright, 2002). Even small changes in elevation can lead to changes in plant community composition (Harms et al., 2001). Acting together, local or regional factors may combine to produce outcomes that are difficult to trace back to a single dominant cause. Large-scale disturbances can also have an important influence on most ecosystems. Juxtaposition, however, of large-scale disturbance events may produce results that are not predictable from the events in isolation. An initial disturbance event may, for example, effect changes incurred during a subsequent event (Platt et al., 2002 and refs therein).

Chance events may be another important source of community variability. In tropical rainforests, for example, it has been established that tree species are clearly differentiated by regeneration ability in gaps versus closed canopy forest. The stochastic nature of gaps however leads to gap assemblages that are filled mostly by chance occupants rather than by species best adapted to gap environments (Brokaw and Busing, 2000). Although species are clearly defined by their ability to tolerate shade or grow quickly in light gaps, the size advantage of surviving juveniles often offsets the high growth rates achieved by pioneer-type species. This means that beta diversity is often independent of gap size, and gap history, and the assemblages of gaps are primarily due to multiple stochastic events (Wright, 2002).
Importantly, the relative dependency on external sources for ecosystem resilience will increase following large-scale and/or intense destruction of habitat. Propagules from adjacent intact habitat will be required to stimulate succession towards the pre-disturbance state. In the absence of these sources succession may be delayed indefinitely (Nystrom et al., 2000). The scale of disturbance thus matters.

Chance events also play an important role in influencing recruitment and survival. Falling debris, for example, in Panama killed 33% of liana saplings over a two-year period and falling debris in Costa Rica killed 19% of artificial seedlings over a one-year period (Wright, 2002 and refs therein). The importance of chance, and of factors such as dispersal limitation in influencing local species assemblages has stimulated the development of important alternative non-niche based models that can explain community dynamics. These models are generally called neutral models.

Neutral Models and dispersal

Whereas niche-based theories have a long history, neutral theories that focus on the random nature of communities are of more recent origin (Caswell, 1976; Harte et al., 1999; Hubbell 2001). According to neutral theory the species in a given habitat patch have been thrown together indeterminately from a larger pool of species (Hubbell, 2001). Neutral models "provide a view of what community structure would look like if there was no interactions among the component species" (Caswell, 1976).

Neutral theory has already proved a good predictor of patterns of tree beta diversity in Central and South America at intermediate spatial scales, but performed less well at small and large spatial scales (Condit et al., 2002). At the smaller spatial scales, Condit et al. (2002) noted that similarity declined more rapidly than expected with distances up to 3 to 5 km. They concluded that dispersal is strongly limited over small spatial scales, while at large spatial scales low species turnover rates (leading to greater than expected similarity) may be bounded by as yet unexplained processes. Condit et al. (2002) suggested that the rapid decline in similarity at short distances was due to species being more aggregated at these distances than predicted by theory. The high levels of similarity over large spatial distances may be due to 'equilibrating processes' such as differences in life history or pest resistance that control densities of species over large areas. Hubbell (2001) also provides a number of examples in which his neutral theory proves a very good predictor of real-life species abundance distributions.

One of the most critical factors in describing communities with neutral models is dispersal limitation (Parsons, 1997). Under very low rates of dispersal a single species is expected to dominate each local community. As dispersal increases immigrants are able to reach neighbouring communities thereby changing the local species abundance distributions to include more rare species (Bell, 2001). The idea of dispersal limitation is somewhat older than the general neutral theories, and points to an early perception that random processes could play a role in structuring communities. Gleason (1923) and Palmgren (1926), for example, suggested that dispersal limitation and passive propagule dispersal were major factors in community composition.

If indeed dispersal regulates community similarity, then proximate plots will contain similar assemblages of species and in similar proportions, and this similarity will decline with distance as dispersal limitation sets in (Hubbell, 2001). A negative relationship between community similarity and distance is expected in most ecological phenomena (Nekola and White, 1999). Alternatively, local environmental conditions may prevail because certain species depend on a given set of environmental conditions for survival. This would lead to a much weaker relationship between distance and dissimilarity.
Both of the processes introduced above are likely to act in concert to determine patterns of community similarity within and among habitats. Partitioning ecological variation exhibited by communities into that explained by purely spatial and that explained by environmental phenomena is crucial to understanding the mechanisms behind patterns of biodiversity (Borcard et al., 1992; Condit et al., 2002; Duivenvoorden et al., 2002). Importantly, the relationship between spatial distance and community similarity is assumed to be a predictor of community-wide dispersal rates (Spencer et al. 2002). Community similarity is analogous to variance in univariate factors such as pH concentration in soils and species density. Community similarity, however, consists of pairwise comparisons of observations from different locations and is a complex function of the occurrences and abundances of many species at each location (Nekola and White, 1999).

It is important to note that in addition to dispersal limitation, the distance decay of community similarity can also be related to spatially structured environmental processes. The relationship between the spatial configuration of habitats within an ecosystem and intrinsic dispersal ability of its occupants will also influence the duration of historical effects. A relationship between dispersal ability and habitat configuration may also influence the rate of succession from a disturbed secondary state to primary-like conditions. In turn, many factors, such as the nature of the habitat configuration, which influence distance-decay in community similarity and the rate at which ecological processes propagate, are themselves related to historic events such as disturbance.

**Disturbance**

Large-scale habitat variation, especially when disturbance-induced, can have an important effect on community rates of dispersal. Disturbance has been defined as “a force, often abrupt and unpredictable, with a duration shorter than the time between disturbance events, that kills or badly damages organisms and alters the availability of resources” (Mackey and Currie, 2000). When optimal habitat is destroyed the upper dispersal threshold of organisms is lowered. Organisms that can survive in a pristine but patchy habitat may go extinct in a partly destroyed landscape because their high dispersal ability allows them to be lost to unsuitable habitat (Casagrandi and Gatto, 1999). These dispersers may leave a patch, and simply not find another. Destruction of intermittent habitat between remnant patches as fragmentation proceeds will initially have three potentially important consequences. First, organisms will move longer distances as fragmentation increases. Second, the proportion of organisms moving will decrease with increasing fragmentation, and third, species will begin to show source-sink dynamics (Diffendorfer et al., 1995).

Disturbance should not be merely seen as a negative factor in structuring communities for it also increases the heterogeneity of the environment and the total amount of ecological space available (Ricklefs, 1987). An increase in habitat heterogeneity should lead to an increase in species (Rozenzweig, 1995). Intermediate levels of disturbance have been suggested to be important for maintaining high levels of diversity in coral reefs and other ecosystems (Connell, 1978). In fact, it is generally believed that coral reefs are disturbance-driven systems that are continually in a state of disequilibrium (Pandolfi, 2002). Without disturbance, competitive exclusion may lead to species loss and thus impoverishment of these diverse ecosystems. Disturbance thus seems to supply space for fugitive or non-equilibrium species (Caswell and Cohen, 1991). Two thirds of the canopy and subcanopy trees of a Costa Rican tropical lowland forest require tree gaps for regeneration and would probably become extinct without this type of disturbance. In addition to affecting dispersal, recent research on the impact of disturbance on community structure has shown the prevalence of multiple equilibria, nonlinearity and threshold effects (Nyström et al., 2000).
Although natural disturbance such as gap-dynamics in rainforests appear to occur in short pulses and may benefit diversity, human-induced disturbances are often chronic and tend to accumulate with time (Nyström et al., 2000). In tropical terrestrial ecosystems Two of the most important forms of human-induced or human-mediated disturbances are logging and ENSO (El Niño Southern Oscillation) -induced forest fires.

**Logging**

How logging affects biodiversity is one of the most important questions facing forest ecologists. Answering this has considerable repercussions for forest management and conservation since both the logging industry and conservation group see sustainable forestry as a key goal (Summerville and Crist, 2002).

Numerous studies have addressed the impact of logging on levels of diversity. Cannon et al. (1998) showed that tree species richness of primary and logged forests in Borneo were similar when re-scaled to the number of individuals sampled instead of using quadrat-based species richness. Selective logging in Belize did not significantly change the species richness of fruit-feeding butterflies or birds and had little effect on assemblage composition (Lewis, 2001). The species richness of butterflies in Asia (Spitzer et al., 1997; Willot et al., 2000) and ants in South America (Vasconcelos et al., 2000) showed either no response or a positive response to logging. Species richness in a Sabahan logging concession was higher in logged forest than in primary forest because of the presence of more forest edge species in the logged forest (Johns, 1996). Rainforest avifaunas, in general, are characterised by losing very few, if any species as a result of logging (Johns, 1996 and refs therein). Some studies, however, have shown some species losses (Thiolay, 1992; 1997). In line with the intermediate disturbance hypothesis (Connell, 1978) the diversity of temperate lepidoptera, coleoptera, and flora increased in selectively logged forest in comparison with unlogged and clear-cut forest (Summerville and Crist, 2002 and refs therein).

In general selective logging does not seem to have a seriously negative impact on levels of species richness. This may be due to a number of factors including the scale of study. Small-scale studies that assessed ecological phenomena in isolation from the larger landscape-context proved successful in elucidating mechanisms such as competition, mutualism, predation, and disease, but proved much less successful in identifying causes for the spatial and temporal variation in the abundance, distribution, and species richness of communities (Brown et al., 2001). Notably, studies that failed to find effects of logging on biodiversity have been frequently small-scale studies (refs in Summerville and Crist, 2002).

Lack of an initial impact of logging on levels of species richness does not, however, mean that logging has no negative effect. The secondary effects of logging may often be worse than the primary. Logging facilitates an influx of hunters, illegal loggers, ranchers, and slash-and-burn farmers (Laurance, 2000). These effects may, also only be manifest after longer periods of time. Illegal logging, especially, is a serious problem in Indonesia. Illegal logging gangs will even resort to terror and have burned concession camps if these interfered with their activities (Jepson et al., 2001). Indeed, the camp I stayed in during my field work in Central Kalimantan in 1998 was burned to the ground, presumably by illegal loggers, very few days after I had completed my fieldwork and left.

Probably the greatest threat to logged forests is from fires (Nepstad et al., 2001). Logging, even at low intensity, can irrevocably change the forest microclimate (Peres, 1999) and lead to a significant increase in total fuel mass (Uhl and Kauffman, 1990). Both logging and fires increase the probability of future fires (Nepstad et al., 1999), which can be much worse than initial fires in flame height, intensity, depth, residence time, and rate of spread (Cochrane et al., 1999). The occurrence of forest fires in the moist tropics is not a purely natural
phenomenon, however. The requisite ignition source is almost always human (Laurance et al., 2001). During a four month period, satellites revealed 44 734 individual fires in the Amazon, most of which were caused by humans (Laurance, 1998). During the 1997/98 El Niño in Amazonia 20 000 Km² of forest burned, but a further 1.5 million km² of forest newly susceptible to burning did not burn because of insufficient ignition sources (Nepstad et al., 2001). In Borneo severe droughts occurred before the infamous 1982/83 and 1997/98 ENSO-induced fire events but the droughts before 1982/83 did not lead to large-scale fires. The fires of 1982/83 and 1997/98 can be largely attributed to greater fire susceptibility of disturbed forests and the increased density of man-made ignition sources (Woods, 1989).

Ironically, burning forests is seen as a cheap alternative to sustainable agricultural investments (Nepstad et al., 2001). Fire, however, also increases forest susceptibility to future fires, and discourages fire-sensitive investments such as agroforestry. Agriculturists who wish to abandon the use of fire and invest in other crops are generally discouraged from doing so by the constant threat of fires from neighbouring lands (Nepstad et al., 2001).

Although fires have always been present in Southeast Asia and in much of the world, population growth, changes in land-use, and ENSO events have increased the probability of catastrophic fires (Kinnaird and O'Brien, 1998). The combination of logging, migrant farmers, and ENSO-induced drought are responsible for the catastrophic fires in 1982/83 and 1997/98 that destroyed huge areas of Bornean rain forest (Laurance, 1998).

**ENSO**

El Niño is defined as "an extensive warming of the upper ocean in the tropical eastern pacific lasting more than five months." The Southern oscillation is a "widespread interannual oscillation in sea-level pressure between one region near northern Australia and one in the central Pacific" (Wang et al., 1999). ENSO events have a variable period of 2.5 to 7 years (Tudhope et al., 2001) and can cause global changes to weather conditions because of the huge expanse of warm waters in the Pacific and concomitant increase in evaporation from the ocean (Fedorov and Philander, 2000). The ENSO phenomenon is in fact the strongest interannual climatic fluctuation with both regional and global impact. It can affect societies and economies of many countries and can have pronounced effects on ecosystem functioning (Timmermann et al., 1999).

Fires associated with ENSO events have been described for East Kalimantan (Indonesian Borneo) as early as 1914, but until recently these were small in scale. This has been attributed to the normally high resistance of undisturbed primary forest to burning, and the lack of ignition sources in such forests. The first recorded major burning event in East Kalimantan was during the 1982/83 ENSO event (Sieger et al., 2001), with the second, even more severe event occurring in 1997/98. Before describing some of the effects of these two catastrophes, I note that some sceptics consider ENSO-induced fires to be a purely natural event with a long history in Borneo, and which should not pose any threat to ecosystem functioning (Stott, 1999).

Mean global temperatures have risen this century, and will continue to rise for the next 50-100 years (Easterling et al., 1997). During the last 20 years ENSO events have increased in both strength and duration as a result of this global warming (Trenberth and Hoar, 1996). Recent models show that predicted global climate change will result in more frequent and more extreme ENSO-like events (Guilderson and Schrag, 1998; Holmgren et al., 2001; Salafsky, 1998; Timmermann et al., 1999), but there are still uncertainties in the exact nature of the predicted changes (Fedorov and Philander, 2000). The amplitude, however, of modern ENSO events already appears to be significantly greater now than during any other time over the past 150,000 years (Tudhope et al., 2001).
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The 1997/98 record breaking ENSO-induced drought followed only 15 years after the previous record drought of 1982/83 (Harrison, 2000; McPhaden, 1999). The 1997/98 ENSO-induced fires in East Kalimantan far surpassed the 1982/83 fires and blanketed approximately 20 million people in smoke for months, having a disastrous impact both on local health and the economy (Jepson et al., 2001). In addition to occurring in most of the previously (1982/83) affected areas, an additional 40% of forests were affected, mainly in recently opened up areas in logging concessions (Siegert et al., 2001). During the 1997/98 ENSO event an estimated 5.2 million ha of East Kalimantan were affected by fires; 24% of this area had moderate damage (25-50% of trees dead), 42% had severe damage (50-80% of trees dead), while 34% had total damage (> 80% of trees dead). In addition to damaging the forests, the fires greatly increased the risk of future fires due to the large amounts of flammable dead wood (Siegert et al., 2001).

Predicted changes in ENSO events have the potential to profoundly alter biodiversity and ecosystem functioning (Holmgren et al., 2001). There is now overwhelming evidence that coral reefs are being affected by global ecological changes that are altering community states and that will result in reduced species richness (Pandolfi, 2002). In coral reefs, the 1997/98 bleaching event was the most severe and widespread ever recorded. Some scientists fear that a threshold may have already been reached where reefs will not be able to cope with the increasing intensity and frequency of future bleaching events associated with ENSO-induced disturbances (Nystrom et al., 2000). In contrast to the impacts of ENSO events on marine ecosystems, those on terrestrial ecosystems have been poorly studied (Holmgren et al., 2001). Hardly anything is known about the response of animal populations to severe ENSO events (Harrison, 2001). Without any quantitative knowledge on how terrestrial ecosystems are affected by ENSO events it will be very difficult to take any protective measures to conserve susceptible areas and species. In the absence of changes in land-use and implementation of reduced-impact logging techniques and land-monitoring recurrent fires may lead to the complete loss of Borneo’s lowland rainforests (Siegert et al., 2001).

Scale

Recently, scientists have become aware of the fact that many taxa are affected by both local and landscape-scale variation in habitat structure (Drapeau et al., 2000 and refs therein). Mechanisms that affect community structure can fall into two scale-related categories. First there are mechanisms that affect communities at small spatial scales such as competition or microclimatic variables that affect physiological traits. Alternatively, there are landscape-scale mechanisms that may not act directly on individuals but may have a strong effect on communities. Fragmentation, to take a well-known example, can decrease rates of dispersal and severely constrain gene flow (Pearman, 2002).

At small spatial scales community structure seems to show greater than expected variance (Pandolfi, 2002). Studies in the most diverse ecosystems, coral reefs, and tropical rainforests, for example, have shown that enlarging the spatial scale of study leads to highly consistent patterns in community structure. The high variability observed within sites declines, often dramatically, as larger areas (landscapes) are sampled (Pandolfi, 2002). Overall, studies at small (and extremely large) spatial and temporal scales show the largest variance in community structure, whereas studies conducted at intermediate (landscape) scales show high degrees of order in community structure. Small spatial scales include plot-based studies of ca. one ha or less, whereas landscape spatial scales include anything in between 1 and 100 Kms. Small and landscape scalar relationships will, however, also depend on the taxon under study and mean community-wide levels of dispersal (Pandolfi, 2002).
Studies that have specifically addressed the impact of scale on community traits have tended to show that responses to scale-related environmental change can vary both among and within taxa. Pearman (2002) found a significant relationship between local-scale habitat structure and species richness in certain bird guilds but not in others. He also found that, for certain guilds, the area of primary forest cover within hundreds of metres of his plots (large-scale) was a better predictor of species richness than local habitat structure.

In another bird study, landscape factors were as important as local factors in determining the community composition of mixed boreal forests in Canada (Drapeau et al., 2000). Other studies, however, failed to find an important impact of landscape scale factors on bird communities. Schmiegelow et al. (1997), for example, concluded that the impact of a landscape scale affect such as fragmentation was small on boreal bird assemblages. Likewise, urban bird species richness was found to be independent of the surrounding periurban landscape and city size in North America and Europe, and to primarily depend on local habitat structure (Clergeau et al., 2001 and refs therein). Bird communities in different cities were more similar in the same type of habitat than within cities in different habitats. Urban bird communities may also be composed of bird taxa that are not common in the surrounding landscape, thus showing the importance of local over regional factors in determining urban bird community composition and species richness. Other taxa, however, such as mammals, insects, and lizards were found to respond to the surrounding periurban landscapes (Clergeau et al., 2001 and refs therein).

Scale is also very important in determining the pattern of distance decay in community similarity. Natural environmental periodicities may, for example, cause the lack of a relationship between community similarity and distance at certain spatial scales. A relationship between community similarity and distance may also be prevalent at small spatial scales, e.g. in a study from a mountain crest to valley, due to the pronounced environmental gradient. This effect may disappear as more mountain crests and valleys are included in the study (Nekola and White, 1999).

By understanding and studying ecological communities at multiple spatial scales we stand to learn the most about processes and mechanisms that regulate the maintenance of biological diversity (Pandolfi, 2002). Given enough resources large-scale field manipulation experiments may provide insight into the importance of scale on patterns of biodiversity (Godfray and Lawton, 2001). As of present, however, few studies have addressed the impact of scale on species communities even in well-known taxa. Pearman (2002) reported that no studies explicitly addressed how tropical forest understory bird communities are associated with habitat variation at different spatial scales. Importantly, the mixed success of relating habitat structure to faunal diversity has often been related to an inappropriate scale of assessment (Williams et al., 2002). High-resolution data sets documenting the occurrence of large numbers of species over extensive areas are therefore badly required (Gaston, 2000).

**Large-scale studies and pseudoreplication**

One of the main impediments to studying ENSO-induced disturbance or landscape patterns of beta-diversity is that these processes tend to occur over too large a spatial scale for standard research techniques. Historical and regional processes in general are less open to experimentation than local processes in ecological time, but they can be studied using comparative studies, pattern analysis, and natural experiments (Ricklefs, 1987). Due to the expense or impossibility of performing manipulated field experiments they should therefore not have priority over 'natural experiments' since neither replication nor control is an essential part of critical experimentation (although they should be obtained when possible) (Oksanen, 2001). The size and severity of disturbances, for instance, can preclude
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experimental manipulation. An example is the conversion of forest to heathland where severe disturbances are required to remove the trees and a large portion of the topsoil. Severe fire is the most likely event that can initiate such a change because it both kills the vegetation and consumes soil organic matter (Petraitis and Latham, 1999). Often, however, the scale and severity of fire necessary to simulate such a natural fire event are beyond the financial and logistical capacities of most ecologists.

In the tropics, the large size and long regeneration times of trees, coupled with very low population densities would seem to preclude an experimental approach to evaluate mechanisms that facilitate or inhibit plant species coexistence in tropical forests. Alternative methods may include measurements that could be used as parameters in models (Wright, 2002). Studies have also shown that the dynamics induced from cellular automata or coupled map lattice models are predicted to arise at spatial scales larger than those studied by most biologists (Rohani et al., 1997).

It is important, therefore, to realise that not all hypotheses can be tested with experimentation, especially where systems are too large and complex, past events are important, and processes are too slow. It is unfortunate that studies using natural experiments over large spatial and temporal scales are often perceived of as being of less scientific relevance than strictly experimental studies. This arises from the "myth of experimental superiority" based on the experimental monopoly of falsification whereby hypotheses are tested and either accepted or rejected. Even in experimental studies, however, the tests often only falsify auxiliary assumptions that often produce non-confirming results. In contrast, hypotheses placed in an historical context may only need a few important comparative assessments in order to provide inferences that are just as rich in explanatory power as confirmatory results in experiments (Arens, 2002).

Another problem with large-scale studies is replication. Obviously, plots of 1-m² are easier to replicate than whole landscapes. Although plots of 1-m² may be useful for assessing the diversity of nematodes they are probably of less use to assessing the diversity of trees, butterflies, or larger animals. Using small plots can even bias results. In a study of corals, local species richness in small 1-m² quadrats was much more sensitive to local variables such as depth and habitat and insensitive to regional richness. Larger 10 m transects, however, were sensitive to regional species richness (Karlson and Cornell, 2002).

Unfortunately, achieving replication at large spatial scales can cause a considerable increase in cost and concomitant logistical problems. Testing general theories would therefore benefit by a larger number of unreplicated or so-called ‘pseudoreplicated’ studies in different areas and on different taxa. Oksanen (2001) notes that “an unreplicated test of strong and critical predictions is likely to be more instructive than a well-replicated test of weak and trivial ones.”

The use of pseudoreplication for qualifying certain studies has also been much abused recently. It is therefore important to specify perceived statistical problems in studies where these exist (Oksanen, 2001). When possible, interval estimates should be given, whether taken over replicated plots within an area or simulated using bootstraps or other methods. The pseudoreplication (Hurlbert, 1984) debate has sometimes led to “entirely unwarranted stigmatisation of a reasonable way to test predictions referring to large-scale systems” (Oksanen, 2001). Strictly speaking, Oksanen (2001) conjectures that replication is even unnecessary from hypothetico-deductivist reasoning. For a deductive study it is therefore perfectly acceptable to assign systems randomly to treatment and control situations where the vigour of the study will depend on a priori hypotheses and their probability of corroboration. This is especially the case when predictions of change are dramatic enough to make any otherwise spontaneous changes in the system of negligible importance.
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Outline of this thesis

In this work, I use various species groups of animals and plants to address the impact of logging and ENSO-induced fires on community composition, species richness, and species evenness. I further assess patterns of beta diversity across landscapes. The species groups used include butterflies, birds, odonates, lianas, and trees. Certain species groups were examined in more detail by using guilds in small- and large-scale analyses. Some taxa, for example, may not be expected to show non-random structure if they are composed of such a heterogeneous mix of ecologically distinct functional groups or guilds that they succumb to the ‘dilution effect’ (Gotelli and McCabe, 2002).

In chapter 2, easy-to-measure habitat structural variables and community attributes of butterflies and birds were assessed in a logging concession located in Central Kalimantan, using an environmental classification based on topography, wetness, and radiation in addition to logging. I report that the habitat structure differed strongly and significantly among forest types (primary and logged) and moderately among classes in the environmental classification. Logging significantly raised butterfly species richness, but had no effect on bird species richness. Both butterfly and bird community composition varied significantly among forest types. Wetness and topography were moderately important factors in structuring the butterfly community and wetness was a moderately important factor in the bird community.

In chapter 3, the impact of logging on species richness and community similarity of five bird guilds (viz., canopy omnivores, canopy insectivores, frugivores, understory omnivores, and understory insectivores) was assessed in the same logging concession from Ch. 2, this time at two spatial scales. Consistent with ch.2, there was no overall difference in mean species richness at the smaller spatial scale among forest types (recently logged, older logged, or primary forest) in four of the five guilds, but pronounced differences in total rarefied species richness at the larger spatial scale among forest types and among guilds. Changes in community similarity (beta diversity) in all guilds was surprisingly unrelated to spatial distance between plots, but was related to changes in the physical environment and habitat structure at local and landscape scales.

In Chapter 4, the degree of congruence in species richness (alpha diversity) and community similarity (beta diversity) of butterflies, odonates, lianas, and trees was assessed in a logging concession and adjacent forest reserve in East Kalimantan. Environmental variables significantly explained variation in all four groups, but geographic distance only proved significant in lianas. There was furthermore no relationship between patterns of alpha diversity among species groups, but patterns of beta diversity proved to be significantly congruent.

In Chapter 5 butterflies and odonates were compared in a remnant area of primary forest and two areas of burned forest in East Kalimantan. Post-ENSO species richness was higher for both taxa in a once-burned habitat than in either primary or twice-burned habitat. All three habitats, however, had a significantly depauperate butterfly fauna compared to values from the same area recorded pre-ENSO. Variation in community similarity was explained by a reduction in similarity between plots in primary and burned forest (49% for butterflies and 6% for odonates) and by a reduction in similarity with distance (22% for butterflies and 21% for odonates). Local habitat structure was relatively unimportant in predicting variation in community similarity of both taxa.
In Chapter 1, butterfly species richness and community composition are compared temporally in two forest reserves, the Sungai Wain Protected Forest Reserve and the Wanariset Research Forest Reserve. In both reserves assemblages are assessed in three habitats, primary and adjacent burned forest in Sungai Wain, and burned forest in Wanariset. Post-ENSO there was no significant change in species richness and evenness in the Sungai Wain primary and burned forest. In the Wanariset burned forest there was a significant decline in species richness and evenness from pre- to post-ENSO. Subsequently there was a significant increase from 1998 to 2000, but levels are still significantly lower than pre-ENSO. Community composition in all three habitats changed significantly from 1998 to 2000 suggesting that all three forests, including the primary forest, are experiencing significant post-ENSO restructuring.

In Chapter 7, I deal with temporal changes following forest fires in density, species richness and community composition of seedlings and saplings in an unburned forest reserve in East Kalimantan and the adjacent burned forest. Densities of seedlings declined in both unburned and burned forest while sapling densities increased. Both saplings and seedling densities remained, however, much lower in burned than unburned forest. There was no significant trend in mean species richness, but total rarefied species richness of seedlings increased in both unburned and burned forest with increasing sample size or geographic scale. The total rarefied species richness of saplings, however, increased in unburned forest, but declined in burned forest. Most unburned forest species, however, failed to germinate in the burned forest over the 3-year study period suggesting that the burned forest will remain in a severely degraded state for a prolonged period of time.

In Chapter 8, scale related changes in species richness of butterflies and of butterfly guilds are compared across Borneo, in both Central and East Kalimantan, in primary, logged, and burned forest. Overall species richness was significantly lower in burned forest than continuous forest. Species richness in the isolates was intermediate. The difference was more pronounced at the large spatial scale than at the smaller spatial scale. In contrast to species richness, there was no significant difference in either dominance or evenness among disturbance classes. Among guilds, tree specialist abundance and species richness was significantly lower in burned forest than continuous forest, and herb specialist abundance (but not species richness) was significantly higher. The largest difference in species richness was, however, in the generalist guild with significantly fewer species in burned forest and isolates than in continuous forest. Our results with guilds indicate that a response to one form of disturbance (logging) provides very little insight into responses for other disturbance forms such as ENSO-induced burning. Surprisingly, ecological generalism in host plant range may make butterflies more susceptible to local or regional extirpation following large-scale disturbances such as ENSO-induced burning, though no mechanism for this is presented.

In Chapter 9 the practical application of butterflies as indicators of logging-induced disturbance is assessed in two logging concessions in Central and East Kalimantan. Few or no taxa have been identified as reliable indicators of logging disturbance (Peres, 1999). I assess the degree to which butterflies respond to logging in terms of species richness, community composition and use an indicator test of individual taxa. I further compare results at three different taxonomic levels 1) species, 2) genera, and 3) subfamilies. This can be of potential use to monitoring programs since identifications to lower taxonomic levels (especially to species) require extra investments in time and money and requires considerable taxonomic expertise. Importantly, genera provide a highly acceptable alternative to species as indicators.
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In Chapter 10 rarefaction curves are explicitly considered as a potential tool for testing the response of butterflies to disturbance. Levels of species richness are compared in areas sampled before and after the 1997/98 ENSO event in a region that did not burn and in a region that was severely affected. After the fires (1998 onwards) levels of species richness are compared in three areas of continuous forest, three unburned isolates now surrounded by burned forest, and three areas of burned forest. Rarefaction curves provide an important means of comparing levels of species richness at large spatial scales and are able to significantly differentiate among differentially disturbed areas. Importantly there was no temporal variation in species richness from pre- to post-ENSO in an area that was unaffected by ENSO-induced burning in Central Kalimantan. In East Kalimantan, however, species richness was reduced by more than 50% in an area that burned during the 1997/98 ENSO event.

A note on statistical focus

Throughout the thesis various statistical techniques are used to assess levels of community composition and species richness across landscapes and disturbance regimes. Species richness and composition are measures for the total number and abundance of species in an assemblage and may be the most fundamental measures in ecology (Pachepsky et al., 2001).

For species richness rarefaction was always used. It is an often-overlooked prerequisite to rarefy samples when comparisons are made of species richness: species richness is based on the number of individuals as is the case in most community ecology-based models where parameter for abundance \( N \) and population growth rates \( \frac{dN}{dt} \) are per capita (individual-based) coefficients (Gotelli and Colwell, 2001). Overall, the best way to compare sampling is to use the number of individuals as the basic unit of comparison (Willott, 2001). This will help to avoid problems such as the impact of trapping efficiency, or observer bias, which can confound genuine differences in species richness between sites. Standardising by area or sampling effort may produce very different results than standardising by the number of individuals (Gotelli and Colwell, 2001). For rarefaction it is furthermore important to note that sample sizes need to be sufficient to distinguish between different patterns of species richness, because rarefaction curves tend to converge at low abundances, making them conservative. Rarefaction can also not be used for extrapolating to larger sample sizes (Gotelli and Colwell, 2001).

For assessment of small-scale species richness, plot-level ANOVAs were used to compare rarefied species richness among habitats. For comparisons of large-scale species richness, rarefaction curves were obtained by resampling individuals (or samples) at random and plotting the average number of species present for a given sample size (of individuals or samples). Rarefaction curves are similar to accumulation curves but accumulation curves record the total number of species obtained chronologically during collection. Both rarefaction and accumulation curves may be individual- or sample-based. Sample-based curves should, however, be plotted using the accumulated number of individuals and not the accumulated number of samples (Gotelli and Colwell, 2001).

Species accumulation or the analogous rarefaction curves are an “essential component” of studies that compare levels of species richness among sites (Willott, 2001). Both ecological processes and sampling processes increase species number with area, but only ecological processes could be expected to increase species richness per unit area. Before a species-area
curve can be used as an indicator of ecological processes it is important to remove the effect of sampling (Hill et al., 1994) and the best method of comparing the actual level of species richness is to use the number of individuals as the measure of sampling effort (Willott, 2001). Species accumulation curves, furthermore, reduce sampling bias and avoid the problem of pseudosaturation when comparing local and larger-scale levels of species richness (Caley and Schluter, 1997; Karlson and Cornell, 2002). There are some alternatives to individual-based rarefaction estimates of species richness, including a number of species richness estimators that can be used to estimate ‘true species richness’. These estimators, however, often fail to reach any asymptote when applied to datasets of diverse taxa (Gotelli and Colwell, 2001).

**Analysis of species composition and beta diversity**

Biodiversity cannot be encompassed by a single measure such as species richness; instead, species distributions, and especially community composition should be included during assessments. Beta diversity is the change in community composition along a gradient. Very few studies have assessed patterns of beta diversity (but see Condit et al., 2002 and Ellingsen, 2002). Multivariate measures of beta diversity have proven much more sensitive to small changes in faunal composition of marine benthos than univariate measures (Ellingsen, 2002). These multivariate measures include the use of similarity indices, which assess comparisons of similarity between pairs of sites. These values are then used to construct a matrix of pairwise comparisons for a given set of sites. There are numerous similarity indices that can and are used. In the present set of studies I used the Bray-Curtis similarity index (Bray and Curtis, 1957) often used in ecological studies (see, e.g., Clarke and Gorley, 2001; Ellingsen, 2002; Pandolfi, 2002).

Spatial patterns of beta diversity using the Bray-Curtis similarity index were assessed across landscapes. Community patterns may be due to patterns of dispersal or due to the spatial arrangement of environmental conditions. Similar communities in adjacent habitats may in fact be due to either or both of these conditions. Separating the contribution of space and the contribution of environment to patterns of community similarity is necessary, however, for understanding the mechanisms of community structure across landscapes (Spencer et al., 2002).

Because values of matrices of community similarity are not independent, I used multiple matrix regression based on permutations to assess the significance of regression models and to compare the relative proportion of variance explained by spatial and environmental processes in each taxonomic grouping (Nekola and White, 1999). Importantly, multiple matrix regression allowed me to separate the contribution of environmental and purely spatial phenomena to explaining patterns of community similarity.

In all studies, I used a system of small-scale (generally less than 1 ha) plots nested in a larger landscape context (450 ha landscape-scale ‘plots’). This allows me to assess levels of species richness at both small and intermediate spatial scales. Within the 450 ha landscapes, plots were randomly allocated, or located on maps in advance using previously determined environmental criteria, such as topographical position. In the field these plots were then located with the use of compass, clinometer, and georeferenced with standard GPS devices. In addition to sampling species, I also measured a number of environmental or habitat structural variables in each plot in order to relate community traits to environmental traits.

After describing patterns of diversity across pristine, logged and burned landscapes, several additional questions and hypotheses were addressed with this study. Examples include the hypothesis that changes in community composition were related to logging-induced shifts in habitat structure. Further I asked: is there a relationship between community similarity and distance, and if so is this related to environmental or spatial processes? Is this
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relationship scale-dependent, i.e., is there a difference between large-spatial scales (among landscapes) and small spatial scales (within landscapes)?

The analyses presented in this thesis only hint at the ultimate goal of predictive species-habitat models. The rich dataset, and explicit scale-dependent sampling should aid in tuning of such models, both generally, and for the specific areas (here, Borneo) where they are most sorely needed.

References

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