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MAN AND THE BIOSPHERE SERIES

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FOREST BIODIVERSITY RESEARCH, MONITORING AND MODELING

Conceptual Background and Old World Case Studies

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CONTENTS

PREFACE

UNESCO's Man and the Biosphere Programme

Improving scientific understanding of natural and social processes relating to human interactions with the environment; providing information useful to decision-making on resource use; promoting the conservation of genetic diversity as an integral part of land management; enjoining the efforts of scientists, policy-makers, and local people in problem-solving ventures; mobilizing resources for field activities; strengthening of regional cooperative frameworks – these are some of the generic characteristics of UNESCO's Man and the Biosphere (MAB) Programme.

The MAB Programme was launched in the early 1970s. It is a nationally based, international programme of research, training, demonstration, and information diffusion. The overall aim is to contribute to efforts for providing the scientific basis and trained personnel needed to deal with problems of rational utilization and conservation of resources and resource systems and problems of human settlements. MAB emphasizes research for solving problems. It thus involves research by interdisciplinary teams on the interactions among ecological and social systems, field training, and application of a systems approach to understanding the relationships among the natural and human components of development and environmental management.

MAB is a decentralized programme with field projects and training activities in all regions of the world. These are carried out by scientists and technicians from universities, academies of sciences, national research laboratories, and other research and development institutions under the auspices of more than one hundred MAB National Committees. Activities are undertaken in cooperation with a range of international governmental and non-governmental organizations.

Man and the Biosphere Book Series

MAN AND THE BIOSPHERE SERIES

ACKNOWLEDGMENTS

upper level university students, scientists, and resource managers, who are not necessarily specialists in ecology. The books are not normally suitable for undergraduate text books but rather provide additional resource material in the form of case studies based on primary data collection and written by the researchers involved; global and regional syntheses of comparative research conducted in several sites or countries; and state-of-the-art assessments of knowledge or methodological approaches based on scientific meetings, commissioned reports, or panels of experts.

Documenting and analyzing forest biodiversity in Europe, Australasia, and Africa

A heightened awareness of the importance of biological diversity, at all of its levels, to humankind has generated increased support for on-going and new efforts targeted at documenting biodiversity and analyzing the results of such work. While it may be that no amount of financial and technical support will be sufficient to identify and monitor the millions of species that have yet to be discovered, there is little doubt about the usefulness of continued research in this arena. What scientists are discovering about known species and what they hope to discover as unknown species come to light can be immensely helpful to resource managers and decision-makers who are responsible for rational allocation of scarce as well as seemingly abundant resources and who desire to bring about sustainable use and conservation of those resources.

Throughout the world, work in this area is progressing. The introductory chapters in this book provide the theoretical framework behind plot-based monitoring. The second section describes how plot-based results have been put to a variety of uses such as defining the number of trees to be sampled in smaller plots, monitoring climatic change, ground-truthing satellite imagery to map forests, analyzing global trends in tree mortality, determining seed-dispersal patterns, and developing new analytical techniques for assessing patterns of diversity. Section three outlines some of the monitoring programs and networks currently in place in Europe. The remainder of the volume presents case studies from Africa, Australia, and Southeast Asia. Many of the studies have been underway for several years or have been recently initiated to document biodiversity and then monitor changes in species composition and ecosystem functions. These chapters provide details about specific biodiversity research sites – locality and geographic information, methodologies employed in measuring and monitoring biodiversity at the sites, and results of on-going research at the long-established sites and initial inventories at the more recent sites. In most cases, plots that are representative of a larger area have been chosen for the work, with the expectation that the results will be applicable elsewhere.

sections to both books, the majority of the chapters are based on papers presented at the first international symposium on measuring and monitoring biodiversity, organized by the Smithsonian Institution/MAB Biological Diversity Program in May 1995. It is hoped that the information presented in both volumes will prove useful to researchers as well as decision-makers and on-site managers in meeting the challenge of maintaining the Earth's valuable storehouse of biodiversity.

Geoffrey G. Parker, Ganapati Patil, John J. Pipoly III, Andrew Plumptre, Marsha Pomeroy, Richard B. Primack, Jamie Reaser, Anne E. Reilly, Earl Saxon, Fred N. Scatena, Douglas Sheil, Andrew Small, Sy H. Sohmer, Roger Soles, Heinrich Spiecker, Thomas J. Stohlgren, R. Sukumar, I-Fang Sun, Michael D. Swaine, Chang Hung Ta, Edmund V.J. Tanner, Janne Uuttera, Timothy C. Whitmore, Alex Widmer, Michael R. Willig, Wen-Jer Wu, and Ping-Shih Yang.

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Forest biodiversity monitoring is a science in the process of development. Most of the initial approaches were oriented to improving the prospects of intense logging in temperate forests. For the more complex tropical forests ecosystems, researchers are still defining the most appropriate methodologies for biodiversity sampling and monitoring.

In this paper, we describe the evolving framework initiated by the Smithsonian Institution/Man and the Biosphere Biological Diversity Program (SI/MAB) a decade ago for multi-taxa forest biodiversity monitoring. The SI/MAB program operates through an international network of forest biodiversity monitoring plots.

SI/MAB FOREST MONITORING FOR ADAPTIVE MANAGEMENT

SI/MAB was born of the critical need to create new approaches for gathering, analyzing, and disseminating information about biodiversity. In 1986, UNESCO MAB and the Smithsonian Institution joined to create SI/MAB with the express purpose of developing a protocol for surveying and monitoring biodiversity in a global network of forested areas under different management regimes (SI/MAB Biodiversity News, 1992, 1994).

SI/MAB staff, aided by researchers throughout an international network of forested sites, have developed a series of protocols for monitoring biodiversity. The vegetation protocols have been adopted at nearly 200 research sites in 23 countries, facilitating the transfer of comparable data, and providing the framework for data analysis and dissemination (Dallmeier, 1992; Dallmeier and Comiskey, 1996). Other protocols are being developed, tested, and implemented in conjunction with the vegetation monitoring. It is envisioned that the protocols will enable users to integrate scientific research methods and analysis with strategies for getting the resulting information into the hands of a wider range of user – in particular, decision-makers and resource managers involved with issues of sustainable use and conservation of natural resources.

The SI/MAB program incorporates aspects of the adaptive management process, including setting objectives, assessing and monitoring forest biodiversity, evaluation, and decision-making. This process is represented as a cycle (Figure 1.1; Holling, 1978; Walters, 1986; Hilborn, 1992), all aspects of which can be calibrated periodically to assure that the appropriate information feeds the next level. Adjustments to each component are made as needed to achieve the objectives. It is important to maintain the cyclical nature of the process and to refine the monitoring objectives and management decisions based on the ongoing results.

Setting the objectives

At each monitoring site in the network, the SI/MAB protocol emphasizes the following objectives:
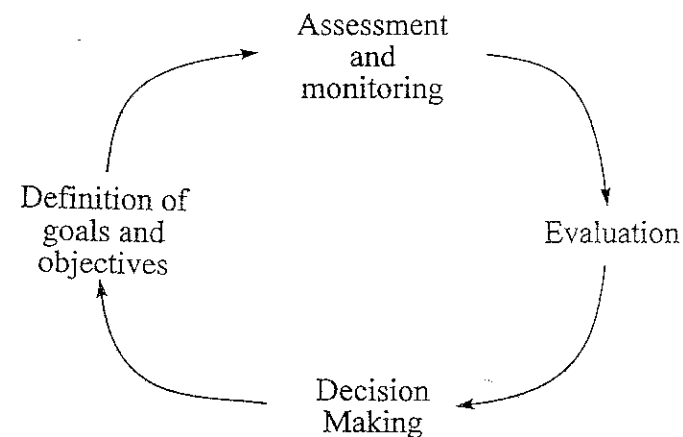
Figure 1.1 Adaptive management process

(1) gather baseline information about forest structure, composition, and diversity within a vegetation plot;

(2) assess changes in these forest components over time;

(3) use the information to link forest vegetation parameters with multi-taxa monitoring.

In addition, site-specific monitoring objectives are developed for each project. Some examples include monitoring the effects of acid precipitation on forests in the Kejimkujik National Park, Nova Scotia, Canada (Drysdale and Howell, volume 21); changes in the monsoon evergreen forests of the Dinghushan Biosphere Reserve in China to assess the impact of climatic change (Kong *et al.*, chapter 31); land management on the different forest types in the Beni Biosphere Reserve, Bolivia (Comiskey *et al.*, volume 21); and the impact of hurricanes on Caribbean forests and their subsequent recovery in the Luquillo Experimental Forest of Puerto Rico (Dallmeier *et al.*, volume 21).

Important questions in planning site-specific monitoring under the SI/MAB protocol are: What are the objectives and are they realistic? What monitoring protocols are required to achieve the site-specific objectives? What is the time line for accomplishing the objectives? Will the information that is gathered assist managers in making informed decisions? Can the results of the management decisions be statistically analyzed? Has a cost/benefit analysis been completed? What is the scale of the monitoring program (protected area, entire forest, selected number of habitats)? Is a consortium of organizations needed to achieve the objectives?

Assessment and monitoring

CHAPTER 1

FOREST BIODIVERSITY ASSESSMENT, MONITORING, AND EVALUATION FOR ADAPTIVE MANAGEMENT

Francisco Dallmeier and James A. Comiskey

INTRODUCTION

The need for sound forest biodiversity monitoring programs is growing. Pressures on the Earth's natural resources caused by a growing human population, increased public and private involvement in management and utilization of global forest resources, and rapid loss of species richness and viability are creating the need for a better understanding of biodiversity and how it changes over time (WCMC, 1992; IUCN, 1995; UNEP, 1995). Monitoring can aid in evaluating existing management approaches and their impacts on forest ecosystems. Monitoring provides data needed to ensure that the effects of management are within a previously defined range. If data indicate effects are not within this range, management can be adapted to achieve the desired outcome.

Natural influences and human actions continually bring about changes in ecosystems. Examples of such natural events include hurricanes and typhoons, extended out-of-season droughts, and volcanic eruptions. Human-induced effects comprise a large and varied spectrum – from acid rain or dust deposition and the introduction of exotic species to rapid landscape alterations caused by development. It is becoming increasingly clear that species are less able to adapt to natural changes at local and regional scales when those changes are compounded by human-caused alterations (UNEP, 1995).

Appropriate management of forest ecosystems requires the ability to measure the impact of such changes. Such information is not obtained easily. The value of the information is enhanced through monitoring programs that cover large spatial and temporal scales. As a minimum requirement, properly designed monitoring should discriminate between changes wrought by human and natural phenomena to pinpoint the most effective management choices.

Monitoring programs, even when initially supported by considerable financial and personnel investments, may be of little value if the results are not analyzed and put to use. This is often related to a lack of well-defined program objectives and/or insufficient long-term support. A clear statement of goals, objectives, methodologies, and avenues of disseminating data are key to designing and implementing monitoring programs. This in turn will enable policy-makers and resource managers to make more informed decisions about sustainable use and

comparisons among habitat types and assessing long-term changes within habitats and the effects of disturbance.

The sampling design should address the following questions:

(1) What do researchers need to know about the site (for example, data on forest composition, structure, and diversity as well as site-specific information such as the effects of acid deposition, drought, or typhoon disturbances)?

(2) How will data from the monitoring program be used (scientific and managerial uses)?

(3) Is the site representative of the selected habitat?

(4) Will the design be sensitive enough to detect changes?

(5) What limits of change are expected and are important to detect (for example, mortality rates of forest stands should not exceed 3% to 5%/year)?

(6) What is the degree of confidence expected from the results?

Indicators

For site-specific monitoring, indicators can be identified for use in assessing environmental quality (Spellerberg, 1991). For example, one might choose oak tree species affected by gypsy moths or species whose recruitment and mortality are known to be impacted by extended droughts. Keep the following in mind when choosing indicator species: 1) the species should be good measures of one or more questions that the monitoring program was designed to answer, 2) the indicators should be able to detect a condition far enough in advance to assist in solving the problem, and 3) it should be possible to monitor the indicators within the constraints of a realistic budget.

Assessing temperate woodland flora for conservation using indicator species has been used in the UK (Peterken, 1974). In tropical forests where the indicator species are not known, it is possible to use taxonomic groups as indicators. Birds and vascular plants are the most frequently used taxonomic indicators of environmental health (Spellerberg, 1992). Key habitats may also be important indicators; for example, the aspen and wet meadow habitats of the Colorado Rockies (Stohlgren *et al.*, in press).

Baseline information

Monitoring requires a base or expected norm against which all future change may be compared. Baseline information may come from existing publications or initial surveys. Unfortunately, initial surveys do not give any indication of how representative the results are of the selected habitat. For many tropical

surveillance is desirable before establishing a baseline against which future comparisons will be made (Hellawell, 1991). As an example, when establishing a vegetation plot, the first census results in a list of species and a description of how they are assembled and distributed at the site. Repeated measurements indicate changes in these variables over time and identify trends upon which the baselines may be constructed.

Site-specific sampling

In setting up a scientifically sound monitoring system, it is necessary to define the population to be monitored. The populations may be representative of habitats that are considered to be important within a region. For example, in the Beni Biosphere Reserve of Bolivia, SI/MAB has defined 12 forested habitats for monitoring (Comiskey *et al.*, volume 21).

Some population values, such as the number of individuals of a selected species within a given area, may only be estimated (Tyrrell *et al.*, 1996). A measure of the standard error of the mean, along with the reliability of the calculated value in the form of a 95% confidence limit, should be provided to assess the monitoring intensity (Usher, 1991). If the sampling is repeated, the true mean, which is of particular interest to the monitoring program, should fall within these limits. The confidence limits decrease as a function of increasing sample size. This is important as small confidence intervals provide more accurate estimates for informed management decisions. But obtaining these data is often constrained by logistic and cost factors because of the large sample sizes required.

Within a selected habitat, sampling may be carried out in a systematic, random, or stratified fashion (Cochran, 1977; Stohlgren, 1994; Stohlgren *et al.*, 1995; Tyrrell *et al.*, 1996). Systematic sampling requires establishment of a grid within which a series of points are sampled. For random sampling, all points have an equal probability of being sampled. Systematic random sampling requires that the habitat be subdivided based on topography; samples are then selected randomly (Goldsmith, 1991). The area may also be stratified according to the needs of the monitoring program.

Under SI/MAB's protocol for measuring tree diversity, a 1 ha plot divided into 25 quadrats is established (Dallmeier, 1992; Dallmeier and Comiskey, 1996). It is advisable that the plot location be within a larger adjoining area of representative habitat to allow the establishment of monitoring sites for other taxa. This will reduce disturbance as integrated monitoring can have a large impact on a site (Roberts, 1991). We suggest a minimum area of 25 ha, but this may not always be possible. For example, in the Beni Biosphere Reserve, several forest islands are being monitored, none of which is larger than 2 ha, thus placing limitations on the taxa that can be monitored at the site.

Tyrrell *et al.* (1996) suggest an evaluation of the cost of the sampling design so that objectives and the precision level can be adjusted, if necessary, to budget

detecting the magnitude and duration of changes, how related taxa are changing, and 'early warning' indicators of forest health. They also serve as the basis for formulating additional research hypotheses and, perhaps most importantly, the data can be used to guide management decisions related to biodiversity conservation.

Assessments

Traditional biodiversity assessments have concentrated on species diversity and distributions to enhance the prospects of harvesting desirable species (Hilborn, 1992). More recently, such assessments have also included habitats and population status of rare or endangered species to determine areas that are important for conservation. Assessment should include field surveys, inventories, and literature reviews to gather information and data relevant to the site-specific monitoring program. In all such cases, research objectives should be geared to provide a framework for decision-makers to evaluate the consequences of action (or inaction) regarding the use of forest resources (Spellerberg, 1992).

Biodiversity assessments at multiple scales provide decision-makers with higher quality data and cost-effective choices. Generally, the scale is based on geographical boundaries of the protected area or conservation unit or on subsets of such areas. In addition, participation of all interested parties in the assessment is important during the early stages to create consensus as assessment moves into the planning and monitoring phases. This also aids in addressing research needs and avoiding costly duplication.

Monitoring

Understanding how an ecosystem works requires careful study across scales of space and time. Recent research reveals complex ecological interactions that determine how organisms are distributed and their abundance on local scales (Diamond and Case, 1986; Gentry, 1988, 1992; Ashton, 1992; Hubbell and Foster, 1992). The evidence also indicates that ecological communities experience internal and external long-term changes with sometimes drastic turnover (Weaver volume 21; Dallmeier et al., volume 21). These long-term changes may have radical effects on the composition, structure, and diversity of the communities, resulting in imminent local extinctions and colonizations (Dallmeier et al., volume 21).

Such effects are best perceived through long-term monitoring of ecological communities and environmental changes (Clinebell et al., 1995). The impacts of environmental change on communities operates at various time scales, ranging from days and weeks (gypsy moth defoliation in eastern North America) to decades (hurricanes and typhoons, extended droughts), or centuries and millennia (volcanic activity) (Davis, 1986; Anonymous, 1994). Such scales are often

Further difficulty is encountered when relating ecological processes operating at local scales to those in effect at regional or global scales. (Stohlgren et al., in press). It is important to consider scale because localized or small-scale events can contribute to large-scale impacts. For example, in the Virgin Islands the most severe drought on record (1994–95) produced a dry forest mortality of more than 13% and eliminated most seedlings and saplings (Dallmeier et al., in preparation). The drought's impact on the forest was accentuated by the effects of Hurricanes Marilyn in 1995 and Bertha in 1996. In Bolivia's Beni region (and elsewhere around the world) annual fires intentionally set as a management tool are transforming biologically rich forested areas into less productive grasslands (Comiskey et al., volume 21).

The monitoring programs must measure the effects of such events in space and time and determine their consequences for biodiversity. Reliable scientific information on habitat composition, structure, and dynamics is needed. The greater the knowledge about a particular site, the more options are available for promoting sustainable resource use and conservation and a more stable local economic base. Increasing public awareness of and appreciation for the benefits provided by that ecosystem will assist in its protection. In addition, greater possibilities will exist that the information will prove useful at far-removed sites with similar characteristics.

Biodiversity monitoring consists of measuring and sampling species over time and comparing the results to a predetermined standard or noting their deviation from an expected norm (Hellawell, 1991). Different inventories in time may measure the same variables but with different objectives in mind and without specified standards for comparing the results over temporal scales. Only when standard protocols are clearly defined to allow the results to be compared to a baseline standard does the repetitive inventory become a monitoring program. Significantly, the standards used to compare biodiversity monitoring data provide the basis for assessing the calibration toward or away from an objective or baseline norm (see evaluation section).

In essence, biodiversity monitoring provides information about the status of species and assemblages of species as well as trends in both. Monitoring can also identify potential cause and effect relationships that can be addressed through research with an eye toward use in the decision-making process.

Sampling and data-gathering designs

Sound sampling designs should provide guidelines for the most cost-efficient and effective way to gather and analyze data while maintaining high quality-control standards. The design of biodiversity monitoring plots in the SI/MAB network rests on the program's overall objectives (outlined above) in conjunction with site-specific scientific and management objectives. Both types of objectives help to identify the information required, but the site-specific objectives are

Management approaches should be viewed as hypothetical means to reach operational goals (Ecological Society of America, 1996). Through evaluation of the monitoring data, managers receive timely feedback as these hypothesis are tested. Thus, evaluations are the tools for improving management by checking on management actions and providing guidelines for improvement. For example, when a predetermined degree of change is detected, appropriate action is taken (Hellawell, 1991) and the results must be evaluated.

Decision-making

All the preceding steps lead to decision-making. If the findings determine that the biodiversity trends are within the expected values, monitoring will continue without substantial alterations. If significant changes in the trends are observed, managers or decision-makers need to design the most appropriate response. The reasons for monitoring can be evaluated at this stage. Is the monitoring still required, and, if so, do the objectives still remain the same?

Inconclusive results require adjustment of the objectives and sampling approaches to increase the degree of precision. However, careful planning and design of the monitoring program can reduce the risk of inconclusive information.

Long-term commitment

One of the most critical and challenging issues in the success of the monitoring program is the need to gain long-term support. Project personnel must elicit the endorsement of high-level managers and the commitment of resource experts and technicians in the field. One method of achieving this goal is to incorporate monitoring as a routine duty of appropriate personnel. Another is to implement a reward system for personnel who detect a problem and take steps to devise a management-oriented solution.

A common practice by SI/MAB is to develop partnerships among several organizations to assist in fund raising, standardizing protocols, providing site-specific documentation, and supporting training for high-quality research and monitoring. This has encouraged sound data and information management and reduced duplication.

Such partnerships have also aided in disseminating information about a monitoring program to inform the public of its importance and benefits. Greater public understanding may lead to increased acceptance and support for the program.

DISCUSSION

There is considerable evidence that the SI/MAB approach to measuring and monitoring biodiversity with a view to adaptive management is achieving desired outcomes. As example:

(1) The results of monitoring post-hurricane regeneration in the hard-hit dry tropical forests of US Virgin Islands National Park on St. John's Island are aiding US National Park Service determinations. The threats posed by the activity of feral ungulates on federally endangered tree species is being evaluated within the reserve's management plan (Ray *et al.*, volume 21)

(2) Canada has adopted the SI/MAB frame nationally under Environment Canada's Ecological Monitoring and Assessment Network (EMAN). In conjunction with climatic monitoring stations, EMAN is providing data on the impacts of acid deposition. Drysdale and Howell (volume 21) provide an example of an integrated monitoring program that is currently underway in the Kejimkujic National Park, Nova Scotia.

These examples and many others are encouraging. They hold out the prospect of greater understanding of the importance of biodiversity and the promise of increased incorporation of sound, scientifically based recommendations for maintaining biodiversity in the design of management plans.

SI/MAB is also working to create diverse forums for biodiversity researchers to communicate their findings and share their concerns. In 1995, SI/MAB convened the international symposium that led to publishing of these two volumes. A second symposium will be held in the year 2000. In addition, SI/MAB and the US Man and the Biosphere Program were instrumental in developing an Internet-based communications network among 100 biosphere reserves in the Western Hemisphere. The network, informally known as MABNetAmerica, serves as the mechanism for applying low-cost protocols and data bases to improve scientific communication and cooperation.

In conclusion, SI/MAB has established a global network of forest biodiversity experts who understand the potential that biodiversity holds for bettering the human condition and the need for appropriate management of the biodiversity resource. Getting this combination of science and strategy right was what SI/MAB was established to do. We believe that careful scientific research will increase knowledge and understanding of the Earth's storehouse of biodiversity. By distributing the findings of that research into the hands of decision-makers and on-site managers, the number of opportunities for adapting management to ensure successful maintenance of the biodiversity resource also increases.

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limitations. The desired precision level can be calibrated by changing the sampling plot unit and design as well as the confidence intervals and level.

Data collection

Data collection entails the measurement and assimilation of information in the field. The sampling frequency should be determined based on the taxa to be monitored. For trees this may be on a scale of years (Dallmeier, 1992), while for arthropods the scale may only be weeks (Stork, 1995). In either case, the scale should be sufficient to enable detection of change.

A central issue in data collection is the need to gather data under consistent standards. The data collectors should be trained specifically for the task. Standard protocols should be used to facilitate cross-site comparisons and evaluation in multi-taxa monitoring. For example, in past efforts related to forest management, dead and dying trees were viewed as less important than live trees because they had little value for wood. More recent efforts related to biodiversity recognize the importance of dead trees as elements of the community that support other taxa. The approach promoted by SI/MAB develops and uses standards across disciplines to assure that data can be transformed into information that is comparable.

Data management and analysis

A primary tenet of data management is to assure that data are accurately transferred from field data sheets and securely stored, making them available for future analysis. As defined by Tessler (1995), managing monitoring data sets should include data entry, verification, validation, archiving, and documentation. SI/MAB's protocols for monitoring tree diversity include data management procedures. The Biodiversity Monitoring database (BioMon) was developed to assist the data management process (Comiskey et al., 1994). A new version of BioMon is currently being developed that has enhanced data management, archiving, documentation, and analysis features. Future development of the program will incorporate monitoring data from other taxonomic groups.

Data entry refers to the process of accurately transferring data from the field data forms to the computer. Validity checks are available in BioMon to assist in the detection of errors. Data verification follows data entry; it is the process of assuring that the computerized records match the information from the original data sheets. Data validation is performed on verified computerized data for range and logic errors; data managers must be knowledgeable about the data they are handling. As monitoring may take place over long periods of time, data must be safely archived. Data documentation should accompany the archive, ensuring that all the information required to understand the data is stored for

dates of monitoring along with any other information pertinent to the data. Under BioMon's protocols, a data dictionary is stored with the archived data. When planning a monitoring program, researchers must remember the costs involved in data management, and include these in long-term budgets; it is money well spent.

Data analysis is essential in relating data to the established goals and objectives of the monitoring program. The results from data analysis in the form of synthesis or reports need to be available to other researchers and to managers and decision-makers. The National Academy of Sciences (1990) provides the following guidelines for analysis:

(1) focus the analysis to ensure that the priority question or questions regarding the aspect of biodiversity being monitored are effectively answered;

(2) emphasize the importance of early detection of critical changes to allow lower cost solutions;

(3) recognize that results from the analysis should contribute to knowledge about the biodiversity component being monitored; and emphasize that the results should provide biodiversity managers with a scientific rationale for setting appropriate standards.

While data analysis should synthesize large amounts of data to make the data meaningful to the user (Tyrrell et al., 1996), sometimes the tendency is to over-analyze data. This often produces an overwhelming amount of analytical results and interpretations that can obscure meaningful findings. It is important to maintain the focus of the monitoring program by returning to the specific questions that need to be answered. The results from the data analysis should be presented in a format that enables others to make their own interpretations without difficulty. This may involve the preparation of reports detailing how the findings affect the management of the protected area along with recommendations.

Evaluation

Evaluation elicits answers to the questions underlying the project's objectives, thus allowing for generation of management recommendations and calibration of the monitoring program. In addition, it allows an assessment of the monitoring progress. The National Academy of Sciences (1990) recommends posing the following questions: Are the results of each specific monitoring technique well integrated with the overall monitoring program? Do methods used ensure reliable, timely, and powerful data analysis? Are the collected data subject to the appropriate techniques for data management and analysis? Could the data gathered be coupled with new technologies for analysis and management? What mechanisms exist or can be developed to allow timely transfer of data and

THE MAINTENANCE OF DIVERSITY IN A NEOTROPICAL TREE COMMUNITY: CONCEPTUAL ISSUES, CURRENT EVIDENCE, AND CHALLENGES AHEAD

Stephen P. Hubbell

INTRODUCTION

The agony of community ecology, Lewontin (1974) once wrote, is that its theories lack sufficiency. Twenty-two years later, I would argue that community ecology has the opposite problem. Ecologists now have too many theories to contend with, all of which can explain diversity and do 'work' in some sense. What we lack in ecology are *necessary* theories. This state of affairs is not likely to improve soon, if ever, because strong inference is not a very useful tool in ecology. Unfortunately, most ecological hypotheses are not mutually exclusive. The challenge now is to disentangle and quantify the relative contributions of each potential mechanism to the maintenance of species diversity.

Oversimplifying a bit, one can broadly divide theories of diversity maintenance in community ecology into two classes – niche-assembly theories and dispersal-assembly theories (Hubbell,1997a,b). The mainstream perspective holds that communities are groups of interacting species whose community presence and relative abundance can be deduced from 'assembly rules' that are based on the ecological niches or functional roles of each species (MacArthur, 1970; Diamond 1975; Tilman, 1982). According to this view, species co-exist in interactive equilibrium with the other species in the community. The stability of the community and its resistance to perturbation derive from the adaptive equilibrium of member species, each of which has evolved to be the best competitor in its own ecological niche. The niche–assembly view emerges naturally as the population- and community-level consequence of a Neodarwinian emphasis on adaptation and small-scale events that determine the relative fitness of individual organisms in local populations (Hubbell,1997a,b).

The opposing dispersal-assembly view emerges from a much larger scale biogeographic perspective, dating from Willis (1922) and Gleason (1917, 1926) and more recently formalized by the theory of island biogeography (MacArthur and Wilson,1963, 1967). This perspective holds that communities are largely accidental collections of species whose biogeographic ranges happen to overlap for historical and individualistic reasons. Communities are viewed as non-equilibrium assemblages of species coming and going and locally co-existing in slowly drifting mixtures and shifting relative species abundances. It is argued

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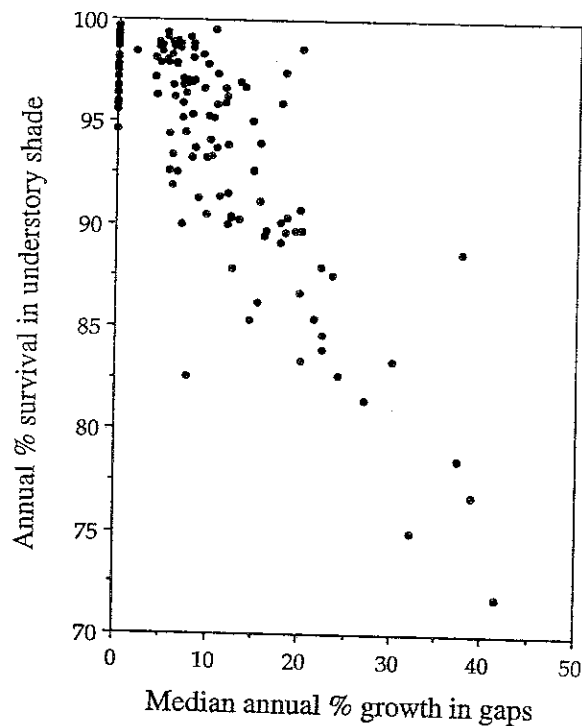
Figure 2.1 Life history trade-off between pioneer tree species and shade-tolerant tree species in saplings 1 to 4 cm dbh. The trade-off is between shade stress tolerance, as measured by annual percentage survival in understory shade (< 2% of full sun) versus median annual percentage diameter growth rate in high light environments (medium and large gaps). Data are for 118 species over a three-year period (1982 to 1985). Some very shade-tolerant species had such slow growth rate in gaps that the median annual percentage diameter growth rate was not detectably greater than zero. However, zero growth is partly artifactual in these species because in the first two censuses, we classified stems into 5-mm dbh classes. In spite of this measurement problem, the trade-off across the tree community between survival in deep shade and growth rate in sun was quite tight

trade-off is the well-known trade-off between seed size and seed dispersability (McKey, 1975; Howe and Estabrook, 1977; Howe, 1986). In general, pioneer species have small seeds that are more widely dispersed, whereas shade-tolerant species have larger seeds that are more locally dispersed. Many of the BCI pioneers also can disperse seeds over time through seed dormancy, whereas the shade-tolerant species all have immediate or at least rapid germination. Because gap sites are a small fraction of the total landscape in closed-canopy forests such as BCI, there should be a strong selection of pioneers for good dispersal. However, we found evidence of severe dispersal limitation in BCI pioneer species. Data on gap occupancy rates for individual pioneer species showed that a mean of only 1% to 3% of the gap sites judged suitable for germination

and growth were actually occupied (Hubbell *et al.*, 1997). This conclusion is supported by the recent work of Dalling (personal communication) on the soil seed bank of pioneer species. By germinating seeds from soil samples as a function of radial distance from isolated individual pioneer species, Dalling has shown that there is a rapid fall-off of seed densities with distance. Moreover, experiments with seeds buried in bags show that the viability of dormant seeds in most species declines rapidly after one to two years, and only one species is estimated to be viable after 10 years. Thus, the ability of the pioneer tree community to disperse in time and wait for canopy gaps to open in the BCI forest is more limited than previously thought.

Similar dispersal limitation is also seen in the gap occupancy rates of mature-phase tree species (Hubbell *et al.*, 1997). This dispersal limitation occurs despite the fact that these species are generally much more common than the pioneers because they have a far greater amount of habitat suitable for germination. Seeds collected in a series of 200 seed traps throughout the 50-ha plot reveal that most mature-phase species do not disperse most of their seeds very far, although many species have a long-tailed dispersal curve, with a small fraction of seeds traveling considerable distances (Wright and Harms, unpublished data). Tilman (1994) argued on theoretical grounds that a strict trade-off between competitive ability and dispersal ability would, in principle, allow an infinite number of species to coexist. We do not know whether large-seeded, poor-dispersing BCI tree species are better competitors in all respects, but their shade tolerance certainly makes them better survivors in the low-light environment of the understory. Leigh *et al.* (1993) report that small forested islands isolated after Gatun Lake was created have become dominated by large-seeded tree species. They attributed this to the absence of most seed- and seedling-eating ground foraging mammals. However, Harms (unpublished data) could find no evidence that seed-predator bruchid weevils have a more difficult time finding *Oenocarpus* palm seeds on these same islands.

Large seed size has been known to be associated with shade tolerance for some time, and the usual explanation is that seedlings need large seed stores to produce their first few leaves in the shaded understory (Foster and Janson, 1985). However, not all shade-tolerant species are large seeded, and other factors may also be involved. For example, Harms and Dalling (personal communication) have shown that large-seeded species survive repeated bouts of partial herbivory better than small-seeded species in the BCI forest. In addition, seed stores are needed to produce non-photosynthetic below-ground tissues. In the shaded understory, seedlings face an allocation problem between roots and shoots, particularly in strongly seasonal tropical forests such as BCI. Seedlings without a sufficiently deep tap root will not survive their first dry season. This may be the primary explanation for the strong species richness gradient observed in the BCI plot: 20-m^2 quadrats on mesic slopes, which retain moisture longer into the four-month dry season (Becker *et al.*, 1988), have 30% to 50% more species than the drier plateau (Hubbell, 1995) (Figure 2.2). This explanation is supported

that species in communities are rarely so tightly co-adapted that they cannot persist without the presence of other specific taxa (Howe, 1984). This perspective does not deny the existence of niche differentiation, as for example, between pioneer tree species and shade-tolerant, mature-phase species. However, it ascribes far less importance to niche in regulating species richness and relative species abundance in local communities. Niche differentiation, according to this view, reflects the time-averaged history of the ever-changing biotic and abiotic selective environment to which species ancestral lineages were exposed during their long, individualistic geographic wanderings – the ghost of competition past (Connell, 1980).

Many ecologists today would probably say that the debate over ecological communities has been won by proponents of niche assembly. In my opinion, this conclusion is premature and contradicts the obvious successes of the theory of island biogeography with its dispersal–assembly assumptions. An extreme equilibrium, niche–assembly view is clearly untenable because colonizations and extinctions of species are observed and are not explained by standard niche-based equilibrium theory. Conversely, we also know that habitat specialization and niche differentiation and not just dispersal limitation are important to the composition of local tropical tree communities (e.g. Tuomisto *et al.*, 1995). Obviously, the truth must lie somewhere in between.

In this paper, I summarize some of the more salient evidence bearing on the niche–assembly and dispersal–assembly perspectives with regard to the tropical forest on Barro Colorado Island (BCI), Panama. There, evidence supports both perspectives. At the end, I attempt a reconciliation of these two perspectives for BCI and for species-rich tropical forests in general. This paper is a mixture of data and blatant speculation, and the views expressed here are my own and may not accurately characterize the views of my collaborators on the BCI Forest Dynamics Project.

THE BCI FOREST DYNAMICS PROJECT

For the past 15 years, my colleagues and I have been studying the structure, tree species composition, and dynamics of old-growth tropical moist forest on BCI. Barro Colorado Island is a 15-km² former hill top in artificial Lake Gatun, which was created by damming the Chagres River in the early 1900s to create the Panama Canal. The island is half covered with old-growth forest that has never been clearcut for agriculture as far as can be determined from the soil phytolith record (Piperno, 1992). The forest is classified as tropical moist forest, and BCI annually receives about 2,600 mm of precipitation distributed mainly between May and December (Leigh *et al.*, 1982). In 1980, a 50-ha permanent plot was established at 150 m above sea level on the central plateau of the island (Hubbell and Foster, 1983). The plot is relatively level, but it does contain 3% to 10% grades on the eastern and southern margins and a small (< 2 ha) seasonal swamp in the middle, drained by a wet-season stream flowing to the southwest.

The first census of all free-standing woody vegetation with stems > 1 cm in diameter at breast height (dbh) was completed in 1982. All stems were tagged, identified to species, measured for diameter, and mapped for a first census total of about 240,000 individuals of slightly more than 300 species. Second, third, and fourth complete censuses of the plot were taken in 1985, 1990, and 1995, respectively, at which times growth, mortality, and new sapling recruitment were recorded. In addition to tree demography, data have been collected annually since 1983 on the dynamics of canopy height and gaps (Hubbell and Foster, 1986a), with measurements of canopy height on a 5-m grid over the entire plot. The canopy height data has enabled us to measure survival, growth, and recruitment in each species in gap and understory environments (Hubbell and Foster, 1986b; Welden *et al.*, 1991; Hubbell *et al.*, 1997). In 1994, a seedling and small sapling census was initiated, with the goal of a 4% stratified sample of 1-m² in every 5-m² quadrat. All woody plants 20 cm in height and 1 cm dbh in these plots are being tagged, measured, and identified. In 1995, we started a large, long-term exclosure experiment with eight 30 × 45-m fenced plots and matched unfenced controls to examine the impact of removing ground-foraging mammals on understory regeneration (Carson and Hubbell, unpublished data).

EVIDENCE FOR NICHE ASSEMBLY: LIFE-HISTORY TRADE-OFFS

One does not have to look far for some evidence of niche differentiation among the tree species in the BCI forest. A major axis of niche differentiation is evident in the spectrum of very shade-intolerant pioneer species to the most shade-tolerant, mature-phase species. This differentiation is expressed most clearly as a set of life-history trade-offs, the most dramatic of which is the trade-off between maximal growth rate in full sun versus survival rate in understory shade. This trade-off results in a narrow manifold of points in the growth-survival state space (Figure 2.1). Many life-history combinations are evidently not possible for BCI tree species. Thus, there are no super species with very fast growth rate in full sun, but also very high survivorship in understory shade. This trade-off reflects specialization, which in turn will promote co-existence. Note, however, that Figure 2.1 does not support the idea of overdispersion of most BCI tree species in niche space. To the contrary, there is a great swarm of species exhibiting very similar slow growth rate and high survivorship at one end of the state space. Three-quarters of the BCI species cluster relatively tightly at the shade-tolerant end of this spectrum. This suggests that a large majority of mature-phase tree species has converged on similar life history and physiological strategies for coping with shade stress. On the other hand, Figure 2.1 does not support the simple dichotomous-guild hypothesis of pioneers and mature-phase species advanced by Swaine and Whitmore (1988) and Whitmore (1989). The points not clustered at the shade end of the axis are distributed nearly continuously all the way to the other extreme of the most heliophilic species.

A second axis of niche differentiation and one related to the growth–survival

EVIDENCE OF NICHE ASSEMBLY FROM FOREST DYNAMICS

While several life-history trade-offs have been identified in the BCI tree community, there is still a need to connect these trade-offs directly to the coexistence of tree species in the BCI forest. In general, connecting evidence is lacking at the species level, but at the guild level, there is stronger evidence. For example, pioneer species are persistently uncommon to rare relative to most shade-tolerant species, which is a direct consequence of the rarity of gap habitats suitable for them coupled with strong dispersal limitation in the pioneers (Hubbell and Foster, 1986c). However, we generally do not know what restricts the local abundance of most of the mature-phase tree species, which constitute more than three-quarters of the BCI tree community (Condit *et al.*, 1992a,b). Where density- and frequency-dependent mechanisms have been identified in the BCI forest, the mechanisms have not been attributable to resource-based trade-offs, but rather to the actions of predators and pathogens (Hubbell *et al.*, 1990; Wong *et al.*, 1990; Gilbert *et al.*, 1995; Gilbert and Hubbell, 1996). Of course, there could be interactions between susceptibility to pathogens and resources (e.g. shade-stressed or drought-stressed plants), but we have no direct proof of such interactions in BCI trees. Tree mortality was elevated after the severe drought associated with the El Niño event of 1982 to 1983 (Condit *et al.*, 1992b), and fungal pathogens are known to attack drought-stressed trees in temperate forests (Gilbert and Hubbell, 1996).

In spite of a lack of clear mechanism in most species, one can still test for the presence of density and frequency dependence in BCI trees and ascertain how strong and pervasive such density effects are throughout the community. Janzen (1970) and, independently, Connell (1971), following up on an idea of Gillette (1962), suggested that host-specific seed predators and pathogens so reduce the local recruitment of seedlings in the vicinity of conspecific parents that *in situ* self-replacement of species would be a rare event. Janzen (1970) postulated that this seed predation would allow more tropical trees to coexist because space currently occupied by one species would be taken by some other species in succeeding generations. A number of BCI tree species have been individually studied for a Janzen–Connell effect, and it has been detected in several (e.g. Augspurger, 1983, 1984; de Steven and Putz, 1984; Howe *et al.*, 1985; Sork, 1987; but see Schupp, 1988). Janzen–Connell effects have also been found in other neotropical forests (e.g. Clark and Clark, 1984).

However, Hubbell (1980) argued that if density-dependent mortality of seeds and seedlings only operated among the progeny from single adult trees, such density dependence cannot regulate the size of the adult population. In any event, Huntly (1991) noted that focal species studies will not be able to test hypotheses about community-level effects. One has to determine how strong and how pervasive Janzen–Connell density-dependent effects are throughout the tree community. We first attempted a community-wide test on the static data from the first census of the BCI plot (Hubbell and Foster, 1986a). This test did not provide much evidence for density dependence in that there was generally a linear positive relationship between the number of adult trees/ha and the number of small saplings of the same species/ha. Only the two most abundant canopy tree species had a negative relationship between adult density and sapling density; these were *Trichilia tuberculata* (Meliaceae) and *Alseis blackiana* (Rubiaceae). Many of the tree species were also highly aggregated, suggesting that Janzen–Connell effects, if present, were not strong enough to overcome limited dispersal of seeds and result in relatively evenly distributed, low-density adult populations.

These conclusions could obviously be faulted because they were based on static data alone (Clark and Clark, 1984). Once the BCI plot had been recensused, however, it became possible to test for Janzen–Connell effects on dynamic data, namely on the spatial patterns of survival, growth, and recruitment. Taking a focal-tree approach as in the Janzen–Connell model, we again found evidence for density dependence in *Trichilia*. When we incorporated the measured distance- and density-dependent mortality, growth, and recruitment into a spatially explicit model of *Trichilia* populations, the measured effects were sufficiently strong to regulate the model population at densities close to those observed (Hubbell *et al.*, 1990). We found evidence for a 'repelled pattern' in the saplings near conspecific adults in 35% of canopy tree species tested, but the fraction of species showing a significant repelled pattern was successively lower in subcanopy trees (17%), treelets (11%), and shrubs (7%) (Condit *et al.*, 1992a; Condit *et al.*, 1994). These results led us to question the importance and pervasiveness of density- and frequency-dependence in the BCI forest (Hubbell *et al.*, 1990; Condit *et al.*, 1992a, 1992b). Unless a substantial fraction of the community exhibited Janzen–Connell effects, the question still remained why species lacking such self-inhibiting effects should not take over the forest.

Schupp (1988, 1992), in a study of density effects on seed mortality in the understory tree, *Faramea occidentalis* (Rubiaceae), concluded that the focal-adult approach of Janzen–Connell was the wrong spatial scale, and that density effects involving predators and pathogens were more likely to operate and be detected on the scale of patches containing multiple adults. Testing this idea, Wills *et al.*, (1997) returned to the quadrat-based approach of Hubbell and Foster (1986a), but this time analyzed the dynamic data from two recensus intervals (through the 1990 census). They found evidence for much stronger and more pervasive density dependence than had previously been detected in the focal adult analyses. In many more species, both sapling survival and growth decreased in quadrats having more conspecifics. Testing density effects on recruitment was more complicated. Wills *et al.*, corrected for mass-effect biases in recruitment of new saplings in quadrats having a low density of adult trees but which were adjacent to high-density quadrats (Schmida and Wilson, 1985). After statistically removing the effect of neighboring adult density on recruitment in a given quadrat, the residual within-quadrat density effects were generally still significant and negative. As predicted by Schupp (1992), the spatial scale on which these effects were significant was much larger than the scale of squared nearest neighbor distances (36 to 225 m^2), and instead ranged upwards from
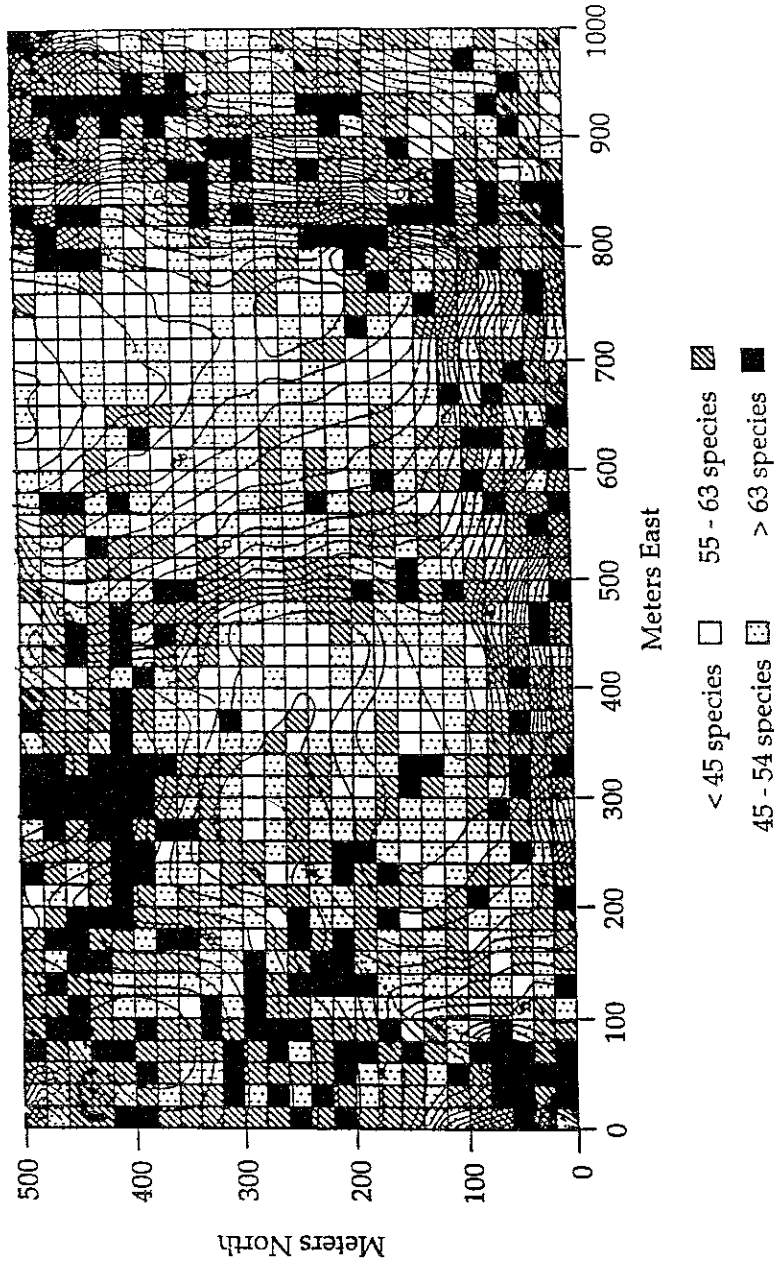
Figure 2.2 Species richness of trees and shrubs > 1 cm dbh in the 50-ha BCI plot on a grid of 20-m² quadrats. Species richness is 30% to 50% higher on the slopes in the plot to the east, south, and northwest than on the seasonally drier plateau (center, right) and the seasonally flooded swamp (center, left). The slopes are more mesic during the four-month BCI dry season than is the plateau

Legend:
- < 45 species (□)
- 45 – 54 species (▨)
- 55 – 63 species (□)
- > 63 species (■)

Meters East

Meters North

by the fact that the soil moisture gradient appears to be a one-way filter; almost all species found on the drier plateau also grow on the more mesic slopes; but many slope species are nearly or completely absent from the plateau. Such a filter may also help explain Gentry's (1982) correlation of plant species richness and mean annual rainfall in a large number of 0.1-ha samples of forests throughout the New World tropics (Clinebell *et al.*, 1995). The filter effect could be much greater on regional spatial scales where a far broader range of moisture regimes is expressed than in the local BCI plot

Another obvious axis of niche differentiation is between understory specialists such as shrubs and treelets, and canopy trees; but exactly which life-history trade-offs are involved are less well understood (O'Brien *et al.*, 1995; Kohyama, 1993). Nearly 40% of the BCI species are shrubs and treelets that reach a mature size at a stature of < 10 m (Hubbell and Foster, 1986a), a relatively high percentage for closed-canopy tropical forests. Most of these are shade-tolerant understory species (e.g. *Hybanthus prunifolius*). A few are small-statured, short-lived gap pioneers (e.g. *Palicourea guianensis*). Terborgh (1985, 1992) hypothesized on a geometrical basis that overlapping cones of light cast by the sun moving over gaps among tree crowns in the canopy will lead to vertical stratification of the forest. He argued that these light cones will produce relatively uniform lighting in the understory up to a certain height above the forest floor and that understory specialists will stop growing when they reach this height. However, the evidence for stratification in tropical forests is not strong (Terborgh, 1992). In addition, overstory trees must still grow through all subcanopy levels to reach the canopy.

I suspect that the explanation is more simple and probably lies in life-history trade-offs, possibly the trade-off between early reproduction but low fecundity of the low-light environment of the understory and delayed reproduction but high fecundity in the high-light environment of the canopy layer (Kohyama, 1993). Given that reproduction is a major carbon cost to plants in a low-light environment, height growth may slow down considerably in mature shrubs and treelets relative to same-sized but immature individuals of canopy trees. Without having to bear the cost of reproduction, immatures of canopy trees can invest a greater percentage of their carbon gain into growth and shoot extension. We have also found that many understory specialists exhibit lower survival in gaps than saplings of mature-phase canopy trees (Hubbell *et al.*, unpublished data). All shade-tolerant species suffer higher mortality in gaps during the thinning that occurs with gap closure (Hubbell *et al.*, 1997), but the mortality is even higher in shrub species, so that saplings of canopy trees in gaps experience reduced competition from understory specialists. Light gaps are not just holes in the canopy. They are also holes in the shrub layer. In addition, I suspect that the development of an understory tree and shrub community will be a function of soil fertility. Competition for light and leaf area indices are highest on the most fertile soils, which should reduce light levels in the understory even further and, therefore, diminish the viability of understory specialization.

Beilschmiedia pendula

Alseis blackiana
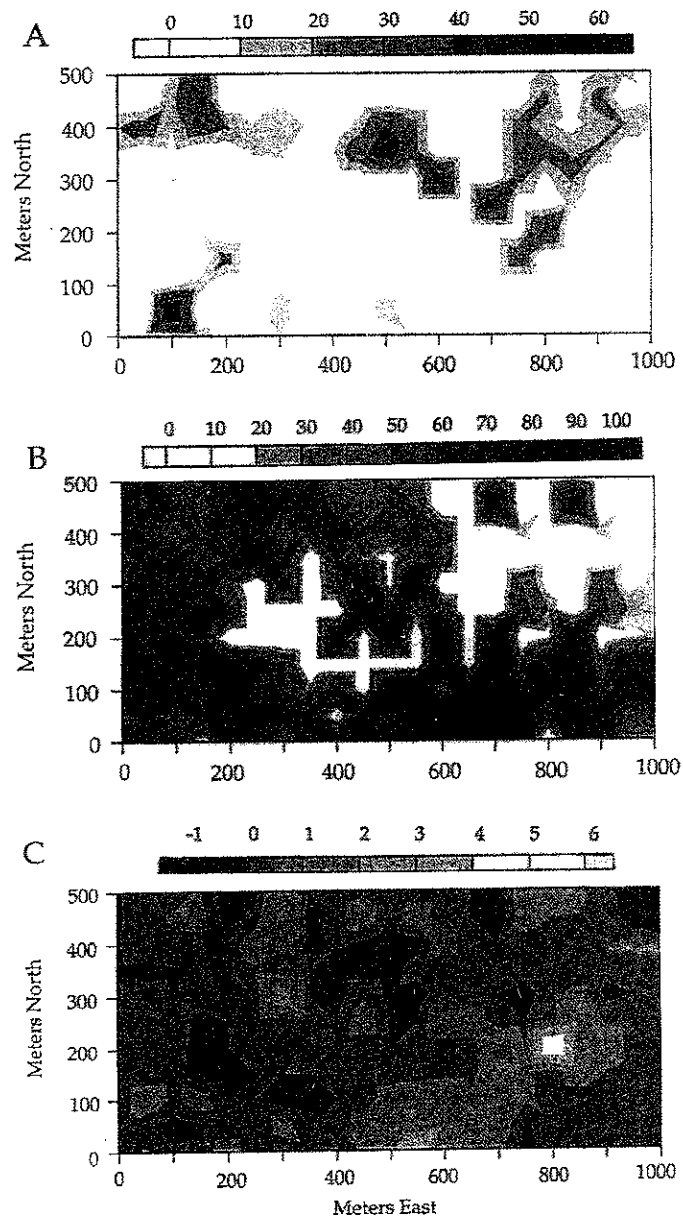
Figure 2.4 Population of the canopy tree *Beilschmiedia pendula* (Lauraceae): panel A contours of percentage of adult trees/0.25 ha in 1982; panel B contours of percentage of saplings 1 to 3.9 cm dbh/0.25 ha in 1982; panel C contours of finite rate of increase (%)/
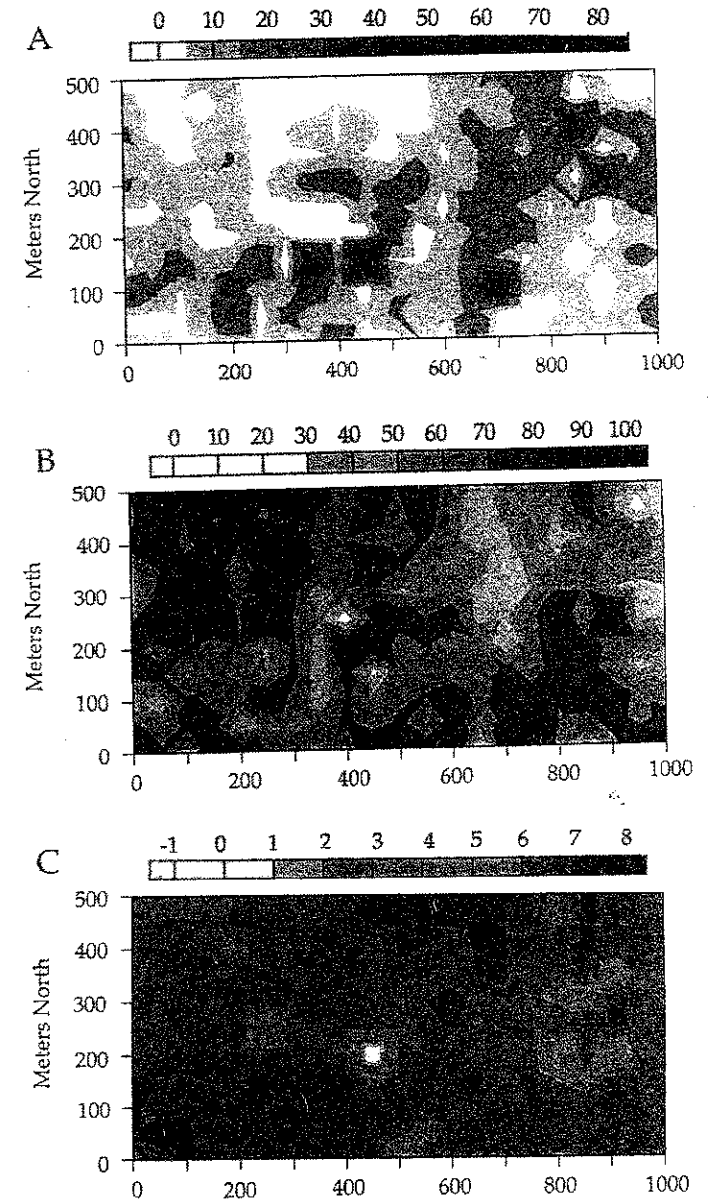
Figure 2.5 Population of the canopy tree *Alseis blackiana* (Rubiaceae): panel A contours of percentage of adult trees/0.25 ha in 1982; panel B contours of percentage of saplings 1 to 3.9 cm dbh/0.25 ha in 1982; panel C contours of finite rate of increase (%)/0.25 ha

400 m² to 10,000 m² and larger, depending on the species. One can visualize these density-dependent effects by plotting contours of the percentage of adult trees and small saplings and observing their spatial complementarity, as shown in Figures 2.3 to 2.5. Full quantitative analysis of these data can be found in Wills *et al.*, (1997), but the complementarity is obvious by visual inspection. I present these figures to emphasize that the spatial scales on which the density effects occur are larger than single adult tree neighborhoods.

There is no mathematical need for this complementarity since large numbers of juveniles and sub-adult trees are not included in the figures. Figure 2.3 shows the sapling and adult contours for the most abundant canopy tree species *Trichilia tuberculata*, with Panel 2.3c displaying contours of the observed finite rate of increase of *Trichilia* over the interval 1982 to 1990. Figures 2.4 and 2.5 show the comparable graphs for two additional canopy trees, *Beilschmiedia pendula* (Lauraceae) and *Alseis blackiana*. All of these species are shade-tolerant, but *Alseis* is unusual in being able to respond with relatively rapid growth when exposed to light. It is the outlier point to the far right of the main trade-off sequence in Figure 2.1. Parenthetically, it should be noted that density-dependent phenomena on these large spatial scales, which may be the scales on which most tropical tree populations are regulated, are not captured by any of the currently popular, individual-based forest simulator models.

It is not immediately obvious what sets up these large-scale density fluctuations. Why, for example, is the percentage of adult trees so variable across the 50-ha plot in most species? Except for species that are restricted to slopes by low dry season soil moisture on the plateau, there is little evidence of habitat restriction for a majority of the abundant, mature-phase tree species (Hubbell and Foster, 1986c). This suggests that the patchiness arises out of a biotic interaction between dispersal and predator and/or pathogen attack. One could imagine a uniform density dependence that would equilibrate nearly constant percentages of each size or age class everywhere. The spatially inconstant percentages of adult and sapling densities shown in Figures 2.3 to 2.5 and the variable finite rate of increase in local stands seem to imply that the factors regulating BCI tree populations are time lagged. Whatever regulates these tree species allows their populations to build up to locally dense stands of conspecifics *before* it acts. If the density-dependent mechanisms were instantaneously responding to current local density, then we should rarely see such patchily distributed populations as those commonly observed – except perhaps during colonization when species were first invading and were most dispersal-limited. Time-lagged host-tree population dynamics is well known in temperate zone tree species that exhibit die-backs because of fungal pathogen attack (Gilbert and Hubbell, 1996).

Our current hypothesis is that many BCI tree species are regulated by fungal pathogens. The known pathogens on BCI can spread locally through roots and the soil by hyphal growth. They also spread across long distances by airborne spores, but with a much lower successful infection rate. Our present model is of

Trichilia tuberculata

Figure 2.3 Population of the canopy tree *Trichilia tuberculata* (Meliaceae): panel A contours of percentage of adult trees/0.25 ha in 1982; panel B contours of percentage of saplings 1 to 3.9 cm dbh/0.25 ha in 1982; panel C contours of finite rate of increase (%)/ 0.25 ha during the interval 1982 to 1990.
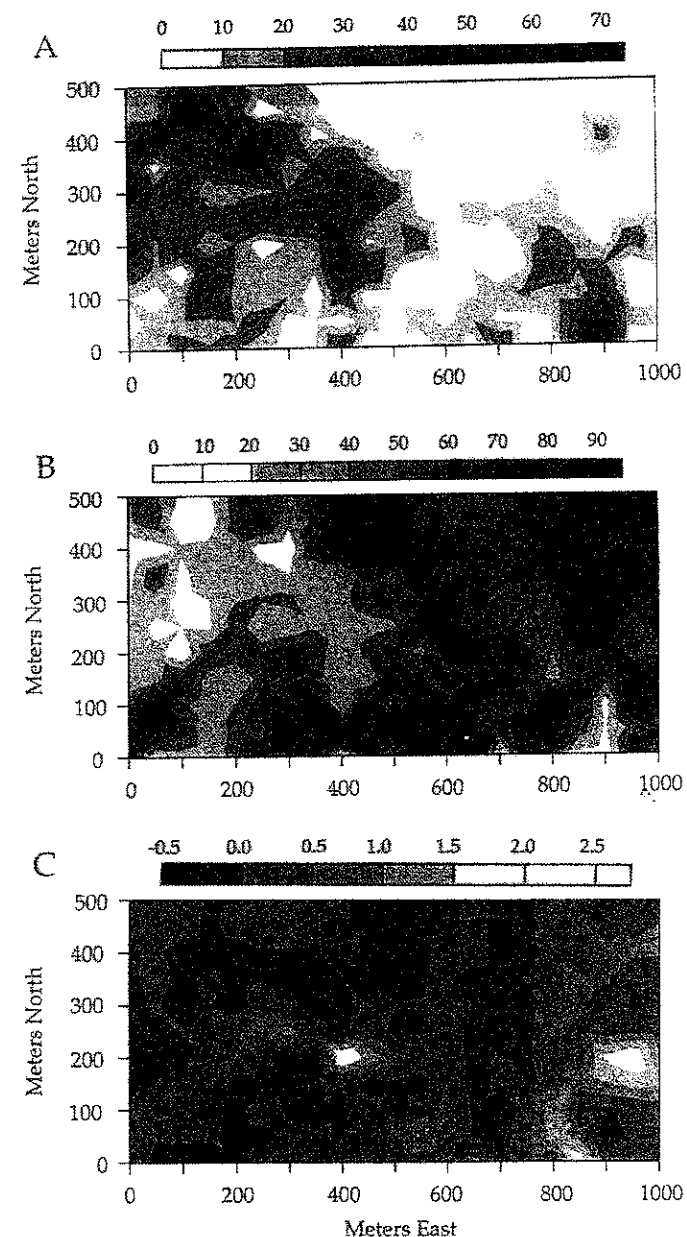
forest is estimated to be 16.6 years. The slowest growing species was the shrub *Ouratea lucens* (Ochnaceae), which had an estimated age > 80 years at 1 cm dbh. The two most common canopy trees, *Trichilia* and *Alseis*, had estimated ages of 21.9 and 27.4 years, respectively, at 1 cm dbh. The fastest growing species of those tested were two pioneer species, *Cecropia insignis* and *Zanthoxylum belizense*, both of which had an estimated age of just 0.9 year at 1 cm dbh. There are two significant conclusions from this analysis. First, mature-phase BCI trees spend an appreciable proportion of their life span in the small sapling stage, where they are exposed to predators and pathogens for possibly several decades. Thus, the understory is where the relative abundance of BCI tree species is largely determined. Second, the age of saplings suggests that it may be methodologically difficult for a focal tree approach to detect density- and distance-dependent Janzen–Connell effects unless prior populations of adult trees are known. Adult tree mortality is on the order of 1% to 2%/year, which means that as many as one-third to one-half of the parents of a given sapling cohort will have died before the saplings reach 1 cm dbh. This fact may help explain why Condit *et al.*, (1992a) failed to find evidence for Janzen–Connell effects in recruitment near conspecific adults in most BCI tree species.

EVIDENCE FOR DISPERSAL ASSEMBLY OF THE BCI TREE COMMUNITY

I have spent the greater part of this paper outlining the evidence for niche assembly of the BCI tree community. While this evidence is strong, there is also sound theoretical and empirical evidence for dispersal assembly of the BCI forest. A bit of background on the theory will be useful. In a forthcoming monograph, I develop a unified theory of island biogeography and relative species abundance (Hubbell, 1997 a,b). This theory predicts not only the number of species on islands or in local communities, but also their relative species abundance at equilibrium between immigration and extinction. The unification of the two theories unexpectedly results from incorporating speciation into the theory of island biogeography (Hubbell, 1997a). Speciation in the source area meta-community is the analog of immigration on islands. The unified theory predicts the existence of a fundamental biodiversity number Θ, which is equal to twice the meta-community size Θ_M (the total number of individuals of all species in the source area) times the speciation rate v ('nu') (Hubbell, 1997b). The number Θ controls not only the species richness but also the relative species abundance distribution in the source meta-community. Observed (fitted) Θ values for tree communities are finite, ranging from a low of about 0.1 for simple boreal coniferous forests containing only a few species to about 200 for the most species-rich evergreen tropical forests (Hubbell,1997a). We can be certain that v is a very small number and, given the range of observed Θ values, we know that meta-community size Θ_M must be a very large number, in the order
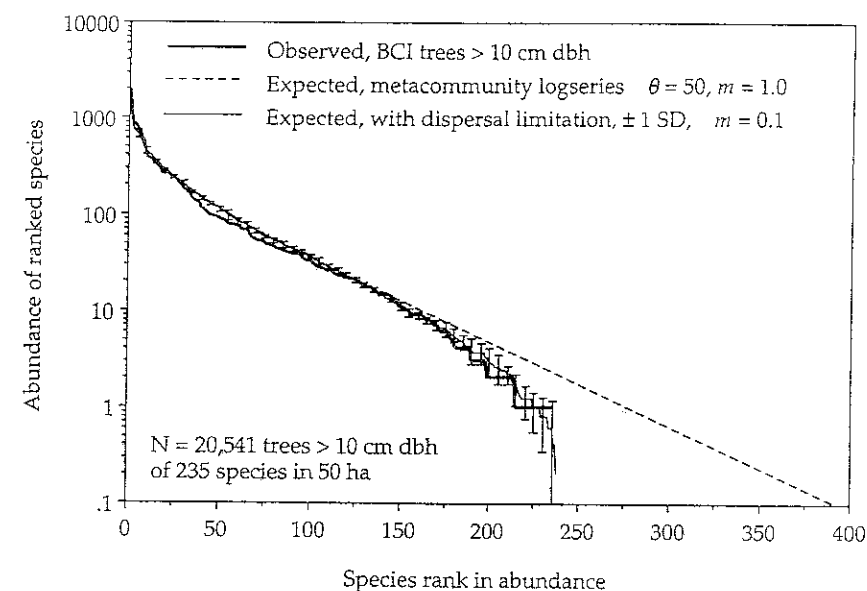
Figure 2.7 Theoretical and observed dominance–diversity distributions for the rank abundance of all trees > 10 cm dbh in the 50-ha BCI plot. The heavy line is the observed distribution. The expected meta-community logseries distribution for a value of $\Theta = 50$ is the diagonal dotted line continuing past the end of the observed distribution for the local 50-ha community. Note the departure of the observed distribution from the meta-community logseries for rare species. However, when the immigration rate was restricted to 10% ($m = 0.10$), the expected distribution (shown with ± 1 SD) fit the observed distribution quite well, including the rare species ($p > 0.8$, log likelihood ratio test). A value of $m = 0.10$ corresponds to 90% local recruitment, a reasonable value based on the fact that 10% of the plot is within 17 m of the perimeter

of one-twentieth to 100 times the inverse of the speciation rate. The theoretical distribution of relative species abundance predicted for the meta-community is the logseries, an empirically fitted distribution of relative species abundance proposed by Fisher *et al.* (1943). It turns out that Θ is equal to Fisher's α, a parameter of the log series and a widely used statistical measure of biodiversity. The unified theory provides the first theoretical justification of Fisher's α in an ecological context.

The relevance of all this to the present discussion is that the unified theory is capable of remarkably accurate predictions of both the species richness and the distribution of relative tree species abundance in the BCI forest – and yet the assumptions of the unified theory are hardly more complex than those embodied in the original theory of island biogeography (MacArthur and Wilson 1963, 1967). The fit of the theoretical distribution to the dominance diversity curve

trees and their fungal pathogens in a slow race over the landscape. The local abundance of a tree species builds up; then the patch is invaded by a pathogenic fungus. The fungus invades living trees, grows slowly in the wood tissue, and eventually kills the tree by structurally weakening it through heartrot, or by girdling. Eventually, the local stand of the host tree begins to decline. Meanwhile, however, the host tree species has dispersed seed far enough away to escape immediate pathogen attack, and the cycle repeats elsewhere. The result will be slow, species-specific population density waves of the host tree moving through the forest. Wills *et al.*, (1997) hypothesize that there may also be a frequency-dependent, 'species herd immunity' phenomenon involved. Each tree should gain some indirect protection in a diverse forest because the spread of host-specific pathogens should be slower when each tree is surrounded by non-host trees of other species. This should allow each species to increase in relative abundance when it is rare. These authors did not find strong evidence for such rare-species advantage when intraspecific density effects were statistically controlled. Whatever the case for frequency dependence, I suspect that fungal pathogens are probably more important than herbivores and seed predators in regulating populations of BCI tree species. This is because it is hard to imagine how highly mobile and short-lived herbivores and seed predators could produce the time-lagged density fluctuations observed in long-lived BCI tree species. Oscillations due to time lags typically do not arise in dynamic systems unless subsystems are coupled that have similar time constants.

Nevertheless, we cannot rule out ground-foraging mammals and herbivorous insects as being important in maintaining tropical tree diversity. Even if mammals and insects are probably not responsible for the time lags in tree populations, their actions may still be density- and frequency-dependent. While a majority of insects is host-specific, the mammals certainly are not. Host-specificity may not be essential for mammals to influence tree species diversity, however. Dirzo and Miranda (1991) noticed a striking difference in the seedling communities in two tropical forests in Mexico. Seedling plots in the Los Tuxlas forest, which has been poached for more than half a century and has few remaining large ground mammals, had high densities of seedlings but low species diversity. In contrast, seedling plots in a large biosphere reserve in southern Chiapas that has an intact mammal fauna, exhibited low densities but much higher species diversity. Diversity in the overstory of the two forests was similar, suggesting that differences in overstory diversity of the two forests had not led to the differences in understory diversity. Based on these findings, they speculated that a loss of large ground mammals may lead to the ultimate loss of tree diversity from tropical forests. On reflection, it is easy to see how this might work. Even if mammals collectively act like non-specific lawn mowers in the understory, dispersal limitation in the trees and the resulting clumped seedling distributions will result in density and frequency dependence in seed and seedling mortality. In addition, mammals undoubtedly seek out dense patches of seedlings for reasons of optimal foraging, even if they are
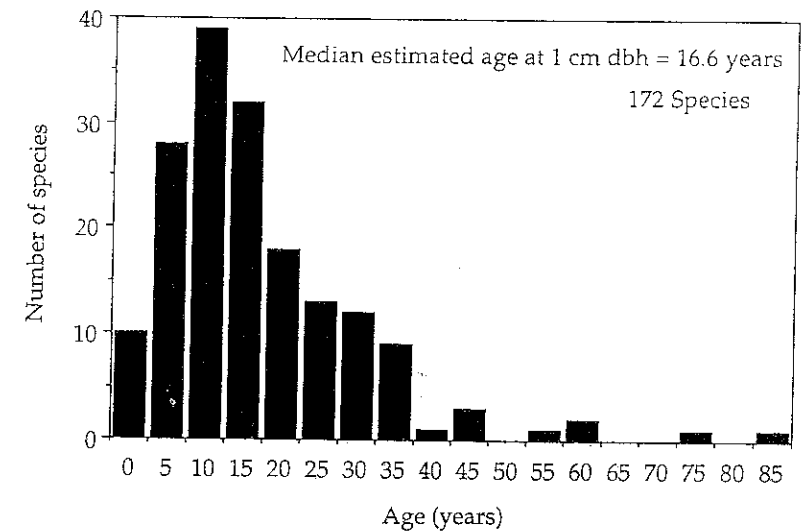
Figure 2.6 Distribution of estimated ages of saplings upon reaching 1 cm dbh for 172 BCI canopy trees, understory trees, treelets, and shrubs. (Ages are probably underestimated (see text)

not host-specific (Howe *et al.*, 1985; Forget, personal communication). Thus, it is probably an interaction between the behavior of foraging mammals and the patchy distribution of the seedlings they eat that generates density and frequency dependence.

The importance of events in the understory, such as predation and herbivory by mammals and insects, has been underscored by the recent discovery that 1-cm dbh saplings of mature-phase BCI trees and shrubs are quite old (Hubbell *et al.*, unpublished data). One can estimate the ages of 1-cm dbh saplings by computing polynomial regressions of dbh against time for plants > 1 cm dbh and extrapolating to smaller diameter classes. There are several problems and assumptions with this estimating procedure, but it is the only method that we currently have available. One problem is that there is a strong positive correlation between prior growth rate and probability of survival to the next census (Hubbell *et al.*, unpublished data). Mean growth rates average the growth of fast-growing plants with those destined to die; thus, ages based on mean growth rates are generally overestimated. For this reason, the regressions were based on the fastest growing 10% of all stems – those most likely to survive. Age estimates for saplings by this method are probably conservative, so we feel confident that the finding that 1-cm saplings are old is almost certainly correct.

Moreover, the estimates are reasonable and correlate as expected with life-history traits. The distribution of estimated ages for 186 tree and shrub species is shown in Figure 2.6. The median age of a 1-cm dbh sapling in the BCI

value of $\Theta = 50$. This number controls the logseries relative abundance distribution for the source meta-community from which immigrants to the local community in the BCI 50-ha plot are drawn. The meta-community logseries is the sloping diagonal line extending beyond the end of the distribution observed for the 50-ha plot.

However, the unified theory also says that the relative species abundance for island or local communities is not the same as a random sample of the meta-community logseries. It deviates especially for rare species (Figure 2.7), which are rarer than expected on islands or in local communities because they are prone to extinction. At equilibrium, the frequency and relative abundance of rare species is lower in the local community than expected from the meta-community because of an interaction between dispersal limitation and local extinction. In the unified theory, the parameter m measures the degree of isolation by dispersal limitation of a local community; m is the probability that a birth in the local community is replaced by an immigrant from the source meta-community. The theory predicts that the shape of the equilibrium island or local dominance–diversity curve will be a function of parameter m. Changes in the shape of the dominance–diversity curve enable m to be estimated (Hubbell, 1997a,b). The m value for the BCI plot is about 0.10, or that 90% of tree replacements are made locally from within the plot and 10% are immigrants from outside the plot. This is a reasonable estimate of immigration rate, given that 10% of the plot's area is within 17 m of the plot's perimeter, a distance over which most BCI tree species could easily disperse. Once dispersal limitation is factored in by parameter m, the unified theory's prediction of the observed dominance–diversity curve is nearly exact, including the loss of rare species (Figure 2.7).

The unified theory predicts that dispersal limitation will not only lead to a reduction in species richness in local communities or islands, as predicted by island biogeography theory, but also that there will be an increase in the variance of relative species abundance and, therefore, an increase in apparent dominance. Rare species become more rare and common species more common. This is not an effect predicted by niche-assembly theory. Rather, it is predicted by the number Θ in combination with restricted immigration ($m < 1$). As equilibrium species richness declines, the mean and variance in abundance of the remaining species increase relative to the meta-community. The predicted increase in dominance is observed in 1-ha subplots compared to the 50 ha-plot as a whole (Figure 2.8). For these smaller plots, the estimated immigration rate m is 0.54, which, as expected, is higher than for the entire 50-ha plot. In a 1-ha plot, 54% of the area is within 16 m of the perimeter – in very close agreement with the calculation for the 50 ha-plot. Terborgh et al.,1996) argue that dispersal assembly is falsified by their data on the high degree of similarity of terra firme forests up to 40 km apart along the Manu River in Amazonian Peru. However, the theory shows that even weak coupling by dispersal of local forest stands to the size-stabilized meta-community is sufficient to produce strongly correlated local species compositions and relative abundances (Hubbell, 1997a,b). There is an analogous problem in population
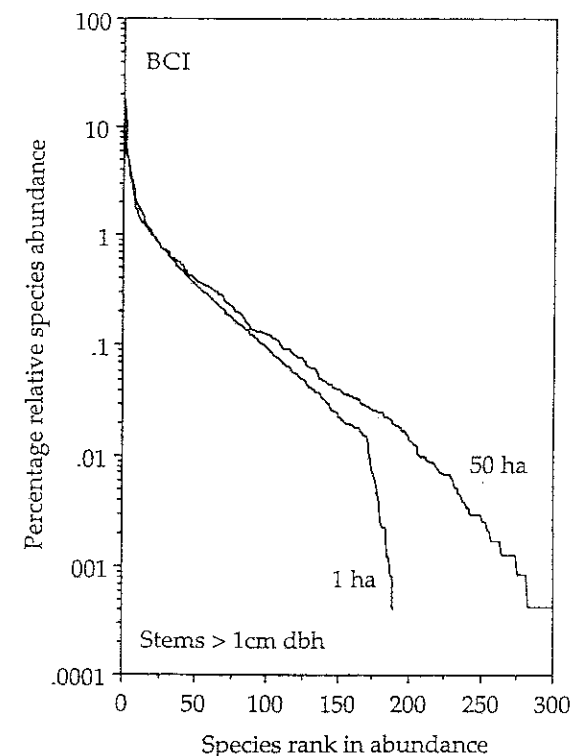
Figure 2.8 Steepening of the dominance-diversity curve of ranked species abundance in 1-ha subplots compared with the curve for the 50-ha BCI plot as a whole. This steepening is explained by the unified theory as an interaction between dispersal limitation and local extinction, particularly of rare species

genetics in which only a very small amount of migration per generation is needed to maintain panmictic populations (Slatkin, 1973).

There are many other predictions of the unified theory that are explored fully elsewhere (Hubbell, 1995; 1997a,b). My purpose here has been to argue that a theory of dispersal assembly is not so casually dismissed. It is capable of explaining a great many of the detailed patterns of species richness and relative abundance in the BCI tree community with a simple three-parameter theory. One could argue that niche-assembly theories may some day do equally well in predicting relative species abundance, even though for the moment they do not. I predict that niche-assembly theory will never provide a satisfactory theory of relative species abundance. However, there are clearly elements of truth in both the niche-assembly and dispersal–assembly perspectives. I conclude now with some speculations on the challenge ahead of synthesizing these two perspectives into a more comprehensive theory of ecological communities in general and of tropical tree communities in particular.
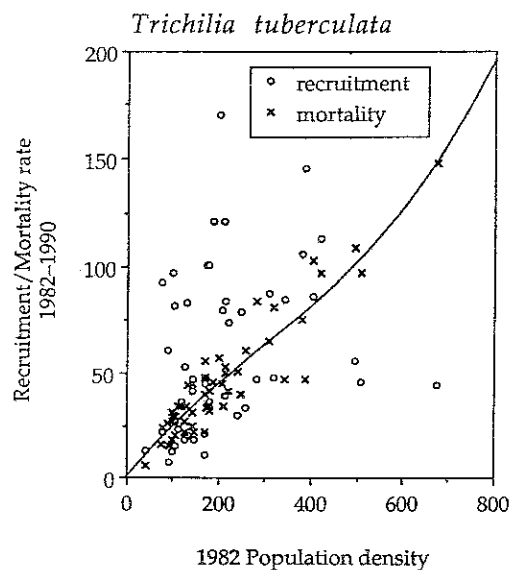
Trichilia tuberculata

Figure 2.10 Density dependence in the canopy tree *Trichilia tuberculata* (Meliaceae) showing a tight functional relationship between density/ha and mortality rate, but density-vague behavior in recruitment rate
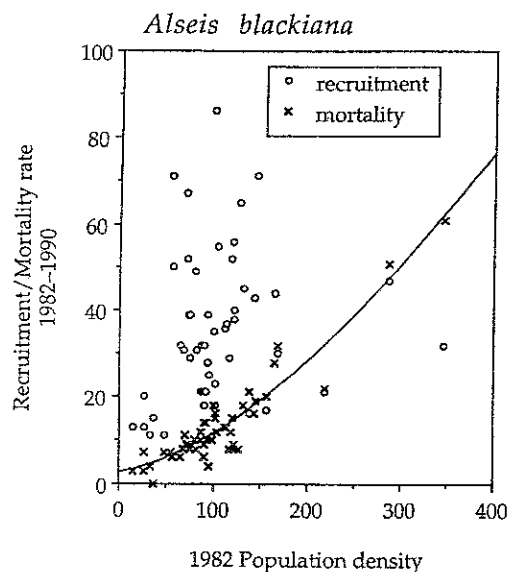
Alseis blackiana

Figure 2.11 Density dependence in the canopy tree, *Alseis blackiana* (Rubiaceae), showing a tight functional relationship between density/ha and mortality rate, but density-

abundance much more often than common species (Condit *et al.*, 1992b). Moreover, Wills *et al.*, (1997) found little quantitative support for rare species advantage predicted by their 'herd immunity hypothesis' when the effects of intraspecific density were removed. We also have recorded new species entering the plot, so the BCI forest can be invaded.

The second major empirical finding and theoretical development that helps to reconcile the niche-assembly and dispersal–assembly perspectives is the importance of dispersal limitation. As discussed earlier, gap occupancy rates at BCI, even for pioneer tree species, are very low – on the order of 1% to 3% of suitable sites. Because of severe dispersal limitation, and a geometrical constraint of how many stems can be packed into a small finite area, the number of saplings 1 to 4 cm dbh competing for each canopy site (25 m²) is very low – just 6.8 ± 1.3 stems (Hubbell *et al.*,1997). Even if all stems were of different species, the diversity among local competitors never exceeds about 2.3% of the primary census species. Therefore, competition always takes place among only a tiny subset of all potential competitors. As a result, the best competitor species is often absent from the site, and a great many canopy positions are won by 'default' in any given canopy-tree replacement cycle. Moreover, the packing constraint will continue to operate, following an allometric rule, throughout ontogeny, so that dispersal and recruitment limitation and winning by default are mechanisms that operate throughout the entire life history of tree species as they compete for positions in the canopy, or in the understory if they are understory specialists.

The importance of this finding for the maintenance of species diversity has been explored theoretically by Tilman (1994), Hurtt and Pacala (1996), and Hubbell (1997a). Tilman (1994) showed that if there was a strict, ordered trade-off between competitive ability and dispersal ability, such that the best competitor was the worst disperser and *vice versa*, then in principle there was no upper limit to the number of co-existing species. As discussed earlier, it is not clear whether this strict trade-off occurs in BCI trees. Hurtt and Pacala (1996), however, showed that dispersal limitation by itself can overwhelm the effects of even strong competitive differences, especially in species-rich communities such as tropical forests. The critical limitation may not in fact be in the dispersal stage, but instead in adult fecundity or in subsequent recruitment stages. These limitations at different stages are functionally equivalent in their theory.

Hurtt and Pacala (1996) analyzed a model of a community of niche-differentiated species partitioning an environmental axis. Each species is the absolutely best competitor in some region of the axis. Without dispersal limitation, each species wins those sites in which it is the best competitor. With dispersal limitation, many sites are won by default, by species that are not the absolutely best competitor for the site. The authors proved that dispersal limitation so slows down the rate of competitive exclusion that large numbers of inferior competitor species can persist as fugitives essentially 'forever', if forever means thousands to hundreds of thousands of generations. I subsequently

THE CHALLENGES AHEAD

The difficulties of reconciling the niche-assembly and dispersal–assembly perspectives are not as widely appreciated as one might expect. It is perhaps not so daunting a task as the wave–particle duality of quantum physics, but nevertheless it is not trivial. On the one hand, there are theories asserting that relative abundances of tree species could in principle (if one knew enough) be deduced from resource-based competition theory (e.g. Tilman, 1982, 1988). On the other hand, island biogeography theory contends that the dynamics of immigration and extinction control presence, absence, and relative species abundance (MacArthur and Wilson, 1963, 1967). By implication niches *do not* control the presence, absence, or current relative species abundance of species; dispersal and extinction do.

How do we reconcile these ideas? I believe two discoveries from the BCI Forest Dynamics Project and some recent theoretical developments may hold the answer. The first discovery is that the regulation of populations of BCI trees is density-vague *sensu* Strong (1986). Ecologists have grown up with a model of population regulation represented by the cartoon in Figure 2.9a. Per-capita birth rates fall with increasing population density, per-capita death rates rise, and where these rates cross is the carrying capacity, or the expected point of regulation. This theoretical construct assumes that the birth and death rates are one-to-one functional mappings onto density; i.e. real mathematical functions. What we find for BCI tree species, however, is better characterized by the cartoon in Figure 2.9b. Death rates are generally good mathematical functions of density. But recruitment (birth) rates are not neat functions of population density, except that there is an upper bound for per-capita recruitment, and this upper bound declines with population density. This lack of functionality in recruitment is the result of environmental stochasticity affecting year-to-year fecundity as well as seed and seedling mortality. Figures 2.10 and 2.11 illustrate these patterns for two common canopy tree species, *Trichilia tuberculata* and *Alseis blackiana*.

There are three important conclusions to be drawn from this result. The first is not to expect tree species to achieve constant equilibrial abundances in the BCI forest, whether or not niche assembly is at work. There *is no* identifiable point of density regulation, for example, in either *Trichilia* or *Alseis*, although there appears to be a cap on maximal density in each species. The second conclusion is that these results are consistent with Chesson and Warner (1981), who have demonstrated that stochastic variation in recruitment rates, but *not* in death rates, will promote coexistence between species. They taught that recruitment variation should not be treated as just 'white noise', but that it actually can be a stabilizing force (Chesson, 1986). The final conclusion is that the abundance fluctuations now expected in all BCI tree species open the door for immigration and extinction processes; i.e. to dispersal–assembly. The community should no longer be viewed as a locked-up assemblage at static adaptive equilibrium that cannot be invaded.
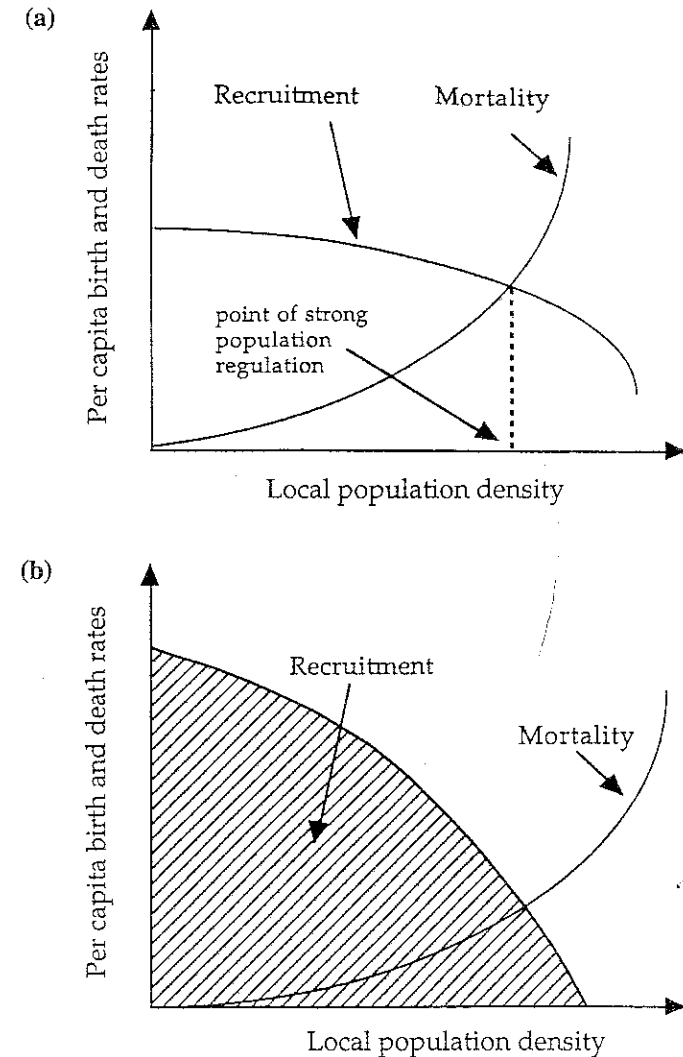
Figure 2.9 Cartoon of classical model of density dependence (panel A) and the density-vague population regulation that appears to apply to BCI tree species (panel B). Note that the per-capita mortality is a reasonably tight mathematical function. The density vagueness is only expressed in the recruitment function

Chesson (1986) argued that species will be 'bounded away' from extinction, and this is certainly true in his model. However, as I have stated elsewhere (Hubbell, 1995), the strength of frequency dependence in the Chesson and Warner model may be unrealistically high. We have found no evidence that the rare species in the BCI plot have a frequency-dependent advantage (Hubbell and Foster, 1992). If anything, the rare BCI species appear to be decreasing in

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equilibrium species richness and relative species abundance is achieved at steady state between speciation and extinction (Hubbell, 1997a). The rates of competitive exclusion under dispersal limitation in Hurtt and Pacala's model are so slow that they become commensurate with rates of speciation. These theoretical results combined show that large numbers of species that would be expected to be eliminated by competition under classical niche–assembly theory reach a steady-state diversity under dispersal–assembly theory. These theoretical and empirical results also explain the apparent paradox of so many very similar species coexisting. The fact is that they hardly ever encounter one another in a species-rich forest, so that direct competition between specific pairs of species almost never happens. Even if they did, in plant communities the winner is usually the larger of the two plants (because of shade competition), regardless of species. Thus, in mixed-species, mixed-age, species-rich tropical forests, the accidents of relative size and age will also operate to greatly slow down rates of competitive exclusion.

These results have potentially profound implications for the current niche–assembly paradigm in community ecology because they show that dispersal limitation, allometric packing constraints, and size-dependent competition all act powerfully and in concert to decouple the control of abundance from the relative competitive abilities of species as defined by their niches. It is for these reasons that I firmly believe that the dispersal–assembly perspective will take far greater prominence in the future in conceptions about how ecological communities, including tropical tree communities, are assembled and maintained. However, if there is one overriding lesson that I have learned in the course of this long-term study, it is that ideas, like forests, change. Perhaps the greatest challenge that lies ahead is to ensure that empirical science keeps pace with theoretical science and keeps ahead of the pace of the burgeoning global destruction of tropical forests.

ACKNOWLEDGMENTS

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Section II

Monitoring and modeling forest biodiversity