Understanding the Role of Chronic Environmental Disturbance in the Context of Island Biogeographic Theory

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ABSTRACT / Island biogeographic theory offers a powerful conceptual framework for understanding and managing insular diversity. The human impact on insular environments is constantly growing, especially because of tourism. We performed a simulation study aimed at improving the understanding of the role of disturbance in islands. We also built an individual-oriented computer model of an archipelago subjected to chronic disturbance of varying degree. Results are discussed in the light of island biogeographic theory. Relevant results show the importance of autoecological characteristics of the species considered, regarding the attainment of equilibrium and the species-area relationship in both disturbed and undisturbed cases. The possibility of bias in the predictions of the equilibrium model is pointed out. Fundamental criticisms concerning the ecological relevance of the equilibrium theory are discussed.

Understanding patterns of species diversity that characterize insular biotas is a major aim of ecological science. The observation that islands usually contain fewer species than comparable areas on the mainland has spawned scientific research that touches all the important fields of theoretical and applied ecology. The contributions of MacArthur and Wilson (1963, 1967) mark the move from the naturalistic realm to a coherent quantitative theory of island biogeography, a milestone in modern ecology.

The large body of subsequent work stimulated by MacArthur and Wilson's theory shows how important the topic is. The theory, in fact, has a potential for applications that extends far beyond the study of insular biotas. The increasing human impact on the environment makes species diversity a resource of high value, whose conservation and management depend primarily on scientific understanding. The theory of island biogeography is discussed in relation to conservation in many different contexts, with arguments that stretch from the correct size and shape of natural reserves (Diamond and May 1981) to recovery rates in perturbed environments (Gore and Milner 1990) and the formulation of pest-control strategies (Stenseth 1981). The rationale for such applications is the ecological analogy between islands and isolated habitats, such as mountain tops, lakes, cultivated fields, or natural parks immersed in an environment disturbed by mankind.

The applied relevance of island biogeographic (IB) theory has been noted since the first years of its introduction. We believe that explicit consideration of environmental disturbance, which until now has been lacking, should greatly enhance the predictive power of real-world applications. The aim of this study is to investigate the role of disturbance in models of small insular environments. In the first section we review the fundamentals of island biogeography, along with the most important criticisms of it; we will deepen the aspects we believe most relevant to disturbance. In the second section we show the results of a simulation study, which was carried out in order to show how patterns of insular species diversity behave in time and space in the presence of chronic environmental disturbance.

Island Biogeographic Theory

Theoretical Basis

Island biogeography, like most "classic" ecological theories, is based on an equilibrium metaphor. At the heart of its formulation, there is the statement that the number of species on islands reaches a dynamic equilibrium when the rate of immigration of new species

KEY WORDS: Computer simulation; Disturbance; Equilibrium theory; Individual-oriented modeling; Island biogeography

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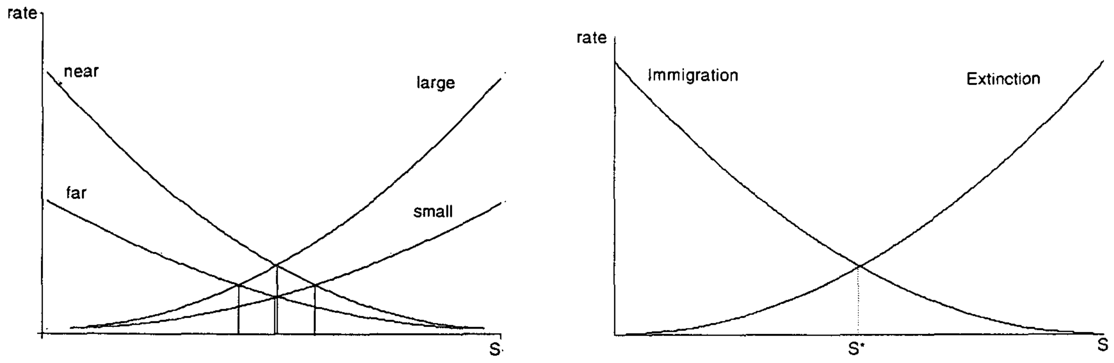

Figure 1. The MacArthur and Wilson equilibrium model.

balances the rate of extinction of ones that are already present. Figure 1 illustrates the equilibrium concept: rates of immigration and extinction are represented as a function of the number, S, of species present on an island; when the island contains more species, the probability of a new one colonizing it is lower, so the rate of immigration from the mainland pool (whose composition is assumed constant) decreases with the increase in S. On the other hand, the probability of extinction of species that are present is higher when the total number of species is high, such that the extinction curve is increasing. Over time, immigration and extinction rates converge towards a stable value, corresponding to the equilibrium number of species (S^*). Under the simplest assumptions immigration and extinction curves are linear: different dispersal abilities of species and interactions among them modify the respective shapes to concave, as shown in Figure 1a.

The steepness of the curves changes with area and degree of isolation, thus modifying the equilibrium value. Immigration rates are assumed to decrease with increasing distance from the mainland, and extinction rates to decrease with increasing island area. Figure 1b shows immigration and extinction curves for islands of different areas and degrees of isolation. One can see how the number of species at equilibrium changes as a function of these variables.

The formulation described above allows quantitative predictions of how the equilibrium number of species changes with area and degree of isolation. If distance from the mainland is equal, IB theory predicts that the number of species on islands of different areas will change as a monotonically increasing function of area (the species–area relationship). Theoretical considerations (Preston 1962) suggest a power model of the type

$$S = CA^z \qquad (1)$$

where S, the number of species at equilibrium, is a direct function of A (area) raised to the constant exponent z. Assumption of a log-normal distribution for relative abundance of species (May 1975, Preston 1962) leads to an expected z value of 0.262. For observation to be in accordance with theory, most authors (May 1975) suggest a range for z of 0.16–0.39.

Observed species–area data very often agree with the above model, with z values that mostly fall inside the suggested range. However, exceptions do occur, both for the best-fit model and for the observed value of z (Connor and McCoy 1979).

Criticisms

Debate on IB theory has been intense since the very year of its introduction. Empirical and theoretical contributions have raised objections on most of its aspects. Fundamental criticisms are briefly listed here.

- IB theory is often considered to be simplistic with regard to immigration and extinction mechanisms. It is assumed that extinction rates depend on area, while immigration rates depend on distance from the mainland and on the presence of intermediate "stepping-stone" islands. Both dependence of extinction rates on distance (Brown and Kodric-Brown 1977) and of immigration rates on area (Lomolino 1990, Osman 1977) have been predicted and experimentally demonstrated (see, for example, Toft and Schoener 1983; a comprehensive reivew of these and other criticisms is found in Williamson 1981).
- A good agreement of observed species–area data with the power model (equation 1), with z values falling inside the expected range, has often been claimed as support for the equilibrium theory. Criticisms have been made mostly on methodological grounds, pointing out errors and the possibil-

ity of statistical artifact in application of equation 1 (Connor and McCoy 1979, Loehle 1990, Sugihara 1981). Attainment of equilibrium has been shown not to relate with z values that fall inside the expected range (Aizen 1989). The biological meaning of the coefficients (z in particular) has also been much discussed (Connor and McCoy 1979), without reaching adequate conclusions (Abbott 1983).

- IB theory does not address fundamental phenomena at the population and community level. While it takes population sizes implicitly into account when dealing with extinction rates, predictions are flawed by lack of the assumption of an underlying distribution of relative abundances among species (Williamson 1981). Habitat dynamics and ecological succession and disturbance are ignored, while later contributors (Seagle and Shugart 1985) suggest that island biogeographic phenomena may result from interaction between habitat dynamics and disturbance. Furthermore, no evolutionary change is assumed to take place, in spite of the importance of evolution in insular environments, which has been known since Darwin (1859).

Applications

The applied potential of island biogeography has been recognized since a few years after its introduction (Diamond and May 1981, Wilson and Willis 1975). Research efforts were directed primarily to assessing its usefulness for the design of natural reserves, whose small size and isolation suit them to the island analogy.

The knowledge of the determinants of species extinction and the species–area relationship have been viewed as the basis for estimating optimal characteristics for a natural reserve, like minimum area and shape. A still-debated issue, usually referred to as the SLOSS (single large or several small) problem, is whether many small reserves have more conservation value than a large one. Island biogeographic theory seemed to be the ideal context in which to look for an answer (Diamond 1976, Simberloff and Abele 1976, Wright and Hubbell 1983). Disillusion followed the scientific debate and the first tentative applications (Reed 1983, Zimmerman and Bierregaard 1986). It is now agreed that any successful conservation plan must take into account questions not addressed by IB theory. In particular, the need for integration of autoecological knowledge is stressed by most authors (Boecklen and Gotelli 1984, McCoy 1982).

In our view, the general formulation of IB theory provides a useful conceptual framework that must be filled with case-specific information when applied to real problems. Species diversity patterns observed in empirical studies have often been proved to agree with predictions (Have 1987, Lomolino 1984). In most real-world cases perturbing phenomena occur, and stochasticity dominates the scene. We believe that knowledge of IB theory is indispensable for the formulation of hypotheses against which to test observed patterns. The equilibrium metaphor provides a valuable context to formulate applied hypotheses. For example, evaluation of times of recovery after perturbation is a fundamental issue in environmental impact assessment and is meaningful only in an equilibrium context. Our contribution tries to clarify the requirements for the equilibrium assumption to hold; suggestions for evaluation of return times as a function of measurable biological parameters are also given.

Environmental Disturbance in Islands

The importance of environmental disturbance in islands is overwhelming. The natural value of insular environments is often very high: in 1986, 30% of the total area of natural reserves was located on islands (World Resources Institute 1986). The attractiveness of the island biota is the cause of high tourist pressure. In addition, any human activity is potentially more disrupting in islands than in any other environment, because of the high fragility due to isolation and small area. Thus, economic development (usually deeply connected to tourism) implies great levels of disturbance of the fragile biota of the insular environment (Beller and others 1990; see also some papers in this issue, e.g., Morey and others).

The nature of perturbations deriving from the phenomena discussed above is, of course, complex. Social and economic systems are involved as well as the ecological one. Disturbance in our work is studied from the ecological point of view and simply modeled on the basis of the definition found in Begon and others (1990, p. 754): "(disturbance is) any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different species." In an insular context, this mechanism gives realistic account of direct reversible aspects of perturbation, like trampling of vegetation or temporary invasion of colonizable habitat. The pattern of disturbance chosen, which is discussed in detail below, mimics the strict periodicity of the tourism phenomenon.

Materials and Methods

Simulation Model

To investigate island biogeographic phenomena, we found a suitable tool in individual-oriented simulation modeling. This technique has recently begun to show its power for the analysis of phenomena ranging from the population to the ecosystem level and is now used for investigation and for predictive purposes (Huston and others 1988). In individual-oriented models, mechanisms and assumptions concern only single individuals. The advantages are usually greater realism and robustness (Hogeweg and Hesper 1990, Huston and others 1988); the drawback is the requirement of huge computational power, which has delayed their introduction until recently.

Our work adopts an approach that has sometimes been called "artificial world modeling" (Hogeweg and Hesper 1990). A complex model universe is built from a narrow set of assumptions and a possibly large set of boundary conditions. A simulation is run, and patterns of interest are recorded. The experimenter compares results with empirical and theoretical expectations and gains knowledge on the underlying mechanisms by changing the boundary conditions and repeating the process. Our model concerns individuals who move from a colonization front to a model archipelago. They can settle on islands, where they reproduce and die according to species-specific life-history parameters. Environmental disturbance acts on settled individuals by killing them and leaving space open to new colonization. Each process is modeled stochastically.

Before each simulation run, the experimenter must define the objects involved in the simulation. These are:

- A habitat map, comprising one or more islands. Islands are conceived as subdivided into cells. The cell size is the same on all islands and is specified by the experimenter. Each cell is assumed to contain at most one individual coming from colonization or reproduction. Cells are usually empty at the start of the simulation. Figure 2 is an idealized representation of the map used in the course of experiments; the numbers above islands are the total cell count for each.
- A species list. Each species involved in the simulation is defined by three life-history parameters. We considered the mean life length (L_i), the mean frequency of reproductive events (R_i), and the clutch size, given as a min–max range ($C_i\min - C_i\max$). These parameters constitute the minimum description for simulating individual mechanisms that led to population growth. In addition, a coefficient is specified that describes the relative ability of dispersal of the species (see below).
- A colonization front. This represents the mainland species pool, which is assumed to be located on one edge of the map. The experimenter specifies the edge chosen and the list of species involved. For each species a number describes the relative abundance in the pool.

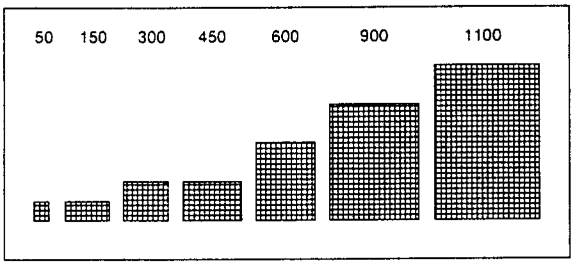

Figure 2. Idealized representation of the model archipelago used in experiments. Numbers above islands are the numbers of cells contained in each.

The pattern of perturbing events desired and other simulation control parameters (e.g., the total simulated time) are also given. At each simulated time unit, three main processes take place: colonization, involving the "launch" of individuals taken from the mainland source pool and their possible settling on islands; birth and death, involving the life-history events of settled individuals; and disturbance, involving perturbations and possible death of settled individuals. The flow-chart diagram of Figure 3 summarizes and complements the model description.

- Colonization. Individuals colonize the islands from the colonization front located on one edge of the model archipelago. They must land on an empty cell to colonize the island successfully. At each simulated time unit, a specified number of individuals is launched from the colonization front. Each individual pertains to a species that is chosen from the source pool; the probability of belonging to a particular one is proportional to its relative abundance. The distance traveled is chosen from a negative exponential distribution (based on a dispersal model by Taylor 1978; see the discussion in Villa and others 1990), whose shape depends on the dispersal coefficient given for that species. The direction is chosen randomly.

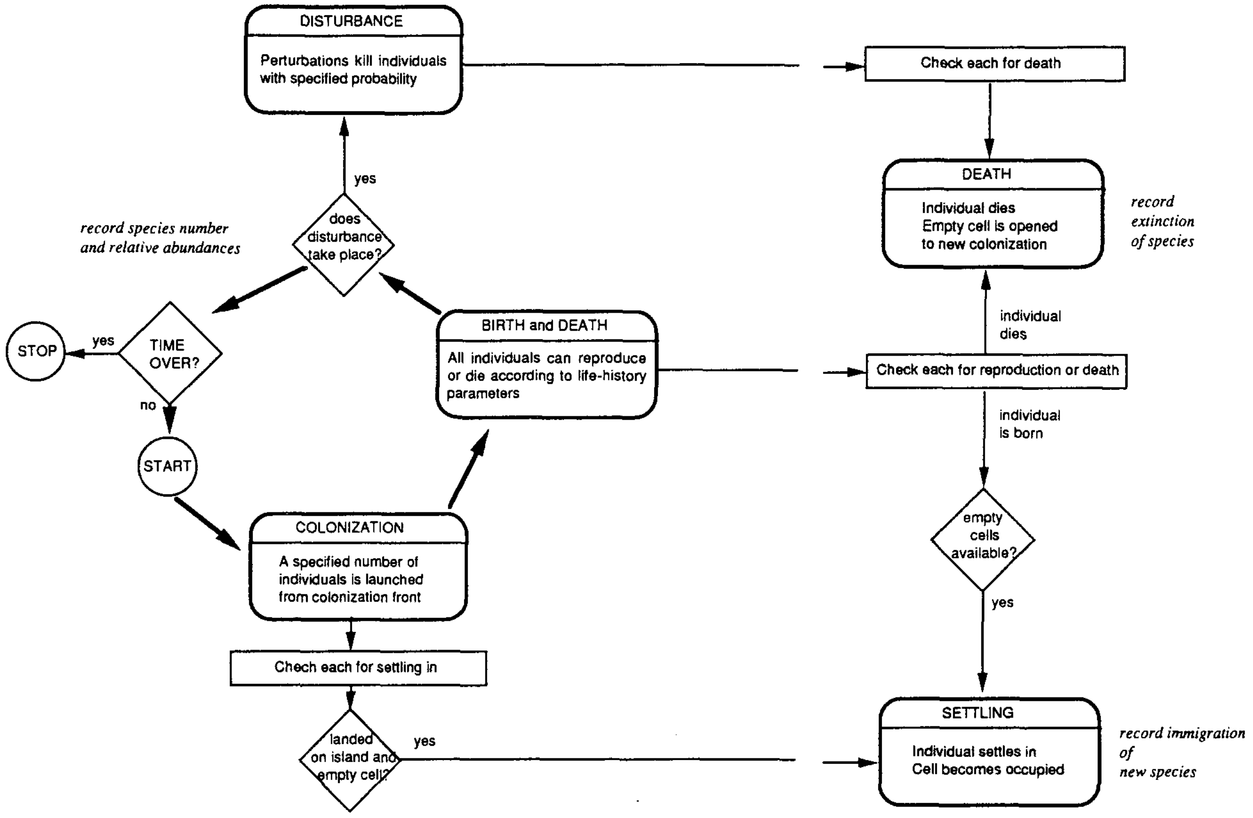

Figure 3. Flow-chart representation of the simulation model. Shaded boxes refer to processes concerning single individuals.

- Birth and death. Individuals that have landed on empty cells reproduce and die according to the simplest possible model based on the species-dependent life-history parameters. The mean frequency of reproductive events for species i (R_i) is used to determine the probability of reproduction for each individual of that species at each time unit; this is simply calculated as $1/R_i$, assuming age-independence for fertility. If reproduction takes place, the number of new individuals produced is chosen randomly in the interval between $C_i$min and $C_i$max, including both extremes. Every new individual is subjected to the same fate of a new colonizer, i.e., a destination cell is chosen randomly on the island and the individual survives only when this cell is empty.

  The probability of dying is computed similarly: if L_i is the mean life-span for an individual of species i, then its probability of dying is $1/L_i$ at each time unit. This computation, like that of reproduction, is based on the assumption of an age-independent death rate. Further parameters related to reproduction and death (choice of partner, time lags due to growth to mature stage, pregnancy, or dormancy) are ignored. The robustness of the individual-oriented modeling paradigm justifies the simplicity of these assumptions: as discussed below, the model has the ability of reproducing known population and community-level patterns in a very realistic way.
- Disturbance. This is globally intended as the result of perturbing events that happen with a specified periodicity and strength. Each perturbation implies a fixed probability of death for the individual contained in each occupied cell. When perturbation strikes, each individual settled on each island can be "killed" with a specified probability, making its cell open to new colonization. All species are assumed to be equally vulnerable to perturbation. Perturbation events can be made to happen with the desired periodicity and strength; this latter is defined by the probability discussed above.

The other assumptions on which the model is founded can be summarized as follows. (1) Immigration is assumed to be purely stochastic, i.e., no "target

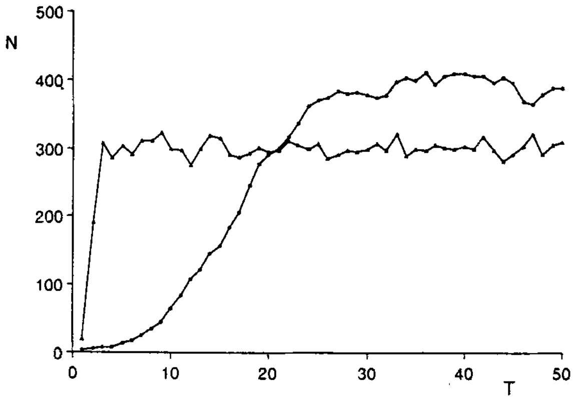

Figure 4. Simulated growth curves [$N = f(t)$] for populations starting with four individuals of two different species, in an island with 450 cells.

area" effect (Lomolino 1990) is incorporated. This is realistic for species whose dispersal is most likely to be random, such as plant seeds or insects. (2) Individuals of different species occupy cells of the same size, so that the carrying capacity of each island is the same for all species considered. This restricts the field of study to species with similar home range, which is in tune with most island biogeographic studies that take into account congeneric or confamiliar species. (3) Explicit species interactions are not considered; however, competition for space and intraspecific competition are built-in features of the model. An individual landing on an occupied cell does not settle in; thus the actual probability of successful individual colonization depends inversely on the density of the already settled populations. (4) Colonization from island to island does not take place, i.e., stepping-stone effects (MacArthur and Wilson 1967) are not considered. (5) Extinction is recorded when no individuals of a particular species are present; this happens only by virtue of demographic processes, i.e., no minimum viable population size (Pimm and others 1988) is assumed.

Experiments Conducted

The model was tested with a number of validation experiments before putting it to work. These preliminary experiments were designed to assess the realism of population- and community-level patterns obtained from simulations. We simulated the growth of a single population and of two populations together, in different islands and with different species characteristics. We also recorded immigration and extinction data under different conditions. The model reproduced realistically the logistic growth curve and the growth of competing populations. Figure 4 shows the population growth curves for a fast-growing and a slow-growing species, in independent islands composed of 600 cells. Immigration and extinction patterns in undisturbed situations behaved as predicted by island biogeographic theory. A significant species–area relationship consistent with the model (equation 1) was always found after about 30 time units.

The model archipelago is composed of seven islands of different areas, located at the same distance from the colonization front. Figure 2 shows the map of the archipelago along with island areas, expressed as the number of cells contained in each island.

The colonization front contains 64 species. The distribution of relative abundances is based upon a study case that was reported by Kempton and Taylor (1974): to avoid introducing any further assumption, we preferred a real distribution rather than a theoretical one, like the log-normal or gamma. Dispersal coefficients for each species have been randomly generated from a normal distribution with a mean of 2.5 and a standard deviation of 1, which accounts for a slight differentiation in dispersal abilities between species. This is more realistic than equal dispersal even among otherwise similar species, given the great variability in dispersal attitude found in nature (see, for example, the discussion in Begon and others 1990).

Two kinds of model organisms were used in this study; their respective life-history parameters were chosen to obtain a slow-growing and a fast-growing species, expressing different life strategies. In a preliminary experiment, four individuals of the same species were put separately on to each island; two simulations, one for each species, were then run, allowing only reproduction and death events (no colonization). In all cases, the logistic curve fitted very well the resulting growth curve (R^2 from nonlinear least-squares fit was never less than 0.95), giving consistent parameter estimates in islands of different size. Table 1 lists the life-history parameters relative to each species, along with values of r (intrinsic rate of increase) obtained by fitting the logistic model to growth curves in all islands. One can see that r values range around 0.06 for the slow-growing population and around 0.5 for the fast-growing one.

We performed ten simulation runs. In five of them, corresponding to five disturbance levels, life-history parameters for all 64 species have been set to obtain the slow population growth; in the other five, fast-growing species were used with the same disturbance levels. Disturbance was modeled keeping in mind the character of the tourism phenomenon, which is very important in islands, as discussed in the

Table 1. Life-history parameters for two typologies of organisms used in experiments[a]

	Life-history parameters and growth rates									
Species	Clutch size ($C_i$min-$C_i$max)	Lifespan (L_i)	Reproductive interval (R_i)	area = 50	area = 150	area = 300	area = 450	area = 600	area = 900	area = 1100
Slow-growing	1 to 1	30	10	$r = 0.065$	$r = 0.093$	$r = 0.056$	$r = 0.074$	$r = 0.076$	$r = 0.052$	$r = 0.066$
Fast-growing	1 to 3	10	2	$r = 0.732$	$r = 0.558$	$r = 0.619$	$r = 0.510$	$r = 0.518$	$r = 0.472$	$r = 0.466$

[a] The intrinsic rate of increase, obtained in each island by fitting the logistic model to a simulated growth curve, is reported.

Table 2. Schematic representation of experiments

	Experiment layout				
Species	1	2	3	4	5
Slow-growing	10 replicates no disturbance	10 replicates disturbance = 10%	10 replicates disturbance = 25%	10 replicates disturbance = 40%	10 replicates disturbance = 75%
Fast-growing	10 replicates no disturbance	10 replicates disturbance = 10%	10 replicates disturbance = 25%	10 replicates disturbance = 40%	10 replicates disturbance = 75%

introduction. Thus we chose a chronic, strictly periodic pattern of perturbation events, whose strength has been made to vary from low (10% probability for each cell of being perturbed) to very high (75% probability). Table 2 is a schematic representation of the experiments conducted, listing the strength of perturbations and the species typology used in each case.

The total simulated time in each case was 120 time units. At each time unit, ten individuals were launched from the colonization front. Disturbance begins at time unit 30, when all islands contain the maximum number of species in the unperturbed case; perturbation strikes at each four time unit's on all islands until the end of the simulation. For each case shown in Table 2, ten replicates were obtained.

The model is computationally intensive, each simulation taking minutes to run on the CRAY Y/MP supercomputer. We recorded the number of species, immigrations, extinctions, and relative abundance of all species on each island at each time unit. Data analysis and all statistical calculations were made by the SAS statistical package, running on an IBM 4341 mainframe.

Data Analysis

The model suggested by MacArthur and Wilson (1963) predicts that immigration and extinction rates depend on the number of species in a well-defined way (see Figure 1). The suggested mathematical relationships are

$$I = k_i\,(P - S)^{n_i} \qquad (2)$$

$$E = k_e S^{n_e} \qquad (3)$$

where I and E are immigration and extinction rates, S is the number of species present on the island, P is the number of species present in the source pool, and k_i, k_e, n_i, n_e are constants. These relationships are often in good agreement with observed data (see, for example, Terborgh 1974); in most cases the exponent is greater than 1 for both immigration (n_i) and extinction (n_e). In biological terms, deviations from linearity arise from differences in dispersal abilities between species ($n_i > 1$) and from species interaction on islands ($n_e > 1$; see MacArthur and Wilson 1967, Diamond and May 1979). The experimental design and the construction of the model (see above) are such that both effects should be expected in our results; in fact, the value 2 for both n_i and n_e gave the best fit to simulated data. We considered absolute immigration and extinction rates, as recommended by Schoener (1988); these are computed as the absolute number of immigration and extinction events recorded at each time unit.

Decision concerning the attainment of dynamic equilibrium with a set of experimental data is a subjective matter. According to McCoy (1982), two conditions should at least be met: (1) the number of species after a particular time unit must remain approximately constant; and (2) immigration and extinction rates should be approximately equal, while remaining greater than zero. The extent to which the approximation should be taken is a subjective choice. To test for equilibrium, we preferred to consider the processes that determine species number, immigration, and extinction. We plotted the difference (d) between immigration and extinction data as a function of time.

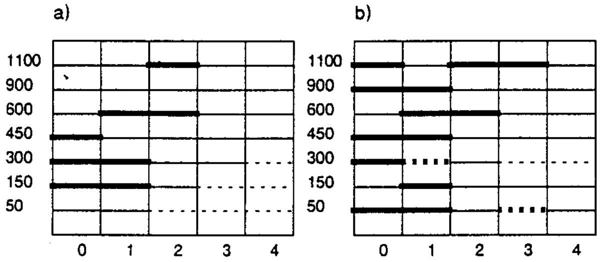

Figure 5. Results of testing for equilibrium on all islands for all levels of disturbance for (**a**) fast-growing and (**b**) slow-growing species. A thick line means equilibrium conditions met. Dashed lines are shown where the fit of equations 2 and 3 was not good.

We performed a linear regression of *d* versus time, over the interval in which the *d* value remained approximately constant. The beginning of this interval was determined by eye. Equilibrium was assumed when: (1) the fit of the regression line was good ($R^2 > 0.7$); (2) the slope value did not significantly differ from 0; (3) confidence intervals (at 95%) for the intercept contained the value 0; and (4) residuals from the linear regression appeared to be normally distributed around mean 0.

Nonlinear models (equations 1–3) have been fitted to data using least-squares nonlinear regression (Gauss-Newton method), with data for all replicates together. The fit was validated by the R^2 value and the analysis of variance: we considered it to be good when $R^2 > 0.7$, when $P < 0.01$, or in both cases.

Results

The equilibrium condition discussed in the Methods section was tested on each island in all study cases. Equations 2 and 3 were also fitted to immigration and extinction data. In most cases the fit was satisfactory. The predicted value of the number of species at equilibrium (S^* in Figure 1) was then computed as the abscissa of the intersection of the fitted immigration and extinction curves. In Figure 5, rows correspond to islands of different areas, while columns correspond to the five classes of disturbance considered. Thick lines are shown for islands where the equilibrium condition was met. A dashed line means that the fit of immigration or extinction data was not good. The two graphs refer to slow-growing species (Figure 5a) and fast-growing ones (Figure 5b).

In Figure 6a, the plot shows the percentage of equilibrium cases as a function of area, computed over the five disturbance levels. Conversely, Figure 6b shows the percentage of equilibrium cases among different areas as a function of disturbance level. In both cases slow-growing and fast-growing species are separated. Graphs in Figure 6 are based on the same information contained in Figure 5.

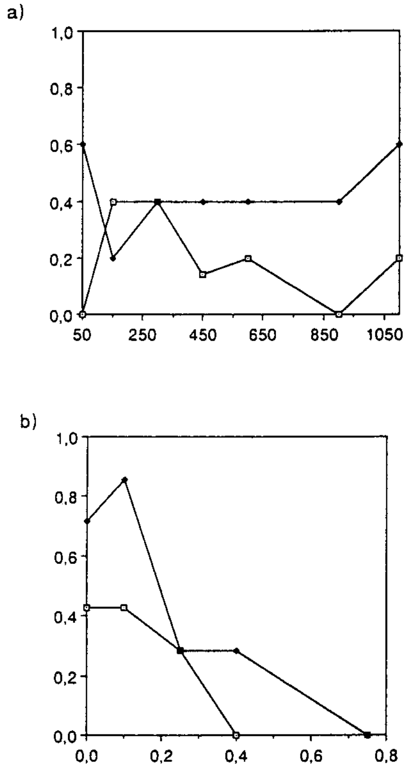

Figure 6. (a) proportion of equilibrium cases as a function of island area, computed over the five disturbance levels. (**b**) Proportion of equilibrium cases among different areas as a function of disturbance level. Solid dots refer to fast-growing species, open dots refer to slow-growing ones.

In each case with good fit of models 2 and 3, we compared the value of the number of species at equilibrium as predicted by the model (S_{pred}) with the observed mean value (S_{obs}). In nonequilibrium cases, S_{obs} was estimated as the mean value of S over the period where no increasing or decreasing trend appeared in data. To test the predictions of the equilibrium model, we performed for each case a linear regression of S_{pred} versus S_{obs}, with islands of different areas. If predictions are good, intercept near 0 and unitary slope are expected. Table 3 lists parameter estimates from the linear regressions obtained in each case.

To test the permanence of populations on islands, we recorded the times to extinction of settled populations for each study case and computed their frequency distribution on each island. Figure 7 shows

Table 3. Parameter estimates from linear regressions of model-predicted S value versus actual mean value found[a]

	Predictivity of MacArthur and Wilson's model				
Species	No disturbance	disturbance = 0.1	disturbance = 0.25	disturbance = 0.4	disturbance = 0.75
Slow-growing	$a = -5.222$	$a = 2.271$	$a = 10.95$	$a = 12.75$	$a = 3.636$
	$b = 1.110$	$b = 1.078$	$b = 0.899$	$b = 1.389$	$b = 6.182$
Fast-growing	$a = 0.706$	$a = 2.289$	$a = 1.295$	$a = 0.676$	$a = 4.216$
	$b = 0.950$	$b = 1.027$	$b = 1.220$	$b = 1.290$	$b = 2.194$

[a] All fittings are significant at the 99% level. See text for explanations.

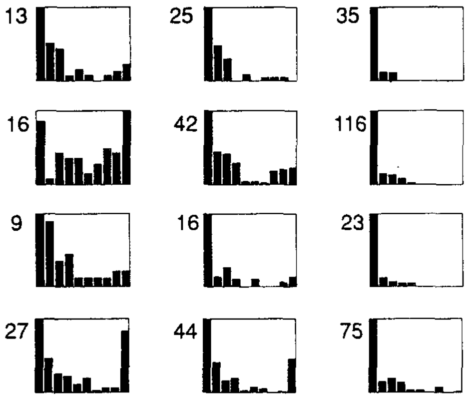

Figure 7. Frequency distribution of population lifetimes on two island with three different levels of disturbance. First row: area = 50, slow-growing species. Second: area = 50, fast-growing species. Third: area = 1100, slow-growing species. Fourth: area = 1100, fast-growing species. Columns refer to levels of disturbance 0, 0.25, 0.7. All histograms have ten time intervals from 0 to 120; the value of the higher class is reported on the ordinate.

some representative cases, chosen among the 70 (seven islands for each case) studied. Distributions for two islands are shown in four rows. The first two refer to slow-growing species and two areas, the smallest and the largest, respectively. Fast-growing species with the same areas as above are shown in the last two rows. The three columns refer to the levels of disturbance 0, 0.25 and 0.75 (columns 1, 3, and 5 of Table 2).

Species–area relationships have been a primary concern of island biogeographic studies. We fitted equation 1 to data in each study case, and obtained estimates of C and z parameters. The resulting values are reported in Table 4. Figure 8 shows the species-area relationships for three levels of disturbance, corresponding to columns 1, 3, and 5 of Table 2. Figure 8a refers to slow-growing species, while Figure 8b refers to fast-growing ones.

Discussion

Island-Level Patterns: Equilibrium and Turnover

Initial examination of Figure 5 suggests that the global attainment of equilibrium is strongly dependent on the rate of increase of the species involved, with different sensitivity to disturbance. More specifically, when slow-growing species are used, equilibrium is reached in eight cases of the total of 35, while fast-growing species give 15 equilibrium cases in otherwise identical conditions.

The temporal scale that characterizes population processes involved in the attainment of equilibrium should be considered in explanations. The broader time scales that characterize slow-growing species imply the equilibrium, if any, is attained in longer times and is "visible" over comparable time scales. This argument raises the issue of the appropriate units with which equilibrium, and all related processes, should be timed. The findings of Schoener (1983, see below) seem to suggest that the mean generation time of the species involved could serve as an appropriate, while tentative, measure. The generation time of our slow-growing species is ten units, while for fast-growing ones it is two (Table 1). This could mean, if the considerations above hold, that equilibrium should be tested for slow-growing species over a time span five times longer, with a proportionally coarser time resolution in measuring immigration and extinction.

In a natural situation, a biological interpretation could be attempted as follows. Species situated on the r side of the r–K continuum (Pianka 1970), which are characterized by their high growth rate, typically show low resistance (ability to withstand perturbation) and proportionally high resilience (ability to recover maximum population density after perturbation). On the other hand, K-selected species work in some way against turnover; they have a high ability to avoid extinction and relatively low success as new colonizers. The community-level equilibrium in species number is reached at the expense of disequilibrium at the pop-

Table 4. Parameter estimates from fitting the $S = CA^z$ model[a]

	Species–area parameters				
Species	No disturbance	disturbance = 0.1	disturbance = 0.25	disturbance = 0.4	disturbance = 0.75
Slow-growing	$C = 7.073$	$C = 4.801$	$C = 2.973$	$C = 1.143$	$C = 0.098$
	$z = 0.283$	$z = 0.327$	$z = 0.337$	$z = 0.371$	$z = 0.501$
Fast-growing	$C = 4.260$	$C = 3.118$	$C = 2.981$	$C = 1.836$	$C = 0.402$*
	$z = 0.320$	$z = 0.360$	$z = 0.355$	$z = 0.409$	$z = 0.496$

[a] All fittings are significant at the 99% level, except the starred (*) case, which is significant at the 95% level.

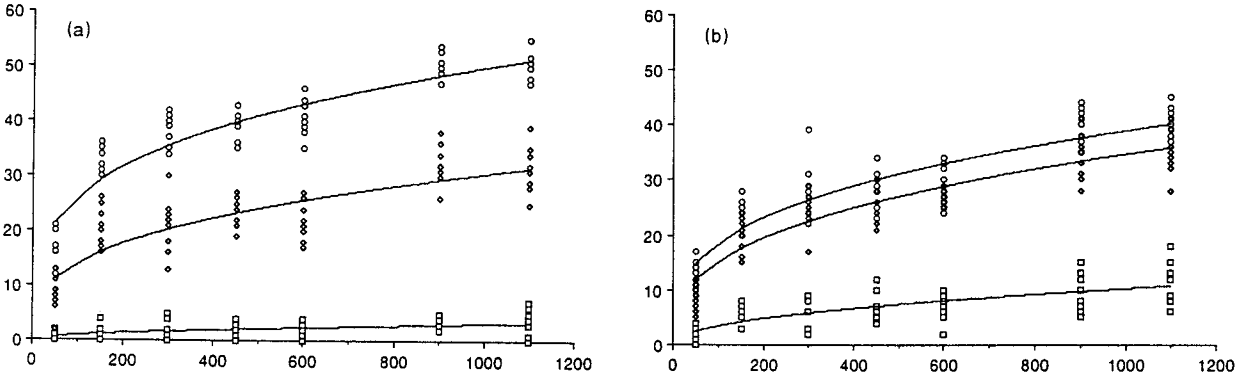

Figure 8. Species–area relationships for levels of disturbance 0, 0.25, 0.7: **(a)** slow-growing species and **(b)** fast-growing species. The solid line is the equation $S = CA^z$ fitted to data. Parameter estimates are found in Table 4.

ulation level; this is a necessary condition for the existence of species turnover.

In the case of *r*-selected, fast-growing species, low resistance implies high susceptibility to extinction, while high resilience implies potentially high success in the first phases of colonization (MacArthur and Wilson 1967); immigration and extinction rates are thus high, and population stability is lower. Conversely, *K*-selected species can reduce immigration and extinction rates up to the point where equilibrium can no longer be attained. In accordance with this agrument, Schoener (1983) found that turnover rates measured in field studies decrease in a predictable way with the increase of generation time, a measure that is strongly related to the population's intrinsic rate of increase (Fenchel 1974, Schoener 1983). These arguments have applied relevance: should the equilibrium hypothesis hold, return times after perturbation would be measurable in time units that are consistent with those that characterize the determining processes. The importance of knowing them is obvious.

Further observations are suggested by examination of Figure 5. One can see that some islands reach equilibrium only when some level of disturbance is present, while in the undisturbed case they are far from equilibrium. Dependence on nonequilibrium population dynamics should explain this observation. Furthermore, there is no clear dependence of equilibrium on area, especially with slow-growing species (see also Figure 6a).

Equilibrium behavior appears not to be related to the good fit of immigration and extinction data to known relations. In ten islands of the 70 considered, data do not fit the equilibrium model. While this occurs with high disturbance and small area for slow-growing species, no such correlation is shown with fast-growing ones. In two cases equilibrium conditions are met, but the fit is bad. The predictive power of the equilibrium model must be tested in all cases where the fit of relations 2 and 3 to data is good. The reason for this is the difficulty of deciding on equilibrium in real-world study cases; often equilibrium is assumed and the goodness of fit is taken as a confirmation.

Linear regression of S_{pred} versus S_{obs} gave a good fit in all cases. When intercept *a* differs from 0, there is an additive bias in the estimation of S^*, which is expressed in units of species number. As Table 3 shows, intercepts for slow-growing species are far from the expected value of 0. Furthermore, they show no clear dependence on disturbance. With fast-growing species, *a* values are far more acceptable, except when disturbance is very high. No clear trend is shown. Except for the first case, all relevant deviations are towards overestimation. Note that it is not possible analytically to compare the intercepts, because of the difference in slopes.

When slopes *b* are considered, dependence on disturbance level is clearer. In cases with low disturbance or none at all, slope values do not deviate much from the expected unitary value. They are much higher when disturbance is strong. For fast-growing species, slope values show an apparently linear increase, while for slow-growing species the situation appears less predictable, with no relevant increase except when the highest level of disturbance is reached. The effect of disturbance on the slope is the expression of a multiplicative bias in the estimation of S^*. This can be viewed as an effect of the interaction between disturbance and area: the application of the equilibrium model leads to overestimation of S^* that is greater in smaller areas.

The predictions of the equilibrium model in the presence of chronic disturbance are thus affected by bias. An additive bias is present in most cases, even when there is no disturbance, and is higher with slow-growing species. In most cases the effect is positive, thus leading to overestimation, and it is not predictable under our assumptions and experimental conditions. A multiplicative bias is also present: it also leads to overestimation of S^* and depends inversely on area. This effect appears to be related predictably to disturbance and is absent in undisturbed cases. It is worth noting that bias is present in cases where disturbance levels are low and species dynamics match the equilibrium conditions. This result is of applied relevance; it suggests caution in applying the equilibrium model to natural situations, especially if human impact is present, so that some level of disturbance can be expected as a rule. Under our assumptions, predictions of S^* based on immigration and extinction records are likely to be higher than they should. This can be of particular relevance should the equilibrium metaphor be applied to predict, for example, rates of recovery after environmental impact; an overestimate of species diversity after recovery could lead to optimistic predictions, resulting in too confident measures. This problem can be even more important if reductions in available area are expected (as usually happens), because of the area-dependent bias discussed above.

An important point about the ecological relevance of the equilibrium model has been made on several occasions by Williamson (1981, 1989a,b). He suggested that although the equilibrium view is realistic, species turnover at equilibrium is in most cases due to locally rare, ecologically irrelevant species. Small population size is the cause of their frequent extinction and reimmigration, while the most ecologically important species do not contribute to species turnover, being dominant and relatively stable. The conclusion drawn by Williamson is that island biogeographic theory may be true but ecologically trivial (Williamson 1989a,b); his argument is, of course, very significant in an applied context.

Figure 7 shows the distribution of population lifetimes in some representative cases. Histograms in the first column refer to undisturbed situations. As predicted by Williamson, short-living populations have high frequencies. However, middle and long lifetimes are also well represented, especially in the large area. Populations in the middle classes contribute to turnover, while remaining ecologically significant: under the assumptions of our model, a lifetime of 60 units (half the experimental time span) corresponds to 30 generations for the fast-growing species, and to six generations for the slow-growing one. Populations that persist more give a lower contribution to turnover or none whatsoever, while still being most important from the ecological point of view.

When disturbance is present, a situation is progressively approached in which no population persists over a few time units. What is most interesting is the progressive disappearance of populations in the middle classes first; dominant populations disappear only when disturbance is very high. Thus, intermediate levels of disturbance give the distribution of times to extinction a shape that matches the situation depicted by Williamson, with most populations living for a short time, and a few dominating the ecological scene. Of course, smallness of area causes more frequent extinctions, accounting for greater sensitivity to disturbance; thus, an interaction effect between area and disturbance is shown, as is to be expected, in this context also. Conversely, the effect of the rate of increase of populations appears counterintuitive: the percentage of populations that persist longer is higher when fast-growing species are used. Results can be summarized as follows.

1. Attainment of equilibrium has relations with the population characteristics of the species involved. In general, species dynamics show an equilibrium behavior more frequently when the intrinsic rate of increase is high. Only here does the frequency of attainment of equilibrium seem to be related to area.

2. The goodness of fit of immigration and extinction data to known models lacks a clear relationship with the actual attainment of equilibrium.

3. Predictions of S^* based on application of the equilibrium model can be biased, most often towards overestimation. Bias is higher with slow-growing species and strong disturbance. This effect can be split into two components, one additive and one multiplicative, of which only the second appears to be predictably related to disturbance.

4. In the presence of disturbance, turnover is mostly accounted for by ephemeral populations, with little ecological relevance. This is true even in equilibrial situations.

Archipelago-Level Patterns: Species–Area Relationship

At first examination, the species–area relationships of Figure 8 show the most marked effect of disturbance. As is to be expected, the overall number of species is proportionally reduced.

Closer inspection of Figure 8 reveals less immediate patterns. When disturbance is low or absent, the overall diversity is higher when slow-growing species are considered. When disturbance is high, this situation is reversed. Again, this can be explained by taking time scales into account: in the present case, perturbation events strike every four time units: this corresponds to two generations of the fast-growing species, while the generation time of slow-growing species is five times longer. The high rate of increase means time to regenerate between two perturbation events, resulting in less sensitivity to disturbance.

On biological grounds, one could say that population resistance (higher for slow-growing, *K*-selected species) plays the most important role in maintaining species diversity high when disturbance is low, while resilience becomes more important when disturbance is high. This is intuitively explained by the following consideration: when environmental conditions are favorable, the advantage is on *K*-selected species, which can maintain the maximum population size. When strong disturbance is present, the ability to colonize the habitat rapidly, which characterizes *r*-selected species, becomes more important, while slow-growing species cannot even reach a significant population size.

High diversity seems to be associated with nonequilibrium. Figures 5 and 6 show that attainment of equilibrium, when disturbance is low or absent, is easier with fast-growing species. These situations are characterized by a comparatively low number of species. This observation seems to be, at first approximation, in tune with theories of community composition that emphasize intermediate disturbance and community nonequilibrium as a means of mantaining a high species diversity (Begon and others 1990).

Examination of Table 4 reveals regularity in the behavior of z values when disturbance is increased. For both species considered, z values increase when disturbance is stronger. The value of z is generally lower for the slow-growing species, but the difference is clear only in undisturbed cases. The z values fall inside the range 0.16–0.39, as suggested by May (1975), only when disturbance is low or absent, and more so for slow-growing species. Higher levels of disturbance raise the value of z outside this range. The species–area relationship becomes steeper when disturbance is present; this means stronger differentiation in species number between small and large islands, which confirms the interaction effect between disturbance and area.

Besides raising the value of z, disturbance strongly decreases the value of the C coefficient. C can be considered a scale factor, which expresses the position of the curve on the ordinate axis when z is held equal (Gould 1979). The difference in C is the mathematical expression of the observed overall difference in species number between study cases. Note that because of different z values, analytical comparison is not possible.

The following conclusions can be drawn from examination of the species–area relationships. (1) Disturbance has the effect of lowering the overall number of species, which is mathematically expressed in the lowered value of C. (2) Population characteristics of the species involved play an important role: if disturbance is low, maximum diversity is attained when species grow slowly. In very disturbed situations, maximum (nonequilibrium) diversity is reached when species are able to maximize their ability to colonization. The relationship between frequency of disturbance and population time scales is probably the most informative criterion to adopt. (3) While the overall species diversity is lower, the steepness of the species–area curve is increased when disturbance is present; this is mathematically expressed by the increased value of z. Species diversity is thus more sensitive to disturbance in small areas than in large ones.

Conclusions

The work presented here is a preliminary contribution, intended to give suggestions for further theoretical and empirical research. We think that the most interesting results concern equilibrium and its assessment. Equilibrium has surprisingly few relationships with measurable parameters. Only the species characteristics seem to play a well-defined role in its attainment; strong disturbance lowers the percentage of equilibrium cases, but low or intermediate disturbance does not have straightforward consequences. The adherence of immigration and extinction records to known models does not bear any relationship with the actual attainment of equilibrium. If the equilibrium concept is considered in an applied context, these preliminary results should sound as a warning against careless assumptions. In particular, equilibrium must be considered over the appropriate time scale, which, at first approximation, is related to the rate of increase of the species involved. Management practices conceptually built on island biogeography should thus take into account autoecological characteristics. It should be kept in mind that equilibrium can mean instability at the population level, which is often opposite to the purposes of conservation practices: it can, anyway, be important for management that overall diversity remains approximately constant.

The role of disturbance is complex even in a simplified system like the one presented here. The overall diversity in disturbed archipelagos is greater if fast-growing species are considered. In several cases it is noted that the effect of disturbance is stronger in small areas. Although this is intuitively clear, it should be kept in mind when planning disruptive intervention. A better understanding of the different roles of immigration and extinction will be useful, for immigration can be managed by artificially introducing species.

Full understanding of the role of disturbance in insular environments will need further research. We think that two main areas need to be explored, with further theoretical research and experimental validation. The first concerns the role of community-level phenomena, such as biotic interactions: competition and mutualism, in particular, should play a major role in determining the sensitivity of the island biota to perturbations of any kind. Simulation modeling can be profitably used here in conjunction with analytical techniques and data analysis.

Another important issue is the full characterization of perturbations in islands. The model of disturbance we used here is very simple if compared to the complex realities of human intervention in islands. Research in this direction will benefit from a multidisciplinary approach, linking socioeconomic factors with environmental ones, and considering the important issue of sustainable development. Case histories will provide the guidelines for this complex research to be carried out. We intend to continue exploring these areas with the final aim of obtaining predictions that are useful for decision-making.

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