

A SYSTEM DYNAMICS MODEL OF ISLAND BIOGEOGRAPHY

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The MacArthur–Wilson equilibrium theory of island biogeography has been one of the more influential concepts in modern biogeography and ecology. In this paper, we synthesize the theory and examine effects of different immigration/extinction rate–species diversity curves on original predictions from the theory by using the System Dynamics simulation modeling approach. Moreover, we develop a comprehensive and generic System Dynamics model to incorporate a variety of recent modifications and extensions of the theory, including area effect, distance effect, competition effect, habitat diversity effect, target effect, and rescue effect. Through computer simulation with STELLA, a more profound understanding of the theory of island biogeography can be gained. The System Dynamics modeling approach is especially appropriate for such a study because it maximizes the utilization of the ecological data by incorporating qualitative information so that a complex, imprecisely-defined ecological system can be studied quantitatively, effectively, and comprehensively.

Our simulation results show that different monotonic rate–species diversity curves do not affect the essence of the theory of island biogeography, while the magnitude of equilibrium species diversity may be greatly affected. Non-monotonic rate–species diversity curves may result in potential multiple equilibria of species diversity. In addition, our model suggests that a non-monotonic relationship may exist between the equilibrium turnover rate and island area and between the equilibrium turnover rate and distance.

1. Introduction. The equilibrium theory of island biogeography, developed independently by Munroe (1948, 1953; see Brown and Lomolino, 1989) and MacArthur and Wilson (1963, 1967), has been highly influential in modern biogeography and ecology (A. Schoener, 1988; Roughgarden, 1989). Modified and extended by many others the MacArthur–Wilson equilibrium theory has stimulated much discussion and research. Studies have been conducted not only on oceanic and continental islands but also in a variety of other insular habitats, involving numerous different taxonomic groups of plants, animals, and microbes. The validity and applicability of the theory have been hotly disputed (Gilbert, 1980; Case and Cody, 1987; Wu, 1989). However, there is no perfect model for any complex ecological system and, despite its limitations and inabilities, the equilibrium model of island biogeography has occupied an important position in ecology and conservation biology. Its heuristic significance for many studies in these and other areas is expected to continue (Haila and Jarvinen, 1982; Begon *et al.*, 1986; Wu, 1989).

We use System Dynamics methodology, through STELLA software, to simulate the theory of island biogeography and to develop a more comprehensive model for it. Our objectives are to (1) construct and demonstrate a System Dynamics model which synthesizes the theory and many of its modifications, (2) examine the sensitivity of the MacArthur–Wilson equilibrium model to assumptions about different immigration/extinction rate–species diversity (richness) relationships, and (3) use the model to evaluate the robustness and to enhance understanding of the theory of island biogeography by computer simulation. Since we essentially use a quantitative method to achieve relatively qualitative conclusions, the following should be kept in mind during interpreting the model results. In all simulation runs, simulation time is not to be confused with actual time required for species diversity dynamics on real islands, the numerical values of variables and parameters used in the models are primarily for exploratory purposes, and the units of variables in the equations are provided mainly for making easier perception of the relationships among them.

2. A System Dynamics Model of the Basic MacArthur–Wilson Theory

The MacArthur–Wilson equilibrium theory. Under the assumption of a log-normal species–abundance relationship, Preston (1962) derived the following species–area relationship:

$$S = cA^z \quad (1)$$

or

$$\log S = z \log A + \log c, \quad (2)$$

where S is the species diversity, A is the area, and c and z are positive constants. While this model has been widely used, it has little explanatory power. Therefore, at least three hypotheses have been proposed to account for the species–area relationship (*sensu* Boecklen, 1986): the habitat diversity hypothesis (Williams, 1964), the passive sampling hypothesis (Connor and McCoy, 1979), and the dynamic equilibrium hypothesis (MacArthur and Wilson, 1963, 1967). According to the habitat diversity hypothesis, the species–area relationship results from the positive correlations existing between area and habitat diversity and between habitat diversity and species diversity. In the passive sampling hypothesis, insular taxonomic groups are simply viewed as subsets or samples from larger communities. Therefore, species diversity is a function of both sampling size and intensity.

MacArthur and Wilson (1963, 1967) theorized that species diversity on an island is determined by two processes: immigration and extinction. Because there are a limited number of empty niches or habitats available on an island,

the more species already on an island, the less likely that a new colonization will be successful and the greater the chance that one of the present species will go extinct. Therefore, for a given area and degree of isolation (usually represented by the distance between an island and its colonization source), immigration and extinction rates will monotonically decrease and increase, respectively, as the number of established species increases. For a given number of species, the immigration rate decreases with increasing isolation because of differences in the dispersal abilities of colonizing species (the “distance effect”). On the other hand, the extinction rate will decrease with greater island area because the larger the area, the larger the species populations, and thus the smaller the probability of extinction (the “area effect”). When the rates of immigration and extinction are equal, the island’s biota is in a dynamic equilibrium, where species diversity is relatively constant despite continual compositional turnover of species.

The MacArthur–Wilson model usually takes the following mathematical form:

$$\frac{dS}{dt} = I - E, \quad (3)$$

Where I is the immigration rate and E is the extinction rate. Assuming that there exist homogeneity, temporal consistency, and additivity among species of immigration and extinction rates, a linear relationship between the rates and species diversity is expected. In other words, if all species involved have very similar per-species rates of immigration and extinction which are constant with changing species diversity, and species interactions are insignificant, it holds that:

$$I(s) = I_0[S_p - S(t)] \quad (4)$$

and

$$E(s) = E_0 S(t), \quad (5)$$

where I_0 is the per-species immigration rate or immigration coefficient, E_0 is the per-species extinction rate or extinction coefficient, S_p is the total number of potential immigrants in the colonization pool, and the term $[S_p - S(t)]$ indicates the number of potential colonists at time t .

The linear model [equations (3)–(5)] can be easily solved analytically and certain properties of a hypothetical island system may be predicted by mathematical manipulations (e.g., Diamond, 1972; Wu, 1989). However, because of heterogeneity in immigration and extinction among species, temporal variability, and species interactions, the above equations are far from being realistic. For example, species with high colonizing abilities are likely to

become established first and weak competitors may go extinct first. A steep gradient in species colonizing abilities would cause a rapid initial drop in the overall immigration rate, and the combined effect of diminishing population size and increasing species interference would yield an exponential extinction curve (MacArthur and Wilson, 1967). The rates of immigration and extinction have approximately log-normal distributions among species and the differences may range over many orders of magnitude (Gilpin and Diamond, 1981). There is empirical evidence suggesting that I_0 tends to decrease and E_0 tends to increase with increasing species diversity, respectively (Pielou, 1979; Diamond and May, 1976).

Therefore, non-linear concave curves may represent the rate–species diversity relationship more realistically than straight lines. Studies on birds have suggested that both curves are very concave, with the concavity of the immigration curve being more pronounced (e.g., Gilpin and Diamond, 1976). MacArthur and Wilson (1967) commented that modifications in shape of the two curves would not significantly affect the essence of the theory as long as the curves are monotonic. Gilpin and Diamond (1976) proposed that the rates of immigration and extinction can each be expressed as a product of two functions with the general form of:

$$I(S, D, A) = i(D, A)h(S) \quad (6)$$

and

$$E(S, A) = e(A)g(S), \quad (7)$$

where the function $i(D, A)$ accounts for the distance effect and the target effect (explained further in later sections), $e(A)$ accounts for the area effect, and the functions $h(S)$ and $g(S)$ reflect the effects of species diversity on immigration and extinction rates, respectively. When the number of species is constant, we may expect that

$$\frac{\partial i(D, A)}{\partial A} > 0, \frac{\partial i(D, A)}{\partial D} < 0, \text{ and } \frac{de(A)}{dA} < 0, \text{ when } \frac{dh(S)}{dS} = \frac{dg(S)}{dS} = 0.$$

That is, immigration rate increases with increasing area, decreases with increasing distance, and extinction rate declines with increasing area. Apparently, $h(S)$ should be equal to zero when $S=0$ and positive for $S>0$, whereas $g(S)$ has to be 0 when $S=S_p$ and positive for $0 \leq S < S_p$. If area and distance are held constant, i.e.:

$$\frac{\partial i(D, A)}{\partial A} = \frac{\partial i(D, A)}{\partial D} = \frac{de(A)}{dA} = 0,$$

the following trends may be expected:

$$\frac{dh(S)}{dS} < 0, \frac{d^2h(S)}{dS^2} > 0, \frac{dg(S)}{dS} > 0, \text{ and } \frac{d^2g(S)}{dS^2} > 0.$$

That is, with increasing species diversity, immigration rate decreases at a slower and slower pace while extinction rate increases with an acceleration (cf. Fig. 6). These trends may be attributed to effects of species differences and competition (MacArthur and Wilson, 1967; Gilpin and Diamond, 1976; Strong and Rey, 1982). However, some exceptions may also be expected, which are to be discussed in the following section.

A basic System Dynamics model of MacArthur–Wilson equilibrium theory. System Dynamics is a modeling methodology developed especially for non-linear, dynamic, complex systems. This approach combines mathematical modeling with computer simulation; therefore, complicated relationships among variables do not have to be oversimplified as in an analytic approach to achieve a solution. One of the salient features of the System Dynamics method is the ability to utilize both quantitative and qualitative information. In System Dynamics modeling, a flow (structural) diagram is constructed to depict the types of variables (i.e., state, rate, and auxiliary variables) and the interrelationships among them. The mathematical equations, corresponding to the flow diagram, are written in a computer language so that simulation is available as soon as the model is completed. While the traditional computer language associated with the System Dynamics method has been DYNAMO, a newly-developed software STELLA is used in this study. STELLA can greatly ease modeling processes and is believed to provide unique contributions for simulating complex biological systems (Costanza, 1987).

A rather simple System Dynamics model can be used to represent and simulate non-linear relationships in the MacArthur–Wilson theory. A flow diagram of such a System Dynamics model is shown in Fig. 1 and the corresponding mathematical model written in STELLA language is presented in Table 1. Species diversity is treated as a state variable; immigration and extinction rates are rate variables; the number of potential colonists, the per-species rates of immigration and extinction, the relative species diversity (defined as $S(t)/S_p$) are all auxiliary variables; the size of the species pool is a constant. Non-linearity of the rate–species diversity relationship makes it difficult to pursue an analytical approach because simple mathematical expressions would not be representative. This problem can be circumvented with the System Dynamics method. As seen in Fig. 1, both the per-species rates are functions of relative species diversity. With STELLA, these mathematical functions can be conveniently expressed as graphical inputs other than

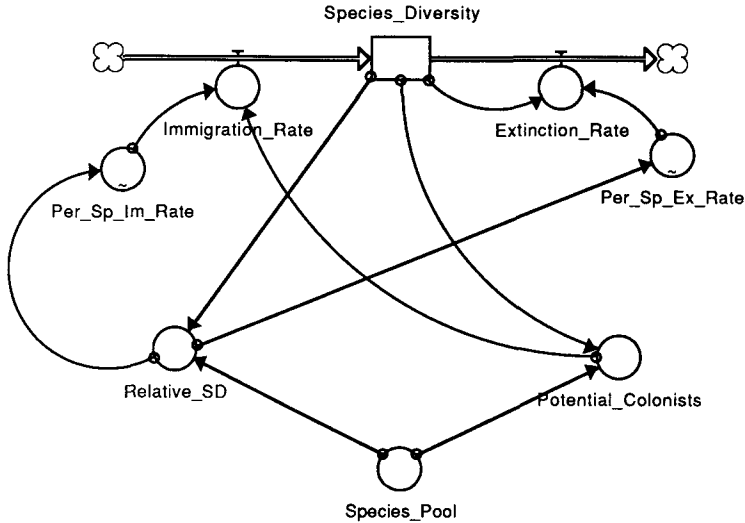


Figure 1. A flow diagram of the basic System Dynamics model of the MacArthur–Wilson equilibrium theory.

Table 1. Equations for the basic System Dynamics model

{Structural equations}
Species_Diversity = Species_Diversity + dt*(Immigration_Rate-Extinction_Rate)
Immigration_Rate = Per_Sp_Im_Rate*Potential_Colonists {Sp#/Year = 1/Year*Sp#}
Extinction_Rate = Per_Sp_Ex_Rate*Species_Diversity {Sp#/Year = 1/Year*Sp#}
{Auxiliary equations}
Relative_SD = Species_Diversity/Species_Pool
Per_Sp_Ex_Rate = graph(Relative_SD)
(0.0,0.0),(0.100,0.0100),(0.200,0.0240),(0.300,0.0440),(0.400,0.0640),(0.500,0.0940),
(0.600,0.128),(0.700,0.172),(0.800,0.230),(0.900,0.300),(1.00,0.400)
Potential_Colonists = Species_Pool-Species_Diversity {Sp#}
Per_Sp_Im_Rate = graph(Relative_SD)
(0.0,0.0792),(0.100,0.0444),(0.200,0.0292),(0.300,0.0200),(0.400,0.0148),
(0.500,0.0108),(0.600,0.00720),(0.700,0.00400),(0.800,0.00200),
(0.900,0.000500),(1.00,0.0)
{Constants}
INIT (Species_Diversity)=0
Species_Pool = 100

algebraic equations. In such a way, assumed relationships between the per-species rates and species diversity are expressed (Fig. 2). This not only eases the modeling process but increases data availability and simulation flexibility as well.

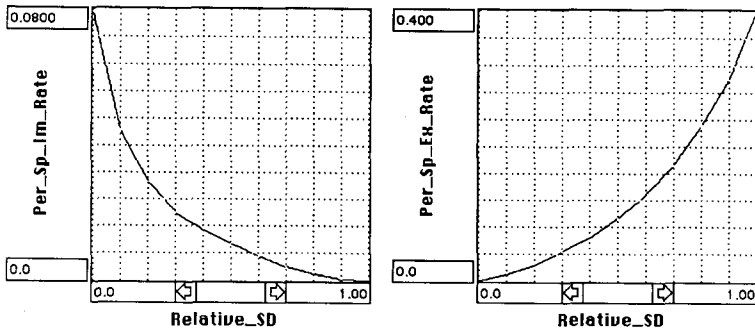


Figure 2. Per species rate–species diversity relationship in the basic System Dynamics model.

Figure 3 exhibits a typical behavior pattern of the model system. Species diversity increases in a decreasing rate in time and reaches a stable equilibrium state when the rates of immigration and extinction become equal. No matter what initial values of species diversity are taken in the simulation, the equilibrium state will eventually be reached asymptotically. The overall rate of

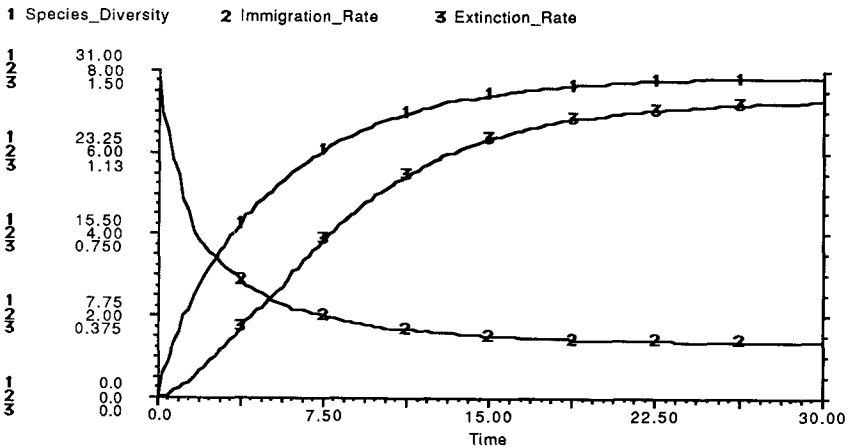


Figure 3. Dynamics of species diversity, immigration and extinction produced by the basic System Dynamics model.

immigration decreases in time because of the continuous drop in the number of potential colonists while the overall rate of extinction increases with species diversity. Because of the per-species rate–diversity relationships assumed in Fig. 2, both the rate–species diversity curves generated by the simulation are concave (Fig. 4). Not surprisingly, these features are basically similar to what the linear model [equations (3)–(5)] would predict. However, the System Dynamics model can serve as a simulation tool to experiment with different

types of relationships among the variables and examine their effects on the dynamics of species diversity.

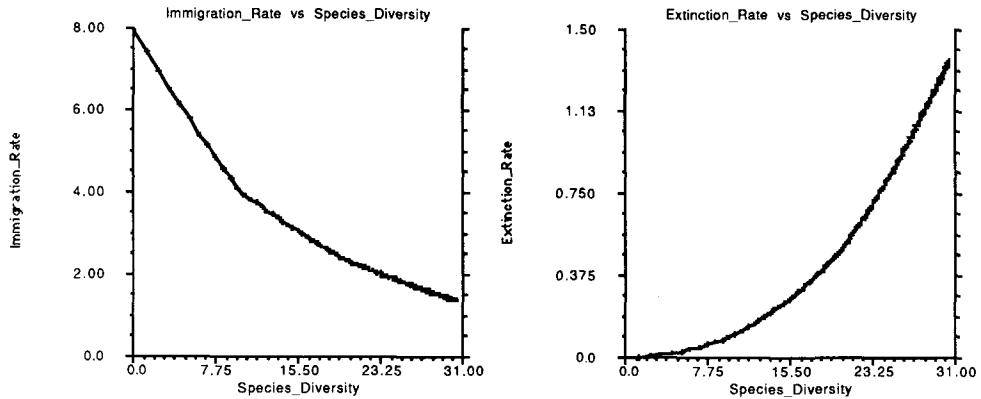


Figure 4. Rate-species diversity curves generated by the basic System Dynamics model.

Examination of rate-species diversity curves by System Dynamics simulation. The curves of immigration and extinction rates are the essence of the equilibrium theory of island biogeography (Strong and Rey, 1982). Gilpin and Diamond (1976) conjectured that in some cases (e.g., for plants, insects, or sessile marine invertebrates), the general trends in the signs of the first and second derivatives of functions $g(S)$ and $h(S)$ in equations (6) and (7) could be varied, becoming:

$$\frac{dg(S)}{dS} < 0, \frac{d^2g(S)}{dS^2} < 0, \frac{dh(S)}{dS} > 0, \text{ and } \frac{d^2h(S)}{dS^2} < 0$$

over some range of species diversity. Pielou (1979) also postulated, at least for plants, that immigration rate might first increase and subsequently decrease with increasing species diversity because initial colonization is greatly inhibited by unfavorable environmental conditions on islands. Dickerson and Robinson (1985) stated that biological interactions among species may cause non-monotonic and dramatic changes in immigration and extinction curves. Strong and Rey (1982) also asserted that, in general, slight rate heterogeneity and slight species interactions may effect both concave and convex curvatures, whereas great rate heterogeneity, temporal variability, and strong species interactions would cause significant changes in the shape of rate curves.

The System Dynamics modeling approach may be used to detect the effects of the different rate-species diversity relationships on the behavior of the model

system. For convenience, a simplified System Dynamics model is used (see Fig. 5 for the flow diagram and Table 2 for the equations). According to

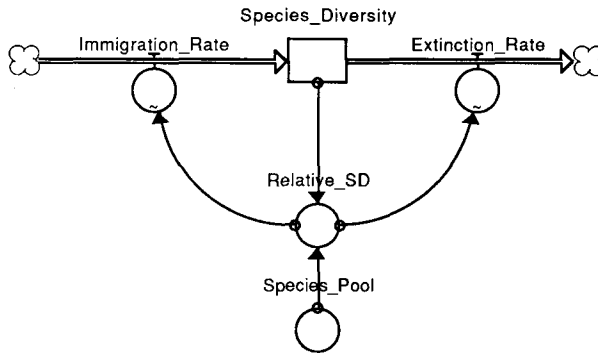


Figure 5. A flow diagram of the simplified System Dynamics model of the MacArthur–Wilson equilibrium theory.

Table 2. Equations for the simplified System Dynamics model

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{Structural equations}
Species_Diversity = Species_Diversity + dt*(Immigration_Rate-Extinction_Rate)
Immigration_Rate = graph(Relative_SD)
(0.0,4.92),(0.100,2.67),(0.200,1.80),(0.300,1.32),(0.400,0.950),(0.500,0.675),(0.600,0.475),
(0.700,0.275),(0.800,0.150),(0.900,0.0500),(1.00, 0.0)
Extinction_Rate = graph(Relative_SD)
(0.0, 0.0),(0.100,0.0500),(0.200,0.250),(0.300,0.500),(0.400,0.720),(0.500,1.08),
(0.600,1.56),(0.700,2.20),(0.800,2.96),(0.900,4.76),(1.00,7.80)

{Auxiliary equations}
Relative_SD = Species_Diversity/Species_Pool

{Constants}
INIT (Species_Diversity) = 0
Species_Pool = 100
    
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suggestions in the previous section, we devise five different sets of rate–species diversity curves and use simulation to examine their impact on the dynamics of species diversity. It ought to be pointed out that because our focus is to study system behavioral patterns, the numerical values used in the simulations are basically hypothetical. The first set (Fig. 6) represents typical concave curves of the two rates, where:

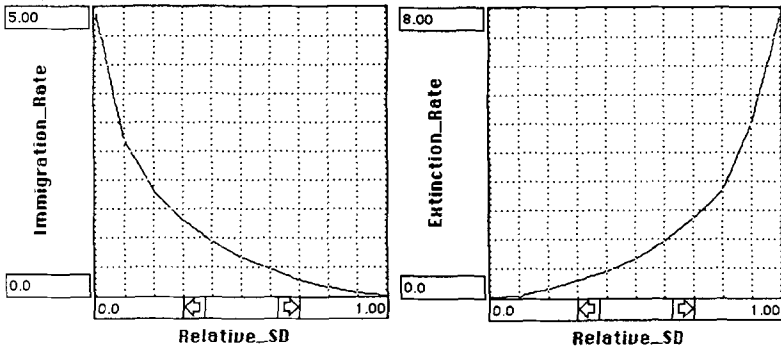


Figure 6. Assumed rate–species diversity curve set 1.

$$\frac{dh(S)}{dS} < 0, \frac{d^2h(S)}{dS^2} > 0, \frac{dg(S)}{dS} > 0, \text{ and } \frac{d^2g(S)}{dS^2} > 0.$$

With this set of curves, the model is similar to the previous one in terms of the behavior mode (Fig. 7). This partially validates our use of a simplified model for examining rate effects and provides a reference pattern for comparison of results with other sets of curves.

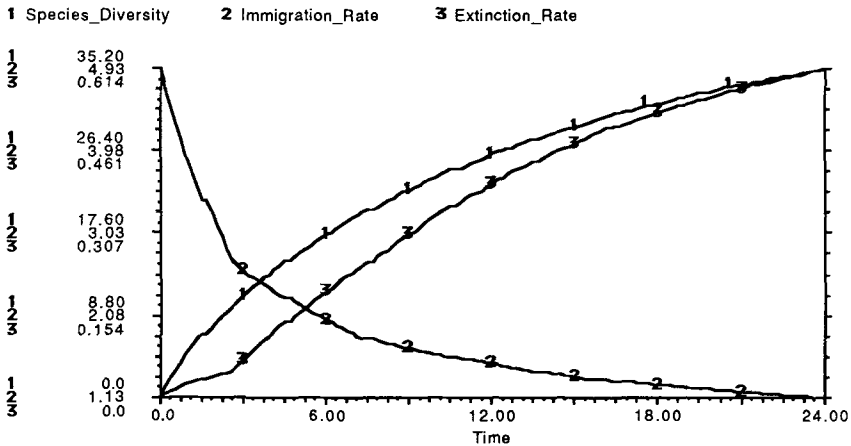


Figure 7. Dynamics of species diversity, immigration, and extinction with rate curve set 1.

The second set of rate–species diversity curves (Fig. 8) reflects Pielou’s (1979) hypothesis that the immigration rate may first increase, i.e.:

$$\frac{dh(S)}{dS} > 0 \text{ and } \frac{d^2h(S)}{dS^2} > 0,$$

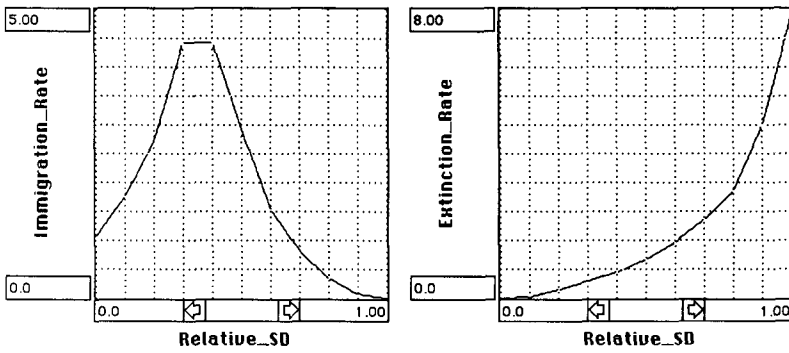


Figure 8. Assumed rate-species diversity curve set 2.

then remain unchanged, i.e.:

$$\frac{dh(S)}{dS} = \frac{d^2h(S)}{dS^2} = 0,$$

and finally decrease, i.e.:

$$\frac{dh(S)}{dS} < 0 \text{ and } \frac{d^2h(S)}{dS^2} > 0.$$

The extinction curve is still assumed to be concave. Although the immigration rate behaves rather differently, the species diversity curve has basically the same shape as the reference pattern (Fig. 9). However, there may be two

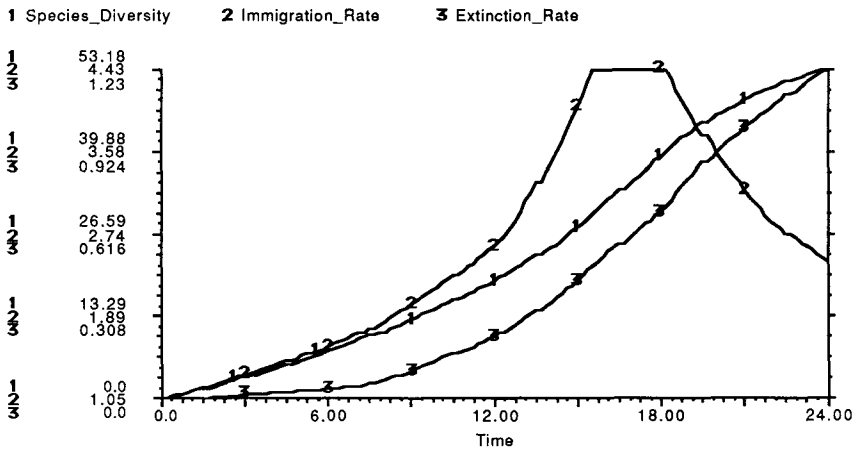


Figure 9. Dynamics of species diversity, immigration and extinction with rate curve set 2.

equilibria occurring in such a system when in Fig. 8 immigration rate is lower and extinction rate higher at the early stage so that they are equal in value twice over the range of species diversity. In addition, the S-shaped feature indicates a rather slower increase in species diversity at early and late stages of the species colonization.

Curve sets 3 and 4 (Figs 10 and 12) might result from species interactions and slight heterogeneity of species' rates in natural communities (Strong, 1979; Strong and Rey, 1982). In curve set 3, a convex immigration curve immigration curve

$$\left(\frac{dh(S)}{dS} < 0, \frac{d^2h(S)}{dS^2} < 0 \right)$$

combines with a concave extinction curve (Fig. 10) and it produces results similar to the reference (Fig. 11). Curve set 4 (Fig. 12) represents the assumption that both the immigration and extinction curves are convex

$$\left(\frac{dh(S)}{dS} < 0, \frac{d^2h(S)}{dS^2} < 0, \frac{dg(S)}{dS} > 0, \frac{d^2g(S)}{dS^2} < 0 \right).$$

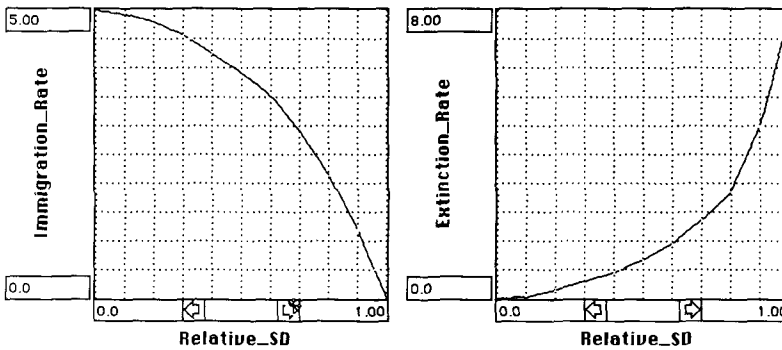


Figure 10. Assumed rate-species diversity curve set 3.

The resultant species diversity curve shows a dramatic increase at the early stage (Fig. 13).

Curve set 5 represents a more complex immigration rate–species diversity relationship (Fig. 14) where the immigration rate decreases at the early stage i.e.,

$$\left(\frac{dh(S)}{dS} < 0 \right)$$

then increases

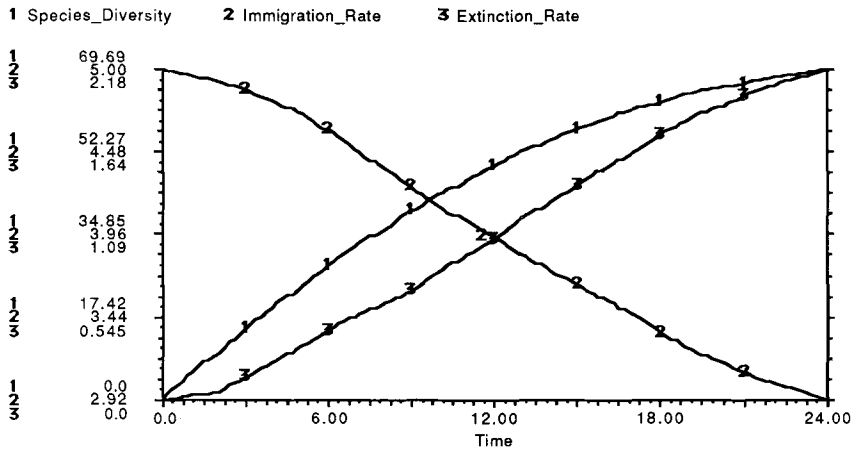


Figure 11. Dynamics of species diversity, immigration and extinction with rate curve set 3.

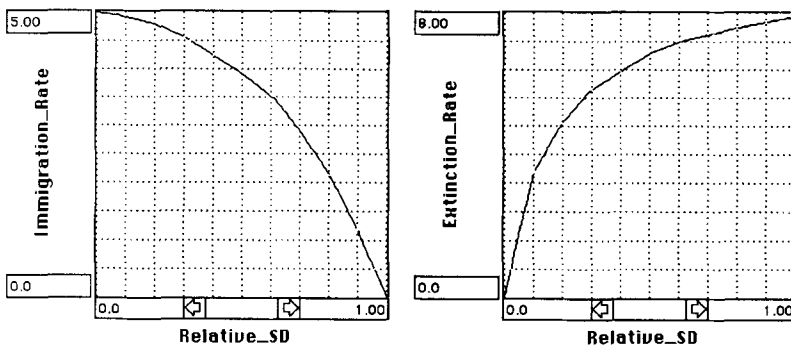


Figure 12. Assumed rate-species diversity curve set 4.

$$\frac{dh(S)}{dS} > 0 ,$$

then levels off

$$\left(\frac{dh(S)}{dS} = 0 \right),$$

and finally drops exponentially

$$\left(\frac{dh(S)}{dS} < 0 \text{ and } \frac{d^2h(S)}{dS^2} > 0 \right).$$

Such situations may occur as a result of a combination of rate inconstancy and

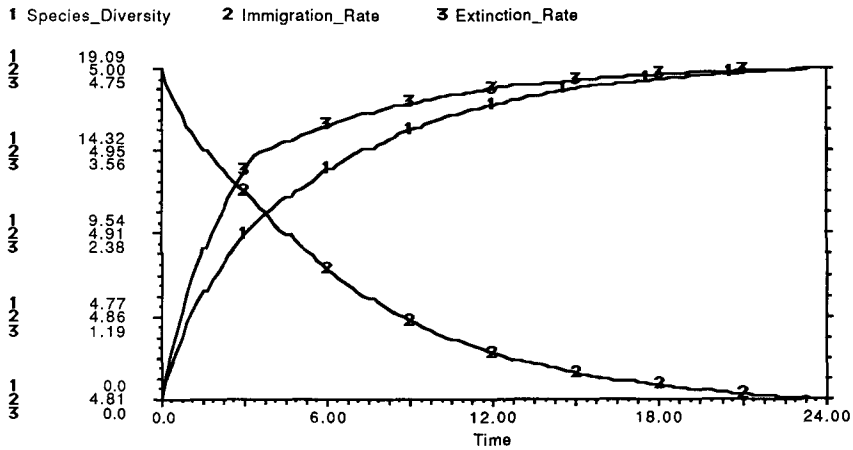


Figure 13. Dynamics of species diversity, immigration and extinction with rate curve set 4.

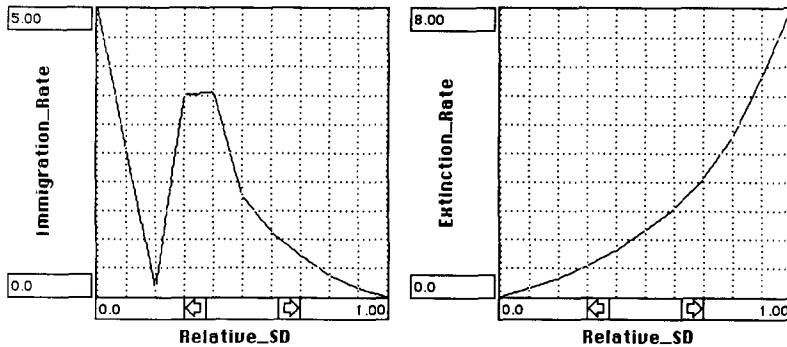


Figure 14. Assumed rate-species diversity curve set 5.

species interactions. Curve set 5 is a modification of curve set 2 based on assertions by Pielou (1979) and Dickerson and Robinson (1985), depicting a drastically non-monotonic immigration rate-species diversity relationship. Without empirical data available, this is rather hypothetical. Nevertheless, simulation with it may not only demonstrate that flexibility in data utilization of the System Dynamics model, but also pose new questions for future empirical studies. Three equilibria (two stable and one unstable) can exist depending on the relative values of the two rates taken in Fig. 14 and the starting species diversity. In this specific case, the lower stable equilibrium (species diversity=19) is reached whenever the starting species diversity is smaller than 22 (Fig. 15, top) while the upper stable equilibrium (species diversity=50) is achieved if the starting species diversity is larger than 19

(Fig. 15, bottom). A species diversity equal to 22 is an unstable equilibrium point in the system.

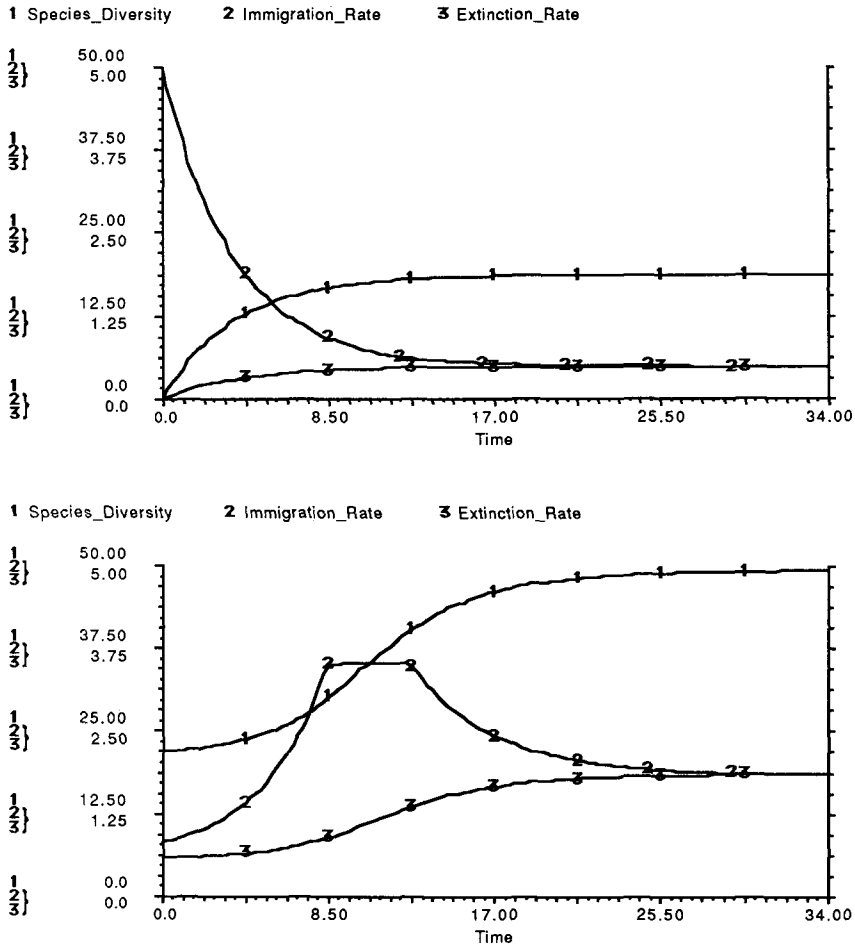


Figure 15. Dynamics of species diversity, immigration and extinction with rate curve set 5. The top: starting species diversity is 0; the bottom: starting species diversity is 19 .

Interestingly, this rather simple System Dynamics model based on the MacArthur–Wilson paradigm can generate diverse behavioral patterns of species diversity, including the phenomenon of multiple equilibria. Mathematically, a non-linear system of equations may in principle produce multiple equilibria. Such examples are found in ecological models of population systems (e.g., Wu and Barlas, 1989), aquatic ecosystems (e.g., Sharma and Dettmann, 1989), and other ecological systems (see Levin, 1979, for a review). With this particular model, multiple equilibria of species diversity clearly result from the

non-monotonic features of the rate curves, which may be caused by biological interactions other than competition (e.g., predation, mutualism; see Dickerson and Robinson, 1985). However, empirical studies are needed to verify these postulations on the rate curves and possibilities of existence of multiple equilibria in species diversity.

3. An Extended System Dynamics Model of the MacArthur–Wilson Equilibrium Theory. Independence between immigration and extinction rates assumed in the basic MacArthur–Wilson model may not be true. Extinction rate of insular populations may be reduced by an influx of conspecific immigrants which provides demographic reinforcement and augments genetic variability (Brown and Kodric-Brown, 1977; Wright, 1985). This was termed the “rescue effect”. Therefore, distance would affect not only immigration rate but extinction rate as well. The rescue effect may take place when immigration rate is very high or at least approaches local recruitment rate and, therefore, it may not apply to truly isolated archipelagos (Brown and Kodric-Brown, 1977; Gilbert, 1980; Wright, 1985).

Also, area will affect immigration as larger islands are more likely to receive immigrants than smaller ones. The phenomenon of increasing probability of immigration with island area has been called the “target effect” (e.g., Gilpin and Diamond, 1976). The effect of area on species diversity can be a combination of the effects of pure area and habitat diversity. MacArthur and Wilson (1967) recognized that factors such as habitat diversity rather than area directly affect species diversity but stated that there exists a “strikingly orderly relation” between area and species diversity. However, such a relationship may not be found in some cases (Gilbert, 1980). A pure area effect, independent of habitat diversity, may be anticipated if the assumption holds that enlarging area monotonically increases population sizes and the latter in turn decreases the probability of extinction (Simberloff, 1974).

The extended System Dynamics model and its behavior. We expanded the previous System Dynamics model to incorporate explicitly the effects of interspecific competition, island area, island–species pool distance and habitat diversity, as well as rescue effect and target effect. The model structure is depicted by the flow diagram in Fig. 16 and mathematical equations corresponding to this diagram are shown in Table 3. Quantitative study of these effects is difficult in most cases and thus numerical data have rarely been available. However, qualitative empirical information can be utilized to analyze the general modes of system behavior with the System Dynamics modeling method. Figure 17 and 18 are the graphical inputs of these effects. Competition among species is assumed to be positively related to species density ratio. Species density is defined as species diversity per unit area and its

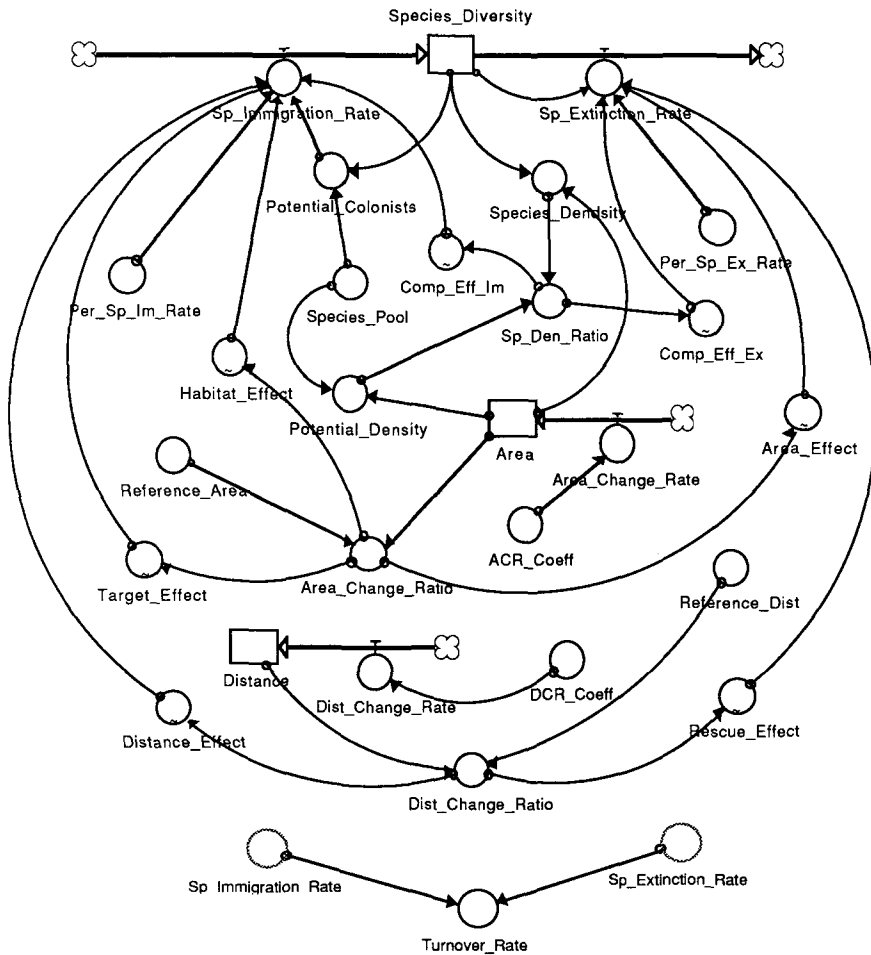


Figure 16. A flow diagram of the extended System Dynamics model of the MacArthur–Wilson theory.

ratio defined as actual vs potential species density. With increasing species density, therefore, competition effect on extinction and immigration will increase. Because *Comp_Eff_Ex* and *Comp_Eff_Im* are used as multipliers in rate equations, increase in competition effect on extinction will increase the former’s value while increase in competition effect on immigration will decrease the value of the latter.

Similarly, area effect, distance effect, habitat effect, target effect, and rescue effect are incorporated into the model by introducing multipliers in the rate equations. These multipliers are, in turn, *Area_Effect*, *Distance_Effect*, *Habitat_Effect*, *Target_Effect*, and *Rescue_Effect*. Specifically, *Habitat_Effect*, *Distance_Effect* and *Target_Effect* are treated as multipliers in the immigration

Table 3. Equations for the extended System Dynamics model

{Structural equations}

Area = Area + dt*(Area_Change_Rate)

Distance = Distance + dt*(Dist_Change_Rate)

Species_Diversity = Species_Diversity + dt*(Sp_Immigration_Rate-Sp_Extinction_Rate)

Sp_Immigration_Rate = Per_Sp_Im_Rate*Potential_Colonist*Target_Effect*Habitat_Effect*Distance_Effect*Comp_Eff_Im {Sp#/Year}

Sp_Extinction_Rate = Per_Sp_Ex_Rate*Species_Diversity*Area_Effect*Comp_Eff_Ex*

Rescue_Effect {Sp#/Year}

{Auxiliary equations}

Area_Change_Rate = if (TIME ≥ 5) and (TIME ≤ 10) then (ACR_Coeff*TIME) else 0

Area_Change_Ratio = Area/Reference_Area

Dist_Change_Rate = if (TIME ≥ 5) and (TIME ≤ 10) then DCR_Coeff*TIME else 0

Dist_Change_Ratio = Distance/Reference_Dist

Potential_Colonists = Species_Pool-Species_Diversity {Sp#}

Potential_Density = Species_Pool/Area {Sp#/Square km}

Species_Density = Species_Diversity/Area

Sp_Den_Ratio = Species_Density/Potential_Density

Turnover_Rate = .5*(Sp_Immigration_Rate + Sp_Extinction_Rate)

Comp_Eff_Im = graph(Sp_Den_Ratio)

(0.0,0.995),(0.100,0.955),(0.200,0.900),(0.300,0.830),(0.400,0.760),(0.500,0.670),
(0.600,0.565),(0.700,0.445),(0.800,0.310),(0.900,0.175),(1.00, 0.0)

Comp_Eff_Ex = graph(Sp_Den_Ratio)

(0.0,1.00),(0.100,1.04),(0.200,1.10),(0.300,1.19),(0.400,1.29),(0.500,1.44),(0.600,1.61),
(0.700,1.81),(0.800,2.08),(0.900,2.43),(1.00,2.98)

Area_Effect = graph(Area_Change_Ratio)

(0.0,1.95),(0.500,1.40),(1.00,0.990),(1.50,0.790),(2.00,0.610),(2.50,0.430),
(3.00,0.330),(3.50,0.260),(4.00,0.220),(4.50,0.180),(5.00,0.140)

Rescue_Effect = graph(Dist_Change_Ratio)

(0.0,0.0100),(0.500,0.590),(1.00,1.00),(1.50,1.00),(2.00,1.00),(2.50,1.00),
(3.00,1.00),(3.50,1.00),(4.00,1.00),(4.50,1.00),(5.00,1.00)

Target_Effect = graph(Area_Change_Ratio)

(0.0,0.0750),(0.500,0.135),(1.00,0.215),(1.50,0.340),(2.00,0.495),(2.50,0.635),
(3.00,0.755),(3.50,0.845),(4.00,0.920),(4.50,0.970),(5.00,1.00)

Habitat_Effect = graph(Area_Change_Ratio)

(0.0,0.0),(0.500,0.610),(1.00,1.02),(1.50,1.23),(2.00,1.38),(2.50,1.53),(3.00,1.63),
(3.00,1.63),(3.50,1.71),(4.00,1.79),(4.50,1.85),(5.00,1.88)

Distance_Effect = graph(Dist_Change_Ratio)

(0.0,1.90),(0.500,1.39),(1.00,1.02),(1.50,0.800),(2.00,0.610),(2.50,0.450),(3.00,0.330),
(3.50,0.210),(4.00,0.130),(4.50,0.0800),(5.00,0.0400)

{Constants}

INIT(Area) = 20 {sq. kilometers}

INIT(Distance) = 50 {kilometers}

INIT(Species_Diversity) = 13.74

ACR_Coeff = 1 {to be changed for different simulations}

Reference_Area = 20 {sq. kilometers}

DCR_Coeff = 0 {to be changed for different simulations}

Reference_Dist = 50 {kilometers}

Per_Sp_Ex_Rate = 0.1

Per_Sp_Im_Rate = 0.08 {Sp#/Time Unit}

Species_Pool = 100

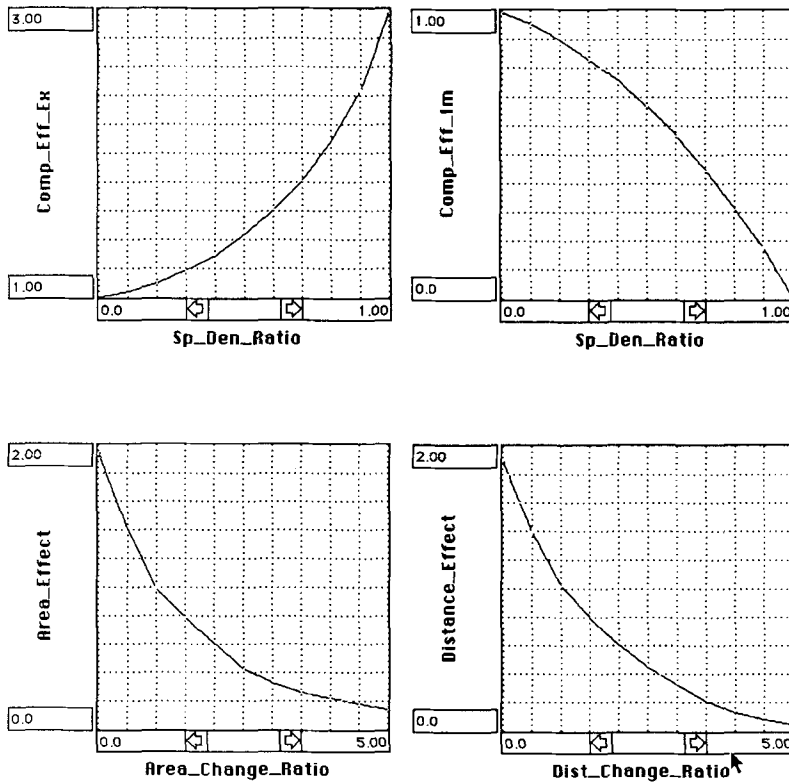


Figure 17. Assumed competition effect, area effect and distance effect.

rate equation, whereas Area_Effect and Rescue_Effect are multipliers in the extinction rate equation. We define Area_Change_Ratio as changed area divided by a reference area and Distance_Change_Ratio as changed distance divided by a reference distance. Therefore, these effects have a value of 1 when the change ratio of area or distance is 1 (i.e., area or distance remains the same). In other words, the effects are studied in a comparative sense.

As a reference pattern, Fig. 19 is a base run of the model where the variables area and distance are kept constant, with a stable equilibrium (14 species). To examine impacts of all the effects mentioned above along with changing area and distance, this equilibrium value is chosen as starting species diversity in each of the following simulations. As mentioned earlier, the numerical values in the simulations should be understood only in a comparative sense, and simulation time is not to be confused with actual years in the sense of time for island dynamics.

A higher new equilibrium species diversity (53 species) is reached when the island area increases (from 20 to 57 km², Fig. 20) with the distance being held constant. The sharp increase in immigration rate with the area change is

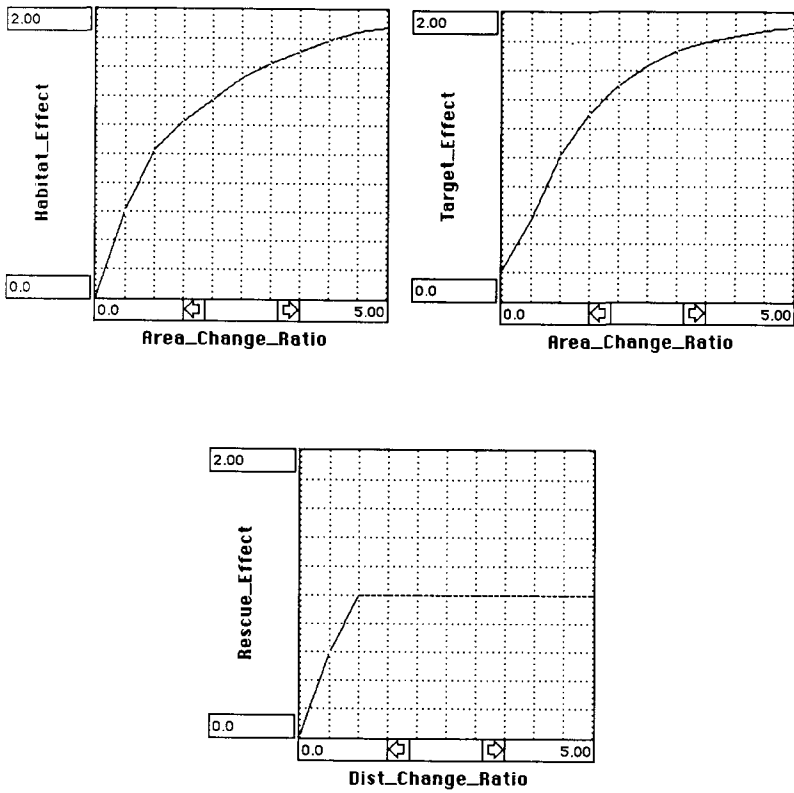


Figure 18. Assumed habitat diversity effect, target effect and rescue effect.

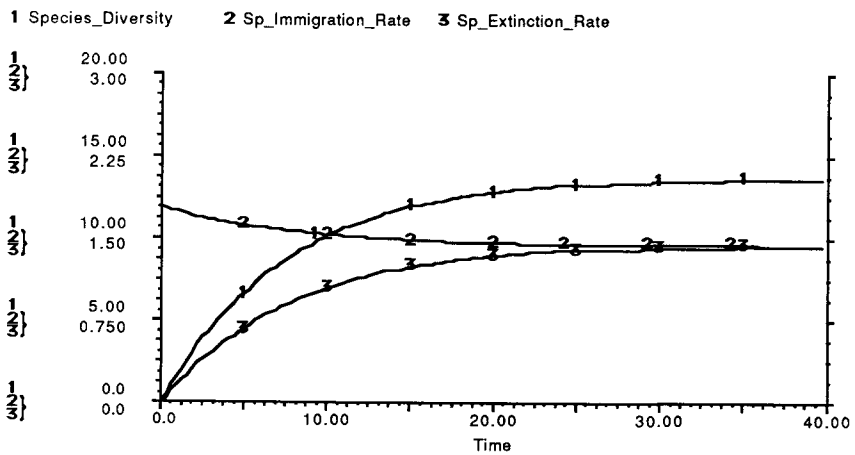


Figure 19. Dynamics of species diversity, immigration and extinction produced by the extended model with constant area and distance.

partially due to the combination of increased habitat diversity and target effect, while the decrease at that time in the extinction rate reflects in part the area and competition effects. Dynamics of species diversity, immigration, and extinction with a decrease in area (from 20 to 12.5 km²) bring the equilibrium to a lower value (six species, Fig. 21). This results from the interactions of different effects related to the variable of area. Of course, for real situations different effects may have varying influences in magnitude and some may be negligible. These variations can be easily included in the model because of STELLA's ability to utilize graphical data.

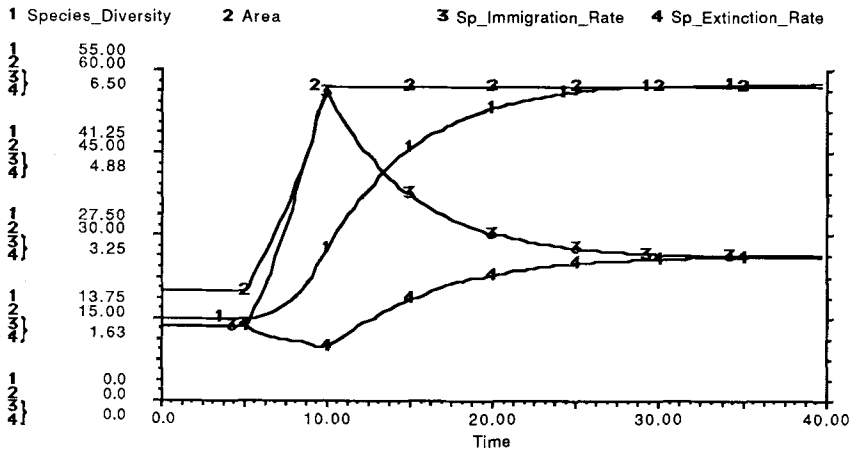


Figure 20. Dynamics of species diversity, immigration and extinction with an increase in area.

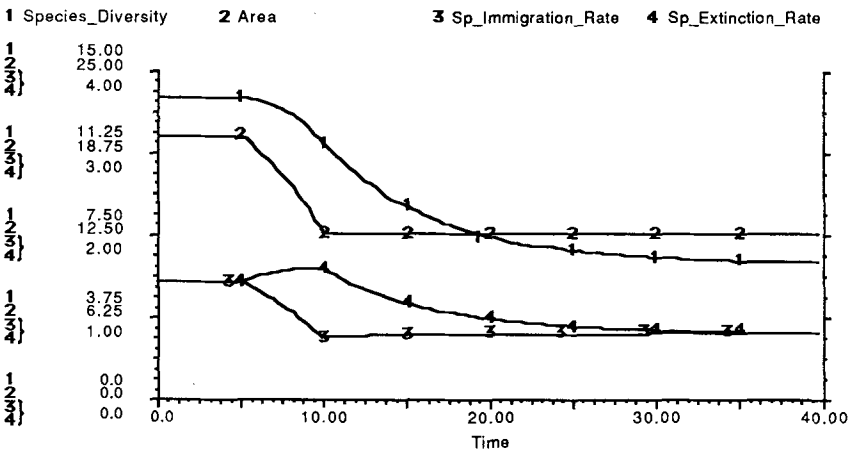


Figure 21. Dynamics of species diversity, immigration and extinction with a decrease in area.

Figures 22 and 23 demonstrate the system behavior when distance increases and decreases, respectively, with island area being kept constant. The increase in distance (from 50 to 87 km) results in a lower new equilibrium (10 species, Fig. 22), whereas the decrease in the distance (from 50 to 31.5 km) increases the equilibrium (to 21 species). Immigration rate is augmented by distance effect and extinction rate is decreased by rescue effect when the distance decreases.

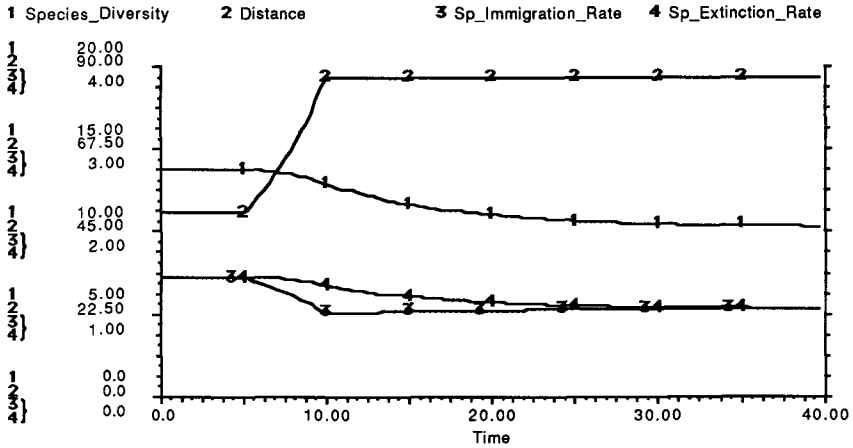


Figure 22. Dynamics of species diversity, immigration and extinction with an increase in distance.

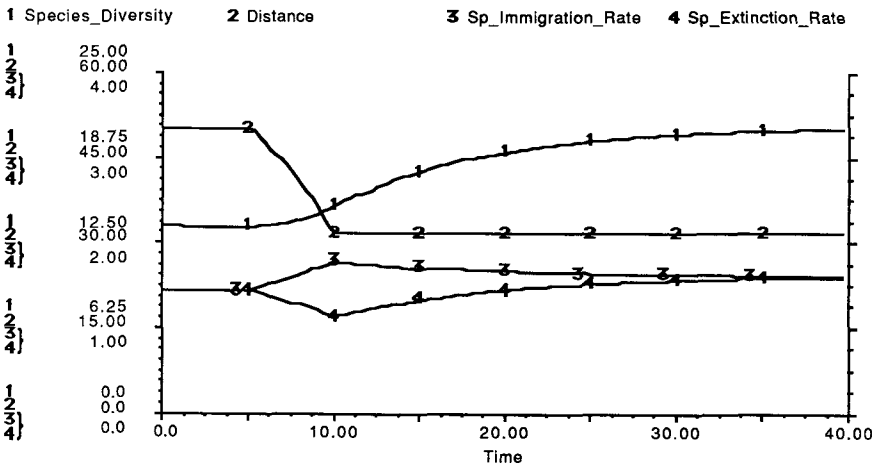


Figure 23. Dynamics of species diversity, immigration and extinction with a decrease in distance.

Impacts of changes in both area and distance may also be examined by simulation. Figure 24 shows the dynamics of species, immigration, and extinction with decrease in area (from 20 to 12.5 km²) and an increase in distance (from 50 to 87 km), in which the equilibrium species diversity drops to the lowest value (four species) among all the simulations. Alternatively, when the area increases (from 20 to 57 km²) simultaneously with a decrease in the distance (from 50 to 31.5 km), the highest equilibrium (62 species) is achieved (Fig. 25). In such a way, different relationships among the structural elements and their influences on the dynamics of species diversity, immigration, and extinction can be examined by simulation. However, an accurate prediction of the numerical values of these variables, of course, requires the model inputs to be from actual studies for real island systems.

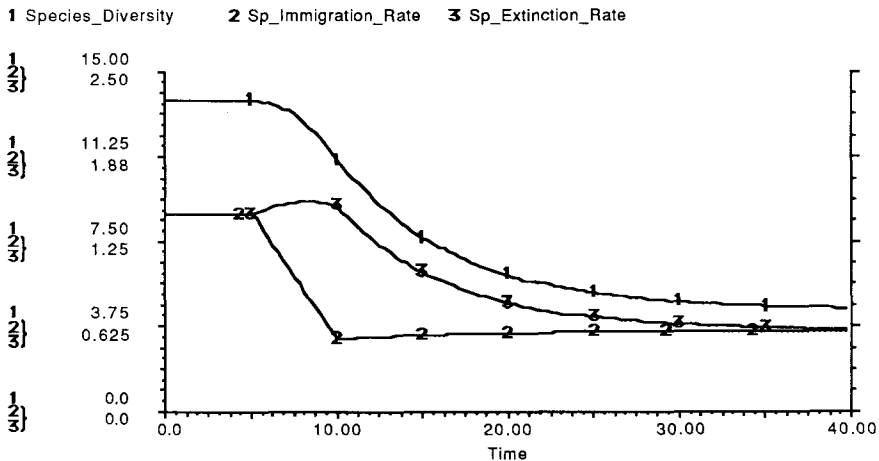


Figure 24. Dynamics of species diversity, immigration and extinction with a decrease in area and an increase in distance.

Examining of relationships of the species turnover rate to island area and distance by simulation. The concept of species turnover, which refers to the continual change in species composition at equilibrium, is an important aspect of the MacArthur–Wilson theory. The species turnover rate is usually defined as the “number of species replaced by new species per unit time at equilibrium” (A. Schoener, 1988) and is also called the “replacement rate” (cf. Pielou, 1979). To avoid confusion in the use of terminology, in this paper we refer to this turnover rate, defined as above, as the equilibrium turnover rate, whereas the species compositional replacement rate at any non-equilibrium states is called the transient turnover rate. Also, it is necessary to distinguish between the absolute turnover rate and the relative turnover rate. Although both of them have been used in biogeographical studies, the absolute turnover rate is more

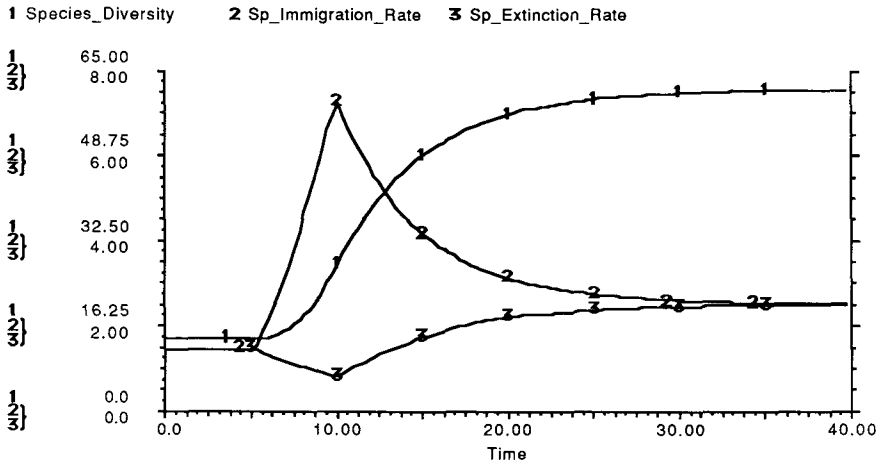


Figure 25. Dynamics of species diversity, immigration and extinction with an increase in area and a decrease in distance.

appropriate, especially in relation to the MacArthur–Wilson model, than the relative one which contains potential statistical artifacts involving ratios (T. Schoener, 1988).

MacArthur and Wilson (1967) asserted that the equilibrium turnover rate should be inversely related to both island area and the degree of island isolation. This prediction has been challenged by several experimental and empirical studies. In a field study of the distribution of arthropods among isolated plants, Brown and Kodric-Brown (1977) found that the turnover rate was directly, rather than inversely, related to the distance to the source of colonizing species. They further hypothesized that, because of the rescue effect, the equilibrium turnover rate first increases and then declines with increasing distance. Wright’s (1985) study on birds confirmed the existence of a similar non-monotonic relationship between the equilibrium turnover rate and distance, and also found a weak inverse relation between the turnover rate and island area. Direct measurements of the equilibrium turnover rate from field or experimental work are difficult because of the problems involving “pseudo-turnover” (resulting in overestimates), “cryptoturnover” (resulting in underestimates), and rescue effect (A. Schoener, 1988; Brown and Kodric-Brown, 1977). Therefore, evaluating turnover rates and their relations to island area and isolation through the mathematical models is of great significance.

We use the extended System Dynamics model to calculate the absolute equilibrium turnover rate and examine its relationships to island area and distance. The turnover rate is obtained from the equation (cf. T. Schoener, 1988):

$$T_{\text{abs}} = 0.5(I + E), \tag{8}$$

where T_{abs} is the absolute turnover rate.

When island area and distance are constant, the transient turnover rate increases with increasing species diversity until the equilibrium state for the particular island is reached (Fig. 26). Then the transient turnover rate becomes the equilibrium turnover rate, which is equal to the immigration or extinction rate at equilibrium. Figure 26 also shows a shift in the equilibrium species

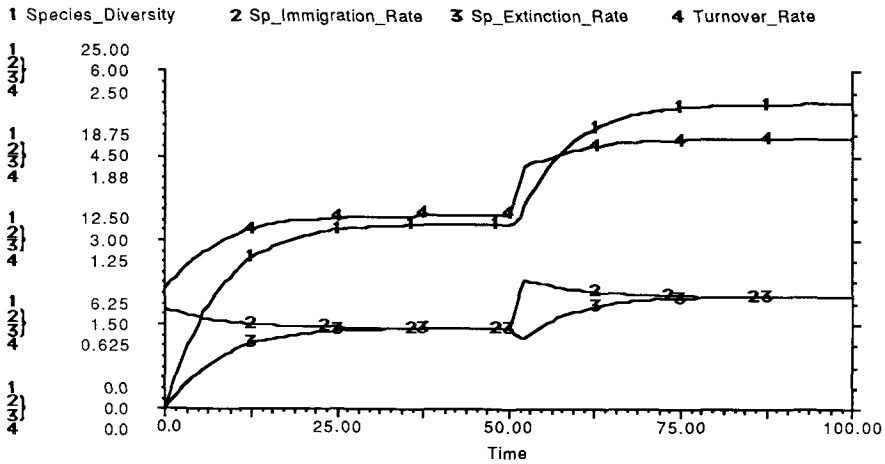


Figure 26. Dynamics of species diversity, turnover rate, immigration and extinction with a stepwise change of island in both size (from 20 to 30) and distance (from 50 to 66) starting at simulation time 50.

diversity and turnover rate when the island area increases stepwise from 20 to 30 units and the distance increases from 50 to 66 units. In order to examine the relations of the turnover rate to area and distance, we use step functions in the equations of area change rate and distance change rate [i.e., $AREA_CHANGE_RATE = STEP(ACR_COEFF, 0) + STEP(5,5) + STEP(-5,7) + STEP(5,50) + STEP(-5,52) + STEP(5,100) + STEP(-5,102) + STEP(5,102) + STEP(5,150) + STEP(-5,152) + STEP(5,200) + STEP(-5,202) + STEP(5,250) + STEP(-5,252) + STEP(5,300) + STEP(-5,302)$, and $DIST_CHANGE_RATE = STEP(DCR_COEFF, 0) + STEP(5,5) + STEP(-5,7) + STEP(-5,52) + STEP(5,100) + STEP(-5,102) + STEP(5,150) + STEP(-5,152) + STEP(5,200) + STEP(-5,202) + STEP(5,250) + STEP(-5,252) + STEP(5,300) + STEP(-5,302)$]. These functions are used in such a way that area or distance increases stepwise and that a new equilibrium of species diversity is achieved at each step (Figs 27a,b and 29a,b). The simulation results suggest that the equilibrium turnover rate first increases and then declines with increasing area (Fig. 28). A similar non-monotonic relationship is found between the turnover rate and distance (Fig. 30). These findings are different from what were predicted by the MacArthur–Wilson

equilibrium theory. The relationship between distance and turnover rate found here confirms the conclusions made by Brown and Kodric-Brown (1967) and Wright (1985). However, the non-monotonic relationship between area and turnover rate still requires empirical confirmation. A possible biological explanation for this is that, for small islands, not only the equilibrium species diversity but also the number of potential colonizing species may be rather low in some cases.

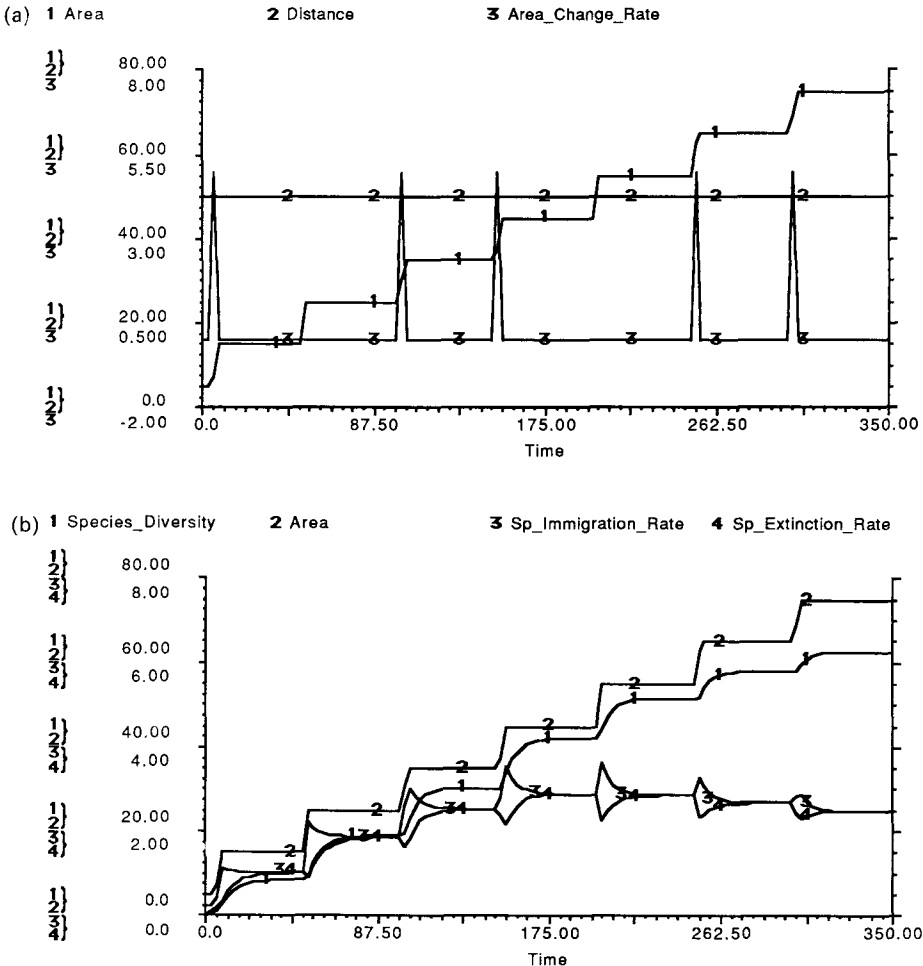


Figure 27. (a) Changes in area and area change rate in the simulation run for examining the relationship between equilibrium turnover rate and island area. (b) Dynamics of species diversity, immigration and extinction with changing area in the simulation run for examining the relationship between equilibrium turnover rate and island area.

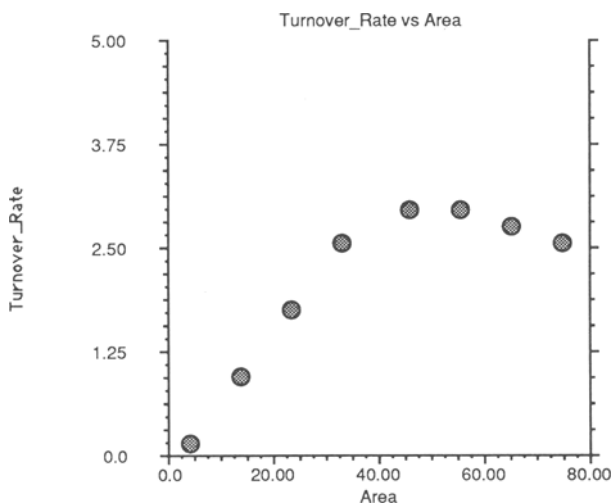


Figure 28. Relationship between island area and the equilibrium turnover rate simulated by the extended System Dynamics model.

4. Discussion and Conclusions. Our System Dynamics model is able to synthesize current perspectives on the theory of island biogeography comprehensively without sophisticated mathematics. The simulations provide for greater understanding of the internal structure of the theory. The model can be used to examine the sensitivity of the MacArthur–Wilson equilibrium theory to a variety of assumptions about the rate–species diversity curves. Also, it can be used to test the relationships between the turnover rate and island area or distance. However, although in a sense search for causality produced the theory of island biogeography, it is important to realize that most relationships in the theory are not causal but actually correlative. Because the model takes these relationships as causal ones, weak correlations between certain variables in some specific cases will weaken the validity of the model. This should lead to corresponding modifications of the model. Nevertheless, the System Dynamics methodology can maximize the utilization of ecological data by incorporating qualitative information so that a complex, ill-defined ecological system can possibly be quantitatively approached. With reasonable estimates of relationships among structural elements and model parameters, the methodology produces reliable results.

Our findings from System Dynamics simulation basically support MacArthur and Wilson's (1967) comment that different monotonic rate–species diversity curves do not affect the essence of the theory of island biogeography. However, they also show that the equilibrium species diversity value can be changed greatly and that non-monotonic rate–diversity curves may result in potential multiple equilibria of species diversity. In addition, the

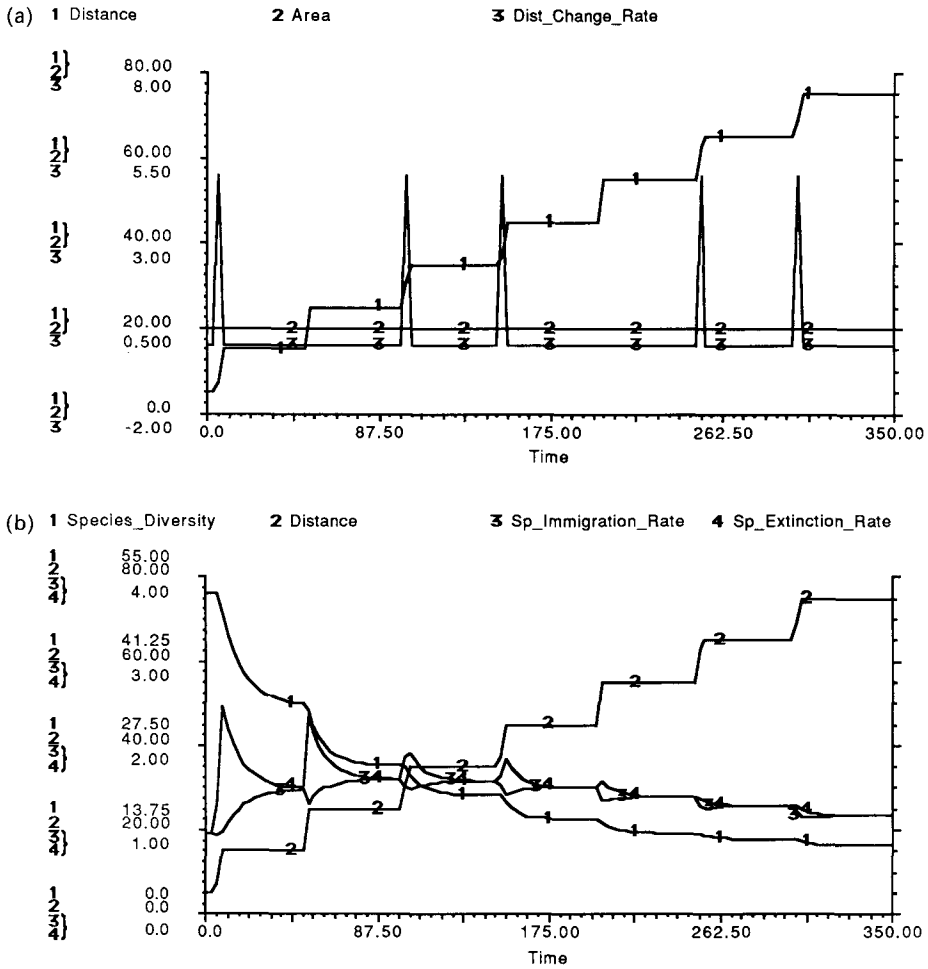


Figure 29. (a) Changes in distance and distance change rate in the simulation run for examining the relationship between equilibrium turnover rate and distance. (b) Dynamics of species diversity, immigration and extinction with changing area in the simulation run for examining the relationship between equilibrium turnover rate and island area.

relations of the turnover rate to island area and distance obtained by the model differ from predictions by the MacArthur–Wilson equilibrium model. While the non-monotonic relationship with distance found here is consistent with some previous studies, the non-monotonic relationship with area deserves further empirical and theoretical investigations.

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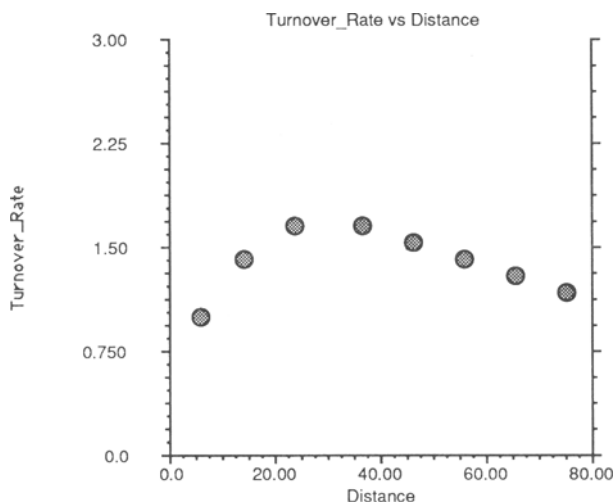


Figure 30. Relationship between the distance to the source of colonizing species and the equilibrium turnover rate simulated by the extended System Dynamics model.

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