

TURNOVER RATES IN INSULAR BIOGEOGRAPHY: EFFECT OF IMMIGRATION ON EXTINCTION¹

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Abstract. Demographic and genetic contributions from conspecific immigrants tend to reduce extinction rates of insular populations. The MacArthur-Wilson model of island biogeography is modified to provide for this effect of immigration on extinction, which we call the rescue effect. This new model predicts that when immigration rates are high relative to extinction rates, turnover rate is directly related to the distance between an island and the source of colonizing species. A field study of the distribution of arthropods among isolated plants supports the model.

Key words: Arizona; biogeography; colonization; extinction; insular biogeography; island; turnover.

INTRODUCTION

More than a decade ago MacArthur and Wilson (1963, 1967; *see also* Preston 1962) proposed a general model of insular biogeography. This model represents the number of species inhabiting an island as a dynamic equilibrium between opposing rates of extinction and colonization, which are functions of the size of the island and its distance from a source of dispersing species, respectively (Fig. 1). The model is attractive because it is elegantly simple and generates several robust predictions which can be tested with appropriate field observations and experiments. There have been numerous attempts to test the model and to use it to account for the distribution of diverse organisms among islands and insular habitats. Although some distributions that do not conform to the predictions have been reported (e.g. Barbour and Brown 1974; Brown 1971; Culver et al. 1973; Diamond 1972, 1973; Simpson 1974; Terborgh 1975), the majority of empirical analyses have supported the model. Thus Simberloff (1974) in a recent review stated "...the equilibrium hypothesis has been experimentally confirmed for oceanic islands, proved useful for interpreting many other insular situations, and spawned a mass of research which has given biogeography general laws of both didactic and predictive power."

The primary innovation of the MacArthur-Wilson (M-W) model was the suggestion that recurrent colonizations and extinctions create a dynamic equilibrium in which the number of species remains relatively constant while the identity of species varies over time. The model predicts that species are replaced at a rate inversely related to both island size and distance to a source of colonists (Fig. 1). Species turnover on islands has been reported (Diamond 1969; Simberloff 1976; Simberloff and Wilson 1969, 1970; Terborgh and Faaborg 1973; however, *see* Lynch and Johnson 1974, for a critique of the first and last papers), but the predicted relationship between turnover rate and island

size and isolation has not been observed empirically. A rigorous test of these predictions is essential to support the M-W model, because a simple, intuitively attractive modification of the model predicts that turnover rate often will be directly related to insular isolation.

AN ALTERNATIVE MODEL

The M-W model represents extinction rate as a function of island size and colonization as a function of insular isolation; the interaction of these two independent and opposing rates determines the equilibrium number of species and turnover rate (Fig. 1). Realistically, however, the same parameters that affect colonization rate (e.g., proximity to a continent or other source of dispersing species) also similarly affect the rate of immigration of individuals belonging to species already present on the island. When this immigration rate is sufficiently high, it will reduce the extinction rate. This is primarily because demographic and genetic contributions of immigrants tend to increase the size and fitness of insular populations, thereby reducing the probability that they will become extinct. In addition, a high immigration rate also will have a statistical effect in reducing the apparent extinction rate simply by decreasing the probability that a given species will be absent during any census.

We suggest that this effect of immigration upon extinction, which we call the rescue effect, makes the M-W model inadequate to predict the relationship between turnover rate and isolation for many kinds of true islands, insular habitats, and isolated patches of resources. Whenever immigration rates are sufficiently high relative to extinction rates, islands that are closer to sources of dispersing species will have higher immigration rates, and hence lower extinction and turnover rates than more isolated islands. The rescue effect will be increased by the tendency (Diamond 1975) for those species that are present on an island to be good dispersers and hence have high immigration rates. When immigration and colonization rates are

¹ Manuscript received 11 May 1976; accepted 28 October 1976.

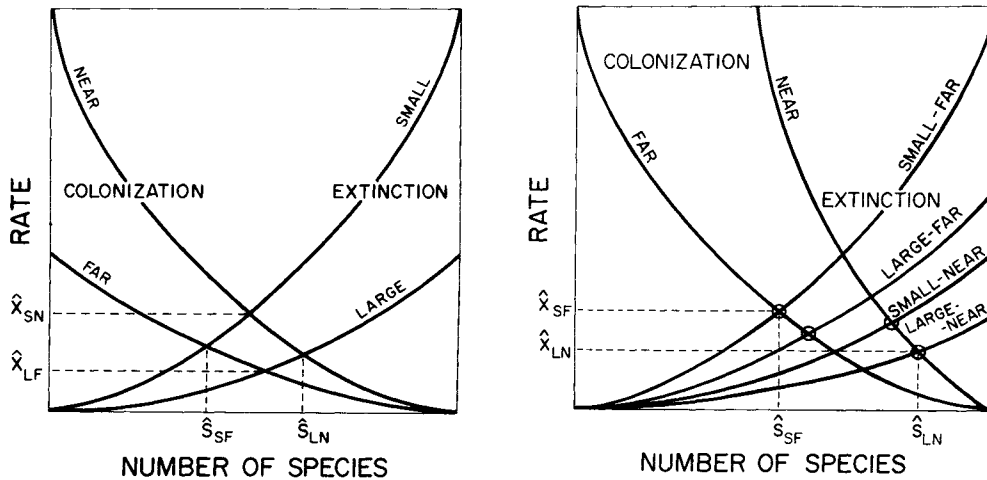


FIG. 1. Two models of equilibrium insular biogeography. Left, the MacArthur-Wilson model, which portrays extinction and colonization rates as functions of island size and isolation, respectively. Right, a modification of the M-W model which incorporates the rescue effect of immigration on extinction. In both models intersections of the curves can be extrapolated to the abscissa and ordinate to give equilibrium numbers of species (\hat{S}) and turnover rates (\hat{X}) respectively. Note that the two models predict the same relative order of numbers of species but different orders of turnover rates.

low relative to extinction rates, the rescue effect should be small and the turnover rate should be inversely related to insular isolation as predicted by the M-W model. Thus turnover rate as a function of increasing distance from a source of species should first increase, reach a maximum where colonization and extinction rates are both high, and then decrease (Fig. 2). On islands more distant from a source of colonists than the maximum turnover rate, the M-W model should correctly predict the relationship between turnover rate and insular isolation. However, for islands nearer a source (to the left of the peak in turnover rate in Fig. 2) a modification of the model is required. We present a model similar to that of MacArthur and Wilson, but which incorporates the rescue effect on the rates of extinction for islands of varying isolation and size (Fig. 1). In comparison to the M-W model, our model predicts the same effect of island size and isolation on equilibrium number of species, and the same effect of island size but the opposite effect of isolation on equilibrium turnover rate.

TURNOVER OF ARTHROPODS ON THISTLES

We were led to reexamine the M-W model and propose an alternative on the basis of a short-term study of the distribution of arthropod species among isolated thistle plants. In May 1973 we censused spiders and several orders of insects on individual plants of *Cirsium neomexicanum* near Portal, Arizona. Two large stands of thistles were censused twice, 5 days apart. Recolonization experiments also were performed by defaunating equal numbers of plants near to and far from other thistles supporting large arthropod faunas.

The results of this study confirmed the major predictions of the M-W model, except that turnover rate was

directly related to insular isolation rather than inversely related as expected. The number of arthropod species increased with size of thistle plant and decreased with distance between plants (Tables 1 and 2). The faunas of the plants appeared to be in approximate equilibrium; the number of species remained similar between censuses although there were gains and losses of individual species on particular plants. Turnover rates were high, inversely related to size of plant

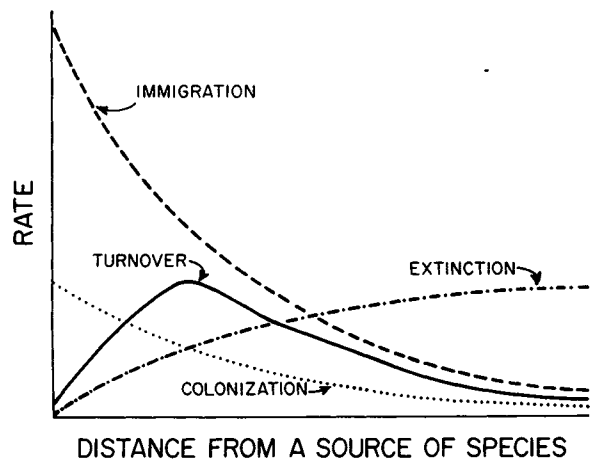


FIG. 2. A graphical representation of the relationship between the distance to a source of species and turnover rate at equilibrium. Note that rates of immigration and colonization decrease with insular isolation as suggested by MacArthur and Wilson; but, in contrast to their model, extinction rate increases with isolation because of the rescue effect. The result is that equilibrium turnover rate first increases and then decreases with distance from a source of species, and turnover is greatest where both colonization and extinction rates are high. The shapes of these curves are hypothetical and should vary with the characteristics of particular insular systems.

TABLE 1. Effects of plant size and isolation on the number and turnover of arthropod species on individual thistle plants. Note that all patterns conform to the predictions of the M-W model except for the relationship between turnover rate and isolation

Size-isolation category ¹	Corral site						Roadside site					
	16 May		21 May		16-21 May		18 May		23 May		18-23 May	
	No. of plants	\bar{x} no. of species	No. of plants	\bar{x} no. of species	No. of plants ²	\bar{x} turnover of species ³	No. of plants	\bar{x} no. of species	No. of plants	\bar{x} no. of species	No. of plants	\bar{x} turnover of species
Large-Near	15	3.00	28	3.82	16	0.67	9	5.78	12	5.25	9	0.29
Large-Far	6	1.67	9	3.78	7	0.78	9	3.67	9	4.44	9	0.42
Small-Near	59	1.61	46	1.89	56	0.78	22	3.23	19	2.21	21	0.69
Small-Far	6	0.67	3	1.33	3	1.00	15	1.27	15	0.80	11	0.91

¹ Categories are defined as follows: Large > 2.5 = number of fresh blossoms + (no. of old blossoms ÷ 2). Near > 8.0 = no. of plants within 12.5 m + (no. of plants 12.5-25 m ÷ 2) + (no. of plants 25-50 m ÷ 4).

² Plants that had not arthropods in both censuses were eliminated from calculations of turnover rates; otherwise, they would have given values of infinity.

³ Turnover = (No. of species present only in first census + no. of species present only in second census) ÷ (total no. of species in first census + total no. of species in second census).

and directly related to distance between plants. Recolonization of defaunated plants was rapid. Within 24 h, 94% and 67% of the original number of species had recolonized the near and isolated plants respectively.

In this case the direct relationship between turnover rate and plant isolation probably was produced primarily by the statistical consequences of high immigration rates. The arthropods did not maintain breeding populations on the thistle plants, but visited them for short periods while searching for food or mates. Since several individuals of each of several common species often were present simultaneously on the same plant, high dispersal rates would reduce the possibility that a species would be present in one census but absent in another, thus producing a turnover. This statistical effect of immigration on extinction is similar only by analogy to the reproductive and genetic contributions of immigrant individuals that should reduce extinction rates of breeding populations on true islands or insular habitats.

DISCUSSION

There have been so few studies of equilibrial faunal turnover in insular systems that it is difficult to evaluate the general significance of the rescue effect and the

validity of our model until additional empirical observations are made. The model is consistent with the observed turnover of arthropods on thistles, and also with the conclusions of Diamond (1969; but these have been challenged by Lynch and Johnson 1975) that the turnover rates for bird species on the Channel Islands of California are inversely related to the number of species present. Immigration rates were observed to be high in the former case and assumed to be so in the latter.

Simberloff and Wilson (1969, 1970) observed no significant correlations, either positive or negative, between turnover rates for arthropod species and distance from a source of species in their study of defaunated mangrove islands. It is not clear whether this was due to sampling problems, the fact that their systems were near the point where the relationship between turnover rate and distance from a source of colonists has zero slope, or the difficulty in distinguishing between recolonization and succession, on one hand, and turnover equilibrium, on the other. Although we know of no attempts to measure turnover directly on islands where immigration and colonization rates are very low, the fact that extremely isolated islands have a high proportion of endemics (MacArthur and Wilson

TABLE 2. Partial correlation analysis of the dependence of number of species and turnover rate on plant size and isolation. Values are partial correlation coefficients giving the effect of one independent variable (plant size or isolation) when the other is held constant. These results show the same pattern as Table 1, and indicate the statistical significance of the relationships

Size/Isolation parameter	Corral site			Roadside site		
	16 May No. of species	21 May No. of species	16-21 May Turnover of species	18 May No. of species	23 May No. of species	18-23 May Turnover of species
Plant size ¹	0.53**	0.57**	-0.33**	0.52**	0.62**	-0.64*
Plant isolation ¹	-0.28*	0.13	0.27*	-0.45**	-0.31*	0.32*

¹ As in Table 1 except that plant isolation is the reciprocal of the measure given there.

* P < 0.05.

** P < 0.01.

1967, Darlington 1957) suggests their turnover rates are lower than those islands somewhat nearer to continents. This is consistent with our prediction (Fig. 2) that as colonization rates decrease with increasing isolation, turnover rates should first increase and then decrease.

The rescue effect of immigration in reducing extinction and turnover potentially has two important consequences for insular biogeography and ecology. First, recolonization by conspecifics may be an important mechanism enabling some species to persist on islands. This may be particularly true of species that represent early stages in insular taxon cycles and are characterized by species-area curves of shallow slope (Ricklefs and Cox 1972, Scott 1972); examples are the supertramp and tramp bird species described by Diamond (1975). Previously it had been suggested that the persistence of insular populations might be explained largely in terms of life history features that reduced their probability of extinction (MacArthur and Wilson 1967, MacArthur 1972). The genetic contributions of frequent immigrants may delay or prevent the genetic differentiation of insular populations. There is evidence that the evolution of genetically distinct insular populations represents entry into the taxon cycle which almost inevitably ends with the extinction of endemic populations (Wilson 1961, Ricklefs and Cox 1972, Scott 1972). Second, the rescue effect suggests that the species composition of insular biotas should be more stable and deterministic than expected from the M-W model. High rates of immigration will tend to stabilize and prevent the extinction of species which are favored by suitable habitats, competitive superiority or absence of predators. Thus Brown (In press) has suggested that the primary importance of habitat in determining the number and identity of permanent resident boreal bird species inhabiting isolated mountain ranges in western North America (Johnson 1975) is owing primarily to high immigration rates. Low slope of the species-area curve and other evidence indicate that immigration is sufficient to maintain boreal bird populations wherever habitat is adequate.

In retrospect, the rescue effect is intuitively reasonable and seems likely to influence many insular distributions. The M-W model has received so much attention since it was presented more than a decade ago that it is interesting to ask why this potentially important exception went unreported for so long. We suggest two primary reasons; they testify to MacArthur's and Wilson's biological knowledge and intuition and provide interesting insight on the relationship between theory and empiricism in contemporary population biology. First, because the M-W model is so elegantly simple and most of its predictions correspond to the observations and intuition of ecologists and biogeographers, there was a tendency to accept the model before it had been tested rigorously. Second, the most easily checked predictions were tested repeatedly and

the results usually supported the model (e.g., Culver 1970; Diamond 1969; Simberloff and Wilson 1969, 1970; Vuilleumier 1970, 1973); the few exceptions were readily explained without invoking a rescue effect (e.g., Abbott and Grant 1976, Barbour and Brown 1974, Brown 1971, Culver et al. 1973, Diamond 1972, 1973, Terborgh 1975). As a result the model was widely regarded as having been confirmed empirically before the crucial predictions about dependence of turnover rate on island size and isolation had been tested. The fact that we obtained conflicting data and were able to reconcile them with most of the existing data on insular species diversity and turnover by constructing an alternative model, demonstrates the necessity of testing all possible predictions and assumptions of such models to avoid "making the right prediction for the wrong reason" (Dayton 1973).

Careful analyses of turnovers of insular species populations are required to test and distinguish between current models of island biogeography. There are obvious reasons why such work has proceeded slowly. It is difficult to perform controlled experiments on a biogeographic scale, although Simberloff and Wilson (1969, 1970; Simberloff 1976) have had the imagination and practicality to do so with great success. An obvious alternative is to work with small-scale, analog systems that are easier to observe and manipulate (e.g., Cairns et al. 1969, Maguire 1971, Schoener 1974, Siefert 1975). Valuable insights may come from analyzing the dynamics of colonization and extinction on thistle plants or artificial sponges, but these must be regarded as hypotheses until they can be tested rigorously on a biogeographic scale.

ACKNOWLEDGMENTS

The field study of arthropods on thistle plants was begun as a class project in a field ecology course (Biology 576 at the University of Utah). Students in the class and John F. Addicott assisted in the field and supplied valuable suggestions. Numerous colleagues and graduate students contributed advice and critical discussion; of these Stephen C. Fretwell, Douglas J. Futuyma, Thomas C. Gibson, E. G. Leigh, Graham H. Pyke, and William M. Schaffer deserve special thanks. The work was supported in part by NSF Grant GB-39260 to J. H. B.

LITERATURE CITED

- Abbott, I., and P. R. Grant. 1976. Nonequilibrium bird faunas on islands. *Am. Nat.* **110**:507-528.
- Barbour, C. D., and J. H. Brown. 1974. Fish species diversity in lakes. *Am. Nat.* **108**:473-478.
- Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.* **105**:467-478.
- . In press. The theory of insular biogeography and the distribution of boreal birds and mammals. In K. T. Harper [ed.] *Biogeography of the Intermountain West*. Brigham Young University Press, Provo, Utah.
- Cairns, J., M. L. Dahlberg, K. L. Dickson, N. Smith, and W. T. Waller. 1969. The relationship of fresh-water protozoan communities to the MacArthur-Wilson equilibrium model. *Am. Nat.* **103**:439-454.
- Culver, D. C. 1970. Analysis of simple cave communities. I. Caves as islands. *Evolution* **29**:463-474.

- Culver, D., J. R. Holsinger, and R. Baroody. 1973. Toward a predictive cave biogeography: the Greenbrier Valley as a case study. *Evolution* 27:689-695.
- Darlington, P. J. 1957. *Zoogeography: the geographical distribution of animals*. Wiley, New York. 675 p.
- Dayton, P. K. 1973. Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *Am. Nat.* 107:662-670.
- Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proc. Natl. Acad. Sci. USA* 64:57-63.
- . 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. *Proc. Natl. Acad. Sci. USA* 69:3199-3203.
- . 1973. Distributional ecology of New Guinea birds. *Science* 179:759-769.
- . 1975. Assembly of species communities, p. 342-444. *In* M. L. Cody and J. M. Diamond [eds.] *Ecology and evolution of communities*. Harvard Univ. Press, Cambridge.
- Johnson, N. K. 1975. Controls of number of bird species on montane islands in the Great Basin. *Evolution* 29:545-657.
- Lynch, J. F., and N. K. Johnson. 1974. Turnover and equilibria in insular avifaunas with special reference to the California Channel Islands. *Condor* 76:370-384.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York. 269 p.
- MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- . 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton, New Jersey. 203 p.
- Maguire, B. 1971. Phytotelemata: biota and community structure determination in plant-held waters. *Annu. Rev. Ecol. Syst.* 2:439-464.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43:185-215.
- Ricklefs, R. E., and G. W. Cox. 1972. Taxon cycles in the West Indian avifauna. *Am. Nat.* 106:195-219.
- Schoener, A. 1974. Experimental zoogeography: colonization of marine mini-islands. *Am. Nat.* 108:715-738.
- Scott, J. A. 1972. Biogeography of Antillean butterflies. *Biotropica* 4:32-45.
- Seifert, R. P. 1975. Clumps of *Heliconia* inflorescences as ecological islands. *Ecology* 56:1416-1422.
- Simberloff, D. S. 1974. Equilibrium theory of island biogeography. *Annu. Rev. Ecol. Syst.* 5:161-182.
- . 1976. Experimental zoogeography of islands: effects of island size. *Ecology* 57:629-648.
- Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands. The colonization of empty islands. *Ecology* 50:278-296.
- . 1970. Experimental zoogeography of islands. A two-year record of colonization. *Ecology* 51:934-937.
- Simpson, B. B. 1974. Glacial migrations of plants: island biogeography evidence. *Science* 185:698-700.
- Terborgh, J. 1975. Faunal equilibria and the design of wildlife preserves, p. 369-380. *In* F. B. Golley and E. Medina [eds.] *Tropical ecological systems*. Springer-Verlag, New York.
- Terborgh, J., and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *Auk* 90:759-779.
- Vuilleumier, F. 1970. Insular biogeography in continental regions. I. The northern Andes of South America. *Am. Nat.* 104:373-388.
- . 1973. Insular biogeography in continental regions. II. Cave faunas from Tesin, southern Switzerland. *Syst. Zool.* 22:64-76.
- Wilson, E. O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95:169-193.