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Birds of the Solomon Islands

THE DOMAIN OF THE DYNAMIC EQUILIBRIUM THEORY AND ASSEMBLY RULES, WITH COMMENTS ON THE TAXON CYCLE

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BIRDS OF THE SOLOMON ISLANDS have played a prominent role in two of the most influential ecological theories of the last forty years. Robert MacArthur and Edward O. Wilson cited these birds in both their 1963 paper introducing the dynamic equilibrium theory of island biogeography and their 1967 monograph on the theory (MacArthur and Wilson 1963, 1967). In 1976, Jared Diamond, Ernst Mayr, and Michael Gilpin published three papers on Solomon Islands avifaunas, interpreting them in terms of dynamic equilibrium turnover, relating the area and isolation of islands to hypothesized immigration and extinction curves (Diamond and Mayr 1976, Diamond et al. 1976, Gilpin and Diamond 1976). At about the same time, Diamond (1975) elaborated his theory that assembly rules govern island species composition and are largely determined by resource competition but influenced by other factors (e.g., dispersal ability), based primarily on birds of the Bismarck Archipelago but with many examples from and references to birds of the Solomons. Remarkably, Philip J. M. Greenslade (1968) first applied the taxon cycle model (Wilson 1959, 1961) to birds, using the Solomon Islands avifauna.

For the equilibrium theory, four decades of research have cast doubt on its applicability to many natural systems (references in Whittaker and Fernández-Palacios [2007]; cf. Schoener, this volume). The range of systems described well by the assembly rules remains highly controversial. In a meta-analysis, Gotelli and McCabe (2002) find that certain distributional patterns predicted by the rules are more common in nature than a noncompetitive null model would predict, but for very few systems is there direct evidence on the reasons for these patterns. The notion of a taxon cycle has also been quite controversial, particularly as regards its applicability to birds (Ricklefs and Bermingham 2002; Ricklefs, this volume). Strikingly, distributions of Solomon Islands birds, though prominent in the development of all three theories, have barely been scrutinized after the original papers. This neglect is because the distributions—which species are on which islands—were unavailable until they were published by Mayr and Diamond (2001). Here we use these data to reassess whether these three theories apply to this biota and to address the implications of our results for the status of the theories and, more generally, for the nature of the evidence required to test them.

The iconic "crossed-curves" equilibrium model of MacArthur and Wilson (1963, 1967) focuses on demography of individual species, leading to stochastic extinction, and not on interactions among species. It does not account for species' identities, looking only at numbers of species. However, MacArthur and Wilson (1967) also stressed the possible role of diffuse competition in generating turnover and recognized that deterministic forces related to species composition and interactions may partly determine how many and which species are found on islands: "A closer examination of the composition and behavior of resident species should often reveal the causes of exclusion, so that random processes in colonization need not be invoked" (p. 121). Diamond's theory that assembly rules govern species composition is based on exactly that sort of examination of the identities and behavior of resident species. The two theories need not conflict so long as substantial turnover occurs and interactions are a major contributor to it. In fact, in an archipelago of islands in which all are conceived as potential sources for one another of multiple potentially interacting species, as in the birds of the Solomon Islands, the equilibrium theory describes what is now recognized as a metacommunity (Leibold et al. 2004). Several authors, beginning with Wilson (1969), have suggested extending the equilibrium theory to an evolutionary scale by adding adaptation and speciation, while the assembly rules were seen as acting in ecological time. As do the assembly rules, the taxon cycle model treats species identities and assigns a key role to competitive interactions: these drive the range and habitat contraction phase of the cycle (Ricklefs, this volume). However, unlike in the assembly rules and most interpretations of the equilibrium theory, evolution is prominent in the taxon cycle, with morphological differentiation aiding assignment of species to particular cycle phases and hypothesized behavioral and physiological changes driving species' trajectories through the phases.

The Equilibrium Theory

To calculate the immigration and extinction curves of the equilibrium theory, Gilpin and Diamond (1976) examined the 106 lowland breeding land and freshwater birds on 52 of the Solomon Islands,[1] including all

[1] We designate by "Solomon Islands" the geographic archipelago, not the nation of the Solomon Islands. We include Bougainville and Buka (part of Papua New Guinea) but not the Santa Cruz Islands, far to the east of the archipelago, just north of Vanuatu, but part of the nation of the Solomon Islands.

major islands. Some species that reach sea level on one island may be restricted to higher elevations on another (a pattern Mayr and Diamond [1976] ascribe to competition); the species pool for this exercise was all species reaching sea level on any island. Assuming all islands to be in equilibrium, they constructed immigration (I) and extinction (E) functions in terms of the area (A), distance (D), and number of species (S) for each island, set these functions equal, and sought functional forms such that variation in area and distance explained as large a fraction as possible of the variation in number of species. For islands with more than 50 species total, or for islands within 6 miles of such an island, distance was taken as 0. For other islands, the distance was the distance to the nearest island with more than 50 species. The upshot is that 37 islands had $D=0$.

As a benchmark, Gilpin and Diamond (1976) found a phenomenological model with five fitted parameters (a, b, c, d, and e) that explained 98% of the variance in S:

$$S=(a+b \log A) \exp(-D^c/dA^e). \tag{9.1}$$

However, the parameters have no straightforward biological interpretation. The goal was to equal this explanatory power with biologically reasonable immigration and extinction functions.

Thus, extinction (E) was assumed to be a function of A and S, and immigration (I) a function of A, D, and S. In addition, Gilpin and Diamond (1976) assumed that any valid extinction function should have at least three parameters:

R: a fitted constant
n: so that E is a concave upward function of S, proportional to S^n ($n>1$)
x: so that, with decreasing A, and extinctions solely the result of demographic fluctuations, E is a function of A^{-x}, with $x>1$

and any valid immigration function should have at least four parameters:

m: so that I is concave upward ($m>1$)
D_0: in accord with a model with a constant direction and risk of death per unit distance traversed (the exponential model of MacArthur and Wilson [1967])
y: accounting for differences among species in overwater flight distances ($y<1$)
v: because a bigger island will present a larger target to a disperser at sea level, and increasing island elevation may make the target more visible ($v \geq 0.5$).

Gilpin and Diamond (1976) found a best-fit model matching the phenomenological model in explaining 98% of the variation in S, even without one parameter (x):

$$E=RS^n/A, \quad I=(1-S/P_0)^m \exp(-D^y/D_0A^v). \tag{9.2}$$

Here P_0 is the size of the species pool, 106. S is then an implicit function when I is set equal to E.

Noteworthy in this exercise are four features:

1. No unequivocal bird extinctions in the Solomon Islands have been observed in historic times. However, this fact does not conflict with the theory because
2. Time is not a factor in any parameters and variables of the equations for I and E. That is, the immigration and extinction curves, plotted against S, are in arbitrary time units.
3. The island avifaunas are assumed to be at equilibrium.
4. The same data were used to produce the equations as to test them.

With respect to point 1 and the fact that the equations do not predict what the extinction and immigration rates are, only that they are equal, it is interesting to consider possible extinctions in the Solomons. Mayr and Diamond (2001) list four species (*Gallicolumba jobiensis*, *G. salamonis*, *Microgoura meeki*, and *Zoothera dauma*) not recorded in the archipelago since 1927 and a fifth (*Anas gibberifrons*) not seen since 1959. These may be extinct (some globally, others just in the Solomons). They also observe that all five are ground-nesters, "suggesting that introduced cats may have been the culprits" (p. 38).

Other introduced species may also have been involved. For example, the teal, *A. gibberifrons*, disappeared from the one island it occupied (Rennell) right after *Oreochromis* (*Tilapia*) *mossambica* was introduced (Mayr and Diamond 2001). Diamond (1984) surmised that the fish somehow eliminated the teal, and he may have been prescient. This species is the most ecologically damaging introduced tilapia (Pullin et al. 1997) and is believed to be one of several threats to the Eurasian white-headed duck, *Oxyura leucocephala*, by virtue of competition (Hughes et al. 2004). Rats are also present in the Solomon Islands and prey on birds. The Pacific rat, *Rattus exulans*, was introduced prehistorically by humans, probably to all inhabited islands. The black rat, *R. rattus*, present on many of the islands (Yom-Tov et al. 1999), was introduced at unknown times after European arrival in the sixteenth century. Other species than the above five may have been extirpated from particular islands during this period but remain on others (cf. BirdLife International 2000); there is no published record of such extirpations.

If these five species are extinct in the Solomons, then they are not examples of equilibrium turnover driven by the demography of small populations or diffuse competition. Rather, these would probably be deterministic extinctions caused by human activities. This is the same distinction Caughley (1994) drew in conservation biology between the small-population paradigm (focusing on inherent extinction risk for all small populations, by virtue of smallness) and the declining-population paradigm, which seeks for each dwindling species the specific, deterministic reasons for its decline. In any event, and returning to point 2 above, because the Gilpin-Diamond model lacks a time scale, it cannot conflict with any extinction rate data, including data that show few or no extinctions over a century.

With respect to point 3 above, the proposition that these avifaunas have been in *any* sort of equilibrium for tens of thousands of years is unconvincing because of enormous anthropogenic change. Although Pleistocene archeology is poorly known in the Solomons except for Buka, humans have occupied most or all of the main islands for at least 30,000 years; Kilu Cave on Buka has been well studied and anthropogenic deposits date to ca. 29,000 B.P. (Steadman 2006). On mid-sized Buka, the only island in the Solomons for which avian fossil evidence is not sorely lacking, 61% of the prehistoric avifauna is no longer present (Steadman 2006). This is a staggering figure, high even among massive post-human colonization extinctions widely documented among Pacific island birds. Steadman (2006) argues that most if not all absences today from the large islands, including Buka, are anthropogenic. An alternative in the spirit of the equilibrium theory is "faunal relaxation," in which the decrease in area (and, for Buka, separation from Bougainville) owing to higher sea levels since the end of the last Ice Age would, simply by the demography of smaller populations, have led ultimately to fewer species. Of the four species extinct on Buka but persisting elsewhere in the Solomons (Steadman 2006), two (*Nesasio solomonensis* and *Nesoclopeus woodfordi*) are present only on islands larger than Buka, while the other two (*Gallicolumba rufigula* and *Caloenas nicobarica*) are on many islands both smaller and larger than Buka (data in Mayr and Diamond [2001]), providing at most weak support for the relaxation hypothesis.

Arrival of the Lapita people to Pacific islands was particularly catastrophic to birds (Steadman 2006), and their colonization of the Solomons, ca. 3000 B.P., was probably devastating. There is almost no evidence for bird extinctions before human arrival throughout Oceania, including the Solomons (Steadman 2006). However, human population growth as well as animals and plants introduced by humans are believed to have massively affected island bird communities. In addition to cats and rats, humans deliberately introduced dogs and pigs to many islands. All prey on birds and/or their eggs. Also, pigs, introduced to many of the Solomon Islands (Long 2003), have greatly modified habitat in many places (Long 2003). Prehistoric humans also carried many alien plants to

Pacific islands, and there was rampant deforestation (often by burning) to cultivate these plants, most of which were of little use to native birds (Steadman 2006). Today there is tremendous habitat destruction by logging (BirdLife International 2000).

Native rodents on some larger islands in the Solomons may have rendered their avifaunas less vulnerable to introduced predators than were birds on remote Pacific islands (Steadman 2006). Nevertheless, the Buka data suggest that massive extinction did occur with human colonization. Not only was this extinction not a form of equilibrium turnover, but it left an avifauna that one could hardly expect to be in equilibrium. All the numbers of lowland bird species cited in the exercise of Gilpin and Diamond (1976) are lower, probably far lower, than those that obtained before humans arrived. And they are still falling rapidly. For land birds of the Solomon Islands (minus Bougainville and Buka), BirdLife International (2000) lists eighteen species as threatened and sixteen as near-threatened (a total of ca. one-fourth of the avifauna). The suspected threats listed in the individual species accounts in the same reference are overwhelmingly anthropogenic, with many citing logging; for only two species are "natural" causes even mentioned as a possibility.

Just as few (if any) nonanthropogenic extinctions are documented in the Solomons, neither is immigration of new species recorded. Given the difficulty of working in these islands, it would be difficult to attribute a new record to immigration rather than to better sampling. For instance, Kratter et al. (2001) recorded three new land bird species on Isabel in three weeks in a dry forest; they do not regard these as new immigrants. Notably, no instance is known in the Solomons of a species lost, then recolonizing on its own (Steadman 2006). Although it would not constitute equilibrium immigration, the Solomons, lacking the acclimatization societies that introduced entire avifaunas to such islands as New Zealand, the Hawaiian Islands, and the Mascarenes (cf. Lever 1992), do not even have many introduced bird species. At most three are established, and these are on very few islands (Long 1981). Thus, given the many documented extinctions (Steadman 2006), the Solomon Islands contradict the pattern noted by Sax et al. (2002), of an approximate equality of immigrations and extinctions for birds on oceanic islands.

Finally, the equations in (9.2) were derived from the data set that was then used to test them, with no attempt at cross-validation. It is not clear that any other biota could be used to test this model. Gilpin and Diamond (1976, p. 4134) observe that "a fauna or flora other than Solomon birds will certainly require parameter values, and maybe require functional forms, different from those of Eqs 7b and 7a [equations in (9.2)], respectively."

Assembly Rules

Just as Gilpin and Diamond (1976) attempted to demonstrate a process (turnover) from a static pattern, so the assembly rules (Diamond 1975) constituted an effort to use a more detailed static pattern (the species composition of each island) to implicate a process (competition) as far more important in generating the pattern than other alternatives (habitat requirements and dispersal limitation). Diamond (1975) assumed that the current island avifaunas are for the most part in a species-number equilibrium and that the processes yielding the assembly-rule patterns operated much more quickly than those yielding a species-number equilibrium.

Here we explore Diamond's basic assembly rule, number 5: "Some pairs of species never coexist, either by themselves or as part of a larger combination" (Diamond 1975, p. 423). Such "checkerboard" distributions have often been taken as evidence for interspecific competition (Gotelli and Graves 1996). Controversy has largely revolved around two issues. First, depending on the numbers of islands and species, some checkerboard distributions might have been expected even if species colonized islands independently of one another (Connor and Simberloff 1979). Second, even if some checkerboards are statistically unlikely to have resulted from independent colonization, other explanations than interspecific competition are possible (Connor and Simberloff 1979, Simberloff and Connor 1981). Two species might have distinct habitat requirements, for example, or might be sister species that have recently speciated allopatrically, or might have arrived in an archipelago by different routes and/or at different times.

We examined the Solomon Islands avifauna (45 islands, 142 species) as described by Mayr and Diamond (2001) for checkerboard distributions. To avoid the "dilution effect" (Diamond and Gilpin 1982; cf. Colwell and Winkler 1984), we looked only at the subset of species pairs in which competition would be expected. First we examined just congeneric pairs of species. Taxonomic groups are not always congruent with guilds (Diamond and Gilpin 1982, Simberloff and Dayan 1991), but many authors have argued that congeners are on average ecologically more similar to one another than are heterogeneric species, and many studies have partitioned biotas into guilds by taxonomy (e.g., MacArthur 1958). Also, all mapped checkerboards in Diamond (1975) consisted of congeners, so we feel this convention suffices for our purposes. We then examined checkerboards in four multigenus guilds (table 9.1) specified by Diamond (1975).

TABLE 9.1
Guild Memberships in the Solomon Islands for Multigenus Guilds Specifically Designated by Diamond (1975)

Guild	*Genera*	*No. of species*
Cuckoo dove	*Macropygia*	2
	Reinwardtoena	
Gleaning flycatcher	*Monarcha*	7
	Myiagra	
	Pachycephala	
Myzomela-sunbird	*Myzomela*	3
	Nectarinia	
Fruit pigeon	*Ducula*	8
	Ptilinopus	

Finally, Diamond (1975; cf. Mayr and Diamond 2001) defined as "supertramps" species found only on islands (generally small ones) with few species, a pattern he also attributed primarily to competition. However, a species could be a supertramp for other reasons (Simberloff and Martin 1991), for example, a preference for habitats especially common on small islands, or exclusion from larger islands by predators. Supertramps would dominate a search for checkerboards, even if the reasons for their status had nothing to do with the competitive interactions that are posited as causal. Because they are on islands with only a few species, they are likely automatically to comprise many checkerboards. We therefore conducted our entire analysis both with and without supertramps. Diamond (1975) did not provide quantitative criteria for qualification as a supertramp. We defined them statistically (Collins et al. in preparation). By our method, the three supertramps in the Solomons are *Ducula pacifica*, *Monarcha cinerascens*, and *Aplonis* [*feadensis*].[2] To these, Mayr and Diamond (2001) add *Ptilinopus* [*purpuratus*], *Caloenas nicobarica*, and *Pachycephala melanura*.

To evaluate the assembly rules, it is necessary to consider historical geography. According to Mayr and Diamond (2001), five island groups occur in the Solomons: (1) the Bukida group, or Main Chain—Greater

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[2] We follow the convention of Mayr and Diamond (2001) in designating superspecies by square brackets. Taxa within superspecies in the Solomons have been assigned different ranks by different authors.

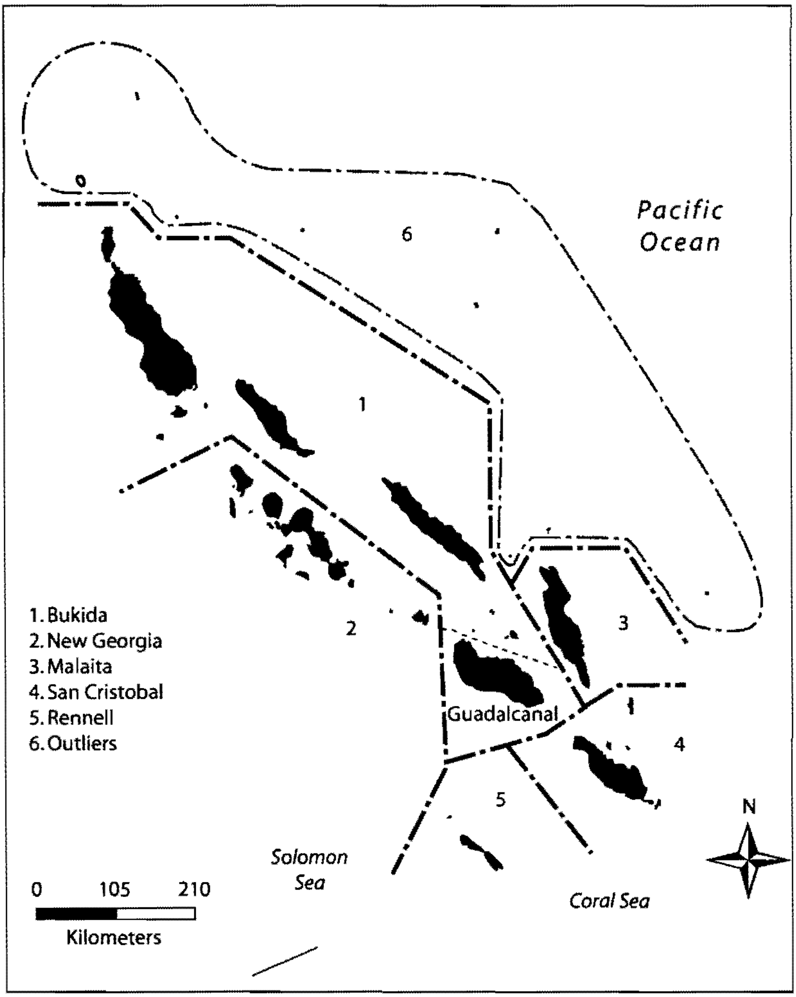

Figure 9.1. Island groups as currently configured in Solomons separated by hypothesized dispersal barriers (cf. Mayr and Diamond 2001).

Bukida, a Pleistocene land-bridge island running from Buka to Florida, and Guadalcanal, which was separated from Greater Bukida by a narrow channel (cf. Steadman 2006), (2) the New Georgia group—three Pleistocene land-bridge islands with current islands from Vella Lavella to Gatukai, and two unconnected islands (Gizo and Simbo), (3) Malaita, (4) the San Cristobal group—San Cristobal (Makira), Ulawa, Ugi, Three Sisters, Santa Anna, and Santa Catalina, and (5) the Rennell group—Rennell and Bellona (figure 9.1). Finally, a sixth group consists of outliers,

TABLE 9.2
Observed and Expected Numbers of Congeneric Checkerboards (CH) in the Solomon Islands (Including Supertramps)

Genus	*No. of taxa*	*ObservedCH*	*Expected CH*	*Probability*
Accipiter	5	5	1.52	<0.001
Aplonis	5	2	0.11	<0.001
Monarcha	3	2	<0.001	<0.001
Pachycephala	3	2	0.95	0.157
Rhipidura	6	3	3.06	0.659
Zosterops	5	8	4.23	0.006

Source: Matrix data extracted from Mayr and Diamond (2001).

Notes: Checkerboards derived by matrix randomization (see text). Depending on ranks of taxa within superspecies, observed and/or expected numbers of checkerboards may increase.

small, remote islands north and east of the archipelago (Fead, Kilimailau, Tauu, Nukumanu, Ontong Java, Ramos, Gower, Nissan, and Sikaina). Although the mega-islands of Greater Bukida, the expanded New Georgia, and the expanded San Cristobal would all have been within sight of each other during the late Pleistocene (Steadman 2006), Mayr and Diamond (2001) argue that, even during the Pleistocene when sea levels were much lower, these groups were separated by barriers to dispersal, differentially permeable to different species but sufficient to generate morphological differences among populations within species (or species groups) on islands in different island groups and compositional differences in bird communities on islands in different groups.

To assess the null probability of the observed numbers of checkerboards, we used the Miklós and Podani (2004) "trial-swap" method to randomize repeatedly the binary presence-absence matrix, maintaining column sums (species richness on each island) and row sums (number of islands occupied by each species). These conventions are explained by Gotelli and Graves (1996). We then sought tail probabilities for the observed numbers of congeneric checkerboards (and later for numbers of checkerboards in the multigenus guilds).

The Solomon Islands have 22 congeneric checkerboards in six genera (table 9.2); in four of these genera, these numbers appear improbably large if species were colonizing islands independently of each other. However, minus supertramps, which occur in two of these six genera, these two genera and four of the checkerboards disappear, and the numbers of

TABLE 9.3
Observed and Expected Numbers of Congeneric Checkerboards (CH) in the Solomon Islands with Supertramps Omitted

Genus	*No. of taxa*	*Observed CH*	*Experienced CH*	*Probability*
Accipiter	5	5	1.52	<0.001
Pachycephala	3	2	0.95	0.157
Rhipidura	6	3	3.06	0.659
Zosterops	5	8	4.23	0.006

Note: Depending on ranks of taxa within superspecies, observed and/or expected numbers of checkerboards may increase.

checkerboards are significantly large only in *Accipiter* and *Zosterops* (table 9.3).

At first blush then, it appears that at least some checkerboards are inconsistent with a hypothesis of independent colonization and in accord with the notion that they represent pairs mutually exclusive by virtue of competition. However, our close examination of all of these congeneric checkerboards, whether or not we include supertramps, yielded a surprise: the checkerboard metaphor, based on red and black squares filling an entire board, does not describe them. Usually there are very few representatives of one or both members of such a distribution, and rather than being spread throughout the Solomons, each representative is usually restricted to one or a few island groups. In other words, they are allopatric at a much broader scale than is implied by the metaphor (figure 9.2), and the boundaries of the allopatric regions coincide with the partitions that Mayr and Diamond (2001) describe as long-standing dispersal barriers. This fact plus the apparently relatively recent arrival of some members of checkerboards and the fact that many have never been seen flying over water suggest that history, in geological time, of the colonization of the archipelago may have led to many of these mutually exclusive distributions.

Of the five *Accipiter* species in the Solomons, *A. fasciatus* accounts for four of the five checkerboards and occurs only in the Rennell group; no other *Accipiter* is found there. Mayr and Diamond (2001) believe this population arrived in Rennell and Bellona from Australia via Vanuatu, bypassing the Bismarck Archipelago. *Accipiter fasciatus* may be excluded from other groups by competition with congeners, but it could also simply not have reached them, or reached them often enough to establish a population, because of the minimum 171 km it would have to fly to get there.

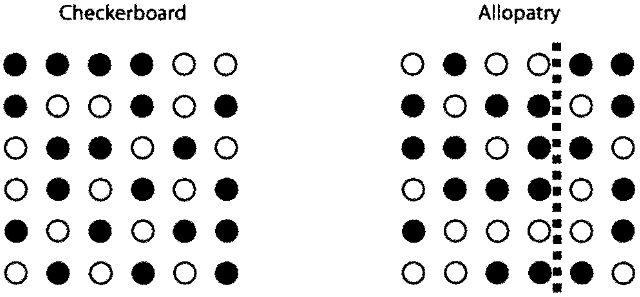

Figure 9.2. Contrast between checkerboard and allopatric conceptions of biogeographic patterns.

The fifth *Accipiter* checkerboard is between *A. imitator* and *A. meyerianus*, each occupying only three islands. *Accipiter imitator* is found only on Greater Bukida islands and has never been seen flying over water (Mayr and Diamond 2001). The three islands occupied by *A. meyerianus* include Guadalcanal of the Bukida group plus two islands in the New Georgia group. A goshawk, it is a strong flyer. It is quite possible that *A. imitator* is not on other islands for historical and behavioral reasons. Mayr and Diamond (2001) suggest it is not on Guadalcanal, though that island is in the Bukida group, because a small channel probably separated Guadalcanal from the rest of the chain. They also suggest that it probably was formerly on other islands that had been part of Greater Bukida but was subsequently extinguished. Competition with *A. meyerianus* would have been an unlikely cause for such extinctions, because (1) *A. meyerianus* is not found on any of these islands; (2) *A. meyerianus* is largely montane in the Solomons (Mayr and Diamond 2001) and *A. imitator* is not; (3) *A. meyerianus* is twice the size of *A. imitator*, suggesting a different diet and/or foraging mode.

Eight pairs among the five *Zosterops* taxa show checkerboard distributions in the Solomons. Except for the superspecies *Z.* [*griseotinctus*], all taxa are restricted to one or two island groups and each occupies six or fewer islands (table 9.4). Mayr and Diamond (2001) stress that, with only two exceptions (discussed below), none of the *Zosterops* taxa occupy the same island, and they see this as an assembly rule determined by competition. However, it is equally true that, with the same two exceptions, the *Zosterops* taxa do not occupy the same island groups, and they are highly restricted in the groups they occupy (table 9.4). Further, three of the species (*Z. stresemanni*, *Z. murphyi*, and *Z. metcalfii*) are believed to be sedentary and not to cross even narrow water gaps (Mayr and Diamond 2001). A plausible, parsimonious hypothesis is therefore that, his-

TABLE 9.4
Occupancy of Island Groups by Solomon Islands *Zosterops* Taxa

Species	*No. of islands*	*Island groups occupied*
Z. [*griseotinctus*]	14	New Georgia, Rennell, Nissan (outlier)
Z. murphyi	1	New Georgia
Z. metcalfii	6*	Bukida
Z. ugiensis	3	Bukida, San Cristobal
Z. stresemanni	1	Malaita

Source: Data from Mayr and Diamond (2001).
* +2 small islets in Bukida group.

torically, each species first reached the island group(s) it currently occupies and simply has not dispersed further.

In arguing for their competitive assembly-rule interpretation, Mayr and Diamond (2001) suggest that at least the three single-island-group species have occupied other, smaller islands (presumably in the same group, as they are not believed to cross water), went extinct, and failed to recolonize. However, no such extinctions have been documented. These hypothesized extinctions would have been facets of "equilibrium" turnover, the consequences of demographic variation in small populations (or perhaps "relaxation" with rising sea levels and decreasing area?). Above, we question the proposition of equilibrium turnover in this archipelago, especially the notion that extinction is "equilibrial." Here we can only add that white-eyes are often enormously abundant, and islands the size of Fauro (71 km^2) and Buena Vista (14 km^2) could have supported thousands of individuals, making extinction from demographic stochasticity unlikely. Of course, populations on smaller islands, such as these, might well be more susceptible to both anthropogenic pressures (cf. Steadman 2006) and the vagaries of environmental stochasticity and catastrophes. And equilibrial turnover might be more likely on islands still smaller than Fauro and Buena Vista (see below).

Two of the ten possible *Zosterops* pairs do not form checkerboards. *Zosterops murphyi* and *Z.* [*griseotinctus*] coexist on Kulambangra, while *Z. ugiensis* and *Z. metcalfii* coexist on Bougainville. Mayr and Diamond (2001) note that, in each pair, the first-named species is montane on the island of co-occurrence, while the other is found only in lowlands, a pattern they also ascribe to competition. This contention is buttressed by the fact that, on San Cristobal, where it is alone, *Z. ugiensis* is found in lowlands.

In any event, the elevational separation and the absence of species from certain islands *within*-island groups they occupy do not bear on the cause of the main pattern driving the number of checkerboards—the restriction of each species to a minority of island groups. This pattern is as compatible with an historical explanation as with one invoking present-day competition.

Three *Pachycephala* taxa occupy the Solomons (Mayr and Diamond 2001): the superspecies *P.* [*pectoralis*] occupies many islands in all five major groups, plus the isolated Russell Islands. *Pachycephala implicata* is a montane species on the Bukida islands of Bougainville and Guadalcanal, where it co-occurs with *P.* [*pectoralis*] but is segregated by elevation. The checkerboards are formed by each of these taxa with *P. melanura*, in the Solomons found only on the isolated island of Nissan plus several islets near Buka, Bougainville, and Shortland in the Bukida group (Mayr and Diamond 2001). *Pachycephala melanura* does not qualify as a supertramp by our statistical test, but Diamond (1975) and Mayr and Diamond (2001) designate it as a supertramp, and it would doubtless qualify statistically if avifaunas of many small islands it inhabits had been tabulated by Mayr and Diamond (2001). The montane habitat of *P. implicata* implies its checkerboard with *P. melaneura* is caused by habitat differences, not competition. However, the fact that islets occupied by *P. melanura* are close to large islands occupied by *P.* [*pectoralis*] suggested to Mayr and Diamond (2001) that competitive exclusion operated between these two species. Two considerations, both noted by Mayr and Diamond (2001), suggest that other factors may be at play.

First, even in allopatry, *P.* [*pectoralis*] does not use very small islands and *P. melanura* does not use large ones, a point also made by Lomolino (1999) for the Bismarck Archipelago. Mayr and Diamond (2001) suggest that this observation may imply the habitat preferences evolved in allopatry. If this were so, it would cast doubt on whether the Solomons checkerboard is competitively driven. Second, Mayr and Diamond (2001) believe *P. melanura* relatively recently invaded the Solomons and has not yet had time to spread beyond the Shortlands region. In that case, the checkerboard would at least partly reflect differing colonization histories. *Pachycephala melanura* has also never been seen flying over water (Mayr and Diamond 2001), again suggesting that, as a recent arrival in the Solomons, it may still be spreading. In Australia, Gotelli et al. (1997) found these species co-occurring less frequently than expected for individual colonization. However, their figure 6a shows the two taxa to be almost allopatric, with large ranges overlapping only in a small section of the northeast coast.

The two *Aplonis* checkerboards both include the supertramp *A.* [*feadensis*], which occupies small outlying islands plus Rennell. Neither of the two species exclusively distributed with it, *A. grandis* and *A. brunneicapilla*, is found on Rennell or any outlying island, so the checkerboard distributions also constitute regional allopatry. Why *A.* [*feadensis*] is a supertramp and is not found on other islands is uncertain; it is highly vagile. Mayr and Diamond (2001) suggest competition with *A. cantoroides* may exclude it from some islands, although these two species coexist on Rennell.

Rhipidura has six species in the Solomons, none supertramps. Of the fifteen possible two-species combinations, three form checkerboards. For all three checkerboards, the species occupy different island groups. *Rhipidura fuliginosa*, found only in the mountains of San Cristobal, forms checkerboards with *R. malaitae*, found only in the mountains of Malaita, and with *R. cockerelli*, found on Malaita and most of the big islands of Bukida and New Georgia. The third checkerboard is between *R. malaitae*, a montane endemic of Malaita, and *R.* [*spilodera*], found only on Bougainville and Guadalcanal in Bukida plus Rennell and San Cristobal. In sum, at least from the distributional data, history is as plausible as competition as an explanation for these checkerboards.

Last among genera with checkerboards, *Monarcha* in the Solomons consists of three taxa (*M. cinerascens*, *M.* [*melanopsis*], and *M.* [*manadensis*]). *Monarcha cinerascens*, a supertramp, coexists with neither of the other taxa. It occupies all nine outlier islands plus the small, isolated island of Borokua between the Bukida and New Georgia island groups, as well as small islets near major islands of the Bukida group, but not large islands. The other two taxa coexist on many large islands in all the other groups except Rennell. Mayr and Diamond (2001) point to competition with *M.* [*melanopsis*] as the likely reason *M. cinerascens* is a supertramp. Although it has not been seen flying over water (Mayr and Diamond 2001), surely *M. cinerascens* can reach at least the major Bukida islands, given its presence on nearby islets. Thus its colonization history cannot explain the checkerboards. However, *M. cinerascens* is a small-island specialist even where *M.* [*melanopsis*] is absent, as in the Bismarcks, so habitat preference may account for these checkerboards. The systematics of *M.* [*melanopsis*] and *M.* [*manadensis*] need revising, as the former is paraphyletic and the latter polyphyletic (Filardi and Smith 2005). Depending on the ranks of component taxa, the number of checkerboards with *M. cinerascens* may greatly exceed two. However, the habitat differences will remain.

Of the 22 congeneric checkerboards, then, 17 consist of pairs of taxa occupying different island groups, while for one (in *Accipiter*), historical dispersal limitation appears to account for the checkerboard even though the species are in the same group (table 9.5). For one checkerboard (in *Pachycephala*), a habitat difference seems to be the cause, while in the remaining three (one in *Pachycephala* and two in *Monarcha*), one taxon occupies very small islands and the other larger islands, and in each of

TABLE 9.5
Proposed Factors Explaining Congeneric Checkerboard Distributions of Solomon Islands Birds

Genus	*CH*	*DG*	*HI*	*HA*	*LS*
Accipiter	5	4	1		
Aplonis	2	2			
Monarcha	2				2
Pachycephala	2			1	1
Rhipidura	3	3			
Zosterops	8	8			
Totals	22	17	1	1	3

Notes: CH=number of checkerboards, DG=different island groups, HI=historical (other than different island groups), HA=habitat difference, LS=one species on small islands, the other on larger islands.

these instances the small-island specialist is still restricted to small islands in other regions where the other taxon is absent.

Among multigenus guilds defined by Diamond (1975), only one, the gleaning flycatchers, has checkerboard distributions in the Solomon Islands. Of the seven species in this guild, one (*Monarcha cinerascens*) is a supertramp by our statistical definition, while *Pachycephala melanura* is also classed as a supertramp by Mayr and Diamond (2001). If we exclude both of these species, there are no checkerboards. If we exclude only *M. cinerascens*, there are five. These all consist of *Pachycephala melanura* with another taxon: *P.* [*pectoralis*] and *P. implicata* as discussed above, plus *Monarcha* [*melanopsis*], *M.* [*manadensis*], and *Myiagra* [*rubecula*]. As observed above, *M.* [*melanopsis*] and *M.* [*manadensis*] are both found on many large islands in all groups except Rennell. *Myiagra* [*rubecula*] is also found on many large islands in those groups, and also on Rennell. We pointed out above that *P. melanura* inhabits small islands even outside the Solomons (including outside the range of *P.* [*pectoralis*], *Monarcha* [*melanopsis*], and *Myiagra* [*rubecula*]), it has also not been seen flying over water, and it is a recent arrival in the Solomons, possibly expanding its range there (Mayr and Diamond 2001). Therefore, both habitat preferences and the history of colonization may at least partly explain these checkerboards.

In sum, looking specifically at the subset of species pairs in which competition would be most expected, we found that no exclusively distributed pairs quite conformed to the checkerboard model and that the exclusive patterns might be explained by a combination of colonization history and timing, behavioral traits (especially propensity to fly over water), and habitat preferences. For three congeneric bird checkerboards in the Bismarck archipelago, Lomolino (1999) suggested a combination of interspecific interactions, habitat preferences, and propensity for overwater flight as causes, while Collins et al. (in preparation), examining all the congeneric and multigenus-guild checkerboards in the Bismarcks, found colonization history, habitat preferences, and propensity for overwater flight to be possible explanations for most of them. Gotelli et al. (1997), studying congeneric checkerboards of mainland Australian birds (including several genera found in the Solomons), saw a major role for habitat preferences and found competition to be unimportant.

Many Solomons checkerboards include one species found exclusively or almost exclusively on small islands, including supertramps. Some may be only on small islands because they are excluded elsewhere by competition. Other explanations are possible, however. They may prefer habitats disproportionately present on small islands (cf. Simberloff and Martin 1991). Holyoak and Thibault (1978) suggest that predation by *Accipiter* hawks may restrict one supertramp, *Ducula pacifica*, to small islands. That competition is unlikely to be the only factor restricting at least some of these supertramps to small islands is suggested by the fact that *Monarcha cinerascens*, *Aplonis* [*feadensis*], and *Pachycephala melanura* all occupy only small, remote, or recently volcanically disturbed islands throughout their ranges, including beyond the Solomons, even when possible competitors are absent.

Finally, the same caveat must be raised with respect to assembly rules in the Solomons as was raised with the respect to the equilibrium theory: anthropogenic extinction must have been staggering, but most of it cannot be specified. The overall picture with respect to checkerboard distributions might not have changed much, especially as regards restriction of species to particular island groups. However, it is also possible that some checkerboards have been created by undocumented anthropogenic extinction. Additionally, the possibility of incomplete censuses noted above should be borne in mind; some absences may be artifacts, and rectifying them would be more likely to obliterate checkerboards than to generate them.

Taxon Cycle

Classifying species by range, subspecific differentiation, and habitat use, Greenslade (1968) saw distributions of land and freshwater birds of the Solomons as reflecting a three-step process in accord with the taxon cycle of Wilson (1959, 1961) for Melanesian ants. First is expansion of a species to form a continuous range encompassing at least the major islands of groups 1–4 described above. This expansion is followed by range fragmentation, accompanied by extinction on small and/or isolated islands. As examples of second-stage species, Greenslade (1968) suggested *Pachycephala* [*pectoralis*] and *Rhipidura cockerelli*, both discussed above. The second stage also entails evolution of island endemics. The final stage consists of a highly fragmented, contracted distribution (often into mountains of the largest islands), presumed to have arisen by substantial extinction even on major islands. Noteworthy in this scenario are the assumption of much undocumented extinction in the second and third stages and the suggestion that restriction of many third-stage species to montane habitats may be due to competition at lower elevations. Greenslade (1968) did not elaborate on the causes of the hypothesized extinctions on small islands during the second stage but did refer to the ongoing extinction hypothesized by MacArthur and Wilson (1963).

Independently of Greenslade (1968), Mayr and Diamond (2001) also attempted to match bird distributions in the Solomon Islands, and Melanesia generally, to the taxon cycle of Wilson (1959, 1961), dividing the avifauna into temporal, evolutionary stages. However, the stages correspond only partially to those proposed by Greenslade (1968) (and by Wilson [1961]), and there is one major difference. The geographic distributions and their relationship to endemicity play a key role in assignment to stages, as for Greenslade (1968), but the habitat affiliations are generally not as strongly related to stage, in their view.

Unlike Greenslade (1968) and Wilson (1961), Mayr and Diamond (2001) see dispersal ability as characteristically differing among species in different stages and having many distributional consequences. Perhaps "dispersal propensity" describes the trait Mayr and Diamond (2001) stress more aptly than does "dispersal ability," as they focus on behavioral explanations rather than physiological and anatomical features. Mayr and Diamond (2001) also point to undocumented extinctions, especially on small islands, as key features of the later stages, but, at least with respect to the taxon cycle, they attribute these extinctions, and the resulting distributional patterns, to the loss of dispersal propensity, arguing that populations occasionally go extinct, but only vagile species "capable of reversing those extinctions" (p. 292) can persist on many islands or on small islands. Just as did Greenslade (1968), Mayr and Diamond (2001) suggest that some late-stage montane species are restricted to upper elevations by competition, an argument buttressed most forcefully by elevational distributions of species with some populations montane and others not, depending on co-occurring species (e.g., *Zosterops ugiensis*, discussed above).

For both Greenslade (1968) and Mayr and Diamond (2001), then, bird distributions in the Solomon Islands result from a cyclic process operating on an evolutionary time scale. The factors driving the process differ somewhat in the two conceptions, but in each, extinctions in the later stages of the cycle play a key role, including extinctions on both large and small islands. Neither proposal discusses evidence for such extinctions, though Mayr and Diamond (2001) call for an expanded search for fossil evidence to determine the extent and causes of past extinctions. Their preliminary assessment is that the hecatomb afflicting other Pacific islands with the arrival of humans may not have been as severe in northern Melanesia because of the presence of native predatory mammals and reptiles. Steadman (2006), by contrast, emphasizes the wave of anthropogenic extinctions and absence of evidence for nonanthropogenic ones.

Discussion

Birds of the Solomons

Our examination of the distributions of these birds, and of evidence and speculation regarding distributional changes, suggests that the processes regulating community composition on large islands may differ greatly from those operating on small ones. With respect to the equilibrium theory in the Solomons, Gilpin and Diamond (1976) probably erred in considering large and small islands together. For large islands in the Solomons, there is virtually no evidence for nonanthropogenic extinction over a time frame of millennia (Steadman 2006). This is not to say that extinctions never occur, or even that no equilibrium richness obtains, but if we are dealing with rare events over time scales of millions of years, it is unlikely that the stochastic demography originally envisioned as mainly driving the dynamism would be important, or that the original assumption of unchanging physical characteristics would be valid. For birds on these large islands, the dynamic equilibrium model may not be appropriate.

By contrast, birds of the small islets near the major islands of each group might operate as envisioned by the original equilibrium theory, though there are insufficient data on turnover to know. One potential disqualifier would be if populations on such islands are insufficiently isolated for persistence to result mainly from in situ reproduction rather than continuing recruitment from the mainland (the "rescue effect" of Brown and Kodric-Brown [1977]). One of the earliest sources of criticism of the applicability of the equilibrium theory was concern about this very point—do individuals in the various island populations constitute separate populations or are they just parts of one widely ranging population, what might now be termed a metapopulation (references in Hanski and Simberloff 1997)?

In the original model, for the equilibrium to be dynamic, another requirement is that extinction must occur, and it must be a consequence of equilibrium demographic processes and perhaps interactions of members of the species pool rather than change in the island environment. Because many small islands in the Solomons are uninhabited, the massive anthropogenic changes found on large islands might not be as severe, and introduced species may not be as numerous. Steadman (2006) describes a 7 km^2 forested island in the Marianas that appears unscathed by humans aside from the presence of Pacific rats, which still contains all bird species recorded from prehistoric sites except for two rails, and which might be able to support populations of other birds. Perhaps islets in the Solomons exist that are also relatively unaffected by humans, are small enough that extinction occasionally occurs, and are sufficiently remote that propagules rarely arrive.

If there were turnover on such small islands, this would clearly be in the spirit of MacArthur and Wilson's conception of turnover, even if competition as envisioned by the assembly rules accounted for at least some of it, as noted above. One would also want a substantial proportion of the species to engage in the turnover. A common knock against the wide applicability of the dynamic equilibrium model is captured by Schoener and Spiller (1987): "in general turnover involves only a subset of fugitive populations, with many others, mostly much larger, being permanent" (p. 477; cf. Simberloff 1976, Whittaker and Fernández-Palacios 2007, Schoener, this volume).

Such turnover could also be consistent with the assembly rules as originally posited by Diamond (1975). He was agnostic about how dynamic the competitive checkerboards are but often cited birds with sufficient dispersal ability to reach many islands from which they are absent, suggesting that such species must frequently arrive on islands occupied by their competitors, only to fail to establish or to suffer quick extinction. Small islands might be a far more likely locus than the large ones of the Solomons for competition to play a decisive role in presence and absence, as required by the assembly rules, and perhaps for a new arrival to persist and the resident to disappear rather than vice versa. The examples cited above from Mayr and Diamond (2001), of species they feel are competitively incompatible but can coexist on large islands by virtue of elevational separation, come immediately to mind: smaller islands would offer fewer opportunities than large ones for habitat partitioning not only in terms of elevational gradients but in other ways as well. Historical factors would also play less of a role on small islands near enough to large ones that immigration is not very rare.

The taxon cycle as envisioned by both Greenslade (1968) and Mayr and Diamond (2001) encompasses both large and small islands, but the evolution driving the cycle in both conceptions occurs on much larger islands than those we suggest may fit the equilibrium theory and the assembly rules. Avifaunas of small islands in the taxon cycle are epiphenomena of processes (evolution of morphology, habitat preference, and dispersal behavior) occurring on larger islands. Thus, should turnover and/or competitive exclusion be demonstrated on small islands in the Solomon archipelago (say, those smaller than 50 km^2), they would be consistent with the cycle but not strong evidence for it.

Both the equilibrium theory and the taxon cycle posit extinctions. The equilibrium theory envisions these as being relatively frequent, albeit less so the larger the island. In the taxon cycle, on small islands extinctions may be relatively rapid; Greenslade (1968) relates them to equilibrium turnover. On large islands, however, these take much longer, associated as they are with the evolution of island endemics and, for Mayr and Diamond (2001), behavioral evolution. Extinctions do not play such a major role in the assembly rules (except, perhaps, for rapid extinction of immigrants that form forbidden combinations), although Mayr and Diamond (2001) invoke extinctions in partial explanation for the *Zosterops* checkerboards and suggest that undocumented extinctions occurred among members of other checkerboards. However, as noted above, there is no direct evidence in the Solomons for any of these extinctions except on Buka. The geographic distributions among the islands themselves can be seen as indirect evidence of extinction, but it seems tautological to use the distributions to support theories that aim to explain the distributions.

Evidentiary Needs for Birds of the Solomons

What other sorts of evidence, in addition to many more fossils from many more sites, could one marshal to support claims of nonanthropogenic extinction? This same concern was voiced early in the most detailed attempt to apply the taxon cycle model to birds, by Ricklefs and Cox (1972) for land birds (exclusive of raptors) of the West Indies, especially the Lesser Antilles. The largest of these islands are much smaller than the largest of the Solomons, with areas in the range of that of Buka. Ricklefs and Cox (1972) hypothesized that extinctions occur on average every few million years on larger islands and much more frequently on smaller ones (cf. Ricklefs and Bermingham 1999; Ricklefs, this volume). They also worried about the confounding effects of anthropogenic extinction, arguing that at least a few documented recent extinctions in the Lesser Antilles cannot be attributed to humans. In response to a battery of criticisms by Pregill and Olson (1981), Ricklefs and Bermingham (1999) (cf. Ricklefs and Bermingham 2002) undertook molecular phylogenetic analyses of West Indian birds that supported many aspects of the hypothesized taxon cycle in the Lesser Antilles and adduced further evidence that anthropogenic impacts and late Pleistocene climatic events did not lead to so much extinction that evidence of a taxon cycle would be obliterated. They also showed that species restricted to few islands, interpreted as in the late (declining) phase of the taxon cycle, were in fact much older than other species. They observed that this fact and the fact that some assigned late-stage species have gaps between the few occupied islands are consistent with the hypothesis of extinction on some unoccupied islands. The argument that occupancy gaps represent extinction is identical to that of Mayr and Diamond (2001), but taxon ages constitute a different sort of evidence. The inference of higher extinction rates on small islands derives from the observation that older taxa also tend to be absent from small islands (Ricklefs and Bermingham 2004; Ricklefs, this volume).

The first item in the wish list of Mayr and Diamond (2001) for additional data to elucidate the distributional trajectories of northern Melanesian birds is molecular phylogenetic research, totally lacking as they published their book. Such research, combined with remedying the striking lack of avian fossil data for the Solomons, would go a long way toward testing claims that current bird distributions there have resulted from a taxon cycle. It would be striking to see if the pattern of older species having patchier distributions and being restricted to larger islands holds there as it does in the Lesser Antilles. Phylogenetic research could also aid in testing whether the timing of colonization (e.g., in *Pachycephala*) or of allopatric speciation (e.g., in *Zosterops*) can explain checkerboards. Molecular evidence might also determine whether populations on small islands are sufficiently isolated to fit the equilibrium model. Such research has just begun for Solomons birds (Filardi and Smith 2005, Smith and Filardi 2007).

Relevance of Solomons Birds to the Three Theories

That Solomon Islands bird distributions, at least on the islands for which data are available and at least since the late Pleistocene, appear not to be determined by the mechanisms envisioned by the dynamic equilibrium theory does not mean the theory does not accurately depict other systems. Similarly, that the checkerboard distributions of birds in the Solomons today do not seem to reflect the processes envisioned in the assembly rules does not mean the rules do not apply elsewhere.

Though the equilibrium theory seems not to apply to many systems (references in Whittaker and Fernández-Palacios 2007; cf Schoener, this volume), it has been enormously fruitful, forcing us to think in new ways about the determinants of extinction and diversity (Brown 1981, Haila and Järvinen 1982, Simberloff 1984, Haila 1986). Among other things, the theory led to (1) consideration of what sets minimum viable population sizes (Shaffer 1981, 1987) and the fate of small populations; (2) the concept of relaxation of insular biotas with changing conditions such as area reduction (Diamond 1972, Faeth and Connor 1979); (3) increased attention to the multiple possible contributors to the species-area relationship (Connor and McCoy 1979); and (4) development of metapopulation ecology, which partially superseded equilibrium theory in both ecology and conservation biology (Hanski and Simberloff 1997, Hanski, this volume). However, for large islands with mean time to extinction of species in the range of 10^6 years, we do not feel the equilibrium theory will be fruitful, as we suggest above for the Solomons. Aside from the likelihood of changing environments, forces that might operate on this time scale (e.g., evolution, plate tectonics, bolides; cf. Ricklefs, this volume) are unlikely to yield any sort of testable equilibrium number of species. The birds of the Solomons may be a particularly difficult system for testing the equilibrium theory because of the human footprint and paucity of fossils. However, the same problems surely arise for many other biotas (Steadman 2006).

As for the assembly rules, in addition to generating controversy, they have contributed to a proliferating literature on and increased understanding of binary matrices, even beyond biogeography (e.g., Snijders 1991, Rao et al. 1996). In instances where there are more checkerboards than expected by matrix randomization (cf. Gotelli and McCabe 2002), there is rarely detailed examination of the distributions or other research to elucidate the cause. This should be a fertile research area and will encompass a wide range of ecological and evolutionary approaches.

The number of systems explored from the standpoint of a taxon cycle pales compared to the many applications of the equilibrium theory and the assembly rules. However, the use of molecular techniques, opening a new avenue of inference about ages of taxa, may spur research on taxon cycles. There are other sorts of taxon cycles than that proposed by Wilson (1959, 1961). For instance, using phylogenetic reconstruction, Losos (1990) was able to refute a taxon cycle that predicted a particular direction of morphological change. Molecular research can also shed light on the possibility of endogenous forces leading to dynamism and extinction (e.g., parasite-host interactions) and singular events such as mass extinctions; Ricklefs (this volume) provides examples for Lesser Antillean birds.

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