species did not affect one another is high. For A. novaehollandiae, a strong disperser (Mayr & Diamond, 2001) on 15 islands including New Ireland outliers, there is no plausible historical geographic explanation for the checkerboard with A. rufitorques, but the null probability of a checkerboard by a two-species balls-in-boxes model even without an interaction is 0.52.

## 2. Ducula

Similarly, all four checkerboards in the genus Ducula include the supertramp D. pacifica, found only on five small islands in the St. Matthias and Northwest groups. Three of the four species with which it forms checkerboards (D. myristicivora, D. rufigaster, and D. pinon) are not found in these island groups. As most colonization of the Bismarcks appears to have proceeded from New Guinea through the island chain towards the St. Matthias and Northwest groups, which are colonized last (Mayr & Diamond, 2001), it is not inconceivable that these three species simply have not reached these islands yet. Holyoak & Thibault (1978) argue that D. pacifica is restricted to small islands because these lack predatory hawks; in the Bismarcks, D. pacifica occupies no islands that contain an Accipiter hawk. The fourth checkerboard is between D. pacifica and D. bicolor, which is found in the Northwest group, but on Manus and Nauna, 160 km east of the islands occupied by D. pacifica. When D. pacifica is excluded from the analysis, the checkerboard score for this genus is not significant (P = 1.0). The key to understanding the Ducula checkerboards in the Bismarcks therefore may lie in historical biogeography plus determining what restricts D. pacifica to small or remote islands.

### 3. Myzomela

Of the 10 checkerboards in the genus Myzomela, four include M. pulchella, a sedentary, non-water-crossing species restricted to mountains of New Ireland (Mayr & Diamond, 2001). Three of these checkerboards consist of M. pulchella plus species found only in the New Britain group (M. eques, M. cardinalis, and M. sclateri). At least for M. cardinalisit is plausible that historical geography explains the checkerboard, as this species is unusual in having invaded the Bismarcks from the east and may not have had time to spread further within the archipelago (Mayr & Diamond, 2001). Although M. sclateri is highly vagile (a supertramp by the classification of Diamond, 1975), for the checkerboards between M. pulchella and both M. eques and M. sclateri, it is possible that M. pulchella has not yet had time to reach New Britain. It is also noteworthy that M. pulchella, M. cardinalis, and M. eques occur on no more than two islands each, yielding a high null probability that each pair of them would form a checkerboard. The fourth checkerboard of M. pulchella is with the supertramp M. lafargei, which occurs on many islands in the St. Matthias and Northwest island groups, on several small, volcanically disturbed islands west of New Britain, and on Tingwon, the westernmost island in the New Ireland group. No other Myzomela occurs in the St. Matthias or Northwest island group, and M. lafargei is involved in three other of the 10 Myzomela checkerboards. When M. lafargei and M.

existence of largely allopatric ranges that may reflect barriers to dispersal between island groups.

### 4. Rhipidura

The two checkerboards in the genus Rhipidura each include R. rufifrons, a species restricted to two islands in the Northwest group. Neither of the other species in the checkerboards (R. Ieucophrys and R. rufidorsa) is found in the Northwest group—the species are regionally allopatric. As the Northwest group is believed, for most species, to be the last colonized in the archipelago (Mayr & Diamond, 2001), it is possible that the latter two species simply have not reached the Northwest islands yet.

# 5. Tyto

The checkerboard formed by the two species of Tyto may also reflect history. Tyto novaehollandiae, a highly sedentary species not seen crossing water (Mayr & Diamond, 2001), is found only on New Britain and Manus (in the Northwest group). This distribution is hypothesized to reflect independent colonizations from New Guinea, and the species is believed to have disappeared from other islands in the New Britain group because they are now too small (Mayr & Diamond, 2001). Tyto alba, by contrast, is believed to have recently colonized Long (volcanically defaunated in the 17<sup>th</sup> century, but geographically in the New Britain group) from New Guinea and Tanga (a small island east of New Ireland and adjacent to the Solomon Islands) from the Solomons (Mayr & Diamond, 2001).

# 6. Pachycephala

The Bismarcks harbour two morphologically and ecologically similar species of Pachycephala:

does not qualify statistically. Diamond (1975; Mayr & Diamond, 2001) argues that M. nigrirostris competitively excludes M. mackinlayi from larger islands. While competitive exclusion is a possible explanation, the pattern may also be influenced, at least in part, by their recent, largely allopatric speciation and the fact that M. nigrirostris is the younger invader and may not have had time to reach other islands (Mayr & Diamond, 2001). Mayr & Diamond (2001) also note that, in regions off the New Guinea coast where M. nigrirostris is alone, it still eschews small islands, and they suggest this indicates that habitat differences may have arisen even before these species achieved regional sympatry. Lomolino (1999) also notes this habitat difference.

# 8. Zosterops

Two

very small ones. Because A. feadensis also exists in the Solomon Islands, it seems unlikely that its distribution in the Bismarcks is restricted by dispersal barriers within the archipelago. Aplonis feadensis, is endemic to the Bismarck and Solomon archipelagoes, is found only on small, depauperate, or remote islands throughout its range, and this fact, combined with the predominance of larger islands among those occupied by A. metallica,

Appendix S2 Intraguild checkerboards of birds in the Bismarcks and possible explanations.

The cuckoo-dove guild contains the two previously discussed congeners, Macropygia nigrirostris and M. mackinlayi [which Mayr & Diamond (2001) consider a supertramp], plus M. amboinensis and one species in the genus Reinwardtoena. The sole checkerboard is between M. nigrirostris and M. mackinlayi. As noted above, both historical factors and possible habitat differences may explain this checkerboard.

The gleaning flycatcher guild has three checkerboards, all including Pachycephala melanura, a sedentary supertramp according to Mayr & Diamond (2001). Above we suggested that habitat preferences may at least partially explain the checkerboard with its congener, P. pectoralis, which is found on larger islands than those occupied by P. melanura. The other intraguild checkerboards are P. melanura with two other quite sedentary species (Mayr & Diamond, 2001) both found primarily on larger islands, Monarcha manadensis and M. chrysomela.

The myzomelid-sunbird guild has 11 checkerboards; ten of these consist of pairs of Myzomela congeners. Above we noted that all but two of these include one species classed as a supertramp by Mayr & Diamond (2001), and either historical biogeography or the statistics of small numbers of occurrences can help explain all of them (including

Lastly, the fruit-pigeon guild has ten checkerboards. Four of these include the supertramp Ducula pacifica with congeners, and above we noted that historical factors could contribute to all of these and that D. pacifica may be restricted to small islands by predation. Four other intraquild checkerboards consist of D. pacifica plus species of Ptilinopus: P. superbus, P. hyogaster, P. rivoli, and P. viridis. Historical geography may play a role in all of these. In the Bismarcks, D. pacifica occupies four islands in the Northwest group, but each is at least 160 km west of the main island of Manus. It also occupies Tench in the St. Matthias group, but this island is 60 km east of the main islands in the group, St. Matthias and Emirau. Ptilinopus superbus is found on several islands in the New Britain and New Ireland groups, but not in the St. Matthias group and only on Manus and an eastern satellite in the Northwest group. Ptilinopus hyogaster is also found on several islands in the New Britain and New Ireland groups, but not in the Northwest group and only on St. Matthias and Emirau in the St. Matthias group. Ptilinopus rivoli is not found in the Northwest or St. Matthias groups. Ptilinopus viridis arrived in the Bismarcks from the Solomon Islands and was restricted to two eastern outliers of New Ireland adjacent to the Solomons until c. 1989, when it colonized Manus (Mayr & Diamond, 2001). The final two checkerboards in this guild are between P. viridis and two other species of Ducula, D. rufigaster and D. pinon. The former rarely crosses water (Mayr & Diamond, 2001) and is restricted to New Britain and a satellite plus New Ireland and a western satellite, Dyaul. The latter is a montane species (Mayr & Diamond, 2001) restricted to New Britain and a satellite, plus New Ireland.

#### REFERENCES

- Diamond, J. M. (1975) Assembly of species communities. Ecology and evolution of communities (ed. by M.L. Cody and J.M. Diamond), pp. 342-444. Belknap Press, Cambridge, MA.
- Holyoak, D.T. & Thibault, J.-C. (1978) Notes on the phylogeny, distribution, and ecology of frugivorous pigeons in Polynesia. Emu, 78, 201-206
- Lomolino, M.V. (1999) A species-based, hierarchical model of island biogeography.

  Ecological assembly rules: perspectives, advances, retreats (ed. by E. Weiher and P. Keddy), pp. 272-310. Cambridge University Press, Cambridge.
- Mayr, E. & Diamond, J. (2001) The birds of northern Melanesia: speciation, ecology, and biogeography. Oxford University Press, Oxford.
- Simberloff, D. & Collins, M.D. (2010) Birds of the Solomon Islands: the domain of the dynamic equilibrium theory and assembly rules, with comments on the taxon cycle. The theory of island biogeography revisited (ed. by J.B. Losos and R.E. Ricklefs), pp. 237-263. Princeton University Press, Princeton, NJ.