

Speciation and endemism under the model of island biogeography

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Abstract. Speciation has been considered as a primary process contributing to species diversity, but its contribution to the diversity of local communities has not been fully appreciated. Based on the theory of classic island biogeography, we derived a model for the number of endemic species as a function of the processes of immigration, speciation, and extinction. The model shows that species endemism on an island is proportional to speciation rate but decreases with the sum of immigration and extinction rates (i.e., the species turnover rate). The model predicts that the contribution of immigration to species richness in local communities decreases with time, while the contribution of speciation to local richness increases with time. It further shows that only when the speciation rate is larger than half of the extinction rate can new species added from speciation eventually surpass those added from immigration. We conclude that, although the model leads to an apparent positive relationship between percentage endemism and species diversity on an island, this positive endemics–diversity relationship is not necessarily driven by speciation.

Key words: *Canary Islands; endemics–diversity relationship; extinction; Hawaiian Islands; immigration; island biogeography model; proportion of the endemics; speciation.*

INTRODUCTION

Speciation is a primary process contributing to species diversity (Brown and Lomolino 2000, Hubbell 2001), but its contribution to the diversity of local communities has not been fully appreciated, leading Heaney (2007) to call for the development of a comprehensive new model of biogeography, reunifying ecological and evolutionary biogeography. This is partly because speciation rate is often thought too small to have a significant impact in the ecological timescale. However, remote islands receive colonists too rarely, and immigration and speciation may occur on similar timescales (Whittaker et al. 2007, 2008). Furthermore, recent studies in island biogeography have shown that speciation occurs faster than previously thought and could be an important source of new species (Heaney 2000, Losos and Schluter 2000, Steppan et al. 2003). These findings suggest it is necessary to more closely examine the role of speciation in determining species richness and endemism of local communities, a problem that has not been well understood (Steppan et al. 2003).

Although theoretical study is still lacking, there are some empirical studies on this topic. Emerson and Kolm (2005a, b, 2007) documented positive relationships between endemics and the numbers of plants and arthropods of the Canary and Hawaiian Islands (i.e., endemics–

diversity relationship). They argued that this positive relationship indicates speciation drives species richness. However, this speciation-driven hypothesis has been challenged by several other studies (Cadena et al. 2005, Kiflawi et al. 2007, Pereira et al. 2007, Whittaker et al. 2007, Witt and Maliakal-Witt 2007, Birand and Howard 2008, Gruner et al. 2008). The point of debate is not so much about how speciation could promote species diversity (this is rather obvious) but about whether the endemics–diversity relationship is a reliable testimony of this speciation-driven hypothesis. The generation of the endemics–diversity relationship is probably much more complicated than speciation alone can predict because the rate of speciation depends not only on the total number of species on an island but also on the abiotic factors of the island. More importantly, migration and extinction would almost inevitably play critical roles in the endemism. Therefore, if the abiotic conditions varied dramatically across time, the potential maximum of species richness and endemism would also be altered, as pointed out by Whittaker et al. (2007). Recently, Whittaker et al. (2008) have developed a theoretical, graphical model based on the dynamic interactions of migration, speciation, and extinction. They showed that the endemics–diversity relationship alone was not sufficient to infer the speciation-driven hypothesis.

Although immigration, speciation, and extinction are the fundamental biogeographical processes, a formal island biogeographical model of the endemics–diversity relationship that ties these three processes has not yet

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been developed. In this study, we developed such a model by linking endemism with the rates of migration, extinction, and speciation. Our objective is to examine the effect of speciation on the endemics–diversity relationship of local communities. Our result shows that an apparent positive endemics–diversity relationship can be generated without invoking increasing speciation rate.

AN ISLAND-BIOGEOGRAPHY MODEL INCORPORATING SPECIATION, IMMIGRATION, AND EXTINCTION

The theory of island biogeography proposes that the number of species (S_t) on an island is determined by the equilibrium between immigration and local extinction (MacArthur and Wilson 1967). We will follow this theory to derive a relationship between the diversity of a local community and the diversity of the region that incorporates speciation, migration, and extinction. The local–regional relationship is considered to be determined by the interplay of both regional processes, such as immigration and extinction, and species interactions at the local scale, such as competition and predation (Ricklefs 2004, Hugueny et al. 2007). The relationship can take linear or curvilinear shapes (Caley and Schuller 1997, Hillebrand and Blenckner 2002, Kiflawi et al. 2003, He et al. 2005, Fox and Srivastava 2006). A linear relationship is often taken as evidence of weak or no competition in local communities, and curvilinear shape is considered to indicate competition, but such relationships can also arise entirely from the interaction of biogeographical processes or spatial sampling scale (Hillebrand and Blenckner 2002, He et al. 2005).

For the purpose of this study, a linear or curvilinear relationship will make no qualitative difference. Therefore, without loss of generality, we base our study on the model of Hugueny and Cornell (2000) that postulates immigration rate (I_t) and extinction rate (E_t) at time t , respectively, as

$$I_t = I_0 S_M \left(1 - S_{I(t)} / S_M\right) = I_0 \left(S_M - S_{I(t)}\right)$$

$$E_t = E_0 S_{I(t)}$$

where I_0 and E_0 are the probability per unit time that a species colonizes an island or goes extinct from the island, respectively, and are independent of the mainland species richness, S_M (Fox and Srivastava 2006). $S_{I(t)}$ is the number of species on the island at time t . The area effect on immigration, extinction and speciation is not explicitly included in the model but is implied in I_0 and E_0 .

In addition to the processes of immigration and extinction, the number of new species arisen from speciation at time t is

$$\lambda_t = \lambda_0 S_{I(t)} \quad (1)$$

where λ_0 is the speciation probability per unit time per species on an island.

Taking stock of the contributions of immigration, extinction, and speciation as described in the above, the

number of species in a local community at time $t + 1$, $S_{I(t+1)}$, is

$$\begin{aligned} S_{I(t+1)} &= S_{I(t)} + I_t - E_t + \lambda_t \\ &= I_0 S_M + S_{I(t)}(1 - I_0 - E_0 + \lambda_0). \end{aligned}$$

Solving this recurrent equation, we have

$$\begin{aligned} S_{I(t)} &= \frac{I_0 S_M [1 - (1 - I_0 - E_0 + \lambda_0)^t]}{I_0 + E_0 - \lambda_0} \\ &\quad + (1 - I_0 - E_0 + \lambda_0)^t S_{I(0)} \end{aligned} \quad (2)$$

where $S_{I(0)}$ is the number of local species at $t = 0$. If we assume $S_{I(0)} = 0$, Eq. 1 can be simplified as follows:

$$S_{I(t)} = \frac{I_0 S_M [1 - (1 - I_0 - E_0 + \lambda_0)^t]}{I_0 + E_0 - \lambda_0}. \quad (3)$$

It is obvious that $1 - I_0 - E_0 + \lambda_0 < 1$ (because speciation rate λ_0 is usually much smaller than immigration and extinction rates). Under this condition, we obtain the number of species at equilibrium ($t \rightarrow \infty$):

$$S_I = \frac{I_0 S_M}{I_0 + E_0 - \lambda_0}. \quad (4)$$

If speciation is negligible (in the case of $\lambda_0 \ll I_0$ or E_0), the equilibrium richness ($I_0 S_M / [I_0 + E_0]$) is the same as that of Hugueny and Connell (2000). It is clear from Eq. 4 that the local species diversity increases with speciation rate (λ_0): the larger the speciation rate, the more species in a local community (Fig. 1).

Although both immigration and speciation can increase species richness of local communities, their contributions to the increase of species richness vary over time. New species added from immigration decreases with time, while new species arising from speciation increases with time (due to the increase of local species richness). The time that speciation would produce more species than immigration does is

$$t \geq \frac{\ln[(2\lambda_0 - E_0)/(I_0 + \lambda_0)]}{\ln(1 - I_0 - E_0 + \lambda_0)}$$

for $\lambda_0 > E_0/2$. It indicates that when λ_0 is larger than half of E_0 , then new species added from speciation will eventually surpass those added from immigration, and the smaller the λ_0 , the longer it takes for the surpassing to occur (Fig. 2). Otherwise, the number of new species added from immigration is always more than that added from speciation. For example, at $I_0 = 10^{-3}$, $E_0 = 0.8 \times 10^{-3}$ and $S_M = 10000$, if $\lambda_0 = 0.8 \times 10^{-3}$, then after $t = 811$, speciation adds more new species than immigration does. If $\lambda_0 = 0.5 \times 10^{-3}$, the t will be 1439.

The increased species diversity resulting from speciation can be considered as endemic to the local community if emigration from local communities to regional communities is negligible at time t when the new species are just formed. Assuming that the single-island endemics are the result of anagenetic or cladogenetic changes, from Eq. 3, the proportion of endemics at time t in the island community (P_E) can be expressed as:

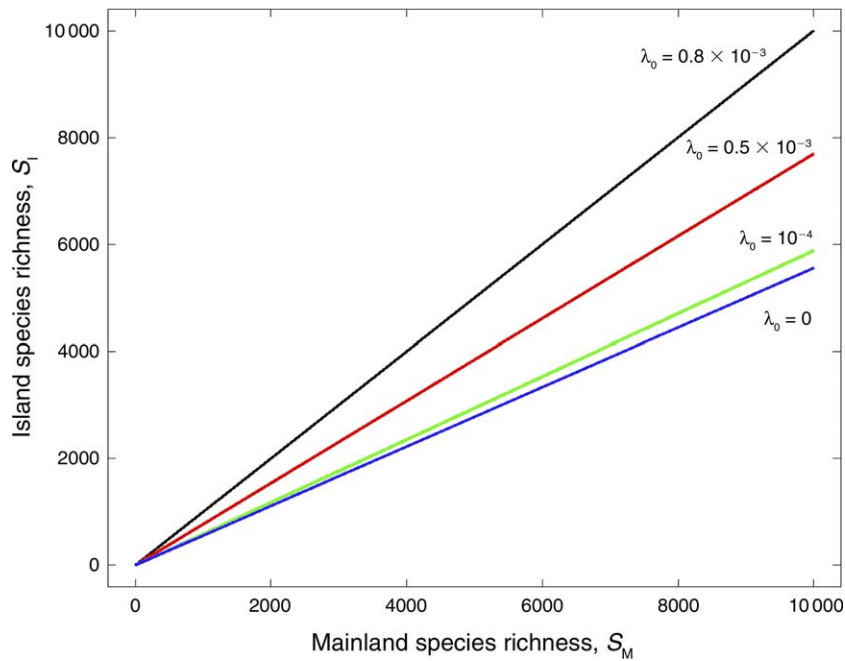


FIG. 1. Effect of speciation on the local–regional diversity relationship (Eq. 4). Speciation rate (λ_0) is varied from 0 to 0.0008. The immigration (I) and extinction (E) rates are kept constant at $I_0 = 10^{-3}$ and $E_0 = 0.8 \times 10^{-3}$. When $\lambda_0 = E_0$ (speciation and extinction rates are equal), S_I (number of species on as island) = S_M (number of species on the mainland).

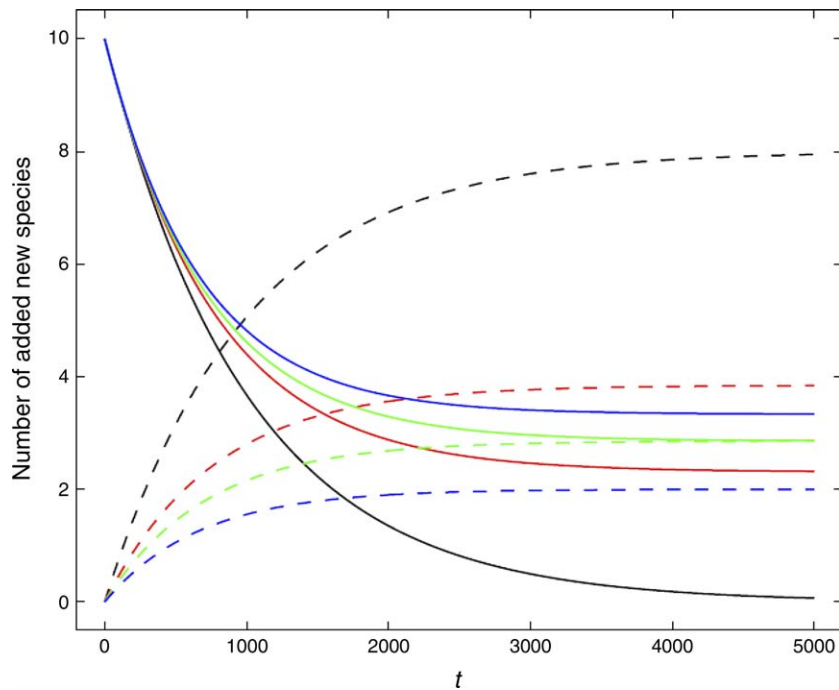


FIG. 2. New species added by immigration (solid lines) or speciation (dashed lines) per unit time, t , at $\lambda_0 = 0.8 \times 10^{-3}$ (black), 0.5×10^{-3} (red), 0.4×10^{-3} (green), and 0.3×10^{-3} (blue), under the conditions of $S_M = 10000$, $I_0 = 10^{-3}$, and $E_0 = 0.8 \times 10^{-3}$.

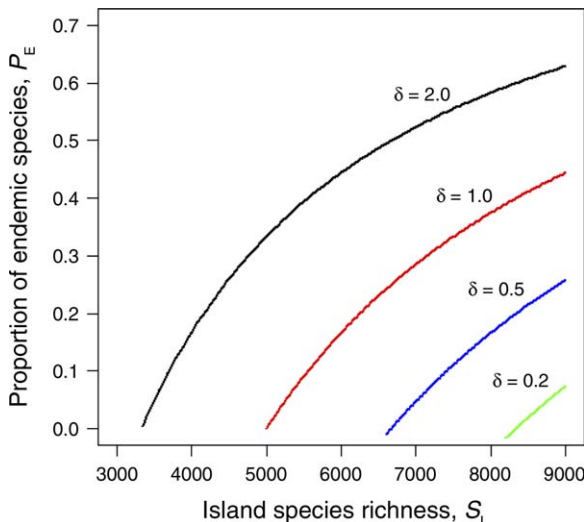


FIG. 3. Relationship between the proportion of endemics and local species richness in island communities, predicted from Eq. 6. The parameters of the model are $S_M = 10\,000$ and $\delta = E_0/I_0 = 2, 1, 0.5,$ and 0.2 .

$$P_{E(t)} = \left\{ \frac{I_0 S_M [1 - (1 - I_0 - E_0 + \lambda_0)^t]}{I_0 + E_0 - \lambda_0} - \frac{I_0 S_M [1 - (1 - I_0 - E_0)^t]}{I_0 + E_0} \right\} \times \left\{ \frac{I_0 S_M [1 - (1 - I_0 - E_0 + \lambda_0)^t]}{I_0 + E_0 - \lambda_0} \right\}^{-1} = 1 - \frac{I_0 + E_0 - \lambda_0}{I_0 + E_0} \frac{1 - (1 - I_0 - E_0)^t}{1 - (1 - I_0 - E_0 + \lambda_0)^t}.$$

At equilibrium ($t \rightarrow \infty$), the proportion of endemics is obtained as

$$P_E = 1 - \frac{I_0 + E_0 - \lambda_0}{I_0 + E_0} = \frac{\lambda_0}{I_0 + E_0}. \tag{5}$$

This equation indicates that, at equilibrium, endemism on an island is dependent on the rates of

speciation, immigration, and extinction but is independent of local diversity. The proportion of endemics is linearly related to speciation rate but is reciprocal to the turnover rate of species diversity (the sum of immigration rate from the mainland and extinction rate on the island). This model provides a theoretical explanation of the Pereira et al. (2007) result that lower extinction rates promote higher endemism, and higher immigration rates leads to lower endemism.

It is worthwhile to note that Eq. 5 may suggest a way to estimate speciation rate on an island from the endemism, and the immigration and extinction rates: $\lambda_0 = P_E \times (I_0 + E_0)$. This equation means that, given the rates of immigration and extinction, a high endemism in a community indicates a high speciation rate. However, a change in endemics does not necessarily mean it is driven by speciation because the change is also subject to the effect of I_0 and E_0 .

Although P_E in Eq. 5 is independent of the number of species on the island (S_I) and the mainland (S_M), an apparent effect of S_I and S_M on P_E can be easily shown. Solving λ_0 from Eq. 4 and substituting it into Eq. 5, we obtain

$$P_E = 1 - \frac{I_0}{I_0 + E_0} \frac{S_M}{S_I} = 1 - \frac{1}{1 + \delta} \frac{S_M}{S_I} \tag{6}$$

where

$$\delta = \frac{E_0}{I_0}.$$

Eq. 6 describes a positive relationship between percentage endemism and the local species diversity (Fig. 3). This apparent relationship was qualitatively observed by Emerson and Kolm (2005b) in plants and arthropods of the Canary and Hawaiian Islands.

DISCUSSION

Based on the theory of island biogeography, we have proposed an endemism model that incorporates immigration, speciation and extinction. Our model (Eq. 5) shows that percentage endemism is a function of the

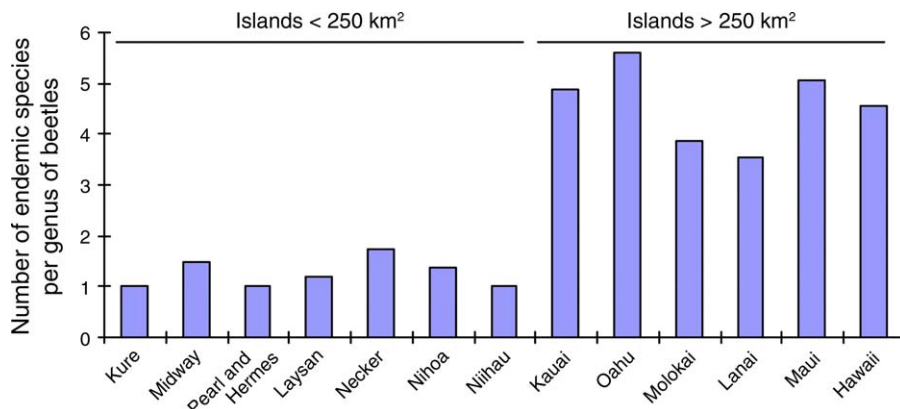


FIG. 4. Mean number of species per genus of endemic beetles on islands of the Hawaiian Islands.

rates of speciation, immigration, and extinction. All else being equal, species richness on an island increases with speciation rate. This result is consistent with the positive relationship between proportional endemics and species diversity as observed by Emerson and Kolm (2005*b*). However, this apparent relationship does not imply that endemics are begotten by local richness. As indicated by models (Eq. 4), species richness on an island is determined by immigration, extinction, and speciation, which in turn determine endemism (Eq. 5). Contrary to the speciation-driven hypothesis of Emerson and Kolm (2005*a, b*), where speciation rate is proportional to species diversity on an island, our model (Eq. 1) assumes the speciation rate λ_0 is a constant, independent of S_i , the number of species on an island.

The role of speciation is often neglected in explaining community assemblages because speciation is usually thought too slow to be significant, particularly in comparing it with the rates of immigration and extinction. While our model does not support the species-beget-species hypothesis, it does not diminish the role of speciation in enriching species diversity or the proportion of the endemics in communities. Recent studies have updated our knowledge that rapid speciation is possible and may not be uncommon in isolated habitats, such as volcanic ocean islands (Mendelson and Shaw 2005). Furthermore, it is possible that speciation could occur at the same timescale as colonization and extinction (Heaney 2000, Steppan et al. 2003). Molecular phylogenetic data have suggested within-community speciation can enrich local species diversity (Losos et al. 1998, Gillespie 2004, Emerson and Oromí 2005).

As the length of time increases, our model predicts that species richness of a local community will increase to an asymptote. In the meantime, the relative contribution of immigration to species richness decreases, but the importance of speciation increases (Fig. 2). The contribution of immigration and speciation to local species richness across time has been analyzed by Whittaker et al. (2007, 2008). Using graphic models, Whittaker et al. (2008) proposed that, when time is long enough, speciation will give rise to more species in remote oceanic islands than will immigration. Our model further shows that whether or not speciation adds more species than immigration does depends on the speciation/extinction ratio. When $\lambda_0 > E_0/2$, speciation will add more species than immigration does, and the larger the λ_0 , the shorter it takes for that to happen (Fig. 2). Otherwise, immigration will always add more species to a local community than speciation does.

From the model, we may deduce several results or predictions, which can be tested directly or indirectly. First, based on Eq. 5, percentage endemism is positively related to isolation, because immigration increases the number of non-endemic species coming from other islands or the mainland. This is consistent with the basic prediction of island biogeography (MacArthur and Wilson 1967) that islands near the mainland have a

low percentage of endemism, and it has been observed in a number of organisms. For example, percentage endemism for spiders in the genus *Tetragnatha* increased with the increase of isolation index (Gillespie and Roderick 2002). For vascular plants of remote Pacific islands, a positive relationship was also observed between isolation and proportion of endemics (Gillespie et al. 2008).

Second, percentage endemism is negatively related to extinction rate (Eq. 5). This is also consistent with previous predictions (Pereira et al. 2007). The prediction might be tested by comparing proportion of endemic species of different taxa with differential extinction rates in the same island system. Extinction rate is usually negatively related to population size, which is negatively related to body size of a species (White et al. 2007). Therefore, taxa of small body size may have a higher percentage endemism than taxa of large body size because the former may sustain for a longer period of time. Data have shown that the proportions of single-island endemism (SIE) in beetles and butterflies of small body size were 51.4% and 51.0%, respectively, while proportions of SIE in birds and mammals of large body size were 15.4% and 6.1%, respectively (data available online).⁴ In a recent study Reaka et al. (2008) also observed an inverse relationship between percentage endemism and species body size in Indo-West Pacific coral reef organisms.

Third, diversification is higher on large, remote islands than on small islands, and higher on older than on younger islands. Remote islands are “seeded” from the source, and the available propagule pool is relatively limited. Therefore, the ecological space is initially unsaturated, and speciation rate will generate significant radiations within a single genus (Gillespie 2004, Whittaker et al. 2008). Larger islands have higher habitat diversity and more species, or larger population sizes and low extinction rates. As the age of islands increases, more species are added by speciation, leading to more species per lineage, given all else is constant. This prediction can be tested by the number of endemic species per genus because species from the same genus form a lineage. We calculated the number of species per genus for endemic beetles on some of the Hawaiian Islands (data source available online).⁵ The mean number of species per genus of endemic beetles on islands $>250 \text{ km}^2$ was higher than that on islands $<250 \text{ km}^2$ (Fig. 4). In the Canary Islands, three older islands ($\geq 10 \times 10^6 \text{ yr}$) have more single-island endemic species of the genus *Tarphius* than two younger islands (1 and $2 \times 10^6 \text{ yr}$, respectively) have (Emerson and Oromí 2005). The two oldest Canary Islands have no species of the genus *Tarphius* due to the loss of habitats by erosion (Emerson and Oromí 2005).

⁴ (<http://hbs.bishopmuseum.org/hbsdb.html>)

⁵ (<http://www2.bishopmuseum.org/HBS/checklist/query.asp?grp=Arthropod>)

It is worth noting that speciation is unlikely constant on an island. Because speciation rate is affected by abiotic factors (Peck et al. 1999, Losos and Schluter 2000, Pereira et al. 2007), when those factors or the effects of their combinations have changed, speciation rate may also increase or decrease. For example, abiotic conditions of a volcanic island may experience dramatic changes, and speciation rate may vary across the development of the island (Gillespie 2004, Whittaker et al. 2007, 2008). It remains a challenge how we may take account of varying speciation rates in the island-biogeography model.

In conclusion, the present study proposes the first attempt to integrate speciation into the classic island-biogeography model to investigate the endemics-diversity relationship. Our model shows that percentage endemism is a function of the rates of speciation, immigration, and extinction. The model also predicts a positive relationship between the proportion of endemics and species richness, but this apparent relationship is not necessarily driven by speciation. Our model predicts that with the increase of time the relative contribution of immigration to species richness decreases, while the contribution of speciation increases. However, only when the speciation rate is larger than half of the extinction rate will the number of species added by speciation eventually surpass that added by immigration.

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LITERATURE CITED

- Birand, A., and D. J. Howard. 2008. The relationship between proportion of endemics and species diversity on islands: expectations from a null model. *Ecography* 31:286–288.
- Brown, J. H., and M. V. Lomolino. 2000. Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecology & Biogeography* 9:87–92.
- Cadena, C. D., R. E. Ricklefs, I. Jimenez, and E. Bermingham. 2005. Is speciation driven by species diversity? *Nature* 438: E1–E2.
- Caley, M. J., and D. Schuller. 1997. The relationship between local and regional diversity. *Ecology* 78:70–80.
- Emerson, B. C., and N. Kolm. 2005a. Is speciation driven by diversity? Reply. *Nature* 438:E2.
- Emerson, B. C., and N. Kolm. 2005b. Species diversity can drive speciation. *Nature* 434:1015–1017.
- Emerson, B. C., and N. Kolm. 2007. Response to comments on species diversity can drive speciation. *Ecography* 30:334–338.
- Emerson, B. C., and P. Oromi. 2005. Diversification of the forest beetle genus *Tarphius* on the Canary Islands, and the evolutionary origins of island endemics. *Evolution* 59:586–598.
- Fox, J. W., and D. Srivastava. 2006. Predicting local–regional richness relationships using island biogeography models. *Oikos* 113:376–382.
- Gillespie, R. G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* 303:356–359.
- Gillespie, R. G., E. M. Claridge, and G. K. Roderick. 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. *Molecular Ecology* 17:45–57.
- Gillespie, R. G., and G. K. Roderick. 2002. Arthropodes on islands: colonization, speciation, and conservation. *Annual Review of Entomology* 47:595–632.
- Gruner, D. S., N. J. Gotelli, J. P. Price, and R. H. Cowie. 2008. Does species richness drive speciation? A reassessment with the Hawaiian biota. *Ecography* 31:279–285.
- He, F., K. J. Gaston, E. F. Connor, and D. S. Srivastava. 2005. The local–regional relationship: immigration, extinction, and scale. *Ecology* 86:360–365.
- Heaney, L. R. 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography* 9:59–74.
- Heaney, L. R. 2007. Is a new paradigm emerging for oceanic island biogeography? *Journal of Biogeography* 34:753–757.
- Hillebrand, H., and T. Blenckner. 2002. Regional and local impact on species diversity—from pattern to processes. *Oecologia* 132:479–491.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Hugueny, B., and H. V. Cornell. 2000. Predicting the relationship between local and regional species richness from a patch occupancy dynamics model. *Journal of Animal Ecology* 69:194–200.
- Hugueny, B., H. V. Cornell, and S. Harrison. 2007. Meta-community models predict the local–regional species richness relationship in a natural system. *Ecology* 88:1696–1706.
- Kiflawi, M., J. Belmaker, E. Brokovich, S. Einbinder, and R. Holzman. 2007. Species diversity can drive speciation: comment. *Ecology* 88:2132–2135.
- Kiflawi, M., A. Eitam, and L. Blaustein. 2003. The relative impact of local and regional processes on macro-invertebrate species richness in temporary pools. *Journal of Animal Ecology* 72:447–452.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279: 2115–2118.
- Losos, J. B., and D. Schluter. 2000. Analysis of an evolutionary species–area relationship. *Nature* 408:847–850.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Mendelson, T. C., and K. L. Shaw. 2005. Rapid speciation in an arthropod. *Nature* 433:375–376.
- Peck, S. B., P. Wigfull, and G. Nishida. 1999. Physical correlates of insular species diversity: the insects of the Hawaiian Islands. *Annals of the Entomological Society of America* 92:529–536.
- Pereira, H. M., V. M. Proenca, and L. Vicente. 2007. Does species diversity really drive speciation? *Ecography* 30:328–330.
- Reaka, M. L., P. J. Rodgers, and A. U. Kudla. 2008. Patterns of biodiversity and endemism on Indo-West Pacific coral reefs. *Proceedings of the National Academy of Sciences (USA)* 105:11474–11481.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7:1–15.
- Steppan, S. J., C. Zawadzki, and L. R. Heaney. 2003. Molecular phylogeny of the endemic Philippine rodent

- Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. *Biological Journal of the Linnean Society* 80:699–715.
- White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323–330.
- Whittaker, R. J., R. J. Ladle, M. B. Araujo, J. M. Fernandez-Palacios, J. D. Delgado, and J. R. Arevalo. 2007. The island immaturity–speciation pulse model of island evolution: an alternative to the “diversity begets diversity” model. *Ecography* 30:321–327.
- Whittaker, R. J., K. A. Triantis, and R. J. Ladle. 2008. A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* 35:977–994.
- Witt, C. C., and S. Maliakal-Witt. 2007. Why are diversity and endemism linked on islands? *Ecography* 30:331–333.