ORIGINAL ARTICLE

Tree diversity on islands: assembly rules, passive sampling and the theory of island biogeography

K. C. Burns[1,2]*, Jenny Berg[1], Ada Bialynicka-Birula[1], Sabrina Kratchmer[1] and Katelyn Shortt[1]

[1]*Bamfield Marine Science Centre, Bamfield, BC V0R 1B0, Canada,* [2]*School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand*

ABSTRACT

Aim Species diversity is distributed heterogeneously through space, for reasons that are poorly understood. We tested three hypotheses to account for spatial variation in coniferous tree species diversity in a temperate island archipelago. The theory of island biogeography (ToIB) predicts that island area affects species diversity both directly (by increasing habitat diversity) and indirectly (by increasing abundances, which in turn reduce extinction rates). The ToIB also predicts that island isolation directly affects species diversity by reducing immigration rates. The passive sampling hypothesis predicts that island area and isolation both affect species diversity indirectly, by increasing and decreasing abundances, respectively. Community assembly rules (i.e. even partitioning of conifer abundances among islands) might also reduce tree species diversity beyond the core predictions of ToIB and the passive sampling hypothesis.

Location Barkley Sound, British Columbia, Canada.

Methods The abundances of eight coniferous tree species were quantified on 34 islands and two (1 ha) mainland plots. The predictions of the ToIB and the passive sampling hypothesis were tested using path analysis, and null models were used to test for abundance-based assembly rules and to further test the passive sampling hypothesis.

Results Path analysis showed that island area and isolation did not have direct, statistical effects on tree species diversity. Instead, both geographic variables had direct statistical effects on total tree abundances, which in turn predicted tree diversity. Results from several passive sampling null models were correlated with observed patterns in species diversity, but they consistently overestimated the number of tree species inhabiting most islands. A different suite of null models showed support for community assembly rules, or that tree species often reached higher abundances on islands that housed fewer heterospecific trees.

Main conclusions Results were inconsistent with the ToIB. Instead, patterns in tree diversity were best explained by a combination of stochastic (passive sampling) and deterministic (assembly rules) processes. Stochastic and deterministic processes are commonly considered to be exclusive explanations for island community structure, but results from this study suggest that they can work synergistically to structure island tree communities.

Keywords

Assembly rules, Barkley Sound, British Columbia, conifers, island biogeography, null model, passive sampling, species diversity.

*Correspondence: K. C. Burns, Bamfield Marine Science Centre, Bamfield, BC V0R 1B0, Canada. E-mail: kevin.burns@vuw.ac.nz

INTRODUCTION

Species diversity often increases with the extent and proximity of discrete habitat patches. These patterns are perhaps best illustrated in island archipelagos, where the number of species inhabiting islands increases with island area and declines with island isolation (see Whittaker & Fernández-Palacios, 2007). A variety of hypotheses have been developed to explain variation in species diversity among islands. However, their relative importance has yet to be fully resolved.

The theory of island biogeography (ToIB) predicts that several processes determine the number of species inhabiting islands with different geographic characteristics. First, MacArthur & Wilson (1963, 1967) predicted that island area affects species diversity directly, because larger islands contain a greater diversity of habitats, which enable them to support species with specialized habitat requirements. Second, they predicted that island area affects species diversity indirectly by regulating total population sizes, because larger populations are less susceptible to extinction. Lastly, they hypothesized that island isolation directly diminishes species diversity, because isolated islands experience lower rates of immigration from the mainland. The ToIB has been tested frequently, but the relative importance of direct (habitat) and indirect (total abundances) effects on species diversity remains contentious (Hortal et al., 2009).

Connor & McCoy (1979) hypothesized that island area influences species diversity only indirectly, by regulating the total number of individuals on islands. This 'passive sampling' hypothesis predicts that species diversity increases with island area in a process akin to randomly sampling individuals from a pool of colonists. Larger islands attract greater numbers of colonists, and as a result they accumulate more species because as the number of sampled individuals increases, so does the likelihood they will belong to different species. Island isolation might also have a similar indirect effect on species diversity, if islands located closer to the mainland attract greater numbers of colonists.

Competition theory predicts that when two species utilize limited resources in similar ways, competition will drive one species to local extinction (Gause, 1934). There is a long history of speculation that this process leads to mutually exclusive distributional patterns or 'assembly rules' (Gotelli & Graves, 1996; Weiher & Keddy, 1999; Gotelli, 2004). Previous work on assembly rules has focused on testing for 'checkerboard' patterns in species occurrences, whereby similar species replace one another among islands (Diamond, 1975). Fewer studies have tested for abundance-based assembly rules (Wilson et al., 1996), which might influence spatial patterns in species diversity. If species are more abundant on islands where other species are less abundant or absent, islands will house fewer species than expected based on the total number of individuals that they support.

We quantified the abundances of eight conifer species on 34 islands and 2 ha of mainland forest in a Canadian fjord to test the ToIB and the passive sampling hypothesis, and to test for evidence of abundance-based assembly rules. We used path analysis to determine the direct and indirect statistical effects of island area, island isolation and total tree abundances on tree diversity (species number). We also used a series of null models to further evaluate the passive sampling hypothesis, in addition to testing for evidence of assembly rules and how they might affect spatial patterns in tree diversity.

MATERIALS AND METHODS

All data were collected in Barkley Sound, British Columbia, Canada (48°80′ N, 125°20′ W), which is located on the west coast of Vancouver Island. Barkley Sound contains hundreds of small islands that were separated from the mainland (i.e. Vancouver Island) by rising sea levels after the Last Glacial Maximum (Fig. 1). However, sea-level changes have not been continuous (see Friele & Hutchinson, 1993). Approximately 5,000 years ago, sea-level changes slowed and then reversed. Consequently, the low-lying islands that formed the basis for this study were recently under water, and their biotic communities result from over-water dispersal. The dominant vegetation type in the region is coniferous forest, which is dominated by a modest number of wind-dispersed conifer species (see Klinka et al., 1989). Of the eight species encountered during sampling, only Taxus brevifolia produces fleshy cones that are dispersed by animals. Environmental conditions on these islands are somewhat different from those on the mainland, with islands having thinner soil horizons, more discontinuous conifer canopies and higher abundances of fleshy-fruited shrubs (Burns, 2004). Cody (2006) provides a detailed description of the environment, natural history and plant communities in the Barkley Sound archipelago.

Thirty-four small islands (range 25–1165 m^2) were visited either by boat or on foot during low tide and thoroughly searched for conifer trees. All trees with a measurable diameter at breast height (d.b.h.) were enumerated. The area of each island was measured by hand with field tape and defined as the total area housing contiguous populations of woody plants. Islands in Barkley Sound are densely grouped together, so measurements of isolation relative to the mainland (i.e. Vancouver Island) do not always accurately represent the minimum distances seeds must travel to reach islands. Islands larger than 3000 m^2 usually house large populations of coniferous trees (Cody, 2006). Therefore, island isolation was measured as the distance to the nearest landmass larger than 3000 m^2 using topographic maps (Canadian Hydrographic Service, 1994).

To characterize tree communities on the mainland, all conifer trees with a measurable d.b.h. were enumerated in two 100 × 100 m^2 plots located within 50 m of the shoreline on the mainland. One mainland plot was located in undisturbed, old-growth forest, while the other was located in secondary forest that was cleat-cut approximately a century earlier and is still undergoing succession. The area surrounding Barkley Sound contains two broad forest types: old-growth forests that have been relatively undisturbed by human activities; and forests at
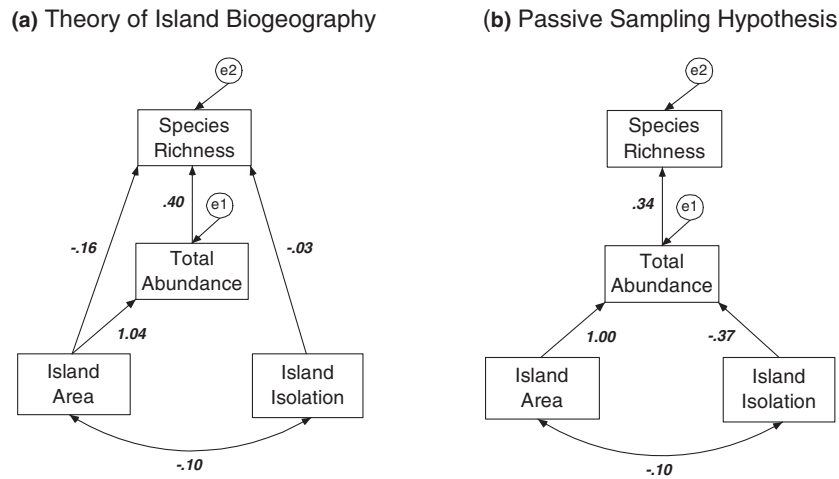
(a) Theory of Island Biogeography　　　**(b) Passive Sampling Hypothesis**

Figure 1 Path diagrams associated with (a) the theory of island biogeography and (b) the passive sampling hypothesis. The theory of island biogeography (ToIB) predicts that island area affects tree diversity directly (by increasing habitat diversity) and indirectly (by increasing abundances, which in turn reduce extinction rates), and that island isolation affects species diversity directly (by reducing immigration rates). The passive sampling hypothesis predicts that island area and isolation both determine tree species diversity indirectly, by increasing and decreasing total tree abundances, respectively. The covariance structure of the passive sampling path diagram provided a better description of the total observed covariance matrix than the path diagram for the ToIB. Numbers are path coefficients, and the circles labelled e1 and e2 refer to error terms ($n = 34$).

various stages of succession following clear-cut logging in the past century. Therefore, the two forest plots on the mainland are broadly representative of the conifer forests flanking the Sound.

Path analysis tests whether the covariance structure of a subset of relationships among a group of variables provides an adequate reflection of the total observed covariance structure (see Kohn & Walsh, 1994, for an application to island biogeography). The first step in path analysis is to formulate a hypothesized subset of relationships between variables, which is referred to as a path diagram. Two path diagrams were constructed to reflect the predicted relationships between island area, island isolation, total tree abundances and species diversity under the ToIB and the passive sampling hypothesis. The path diagram that we constructed for the ToIB predicts that island isolation has a direct statistical effect on tree species diversity, while island area has a direct statistical effect on tree species diversity and an indirect statistical effect mediated by total tree abundances (Fig. 1a). The path diagram that we constructed for the passive sampling hypothesis predicts that island area and isolation have only indirect statistical effects on species diversity mediated by total tree abundances (Fig. 1b).

Our path diagrams reflect the general characteristics of the ToIB and the passive sampling hypothesis. However, each theoretical framework has been interpreted in a number of different ways. Connor & McCoy (1979) originally hypothesized that larger islands randomly sample more individuals and therefore more species. However, island isolation could conceivably have an additional effect on the probability of intercepting dispersing propagules. Similarly, the effect of habitat on species diversity is sometimes treated separately from the ToIB (e.g. Ricklefs & Lovette, 1999; Morand, 2000).

However, it was discussed at length by MacArthur & Wilson (1967), so we decided to include it under the path diagram for ToIB.

We used a likelihood ratio test to assess the fit of both hypothesized path diagrams to the data. A statistically insignificant result implies that the covariance structure of the hypothesized path diagram does not differ from the observed covariance structure, indicating a good fit to the data (see Arbuckle, 2007). All variables were natural logarithm-transformed to conform to assumptions, and analyses were conducted using Amos 16 (Arbuckle, 2007).

To further test the passive sampling hypothesis, two null model simulations were conducted to generate predicted values of species diversity for each island. The first, the 'island' null model, randomly redistributed all trees that were observed on islands during sampling among islands in the archipelago. During each simulation replicate, the total number of trees observed on each island and the total number of trees observed from each species were held constant to that observed. Therefore, row and column totals of the site-by-species abundance matrix were held constant. This procedure is analogous to the 'fixed-fixed' procedure adopted by many null models of species co-occurrence patterns (Gotelli & Entsminger, 2001). The second, the 'mainland' null model, randomly populated islands from the total pool of trees observed in the two mainland plots. During each simulation replicate in the mainland null model, the total number of trees on each island was held constant to that observed. However, the number of individuals from each species was not held constant, to accommodate the differences in species composition between islands and the mainland, and because the mainland plots contained nearly twice as many trees as islands.

To test whether the passive sampling null models could predict observed patterns in species diversity, we conducted a Poisson log-linear model using the generalized linear model procedure in spss (SPSS Inc., 2008). Observed species diversity on each island was used as the dependent variable, and average species diversity for each island based on 1000 simulation replicates was used as the independent variable in separate analyses of each null model. We chose this approach because the dependent variable comprised counts of a small number of tree species that were non-normally distributed. To test whether the null models consistently under- or overestimated observed species diversity, we also conducted two-tailed, paired-sample t-tests for each null model separately.

A different suite of null models was used to test for abundance-based assembly rules. Tests for community assembly rules often use the 'C-score' to evaluate species co-occurrence patterns in binary matrices, wherein species are listed as rows and sites are listed as columns (Gotelli & McCabe, 2002). However, in this instance we wanted to test for non-random patterns in tree abundances, rather than tree species occurrences. We were specifically interested in determining whether tree abundances were evenly partitioned among islands, with species reaching higher abundances on islands where other species were rare or absent. To conduct this test, the 'niche partitioning' module of EcoSim 7 (Gotelli & Entsminger, 2001) was employed. This module is typically used to test whether species assemblages quantitatively partition the use of multiple resources and is conducted by constructing a matrix where species are listed as rows, resources are listed as columns and cells are filled with estimates of resource use. In our application of this null model, islands were considered to be resources, so each was listed as a separate column, and Pianka's (Pianka, 1973) and Czekanowski's (Feinsinger et al., 1981) indices were used to characterize interspecific overlap in the use of resources (i.e. abundance patterns among islands). Lower values of both indices relative to simulated values from the null model would indicate that abundances of each tree species tended to be evenly distributed among islands.

Null model tests based on Pianka's and Czekanowski's indices assume that resource categories are equally abundant, and both indices overestimate resource overlap if some resources are more abundant than others. Therefore, results from this null model are biased against detecting abundance-based assembly rules if some islands house more trees than others. We used two procedures to account for this problem. First, we used the 'user defined resource state' procedure in EcoSim, using the area of islands to account for differences in their capacity to house tree populations. We chose to use island area instead of total tree abundances because the user-defined measure of resource states should not be based on the observations being analysed, and island area is strongly correlated with total tree abundances (see Gotelli & Entsminger, 2001). Second, we converted abundances of each species to a percentage of the total present on each island. Therefore, in this analysis estimates of tree abundances on each island always

Table 1 Total numbers of individuals of eight conifer species inhabiting 34 islands and two (1 ha) plots on the mainland in Barkley Sound, British Columbia, Canada.

Conifer species	Islands	Mainland (1)	Mainland (2)
Abies amabilis	2	6	111
Picea sitchensis	133	5	7
Pinus contorta	77	0	0
Pinus monticola	1	0	0
Pseudotsuga menziesii	19	25	1
Taxus brevifolia	0	2	2
Thuja plicata	277	159	61
Tsuga heterophylla	123	783	254

totalled 100, alleviating the need to use the user-defined resource states procedure.

RESULTS

A total of 632 trees from seven conifer species were quantified on the 34 islands in the archipelago. A combined total of 1416 trees from six conifer species were observed in the 2 ha of forest on the mainland. *Taxus brevifolia* occurred only on the mainland, while *Pinus contorta* and *Pinus monticola* were restricted to islands (see Table 1).

Results from path analyses were consistent with the passive sampling hypothesis and inconsistent with the ToIB (Fig. 1). The path diagram representing the passive sampling hypothesis yielded an insignificant likelihood ratio test ($\chi^2 = 4.058$, d.f. = 2, $P = 0.131$), indicating that the covariance structure of the passive sampling path diagram provided an adequate description of the total observed covariance matrix. Conversely, the path diagram representing the ToIB yielded a significant likelihood ratio test ($\chi^2 = 8.731$, d.f. = 1, $P = 0.003$), indicating an inadequate fit to the observed covariance matrix.

Both the island (Wald $\chi^2 = 15.405$, $P < 0.001$) and the mainland (Wald $\chi^2 = 17.496$, $P < 0.001$) passive sampling null models predicted observed patterns in species diversity (Fig. 2). However, both null models consistently overestimated the observed number of tree species on islands. Paired t-tests showed that the observed number of tree species on islands was consistently lower than that predicted by both the island ($t = 7.447$, $P < 0.001$) and the mainland ($t = 3.260$, $P = 0.003$) null models.

Null model tests for island assembly rules showed that tree abundances were evenly partitioned among islands (Fig. 3). Using the user-defined resource states procedure, the observed value of Pianka's index (0.208) was lower than the average value (0.263) generated in the null model simulation ($P = 0.037$). Similarly, the observed value of Czekanowski's index (0.151) was lower than the average value (0.182) generated by the null model ($P = 0.038$). After standardizing tree abundances among islands, the observed value of Pianka's index (0.116) was again lower than the average value (0.251) generated in the null model simulation ($P < 0.001$). Similarly, the observed value of
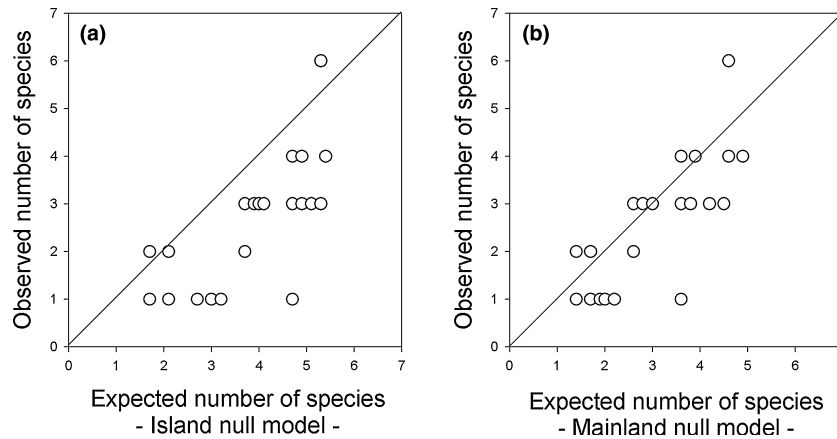
Figure 2 Relationships between observed and expected tree species diversity on 34 islands in Barkley Sound, British Columbia, Canada, based on two null models (several islands had the same values and are therefore obscured from view). (a) The island null model randomized the distribution of all trees observed across the archipelago. (b) The mainland null model randomly populated islands from a source pool of trees in 2 ha of contiguous forest on the mainland. In both instances, the null model predicted, but consistently overestimated, observed species diversity on islands.
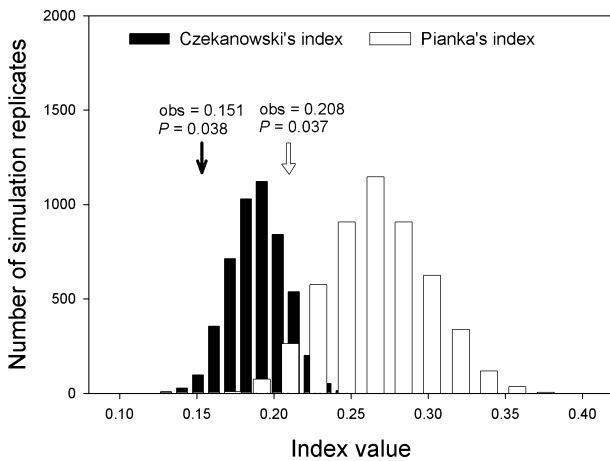

Figure 3 Results from null model tests for even displacement of tree abundances among islands in Barkley Sound, British Columbia, Canada. The numbers of simulation replicates ($n = 5,000$) falling into the categories of Czekanowski's index (black bars) and Pianka's index (white bars) are shown. The black arrow refers to the observed value of Czekanowski's index along with its associated *P*-value, and the white arrow refers to the observed value of Pianka's index. Both null models indicate that the distributions of conifer species are evenly partitioned among islands.

Czekanowski's index (0.082) was lower than the average value (0.154) generated by the null model ($P < 0.001$).

DISCUSSION

Spatial patterns in tree species diversity could be attributed to a particular combination of island geography, total tree abundances and biotic interactions, which is consistent with both the passive sampling hypothesis and abundance-based assembly rules. Path analysis showed that tree species diversity increased with total tree abundances, which in turn increased with island area and declined with island isolation. Direct statistical associations between island area, island isolation and tree diversity were not observed. This path-analytic framework is more consistent with the predictions of the passive sampling hypothesis than with the ToIB, and this result was corroborated by a series of passive sampling null models. Yet passive sampling null models consistently overestimated tree species diversity on islands. Results from an additional suite of null models suggest that this discrepancy results from assembly rules, or from a tendency for conifer abundances to be evenly partitioned among islands.

Kohn & Walsh (1994) used a path-analytic approach to investigate plant species diversity on an archipelago of European islands. They tested whether island area influences plant species diversity directly, or indirectly via area-dependent variation in habitat diversity, and found that both processes are important. Studies in other locales have found a similar effect of habitat on species diversity (Ricklefs & Lovette, 1999; Morand, 2000; Hortal *et al.*, 2009). However, in other archipelagos habitat appears to play a less prominent role (Nilsson *et al.*, 1988). Keppel *et al.* (2009), Morrison (2010) and Rizali *et al.* (2010) provide recent examples of how factors such as the geological age of islands, cyclonic activity and anthropogenic disturbances can also be important determinants of species diversity on islands.

The passive sampling hypothesis postulates that island communities are assembled by randomly dispersing propagules from a source pool of potential colonists. We therefore predicted that larger, less isolated islands would maintain higher total tree abundances, which in turn would promote higher species diversity. Results from path analysis and both passive sampling null models were consistent with this prediction, suggesting that island conifer communities are assembled at random from

mainland source pools. However, several aspects of the results were inconsistent with passive sampling.

If island communities originated via passive sampling from the mainland, tree species composition on islands would recapitulate tree species composition on the mainland precisely. Although passive sampling predicted patterns in species diversity, the composition of mainland conifer communities differed from that of island communities, suggesting that other processes are important. Previous work on islands in Barkley Sound found that dispersal limitations structure the composition of bird-dispersed shrub communities (Burns, 2005). A similar dispersal filter may be at work in conifer communities. Tree species with poor dispersal potential may fail to reach islands, which instead become dominated by species with good dispersal potential (see also Kadmon & Pulliam, 1993; Lomolino, 1993, 1994). Alternatively, islands in Barkley Sound are generally warmer, drier and more exposed to ocean-born disturbances than the mainland (Burns, 2004; Cody, 2006; Burns & Neufeld, 2009). So species with life history attributes that are more compatible with island environments may reach greater abundances on islands than species that are better adapted to mainland environments. Differences in species composition might also result from sampling effects. Mainland tree communities were sampled in only two mainland localities, so they might not accurately represent the pool of potential colonists. However, these plots encompassed the two forest habitats present on the mainland. They were also quite large and contained approximately twice the number of trees sampled on islands. Furthermore, results from the mainland null model were statistically similar to those of the island null model, indicating that overall tests of the passive sampling hypothesis were not biased by the way mainland tree communities were sampled.

Another aspect of the results that could not be explained precisely by the passive sampling hypothesis is that islands consistently housed fewer tree species than expected. Both passive sampling null models held total tree abundances on each island constant, so differences between observed and expected tree diversity estimates result from clumped tree abundances within islands. Several processes may be responsible for this result. Differences in environmental conditions among islands may match environmental tolerances of different species, leading to clumped abundance patterns among islands. Disproportionate rates of within-island dispersal may also lead to clumped abundances by favouring initially colonizing species. However, null model tests for community assembly rules provide an alternative explanation.

Results from both assembly rule null models do not indicate that species simply reach higher abundances on some islands relative to others. Instead, they indicate that species reach higher abundances on islands that maintain lower abundances of other tree species. This type of partitioning of tree abundances is consistent with competition theory, which predicts that competition for limited resources leads to interspecific differences in the use of resources or space (MacArthur, 1972; Rosenzweig, 1995). Assembly rules have a long and tumultuous history in ecology (Diamond, 1975; Connor & Simberloff, 1979; see Gotelli & Graves, 1996, for a general discussion), and it is not clear whether assembly rules consistently structure ecological communities. However, abundance-based assembly rules can account for lower values of species diversity than expected from passive sampling. Future work might benefit from investigating this link more closely, both empirically and theoretically.

Overall results suggest that stochastic processes, whereby larger, less isolated islands passively accumulate more trees and therefore higher tree diversity, are the primary determinants of tree community assembly. On the other hand, deterministic assembly rules, whereby conifer species partition the use of different islands, seem to modify community structure and reduce the total number of species occurring on islands. Therefore, both stochastic and deterministic processes appear to regulate species diversity in this study system.

The history of biogeography is marked by heated debate concerning the processes structuring the assembly of island communities (see Gotelli & Graves, 1996; Whittaker & Fernández-Palacios, 2007). One school of thought argues that interspecific interactions structure island communities deterministically (Diamond, 1975), while an opposing viewpoint argues that island communities are assembled stochastically (Connor & Simberloff, 1979). Results from this study argue against such a dichotomous view of island community structure and suggest that both stochastic and deterministic processes may structure island communities synergistically.

ACKNOWLEDGEMENTS

REFERENCES

Arbuckle, J.L. (2007) Amos™ 16.0 user's guide. SPSS Inc., Chicago.

Burns, K.C. (2004) Relationships between the demography and distribution of two bird-dispersed plants in an island archipelago. Journal of Biogeography, 31, 1935–1943.

Burns, K.C. (2005) A multi-scale test for dispersal filters in an island plant community. Ecography, 28, 552–560.

Burns, K.C. & Neufeld, C.J. (2009) Plant extinction dynamics in an insular metacommunity. Oikos, 118, 191–198.

Canadian Hydrographic Service (1994) Map 3671. Ministry Fisheries and Oceans, Sydney.

Cody, M.L. (2006) Plants on islands: diversity and dynamics on a continental archipelago. University of California Press, Los Angeles, CA.

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. The American Naturalist, 113, 791–833.

Connor, E.F. & Simberloff, D.S. (1979) The assembly of species communities: chance or competition? *Ecology*, **60**, 1132–1140.

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. Harvard University Press, Cambridge, MA.

Feinsinger, P., Spears, E.E. & Poole, R.W. (1981) A simple measure of niche breadth. *Ecology*, **62**, 27–32.

Friele, P.A. & Hutchinson, I. (1993) Holocene sea-level change on the central west coast of Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences*, **30**, 832–840.

Gause, G.F. (1934) *The struggle for existence.* Williams & Wilkins, Baltimore, MD.

Gotelli, N.J. (2004) Assembly rules. *Foundations of biogeography* (ed. by M.V. Lomolino, D.F. Sax and J.H. Brown), pp. 1027–1040. The University of Chicago Press, Chicago.

Gotelli, N.J. & Entsminger, G.L. (2001) *EcoSim: null models software for ecology, Version 7.0.* Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT.

Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology.* Smithsonian Press, Washington, DC.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology*, **83**, 2091–2096.

Hortal, J., Triantis, K.A., Meiri, S., Thébault, E. & Sfenthourakis, S. (2009) Island species richness increases with habitat diversity. *The American Naturalist*, **174**, E205–E217.

Kadmon, R. & Pulliam, R.H. (1993) Island biogeography: the effects of geographic isolation on species composition. *Ecology*, **74**, 977–981.

Keppel, G., Buckley, Y.M. & Possingham, H.P. (2009) Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *Journal of Ecology*, **98**, 87–95.

Klinka, K., Krajina, V.J., Ceska, A. & Scagal, A.M. (1989) *Indicator plants of coastal British Columbia.* University of British Columbia Press, Vancouver.

Kohn, D.D. & Walsh, D.M. (1994) Plant species richness – the effect of island size and habitat diversity. *Journal of Ecology*, **82**, 367–377.

Lomolino, M.V. (1993) Winter filtering, immigrant selection and species composition of insular mammals of Lake Huron. *Ecography*, **16**, 24–30.

Lomolino, M.V. (1994) Species richness of mammals inhabiting nearshore archipelagos: area, isolation, and immigration filters. *Journal of Mammology*, **75**, 35–49.

MacArthur, R.H. (1972) *Geographical ecology.* Princeton University Press, Princeton, NJ.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoography. *Evolution*, **17**, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography.* Princeton University Press, Princeton, NJ.

Morand, S. (2000) Geographic distance and the role of island area and habitat diversity in the species–area relationship of four Lesser Antillean faunal groups: a complimentary note to Ricklefs & Lovette. *Journal of Animal Ecology*, **69**, 1117–1119.

Morrison, L. (2010) Long-term non-equilibrium dynamics of insular floras: a 17-year record. *Global Ecology and Biogeography*, doi: 10.1111/j.1466-8238.2010.00543.x.

Nilsson, S.G., Bengtsson, J. & Ås, S. (1988) Habitat diversity or area *per se*? Species richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology*, **57**, 685–704.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, **4**, 53–74.

Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.

Rizali, A., Lohman, D.J., Buchori, D., Prasetyo, L.B., Triwidodo, H., Bos, M.M., Yamane, S. & Schulze, C.H. (2010) Ant communities on small tropical islands: effects of island size and isolation are obscured by habitat disturbance and 'tramp' ant species. *Journal of Biogeography*, **37**, 229–236.

Rosenzweig, M. (1995) *Species diversity in space and time.* Cambridge University Press, Cambridge.

SPSS Inc. (2008) *SPSS. Release 17.0.0 for Windows.* SPSS Inc., Chicago.

Weiher, E. & Keddy, P. (eds) (1999) *Ecological assembly rules: perspectives, advances, retreats.* Cambridge University Press, Cambridge.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Wilson, J.B., Wells, T.C.E., Trueman, I.C., Jones, G., Atkinson, M.D., Crawley, M.J., Dodd, M. & Silvertown, J. (1996) Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. *Journal of Ecology*, **84**, 527–538.

BIOSKETCHES

K. C. Burns is an assistant professor in biology at Victoria University of Wellington, New Zealand. He is interested in a range of ecological problems, including animal behaviour, plant–animal interactions, plant form and function and community assembly. **Jenny Berg, Ada Bialynicka-Birula, Sabrina Kratchmer** and **Katelyn Shortt** are members of the coastal community ecology research team at the Bamfield Marine Sciences Centre and are particularly interested in island biogeography.

Editor: Nicholas Gotelli

APPENDIX 1

Area, isolation and total number of conifer trees on 34 islands in Barkley Sound, British Columbia, Canada.

Island area (m²)	Island isolation (m)	*Thuja plicata*	*Picea sitchensis*	*Tsuga heterophylla*	*Pinus monticola*	*Pinus contorta*	*Pseudotsuga menziesii*	*Abies amabilis*
42	20	0	1	0	0	0	0	0
25	150	1	1	0	0	0	0	0
44	140	2	0	1	0	0	0	0
77	75	0	2	0	0	0	0	0
84	150	0	1	0	0	0	0	0
86	40	0	0	0	0	0	3	0
81	30	0	0	0	0	5	0	0
192	60	6	2	1	0	0	0	0
117	70	4	4	4	0	0	0	0
108	75	0	1	0	0	0	1	0
180	290	0	1	0	0	0	0	0
112	175	2	0	0	0	0	0	0
163	140	0	5	0	0	0	0	0
175	70	0	5	0	0	0	0	0
320	240	0	2	0	0	0	0	0
285	360	0	3	0	0	0	0	0
378	100	21	4	4	0	0	0	0
300	90	0	1	0	0	0	0	0
205	150	9	0	1	0	0	1	0
240	150	11	1	2	0	0	0	0
212	800	6	0	0	0	0	0	0
542	230	0	4	0	0	0	0	0
780	110	38	2	14	0	0	0	0
725	440	0	29	0	0	0	0	0
624	230	0	3	0	0	0	0	0
720	280	30	3	0	0	1	9	0
294	10	13	10	12	0	0	0	0
1165	10	45	12	36	1	0	0	0
885	20	15	4	7	0	15	0	0
892	15	36	4	8	0	35	2	2
298	9	5	3	0	0	16	3	0
113	8	0	0	0	0	5	0	0
721	10	29	20	33	0	0	0	0
301	8	4	5	0	0	0	0	0