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# History and taxonomy: their roles in the core-satellite hypothesis

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**Abstract** Metapopulation models are important in explaining the distribution and abundance of species through time and space. These models combine population dynamics with stochastic variation in extinction and immigration parameters associated with local populations. One of the predictions of metapopulation models is a bimodal distribution of species frequency of occurrence, a pattern that led to the development of the core-satellite species hypothesis. The spatial scale and taxonomic classification of past core-satellite studies has often been undefined. In our study, we have integrated metapopulation dynamics with the roles that differential dispersal ability and history play in the shaping of communities. The differences in distribution patterns between landbridge islands and oceanic islands, and among various taxa (birds, mammals, herptiles, arthropods, fish, and plants) are analyzed. The majority of landbridge islands comprised locally and regionally abundant species (core species), whereas the majority of oceanic islands had a uniform distribution (or no end-peak in their distribution). The patterns of distribution among the taxonomic groups also showed differences. Birds (good dispersers) consistently showed bimodal- and core-distribution patterns. The bimodal prediction of species distribution is best exemplified in the landbridge islands and in birds, and least in oceanic islands and in organisms other than birds. These results illustrate the importance of testing models with various taxonomic groups and at different spatial scales and defining these scales before formally testing the predictions of the models.

**Keywords** Metapopulation · Core-satellite · Landbridge · Oceanic · Spatial patterns

## Introduction

As fragmentation and isolation of habitats continue to occur, ecological studies of patchy environments become a priority. Further theoretical and empirical studies of the effect of habitat isolation on the distribution and abundance of groups of species at a regional scale, rather than a local scale, are needed. Various researchers have tackled this area (e.g. Holt 1993; Whittaker 1998 and references therein; Hanski and Ovaskainen 2000). The attempt to predict the distribution of animals at various spatial scales and to link this to the abundance of species has been hotly debated for years. Metapopulation dynamics is an area of research that addresses spatial scale effects on species distributions. Simply defined, a metapopulation refers to a network of locally isolated populations connected by infrequently dispersing individuals. Metapopulations rely on the processes of local extinction and the eventual recolonization of vacant sites from neighbouring populations (Hanski and Gilpin 1991). These models provide a helpful setting for the understanding of the distribution, abundance and viability of organisms over time and space.

Levins (1969) developed the basis of a model of a group of interacting populations acting in a manner similar to individuals within a population. Hanski's (1982a) paper re-evaluated Levins' metapopulation model. He considered the potential association between the fraction of sites occupied and the probability of local extinction. In Hanski's model, the probability of local extinction and rate of migration were dependent on the fraction of sites occupied. He demonstrated that the more sites occupied by a given species, the lower the probability of extinction and the higher the probability of migration at any one site. Emigrants from surrounding sites can potentially 'rescue' a site becoming extirpated by immigrating to that site (either from the mainland or other islands); this

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is termed the ‘rescue effect’ after Brown and Kodric-Brown (1977). The assumption that the probability of local extinction and rate of migration are dependent on the fraction of sites occupied, provides an alternative stable equilibrium, which can occur on the basis of immigration affecting the growth rate of existing local populations.

Levins’ original metapopulation model is stable with one equilibrium point, whereas Hanski’s dynamic model is unstable (Gotelli 1991). In Levins’ model, the fraction of sites occupied (distribution) by a species stabilizes around an internal equilibrium, ranging from 0 and 1 (Levins 1969). In Hanski’s model, the distribution of organisms in space or time is bimodal (Hanski 1982a; Hanski 1999). Most species will tend toward regional extinction (distribution close to 0) or regional occurrence (distribution close to 1) if the rate of extinction varies stochastically, although they may switch their position in the distribution over time (Hanski 1982a). Thus, the bimodal distribution of species has peaks close to one and zero. On the one extreme, there exists the core species, which are widely distributed and abundant in space. On the other extreme, there exists a group of rare and patchily distributed species, the satellite species. Hanski’s model suggests that although species have varying immigration and extinction parameters, species are unlikely to occupy intermediate values for long periods of time (Hanski 1982a). This bimodal distribution is obtained because of ongoing recolonization.

One of the most important characteristics of metapopulation models is the presence of regional dynamics, yet rarely do we see the first step of defining spatial regions used in metapopulation studies. The core-satellite prediction of metapopulation models is the focus of this paper. Although there is considerable support for the core-satellite hypothesis (Hanski 1982b, c; Collins and Glenn 1990, 1991; Hanski and Gyllenberg 1993; Eriksson et al. 1995), there have also been many debates on the merit, cause and interpretation of it (Brown 1984; Gotelli and Simberloff 1987; Gaston and Lawton 1989; Scheiner and Rey-Benayas 1997). In addition, most studies provide a qualitative and subjective assessment of whether the results match the core-satellite pattern or not (e.g. Collins and Glenn 1991). Here, we examine the existence of bimodality within archipelago populations. Both the effects of historical connections and taxonomic differences are analyzed to see how each is responsible for the interpretation of evidence for or against the core-satellite model prediction. We also provide a modified version of Gotelli and Simberloff’s (1987) randomization test to assess the presence of bimodality in distribution patterns.

## Landbridge versus oceanic island contrasts

The use of island models in ecological and evolutionary studies aids in understanding both island and mainland systems. Islands can generally be divided into landbridge and oceanic in origin. We acknowledge that this dichotomy is a simple designation, but one that meets the purpose of the present study. Landbridge islands are those that have had recent connections (in a geological or evolutionary time scale) to the mainland as a result of lowered sea levels during glacial periods. The colonists of these islands are ones that did not necessarily cross a water gap (MacArthur 1972). Oceanic islands are islands that were never connected to the mainland, and whose colonists must have arrived via over-water dispersal (MacArthur 1972). During periods of lower sea-level, the islands of an archipelago may have coalesced into one or more larger landmasses. Dispersal would have been easier at this time with subsequent barriers arising as sea-level increased following glaciation.

It is important to consider the effects of historical events and origins on the present day distribution of species on both types of islands. Because of the historical connection to the mainland, a group of landbridge islands potentially should contain a similar group of species. As the landmasses separated from the mainland, these islands were supersaturated with relict populations (Patterson 1987). Theoretically, a snapshot at the time of the break-up should reflect the presence of all species on all islands. In other words, these islands should have originally contained a full complement of mainland species (Worthen 1996). In such a case, a peak in the core species numbers would occur. However, this is hypothetical as the separation of landmasses is not a spontaneous occurrence. It has been suggested that the present-day composition on these islands was determined via faunal relaxation by local, selective extinction events and/or as a consequence of diffuse competition for limited resources, and subsequent recolonization events (MacArthur 1972; Patterson 1987; Worthen 1996). Extinction-prone species (including poor competitors) lower the core peak, and simultaneously heighten the satellite peak, assuming they are not regionally extinct.

Landbridge islands have the advantage of a source pool relatively nearby, which can facilitate colonization events. Thus, they receive new immigrants from both the mainland and the surrounding islands. Extinction, together with increased recolonization events, leads us to believe that landbridge islands should show a bimodal pattern. The extinction of select, local populations on a regional scale without the re-establishment of new colonists, or all species being widely distributed will give rise to a unimodal pattern, with a peak in the core mode. In the first scenario, extinct or very rare local populations may not be recolonized or rescued by surrounding populations because of certain ecological characteristics, such as being poor competitors or poor dispersers. Regionally abundant species remain abundant because they are strong competitors or dispersers. Widely distributed species are also an outcome if we assume these islands are still in the process of faunal relaxation, with most species still occurring on all islands.

In contrast, oceanic islands are both historically and currently insular. When they formed, there were no species present. Therefore, their flora and fauna are derived by either over-water colonization or the formation of novel species. If the rate of endemicity is high enough (as it often is for certain taxa on oceanic islands) the satellite mode will increase in an oceanic archipelago. It has been stated that oceanic islands are dependent on both colonization and extinction events (Patterson 1987; Quinn and Harrison 1988; Cutler 1991), with colonization events being the more important of the two (Williamson 1981; Patterson 1987). The proportion of satellite species will be greater as species infrequently colonize oceanic islands. Assuming colonization events are still taking place, oceanic islands should show one of two distribution patterns. Some groups of islands should have a unimodal pattern, with a peak in the satellite mode attesting to the one-time colonization events without the eventual colonization of surrounding islands or the one-time formation of a species. Other archipelagoes should show a pattern following a "uniform" distribution (i.e. they could follow any of numerous distributions provided a mode is not located at either end). This is because of the absence of common factors responsible for species distribution patterns in oceanic systems.

The observation that a weaker relationship exists between species richness and sample area in continuous habitats as compared with island habitats (Preston 1962), leads us to further believe that landbridge islands will differ from oceanic islands in their species distribution. Relative to island systems, continental regions can gain and maintain more species from other regions and provide safe corridors for long-distance dispersal (Holt 1993; Thiollay 1998). By extending this observation to island systems, we can compare landbridge with oceanic islands (where landbridge islands are more similar to continental regions). Relative to oceanic systems, landbridge islands can gain and maintain more species from nearby source pools, and therefore should have a more shallow species-area curve compared to oceanic islands. A more shallow species-area curve translates into a higher probability of finding most species in most sites (high core species numbers).

### Taxonomic contrasts

Taxonomic differences are important to consider as organisms differ in numerous factors, including dispersal ability, territory size, competition, mode of reproduction, and body size. Implicit in metapopulation dynamics is the concept of population turnover. Population turnover is driven primarily by the dispersal or mobility of organisms (Collins and Glenn 1997). In the present study, differences in dispersal ability are the focus of the effects of taxonomic differences. Taxa with poor dispersal ability will occur only on a few islands, whereas taxa with good dispersal ability will be found on most islands. The objective of this section is to determine whether differences that exist among taxa in their dispersal abilities match particular patterns in their distributions (i.e. bimodal, core, satellite, or uniform distributions).

## Materials and methods

The occurrence of species was gathered from 108 studies of islands and island-like habitats from the island biogeography, species-area and conservation literature. A large number of data sets used were taken from Wright et al. (1998), who compiled 279 presence-absence matrices and a bibliography of sources at the Field Museum of Natural History's World Wide Web site (http://www.fmnh.org/). Although our collection of studies is not a complete inventory, we believe it is a good representation of the island groups and species distribution on these islands. The island groups were chosen based on the following criteria:

1. Original data were available.
2. Island-by-island census was available, and not simply summaries for groups of islands.
3. Species presence-absence data were reported.
4. At least 6 islands were included in the study.
5. At least 8 species were included in the study.

The data sets used in our study are listed in the Appendix. Each set consists of the distribution of species over islands within an archipelago (i.e. each archipelago is a separate study). Forty-four sets were taken from oceanic island surveys, and 64 from landbridge islands. These surveys also include lake systems (10 in total), which have also been considered island systems (Magnuson 1976; Harvey 1982). Lakes that were part of a greater, proglacial lake after the ice retreat of the past glacial event, are similar to landbridge islands, such that they were all connected at one point in the past (Jackson and Harvey 1989; Jackson et al. 1992). The modern-day lakes are fragmented remnants of the proglacial systems as a result of isostatic rebound. "Oceanic lakes" were not covered by proglacial lakes; never shared a common suite of species in their past and species were required to colonize through a series of upstream obstacles (Olden et al. 2001). The landbridge island sets include data from terrestrial habitat isolates (i.e. mountaintop biotae). Islands that were oceanic in origin but have had recent connections to the mainland are classified as landbridge islands because of the free exchange of flora and fauna during the connected phase.

Many studies have looked for bimodal patterns in the distribution of the taxa of interest (e.g. Hanski 1982c), despite the lack of any statistical tests in the literature (Ellison 1993). Studies have relied on subjective assessments with the exception of a test used by Collins and Glenn (1997), a randomization test to assess the significance of the expected versus the observed frequency of species distributions (Gotelli and Simberloff 1987), and a test for unimodality (Hartigan and Hartigan 1985; Scheiner and Rey-Beyanas 1997).

A randomization test modified from Gotelli and Simberloff (1987), which consists of permutating values within rows (islands) of the matrix, and doing this independently from one row to another, was used in the present study. The number of species per island was kept constant. Therefore, the sum of the row vectors or species richness per island remained the same throughout the randomization test. The number of islands on which each species occurred varied from one randomization to another. Therefore, the frequency of occurrence of the species varied, which is the question of interest in the core-satellite hypothesis.

The measure of bimodality, predicted from the core-satellite hypothesis, is based on whether the observed tails contain more values than expected under the null distribution (see Fig. 1). It is based on measuring the fraction of the distribution in the left-tail and the fraction of distribution in the right-tail. First, beginning at the left-most tail of the frequency of occurrence, and stopping mid-way, the statistic measures the degree of bimodality by determining how many consecutive bars have frequencies smaller than the one preceding it (the bar immediately to the left). This is the tally for the left-tail statistic. The same procedure is performed for the right-hand tail. Beginning at the right-most bar, the statistic counting how many consecutive bars have frequencies smaller than the one preceding it (the bar to its right), until the two tails meet. This is the tally for the right-tail statistic. These two statis-

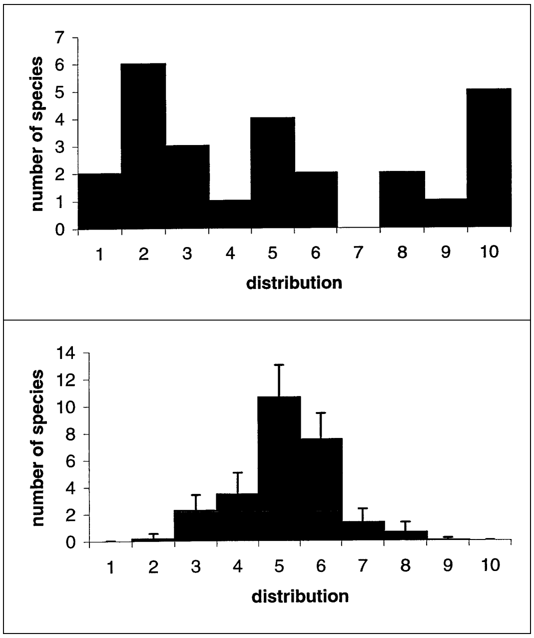

**Fig. 1** An example of the bimodality measure used in the calculation of the left- and right-tail statistics for each of the datasets. The *top graph* represents the pattern observed for the species on the islands. The *bottom graph* represents the mean values obtained under the randomization test and the *vertical lines* are one standard deviation about the mean

tics (left- and right-tail) are the observed values. An example of this method is shown in Fig. 1. The two measures are calculated and compared independently to the randomized distributions (explained below). We do not include tied counts (as do Gotelli and Simberloff 1987) since a flat or uniform distribution would not be bimodal, but could not be distinguished from a bimodal one if tied counts were to be included.

One thousand randomized matrices (including the observed frequency distribution) were run. The bimodal statistic was re-calculated for each of the 999 randomized distributions, plus the observed distribution. The left- and right-tail statistics of the randomized tests were compared to the observed statistics to see whether the null distribution would yield values as extreme as the observed distribution. The associated significance was based on the proportion of randomized values that were equal to or greater than the observed values. This provided a *P*-value for each tail, and for each data set. We have arbitrarily chosen 5% as the cut off for the “significance level”. Where the results bordered this 5% significance level, we used 9,999 matrices (Jackson and Somers 1989). Based on the *P*-values, the data set was categorized as either being bimodal (when both *P*-values were significant), unimodal-core (when the right-tail *P*-value was significant), unimodal-satellite (when the left-tail *P*-value was significant), or a uniform distribution in which a mode is not located at either end (when neither of the *P*-values were significant).

### Statistical analyses

We have examined both the association between the type of island (landbridge or oceanic) and the pattern observed (bimodal, core, satellite, or uniform), as well as between the type of taxa (birds, mammals, herptiles, arthropods, fish, plants) and the pattern observed. For the latter analysis, both separate (landbridge and oceanic separated) and combined (landbridge and oceanic combined) island types were analyzed. Fisher’s exact test was used to calculate the significance of the association between the variables for each contingency table.

In order to identify the pattern most influential in the association between the type of island and the pattern observed, a series of sequential analyses of the original contingency table were performed. One out of the four patterns was deleted each time to test for the presence of association between the remaining values. The same procedure was performed for the second contingency table (4×6), where one taxon was deleted for each test and the association between the remaining taxa and the pattern was analyzed. Additional tests were performed in the taxonomy-by-pattern table (4×6), where one pattern was eliminated for each test, and the association between the remaining patterns and the taxa were analyzed.

Although summarizing results from multiple studies can be done using meta-analysis, it was not appropriate for our study. Meta-analytical methods are designed to determine the relative influence of various study attributes on the resulting significance level of the study. In our case we have two response variables (i.e. the shape of the two different tail distributions) that we are assessing and it is the four combinations of these two response variables that is critical. Therefore meta-analysis was not an appropriate technique to examine this interaction of response.

## Results

A summary of the results from the randomization tests performed for each of the 108 data sets is found in the Appendix. Both the left and right-tail statistics (associated *P*-values) are included, and the category to which the set belongs.

### Landbridge versus oceanic island contrasts

The overall test indicates that the proportion of landbridge islands showing each of the four patterns is significantly different from the proportion of oceanic islands showing each of the patterns (Fig. 2; Fisher’s exact test, two-tail, $P$=0.011). Landbridge islands show a greater proportion of bimodal and core patterns than do the oceanic islands. If we exclude the uniform results (“uniform” represents any distribution other than one having a mode at one or both ends, e.g true uniform as well as Gaussian distributions) from the table and consider the remaining 2×3 table, the nonsignificant *P*-value supports the null hypothesis that the remaining distribu-

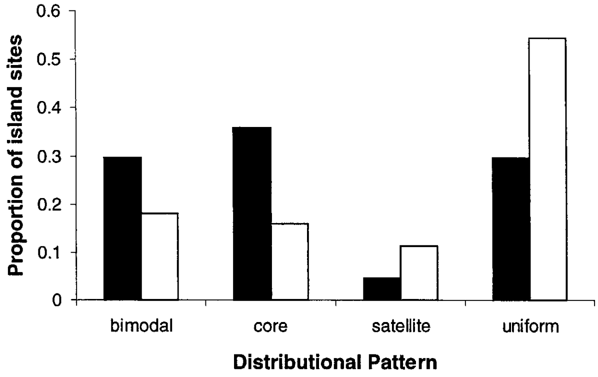

**Fig. 2** The proportion of landbridge (*solid bars*) and oceanic (*open bars*) island systems for each of the four patterns observed

**Table 1** Results of Fisher's exact test on full tables and sequential deletion of individual components

| Contingency table | Table size | Fisher's exact *P* value |
|---|---|---|
| Landbridge vs. Oceanic islands | 2×4 | 0.011 |
| (omitting bimodal columns) | 2×3 | 0.01 |
| (omitting core column) | 2×3 | 0.068 |
| (omitting satellite column) | 2×3 | 0.011 |
| (omitting no peak column) | 2×3 | 0.103 |
| Taxonomic contrasts | 4×6 | 0.0002 |
| (omitting birds column) | 4×5 | 0.451 |
| (omitting mammals column) | 4×5 | 0.371 |
| (omitting herptiles column) | 4×5 | 0.341 |
| (omitting arthropods column) | 4×5 | 0.714 |
| (omitting fish column) | 4×5 | <0.001 |
| (omitting plants column) | 4×5 | <0.005 |
| (omitting bimodal column) | 3×6 | 0.144 |
| (omitting core column) | 3×6 | 0.672 |
| (omitting satellite column) | 3×6 | 0.485 |
| (omitting no-peak column) | 3×6 | 0.446 |

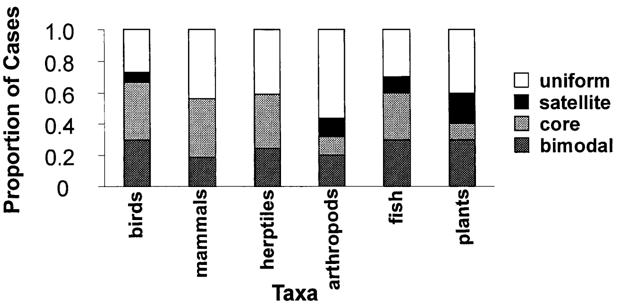

**Fig. 3** The proportion of the distribution patterns of each taxon for the combined landbridge and oceanic island systems

tion patterns are independent of island type (Fisher's exact test, two-tail, *P* =0.103). When the core column is ignored, Fisher's statistic also reports a nonsignificant value (Fisher's exact test, two-tail, *P* =0.068), although marginal. These two distribution patterns are influential in the association between the island type and the pattern observed (see Table 1).

Taxonomic contrasts

The global test for the combined data (landbridge and oceanic together) indicates an association between the type of taxa and the type of pattern observed (Fisher's exact test, 2-tail, *P* <0.0002). The uncombined tests for each island type (landbridge and oceanic separated) yield nonsignificant results (landbridge islands: Fisher's exact test, 2-tail, *P* =0.697; oceanic islands: Fisher's exact test, 2-tail, *P* = 0.347). Figure 3 is a histogram of the proportions of the distribution patterns of each taxon for the combined island systems. A similar histogram, with landbridge and oceanic island systems separated is shown in Fig. 4.

By eliminating the fish column from the original, combined table and considering the remaining 4×5 table, we get significant results (Table 3; Fisher's exact test, two-tail, *P* <0.001). When excluding the plant column, we get similar results (Fisher's exact test, two-tail, *P* <0.005). When excluding any of the other taxa, we get nonsignificant *P*-values, supporting the hypothesis that these two variables are independent of the remaining set. In addition, by eliminating any of the four patterns, and analyzing the 3×6 table, the test reports nonsignificant results. Therefore, all taxa (except fish and plants) and all patterns are necessary for a significant association between the two variables of interest (see Table 1).

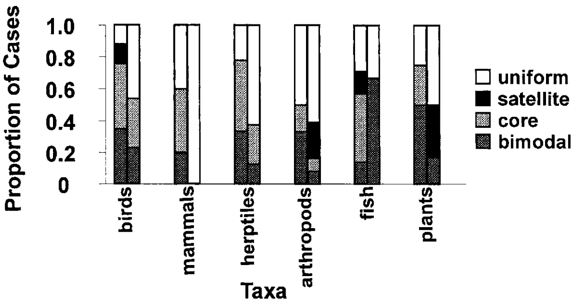

**Fig. 4** The proportion of the distribution patterns of each taxon for the separated landbridge and oceanic island systems. Each pair of *bars* represents the proportions for the landbridge and oceanic islands respectively

## Discussion

The results of this study demonstrate that the distribution of species inhabiting island habitats differ depending on the archipelago's historical connection to the mainland. Landbridge islands show a high proportion of core species, whereas oceanic islands show a high proportion of "uniform" species distributions lacking modes at either end. Within the taxonomical component of the study, we show that different taxa exhibit different distribution patterns.

### Landbridge versus oceanic island contrasts

### *Historical connections*

Present-day distribution patterns of species on islands and isolated habitats reflect historical events and differences in the derivations of their biotae. Thus, it is expected that landbridge and oceanic islands will have different patterns of species richness and distributions. Because landbridge islands have been disconnected from previously continuous extensions of similar habitats (Quinn and Harrison 1988), these islands' biotae have a proportion of their species derived from over-land dispersal prior to island formation. The species composition of these supersaturated islands is highly dependent on extinction events, as suggested in the literature (Patterson 1987; Whittaker 1998). The fact that landbridge islands in an archipelago shared an ancestral biota suggests the presence of a common suite of species on these islands. One would expect a greater number of frequently occurring or core species in this case. Our results show a high proportion of core species on landbridge islands (relative to expected proportions). Patterson and Atmar (1986) indicate that species differ in their relative extinction rates leading to nested subsets of species. Having species exhibiting high rates of extinction relative to others will lead to rare species. This mix of larger numbers of frequently and infrequently occurring species provides a bimodal distribution, as our results suggest.

Oceanic islands are generally more remote than landbridge islands and have never shared a common ancestral biota. These islands' biotae were derived by overwater colonization or by in situ speciation. As a result, they are equally or more dependent on immigration than on extinction events in the formation of their biotae. The fact that they never shared an ancestral biota limits their potential for having core species, as our study illustrates. Our results show that these islands do not have a high proportion of satellite species, although it is still higher than expected under the random model (11.4% as opposed to 7.5%), and higher than the proportion of satellite species on landbridge islands (11.4% as opposed to 4.7% on landbridge islands). Oceanic islands may be expected to show greater numbers of satellite species based on chance colonization events that typically occur on one or a few of the islands, i.e. introductions or passive dispersal. However, the fact that this pattern is not overwhelmingly prevalent can be a consequence of organisms with good dispersal ability (e.g. birds) and successful persistence comprising their biota (Worthen 1996). As good dispersers and successful colonizers, these organisms, after having colonized one island, could have reached and colonized other surrounding islands in the archipelago, i.e. a stepping-stone effect.

Oceanic islands show a high proportion (54.5%) of island sets having a "uniform" pattern (relative to expected proportions) in their species distribution. Variation in environmental conditions and distance from the mainland may be variable on the oceanic islands such that grouping them into one category may mask many sources of variation. Endemism can further affect the species patterns as it has been shown that evolutionary factors have an important role in determining species numbers on larger islands (Losos 1996). Oceanic islands, especially more isolated ones, have higher degrees of endemism than landbridge islands, a result of radiation after the establishment of a few colonists (Lawlor 1983, 1986; Heaney 1986). Although the proportion of endemic species is probably too small in most island groups to have a strong contribution to the distribution patterns (Quinn and Harrison 1988), it may skew the results of the patterns seen.

The fact that organisms have to arrive and successfully colonize and persist on these island habitats is yet another obstacle in the formation of the species composition of these islands. Landbridge islands are free of this problem, as many of the organisms found on them today are primarily relict populations, given the relatively recent rise in sea levels. Also, low-lying oceanic island systems may persist for millions of years; however, they are vulnerable to repeated submergence as sea levels rise and fall. As a result, their biotae are often transitory (Paulay 1994). These factors and the variability around these parameters contribute to the lack of a distinctive pattern in the distribution of their species on oceanic islands.

### *Differential extinction and colonization rates*

Differences in both historical and current colonization and extinction rates could also explain the different patterns seen in landbridge and oceanic islands. Both types of islands are parts of larger groups of islands. The one notable difference between the two is that landbridge islands are often closer to a larger regional species pool than are oceanic islands. When colonization rates are high relative to extinction rates on both types of islands, landbridge islands will inevitably receive a greater number of immigrants as a result of their closer proximity to a nearby source pool. This will lower local extinction rates and aid in the recolonization of vacant sites within the landbridge islands (Brown and Kodric-Brown 1977; Pulliam 1988; Holt 1993; Worthen 1996).

Mean colonization rates will always have to exceed extinction rates in order for populations to persist. Even if we assume that extinction rates on oceanic islands are relatively low and comparable to landbridge islands, we should still expect differences in their faunal and floral distributions, based on their colonization rate alone. Although the mean colonization rate has to be higher than the extinction rate, it is still lower on oceanic islands than that of landbridge islands. Consequently, the proportion of species occurring on all islands is not as great in oceanic islands. If local extinction events are as infrequent as in landbridge islands, the fraction of sites occupied will tend towards an intermediate frequency (or one following a uniform distribution). This partially explains the high proportion of uniform distribution patterns seen in the oceanic island results.

## Taxonomic contrasts

Distributional differences among taxa can be a result of many factors characteristic of the taxonomic group, the islands, and/or a result of sampling errors (Collins and Glenn 1997). Groups that are species-rich tend to have a higher proportion of rare species based on the positive association between rarity and richness (MacArthur and Wilson 1967). Sampling techniques may affect the presence-absence data, as methods are often biased towards capturing common species and relatively ineffective at sampling rare species (Collins and Glenn 1997). Also, large organisms will be easier to detect because of their larger and more evident size. Taxonomic groups will differ greatly in their ability to disperse and colonize a habitat. They will differ in their ability to compete for new, available sites, and in their mode of reproduction, such that the colonizing propagule of asexual organisms will differ from sexual organisms. Thus, differences in distributional patterns among groups may reflect both methodological and biological variation, and thus make it unreliable to test only one group in an attempt to provide a general theory of a model.

An important qualitative prediction from the metapopulation model is that the colonization rate has to exceed a threshold value for species to survive regionally (Lomolino 1986). Colonization can be divided into many parts. Emigration of individuals from a patch is the first component, followed by the dispersal of those individuals over a more or less inhospitable stretch of water. The individuals that make it over successfully (colonizing propagules) must face problems of survival and reproduction. Thus, the emigration of individuals and the subsequent colonizing on a new site are linked through the organism's dispersal capabilities. Differential dispersal abilities play a significant role in the distribution patterns of species as demonstrated in the taxonomic component of this study. We show that there exists a significant association between the type of taxon and the type of pattern shown. Birds, mammals, herptiles, and arthropods all show a strong dependence on the type of pattern associated with them, whereas fish and plants do not.

Birds have good dispersal abilities and therefore they have considerable potential to colonize all islands. Whether they fly voluntarily or are carried by the wind, most are airborne (William 1969). Mammals, on the other hand, are generally poor over-water colonizers. Dispersal among local populations is possible but less frequent than within continuous habitats because of the challenge of the water barrier, which inhibits movement (Lawlor 1986; Krohne 1997). Mainland populations are an important reservoir of dispersers for mammals. As such, mammals rarely inhabit oceanic islands. The high degree of endemism of terrestrial mammals on oceanic islands is evidence of their poor dispersal ability (Lawlor 1986). Although both mammals and herptiles are groups of species with poor dispersal abilities, herptiles survive passive dispersal better than mammals (Schmiegelow and Nudds 1987). The herptiles that do cross water barriers (e.g. lizards) are rafted across. However, they still colonize islands less often than airborne organisms do (William 1969). Arthropods are amongst the most diverse group of organisms. The lack of a distinct distribution pattern within this taxon may be a result of this heterogeneity.

Therefore, pooling all taxa into a single distribution model will mask any taxonomic difference and the additional insight to be gained. Inherent in the metapopulation model is the assumption that the movement of species from one site to any other site should be possible and equally likely. Bimodality can be a result of the strong rescue effect that is found with organisms having high dispersal rates (Hanski and Gyllenberg 1993). It seems likely, then, that birds, a group of organisms that can theoretically disperse over large water barriers, should be the group best fitting this criterion. Of the thirty core pattern sets observed in our study, 23 occur on landbridge islands, whereas 7 occur on oceanic islands. From the 7 oceanic core patterns, 4 are bird data sets. This shows that good dispersal ability can over-ride the isolation or historical factor, as the majority of the core species on oceanic islands are birds. All other taxa show relatively high proportions of uniform distribution patterns. Birds, in general, show more bimodal and core patterns, and fewer uniform patterns, than expected. Oceanic islands contain very few species of mammals, as we could find only a single example in the literature.

In conclusion, despite the empirical and theoretical realism of the core-satellite model, it contains assumptions that do not always reflect the structure and dynamics of natural populations, i.e. similar species and habitat selection where all sites are equally suitable for all species (Hanski 1982a). However, these models have been a focal point in many studies concerning population dynamics and conservation applications. And as such, many studies have recognized the presence of a spectrum in the spatial and taxonomic arenas, such that spatial structures will vary in size, heterogeneity, and connectivity, and organisms will vary in dispersal abilities, geographic ranges and competition (Hansson 1991; Lidicker 1995; Collins and Glenn 1991; Scheiner and Rey-Benayas 1997).

In order to fully understand the dynamics leading to ecological communities on islands, studies must extend their spatial, historical, temporal, and taxonomic scales beyond the level of individual populations in a single region. Our study illustrates the importance of formally testing models with various taxonomic groups and using different island systems, and more importantly, defining these scales before accepting or rejecting the predictions of a model. Previously, many studies failed to differentiate these taxa and islands, as well as relying on qualitative assessments of whether the results matched the core-satellite pattern of bimodality.

The understanding of distribution patterns of species can be of great importance in ecological research. As the fragmentation of habitats continues, studies in geographical ecology provide much insight, as they deal with dynamics at the community level within a geographic context. Landbridge islands represent isolated habitats once connected to each other and to a larger source pool. As the distance between patches of a once-continuous landscape increases, dispersal between fragments becomes increasingly important for the survival of the metapopulation. Recolonization of vacant sites, which have gone extinct, will be required to maintain the species richness that once existed. With habitat fragmentation, as in the break-up of landbridge islands, the number of core species within a group will decrease, as suggested by Collins and Glenn (1991). Species prone to extinction (i.e. poor dispersal ability such as herptiles, or poor competitors) will decrease, whereas species with good dispersal ability will remain as core species within the regional context. Because of the differential dispersal capabilities of organisms, some are more prone to extinction in fragmented habitats than others. The proportion of core species within a taxonomic group, in particular, will be lower in fragmented systems than in similar-sized areas of continuous habitat (Collins and Glenn 1990, 1995). Therefore, it is important to consider each group of taxa, and individual species within a taxon, independently when dealing with management and conservation strategies.

The lack of adequate published results on various taxa (e.g. aquatic taxa and herptiles) from both true islands or from habitat patches limits our abilities to generalize for these taxa and the implications of habitat fragmentation. Such deficiencies need to be targeted in addressing conservation strategies.

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## Appendix

Summary of the datasets compiled in the survey. Location: area of collection; Taxon: taxonomic group in collection. Island type: landbridge or oceanic island (or habitat island); Isl# is the number of islands in the study and Spp# is the number of species in the study

| | Location | Taxon | Island type | Isl # | Spp # | LT: | RT: | Pattern | Source |
|---|---|---|---|---|---|---|---|---|---|
| 1 | W Lake Erie, E N. America | Arthropods | Landbridge | 22 | 12 | 0.005 | 0.001 | Bimodal | Dexter et al. (1988) |
| 2 | Frisian islands | Arthropods | Landbridge | 18 | 25 | 0.024 | 0.001 | Bimodal | Boomsma et al. (1987) |
| 3 | California islands | Arthropods | Landbridge | 8 | 45 | 0.016 | 0.002 | Bimodal | Miller (1984) |
| 4 | Aegean islands | Arthropods | Landbridge | 43 | 71 | 0.001 | 0.001 | Bimodal | Sfenthourakis (1996) |
| 5 | Thimble islands | Arthropods | Landbridge | 12 | 35 | 0.225 | 0.01 | Core | Goldstein (1975) |
| 6 | Georgian Bay | Arthropods | Landbridge | 10 | 26 | 0.081 | 0.025 | Core | Nudds et al. (1996) |
| 7 | Mangrove islands | Arthropods | Landbridge | 9 | 254 | 1 | 1 | Uniform | Simberloff (1976) |
| 8 | Tuscan Archipelago, Italy | Arthropods | Landbridge | 21 | 48 | 0.137 | 1 | Uniform | Baroni-Urbani (1971) |
| 9 | Outer Hebrides, Scotland | Arthropods | Landbridge | 6 | 155 | 1 | 1 | Uniform | Welch (1979) |
| 10 | Outer Hebrides, Scotland | Arthropods | Landbridge | 6 | 38 | 0.989 | 0.24 | Uniform | Welch (1979) |
| 11 | Baltic islands | Arthropods | Landbridge | 10 | 45 | 0.167 | 0.175 | Uniform | As (1984) |
| 12 | Florida keys | Arthropods | Landbridge | 19 | 35 | 0.352 | 1 | Uniform | Peck and Howden (1985) |
| 13 | Faeroe Is. | Arthropods | Oceanic | 17 | 26 | 0.002 | 0.001 | Bimodal | Bengston (1982) |
| 14 | Seychelles islands | Arthropods | Oceanic | 10 | 21 | 0.527 | 0.015 | Core | Muhlenberg et al. (1977) |
| 15 | Antilles (West Indies) | Arthropods | Oceanic | 18 | 51 | 0.016 | 1 | Satellite | Nichols (1988) |
| 16 | Marquesas Is., Polynesia | Arthropods | Oceanic | 10 | 8 | 0.004 | 0.174 | Satellite | Wilson and Taylor (1967) |
| 17 | Polynesia | Arthropods | Oceanic | 62 | 43 | 0.028 | 1 | Satellite | Wilson and Taylor (1967) |
| 18 | Austral Is. | Arthropods | Oceanic | 8 | 15 | 0.081 | 0.128 | Uniform | Wilson and Taylor (1967) |
| 19 | Canary Is. | Arthropods | Oceanic | 7 | 120 | 0.158 | 0.726 | Uniform | Machado (1976) |
| 20 | Gambier Is., Polynesia | Arthropods | Oceanic | 7 | 9 | 1 | 0.759 | Uniform | Wilson and Taylor (1967) |
| 21 | Line Is., central Pacific | Arthropods | Oceanic | 6 | 13 | 0.995 | 1 | Uniform | Wilson and Taylor (1967) |
| 22 | Society Is., Polynesia | Arthropods | Oceanic | 7 | 11 | 0.153 | 0.203 | Uniform | Wilson and Taylor (1967) |
| 23 | Tonga | Arthropods | Oceanic | 6 | 12 | 1 | 1 | Uniform | Wilson and Taylor (1967) |
| 24 | Bahamas and Cuba | Arthropods | Oceanic | 11 | 43 | 0.314 | 0.191 | Uniform | Browne and Peck (1996) |
| 25 | Galapagos islands | Arthropods | Oceanic | 8 | 18 | 0.725 | 0.115 | Uniform | Peck and Roth (1992) |
| 26 | Sea of Cortez | Birds | Landbridge | 9 | 37 | 0.028 | 0.008 | Bimodal | Cody (1983) |
| 27 | Queen Charlotte Is., W Canada | Birds | Landbridge | 41 | 30 | 0.016 | 0.009 | Bimodal | Simberloff and Martin (1991) |
| 28 | Minnesota lake islands | Birds | Landbridge | 56 | 52 | 0.001 | 0.001 | Bimodal | Rusterholz and Howe (1979) |
| 29 | Queen Charlotte Is., W Canada | Birds | Landbridge | 66 | 31 | 0.001 | 0.001 | Bimodal | Martin et al. (1995) |
| 30 | Illinois | Birds | Landbridge | 12 | 49 | 0.015 | 0.005 | Bimodal | Blake (1991) |
| 31 | S Finland | Birds | Landbridge | 34 | 45 | 0.002 | 0.001 | Bimodal | Simberloff and Martin (1991) |
| 32 | Massachusetts | Birds | Landbridge | 33 | 9 | 0.058 | 0.008 | Core | Adler and Wilson (1985) |
| 33 | Great Basin, W USA | Birds | Landbridge | 15 | 81 | 0.118 | 0.001 | Core | Behle (1978) |
| 34 | Great Basin, W USA | Birds | Landbridge | 13 | 11 | 0.432 | 0.001 | Core | Brown (1978) |
| 35 | Maddalena Archipelago, France | Birds | Landbridge | 16 | 61 | 0.4 | 0.001 | Core | Simberloff and Martin (1991) |
| 36 | California islands | Birds | Landbridge | 16 | 45 | 0.365 | 0.015 | Core | Power (1972) |
| 37 | Georgian Bay | Birds | Landbridge | 40 | 112 | 0.92 | 0.001 | Core | Nudds et al. (1996) |
| 38 | Gatun Lake, Panama | Birds | Landbridge | 6 | 102 | 1 | 0.048 | Core | Wright (1985) |
| 39 | New Zealand region | Birds | Landbridge | 22 | 53 | 0.001 | 1 | Satellite | Patterson (1987) |
| 40 | British islands | Birds | Landbridge | 26 | 8 | 0.004 | 0.065 | Satellite | Reed (1980) |
| 41 | Virgin Barrier islands | Birds | Landbridge | 11 | 16 | 0.093 | 0.07 | Uniform | Dueser et al. (1979) |
| 42 | Madagascar | Birds | Landbridge | 12 | 78 | 1 | 0.143 | Uniform | Schulenberg (1998) (in Wright et al. 1998) |
| 43 | Canary Is. | Birds | Oceanic | 7 | 78 | 0.021 | 0.026 | Bimodal | Bacallado (1976) |
| 44 | Faeroe Is. | Birds | Oceanic | 22 | 40 | 0.041 | 0.001 | Bimodal | Bengston and Bloch (1983) |
| 45 | Bahamas and Greater Antilles | Birds | Oceanic | 8 | 35 | 0.003 | 0.025 | Bimodal | Wunderle and Waide (1993) |

**Appendix** (continued)

| | Location | Taxon | Island type | Isl # | Spp # | LT: | RT: | Pattern | Source |
|---|---|---|---|---|---|---|---|---|---|
| 46 | Sea of Cortez | Birds | Oceanic | 13 | 28 | 0.188 | 0.001 | Core | Cody (1983) |
| 47 | Sipoo archipelago, S Finland | Birds | Oceanic | 18 | 50 | 0.166 | 0.001 | Core | Simberloff and Martin (1991) |
| 48 | California Channel Is. | Birds | Oceanic | 16 | 45 | 0.372 | 0.023 | Core | Power (1972) |
| 49 | Galapagos Is. | Birds | Oceanic | 15 | 23 | 1 | 0.001 | Core | Harris (1973) |
| 50 | Hawaii | Birds | Oceanic | 6 | 35 | 1 | 0.561 | Uniform | Scott et al. (1986) |
| 51 | Hawaii | Birds | Oceanic | 8 | 36 | 0.766 | 0.126 | Uniform | Juvik and Austring (1979) |
| 52 | New Zealand region | Birds | Oceanic | 9 | 31 | 0.692 | 0.079 | Uniform | Patterson (1987) |
| 53 | Antilles (West Indies) | Birds | Oceanic | 19 | 211 | 0.943 | 1 | Uniform | Gotelli and Abele (1982) |
| 54 | French Frigate Shoals, Hawaii | Birds | Oceanic | 9 | 18 | 0.077 | 0.191 | Uniform | Amerson (1971) |
| 55 | Cook islands | Birds | Oceanic | 6 | 21 | 0.111 | 0.118 | Uniform | Steadman et al. (1990) |
| 56 | Quetico lakes | Fish | Landbridge | 183 | 49 | 0.001 | 0.001 | Bimodal | Crossman (1976) |
| 57 | Bruce peninsula | Fish | Landbridge | 57 | 46 | 0.99 | 0.001 | Core | Harvey (1981) |
| 58 | La Cloche lakes | Fish | Landbridge | 48 | 32 | 0.839 | 0.001 | Core | Harvey (1982) |
| 59 | Wawa lakes | Fish | Landbridge | 50 | 28 | 1 | 0.001 | Core | Somers and Harvey (1984) |
| 60 | Manitoulin lakes | Fish | Landbridge | 49 | 44 | 0.025 | 1 | Satellite | Harvey (1978) |
| 61 | ELA region | Fish | Landbridge | 147 | 34 | 0.388 | 1 | Uniform | Beamish et al. (1976) |
| 62 | Alberta lakes | Fish | Landbridge | 36 | 11 | 1 | 1 | Uniform | Robinson and Tonn (1989) |
| 63 | Gatineau park lakes | Fish | Oceanic | 45 | 31 | 0.005 | 0.001 | Bimodal | Chapleau et al. (1997) |
| 64 | Black and Hollow rivers | Fish | Oceanic | 52 | 30 | 0.001 | 0.001 | Bimodal | Jackson (1988) |
| 65 | Wisconsin lakes | Fish | Oceanic | 138 | 30 | 0.982 | 1 | Uniform | Rahel (1982) |
| 66 | Sea of Cortez | Herptiles | Landbridge | 8 | 52 | 0.009 | 0.004 | Bimodal | Murphy (1983) |
| 67 | Aegean islands | Herptiles | Landbridge | 91 | 35 | 0.001 | 0.001 | Bimodal | Foufopoulos and Ives (1999) |
| 68 | Central Amazon | Herptiles | Landbridge | 7 | 40 | 0.023 | 0.045 | Bimodal | Zimmerman and Bierregaard (1986) |
| 69 | Guam islets | Herptiles | Landbridge | 21 | 8 | 0.553 | 0.004 | Core | Perry et al. (1998) |
| 70 | Bass Strait | Herptiles | Landbridge | 10 | 17 | 0.687 | 0.008 | Core | Rawlinson (1974) |
| 71 | W Lake Erie, E N. America | Herptiles | Landbridge | 9 | 17 | 0.514 | 0.001 | Core | King (1988) |
| 72 | W Australia | Herptiles | Landbridge | 23 | 69 | 0.9 | 0.001 | Core | Kitchener et al. (1980a) |
| 73 | Lake Michigan, N. America | Herptiles | Landbridge | 9 | 10 | 0.804 | 0.161 | Uniform | Hatt et al. (1948) |
| 74 | Georgian Bay | Herptiles | Landbridge | 41 | 32 | 0.211 | 1 | Uniform | Nudds et al. (1996) |
| 75 | Pacific ocean islands | Herptiles | Oceanic | 30 | 100 | 0.005 | 0.001 | Bimodal | Adler et al. (1995) |
| 76 | Canary Is. | Herptiles | Oceanic | 7 | 14 | 0.327 | 0.003 | Core | Klemmer (1976) |
| 77 | California Channel Is. | Herptiles | Oceanic | 15 | 28 | 0.791 | 0.004 | Core | Savage (1967) |
| 78 | Sea of Cortez | Herptiles | Oceanic | 17 | 56 | 0.416 | 1 | Uniform | Murphy (1983) |
| 79 | California islands | Herptiles | Oceanic | 15 | 27 | 0.845 | 1 | Uniform | Wilcox (1980) |
| 80 | California Channel Is. | Herptiles | Oceanic | 8 | 12 | 0.745 | 0.13 | Uniform | Wilcox (1980) |
| 81 | Seychelles islands | Herptiles | Oceanic | 20 | 12 | 0.833 | 1 | Uniform | Gardner (1986) |
| 82 | Seychelles islands | Herptiles | Oceanic | 30 | 10 | 0.117 | 0.074 | Uniform | Gardner (1986) |
| 83 | Great Basin, W USA | Mammals | Landbridge | 19 | 15 | 0.001 | 0.021 | Bimodal | Brown (1978) |
| 84 | Penobscot Bay, Maine | Mammals | Landbridge | 7 | 32 | 0.025 | 0.001 | Bimodal | Crowell (1986) |
| 85 | American SW | Mammals | Landbridge | 28 | 26 | 0.001 | 0.001 | Bimodal | Lomolino et al. (1989) |
| 86 | Mindanao region, Phillippines | Mammals | Landbridge | 9 | 35 | 0.056 | 0.003 | Core | Heaney (1986) |
| 87 | S Rocky Mnts, USA | Mammals | Landbridge | 28 | 26 | 0.946 | 0.001 | Core | Patterson and Atmar (1986) |
| 88 | Thousand islands | Mammals | Landbridge | 18 | 10 | 0.704 | 0.006 | Core | Lomolino (1986) |
| 89 | Lake Michigan, N. America | Mammals | Landbridge | 12 | 28 | 0.388 | 0.001 | Core | Hatt et al. (1948) |
| 90 | Georgian Bay | Mammals | Landbridge | 35 | 32 | 0.902 | 0.001 | Core | Nudds et al. (1996) |
| 91 | W Australia | Mammals | Landbridge | 22 | 18 | 0.683 | 0.004 | Core | Kitchener et al. (1980b) |
| 92 | W and S Australia | Mammals | Landbridge | 26 | 49 | 0.608 | 1 | Uniform | Kitchener et al. (1980b) |
| 93 | Sea of Cortez | Mammals | Landbridge | 20 | 25 | 0.687 | 1 | Uniform | Lawlor (1983) |
| 94 | Bass Strait | Mammals | Landbridge | 10 | 10 | 0.109 | 0.18 | Uniform | Hope (1973) |
| 95 | Lake Michigan, N. America | Mammals | Landbridge | 14 | 9 | 0.661 | 1 | Uniform | Lomolino (1986) |
| 96 | Lake Huron islands | Mammals | Landbridge | 25 | 16 | 0.789 | 1 | Uniform | Lomolino (1994) |
| 97 | Great Basin/ montane islands | Mammals | Landbridge | 19 | 14 | 0.112 | 0.168 | Uniform | Cutler (1991) |
| 98 | Sea of Cortez | Mammals | Oceanic | 14 | 9 | 0.728 | 1 | Uniform | Lawlor (1983) |
| 99 | Georgian Bay | Plants | Landbridge | 15 | 78 | 0.011 | 0.012 | Bimodal | Nudds et al. (1996) |
| 100 | Georgian Bay | Plants | Landbridge | 16 | 114 | 0.001 | 0.001 | Bimodal | Nudds et al. (1996) |
| 101 | Iowa and Minnesota | Plants | Landbridge | 102 | 39 | 0.997 | 0.001 | Core | Glass 1998) |
| 102 | Illinois | Plants | Landbridge | 15 | 152 | 1 | 1 | Uniform | Clinebell (1920)(in Wright et al.) |
| 103 | Lesser Antilles (West Indies) | Plants | Oceanic | 12 | 102 | 0.008 | 0.001 | Bimodal | Beard (1948) |
| 104 | Lesser Antilles (West Indies) | Plants | Oceanic | 14 | 112 | 0.002 | 0.087 | Satellite | Beard (1948) |
| 105 | French Frigate Shoals, Hawaii | Plants | Oceanic | 8 | 40 | 0.018 | 0.059 | Satellite | Amerson (1971) |
| 106 | Hawaii | Plants | Oceanic | 6 | 66 | 1 | 0.088 | Uniform | Stone (1969) |
| 107 | W Australia | Plants | Oceanic | 49 | 147 | 1 | 1 | Uniform | Abbot and Black (1980) |
| 108 | Lesser Antilles (West Indies) | Plants | Oceanic | 9 | 23 | 0.171 | 0.148 | Uniform | Beard (1948) |

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