

Notes and Comments

Island Biogeography of Genes and Species

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Biodiversity is manifested at two fundamental levels: species diversity and genetic diversity. However, despite important advances in other areas of evolutionary and conservation biology that have resulted from integration of ecological and genetic perspectives (e.g., Real 1994; Young and Clarke 2000), these two levels of diversity have traditionally remained the exclusive domains of community ecology and population genetics, respectively. A number of authors have noted strong parallels between the processes and concepts underlying theories of species diversity and genetic diversity (e.g., Harper 1977; Antonovics 1978; Huston 1994; Amarasekare 2000; Hubbell 2001), but the question of whether parallel process has led to parallel pattern has yet to be explored in a rigorous way. If there is generally a positive correlation between species diversity and genetic diversity, then the parallels between ecological and genetic theories not only may be of heuristic value but also may point to the potential for theories of biodiversity to be unified across organizational levels. This note is an exploration of the hypothesis that a common set of underlying processes results in correlated patterns of species diversity and genetic diversity (within species).

Johnson (1973), in the only study whose primary focus was the relationship between species diversity and genetic diversity, predicted and reported a negative correlation between species diversity and the number of alleles at six allozyme loci for *Drosophila* species on four Hawaiian is-

lands. The prediction was based on the logic that in more stable environments, species diversity should be high because productivity is high and genetic diversity should be low because stability promotes specialization (Johnson 1973). Unfortunately, the negative correlation was an artifact of the method of calculating genetic diversity. By summing the number of alleles across species on each island (with alleles counted once if shared across species) and then dividing by the number of species sampled (with more species sampled on the more species-rich islands), a negative correlation with species diversity was produced despite nearly identical curves of the accumulation of alleles as species are sampled on each island (see app. A in the online edition of the *American Naturalist*). A reanalysis of the data using rarefaction (sensu Gotelli and Colwell 2001) to control for the number of species sampled per island revealed no relationship between the two levels of diversity (app. A).

Hundreds of studies have explored the correlates of within-population genetic diversity at allozyme loci, and occasionally such studies have included species diversity as a candidate variable. For example, allozyme heterozygosity in the lizard *Uta stansburiana* was found to be positively correlated with the number of species of Iguanidae among islands in the Gulf of California (Soulé and Yang 1973). This result was interpreted as evidence that the intensity of interspecific competition (as estimated by the number of co-occurring iguanids) was proportional to the strength of balancing selection on allozyme polymorphisms and therefore heterozygosity. In populations of the salamander *Desmognathus fuscus* in eastern North America, Karlin et al. (1984) found that allozyme heterozygosity was negatively correlated with the number of co-occurring congeners. This result was interpreted as support for the hypothesis that interspecific interactions decrease niche width via directional selection, thereby decreasing genetic diversity. Both of these post hoc interpretations assume a direct influence of the number of co-occurring species on within-population genetic variation; that is, they assume a causal relationship between species diversity and genetic diversity. They also assume that allozyme polymorphisms

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are not only under selection but also under an identical mode of selection across loci. Although there are many clear examples of selection on allozyme variation (Mitton 1997), the effects are invariably locus and taxon specific, leading the majority of authors in the recent literature to favor the assumption of selective neutrality when interpreting empirical patterns of allozyme variation.

Here I propose the hypothesis that species diversity and genetic diversity (within single species) should be positively correlated among islands or habitat patches as the result of processes that influence the two levels of diversity in parallel ways. The hypothesis is based on two of the most prominent theories of island diversity, MacArthur and Wilson's (1967) theory of island biogeography and Sewall Wright's (1940) island model of population genetics. While the mathematical details behind these two theories are quite different, the underlying logic is nearly identical. The theory of island biogeography posits a balance between rates of colonization and local extinction in regulating species diversity, much as Wright's model posits a balance between rates of gene flow and genetic drift in regulating genetic diversity. Small populations on small islands experience high rates of both local extinction and genetic drift. On isolated islands, few migrants arrive over any given time interval, so rates of both colonization (the arrival of new species) and gene flow are relatively low. We therefore predict that diversity should be greatest on large islands that are close to potential sources of colonists and lowest on small isolated islands. This theoretical framework has been used to interpret patterns of either species or genetic diversity in hundreds of studies (Rosenzweig 1995; Frankham 1996, 1997), but it is not until we consider the two levels of diversity simultaneously that a novel prediction arises: we should expect to find a positive correlation between species diversity and genetic diversity across islands. I term this the species-genetic diversity correlation (SGDC).

In this note, I first test for positive SGDCs in 14 data sets compiled from the literature on birds, reptiles, mammals, and plants in a variety of archipelagos. I then test the relative roles of island area and isolation in driving positive SGDCs and the relative importance of first-order correlations (area or isolation \times species diversity or genetic diversity) in driving variation among systems in the magnitude of the SGDC.

Methods

Species diversity is defined here as the number of species in a given taxon (e.g., birds or plants) on each island in an archipelago; genetic diversity is defined as heterozygosity (or some similar measure) estimated for one or more traits (typically molecular-marker variants) in sam-

ples of individuals of one species on each of the same islands. Fourteen data sets were compiled from the literature to test for a positive correlation between species and genetic diversity across islands and to test for the respective influences on the SGDC of island area and isolation (table 1). Island areas were obtained either from the publications in table 1 or from scanning maps and estimating island areas in ArcGIS 8.1 (ESRI, Redlands, Calif.).

Electronic literature searches and compilations of genetic studies on islands (Frankham 1996, 1997) were used to find studies reporting molecular-marker variation within one species on at least five islands per archipelago. One study (Avice et al. 1974) was included in which populations of *Peromyscus* mice in Baja, California, were considered distinct as either subspecies or species on different islands, although the genetic evidence suggested that a single gene pool was shared among islands. If data were reported for more than one subpopulation on a given island, data were combined and considered as one population. Once genetic data were found, additional electronic literature searches and several data compilations (Simberloff 1970; Connor and McCoy 1979; Wright 1981; Lomolino and Weiser 2001) were used to look for corresponding species diversity data. Many genetic studies were excluded because corresponding species diversity data were not found, data were not presented on a per island basis, or too few islands were sampled per species.

For all data sets, species diversity on each island is the number of species present in the group of interest (birds, reptiles [or *Anolis* spp.], mammals, or plants). For one data set (Caribbean *Anolis* lizards), species diversity was log transformed before data analysis to linearize relationships with area and isolation. In seven of the 14 genetic studies, genetic diversity was calculated as expected heterozygosity (H_e) based on Hardy-Weinberg equilibrium at multiple allozyme loci. Four additional allozyme data sets included only observed heterozygosity, H_o (table 1). In the one case where data for more than one class of molecular marker were reported (Wayne et al. 1991), I favored minisatellite DNA data over allozyme or mitochondrial DNA (mtDNA) data because only four polymorphic allozyme loci with very low overall variability were studied and because mtDNA data effectively represent only one locus. For both Wayne et al. (1991) and Degnan (1993), the proportion of dissimilar minisatellite bands among individuals within islands was used as a measure of genetic diversity, and in Seutin et al. (1994) mtDNA haplotype diversity was used.

For most data sets, island isolation was measured in two ways: distance to the mainland and distance to the nearest island or mainland. When measures of isolation were not provided in the genetic or species diversity publications, I either retrieved data from related papers or reviews (Soulé

Table 1: Fourteen data sets with which a positive species-genetic diversity correlation (SGDC) was tested

Study	Place	Species pool	Species for genetic analysis	Molecular markers	No. islands	Max. SD	No. variable loci/bands ^a	Genetic reference	Species reference
A	Canary Islands	Plants	<i>Lobularia canariensis</i>	Az H_c	6	1,079	9	Borgen 1996	Lems 1960
B	Galápagos	Plants	<i>Gossypium darwinii</i>	Az H_c	6	481	23	Wendel and Percy 1990	Yeakley and Weishampel 2000
C	Gulf of California	Reptiles	<i>Uta stansburiana</i>	Az H_o	14	13	≥12	Soulé and Yang 1973	Wright 1981
D	Caribbean	<i>Anolis</i> lizards	<i>Anolis cristatellus</i>	Az H_c	7	10	16	Gorman et al. 1980	Rand 1969
E	Baja California	Mammals	<i>Peromyscus</i>	Az H_o	8	7	25 ^b	Avise et al. 1974	Lawlor 1986
F	British Isles	Mammals	<i>Mus musculus</i>	Az H_c	11	9	8	Berry and Peters 1977	Arnold 1993
G	California Channel	Mammals	<i>Peromyscus maniculatus</i>	Az H_c	8	5	23	Gill 1980	Lawlor 1986
H	California Channel	Mammals	<i>Urocyon littoralis</i>	Minisat	6	5	27.1 ^c	Wayne et al. 1991	Lawlor 1986
I	Gulf of Maine	Mammals	<i>P. maniculatus</i>	Az H_c	5	17	9	Aquadro and Kilpatrick 1981	Crowell 1986
J	Canary Islands	Birds	<i>Fringilla coelebs</i>	Az H_c	6	53	22	Baker et al. 1990	Bacallado 1976
K	Galápagos	Birds	<i>Geospiza fuliginosa</i>	Az H_o	10	20	12	Yang and Patton 1981	Harris 1973
L	Galápagos	Birds	<i>Geospiza fortis</i>	Az H_o	8	20	12	Yang and Patton 1981	Harris 1973
M	Great Barrier Reef	Birds	<i>Zosterops lateralis</i>	Minisat	7	16	6.8 ^c	Degnan 1993	Kikkawa 1976
N	West Indies	Birds	<i>Coereba flaveola</i>	mtDNA	7	66	43 ^d	Seutin et al. 1994	Wright 1981

Note: Mammals include only nonvolant terrestrial mammals, and plants include only vascular plants. Az = allozymes, H_c = expected heterozygosity, H_o = observed heterozygosity, mtDNA = mitochondrial DNA, Minisat = minisatellites.

^a Total number of haplotypes observed for mtDNA and the maximum value (among populations) of mean number of bands scored per individual for Minisat.

^b Total number of loci (proportion variable not reported).

^c Maximum of the mean numbers of bands scored for individuals in any one population (overall number not reported).

^d Number of different haplotypes.

1972; Lawlor 1986) or analyzed digitized maps in ArcGIS 8.1. For the Caribbean islands sampled for *Anolis* lizards (table 1), the largest of the islands (Puerto Rico, ~9,000 km²) is effectively the “mainland” relative to some of the smaller islands (<1 km²), and most islands are in very close proximity to at least some other very small islands. In this case, only one measure of isolation was calculated: the distance to the nearest island at least half the area of the target island. For the British Isles, where many very small islands are in close proximity to larger islands, I calculated the distance to the nearest island at least half the area of the target island or to the mainland as well as distance to the British mainland. For the Galápagos Islands, the distance to the South American mainland is sufficiently far that variation among islands in this quantity is irrelevant. For the three Galápagos Island data sets, two measures of isolation were calculated: the distance to the nearest island and the number of islands with straight-line overseas connections with the target island (see Yeakley and Weishampel 2000 for the latter measure). For the Australian reef islands, distance to the mainland was the only measure of isolation used because of the very small area and wide spacing of the islands.

For each data set, I conducted a one-tailed test for a significant positive correlation between species diversity and genetic diversity with Pearson’s product moment correlation. Because each data set included only 5 to 14 islands (median = 7; see table 1), the power of individual tests was relatively low. As an overall test for a significant positive SGDC, I conducted a one-tailed *t*-test on the 14 correlation coefficients, with studies weighted according to the inverse of the variance of the correlation coefficient (Gurevitch and Hedges 1999). Because these analyses, and those described below, were largely exploratory, no corrections were made for multiple statistical tests on the same data. Interpretations and conclusions were largely based on the composite tests across the 14 data sets rather than individual correlation coefficients.

To test the importance of area and isolation in driving positive SGDCs, I used partial correlation analyses. If the partial correlation between species diversity (SD) and genetic diversity (GD) with area (A) held constant, $r(\text{SD} \times \text{GD}|\text{A})$, is consistently lower than the same correlation with isolation (I) held constant, $r(\text{SD} \times \text{GD}|\text{I})$, then area is the more important driver of the SGDC (and vice versa). As well, if $r(\text{SD} \times \text{GD}|\text{A}, \text{I})$ is significantly >0,

processes unrelated to island area or isolation contribute to the SGDC. In addition to testing the significance of each partial correlation, I conducted weighted one-tailed t -tests for the hypotheses that the mean of each partial $r = 0$ across the 14 data sets (with weights proportional to the inverse variance of r) and a paired t -test for the difference between $r(\text{SD} \times \text{GD}|\text{A})$ and $r(\text{SD} \times \text{GD}|\text{I})$. For these analyses, I used either untransformed or log-transformed area values for each data set, with the choice based on which of the two was more strongly correlated with species and genetic diversity. As a measure of the strength of the correlation of area with species diversity and genetic diversity, I calculated the product of the two correlations: $r[\text{A (or log A)} \times \text{SD}] \times r[\text{A (or log A)} \times \text{GD}]$.

The same procedure as described for area was used to choose a measure of isolation from four possibilities (two untransformed and two log transformed), with one exception. In the Canary Island bird data set, all measures of isolation were poorly correlated with genetic diversity ($|r| < 0.25$), and the largest product of univariate correlations was -0.005 (0.24 for $\text{GD} \times -0.02$ for SD , using untransformed distance to the nearest island). For this study I chose to use log distance-to-mainland as the isolation measure because it showed a fairly strong negative correlation with SD (-0.54) despite a low correlation with GD (0.1) and slightly lower correlation product (-0.05) than untransformed distance to the nearest island. Ultimately, the choice of isolation measures did not influence the conclusions drawn from this analysis.

To the extent that island area and isolation influence diversity, variation in the strength of the SGDC among systems should be a function of four “first-order” correlations: $r(\text{SD} \times \text{A}|\text{I})$, $r(\text{GD} \times \text{A}|\text{I})$, $r(\text{SD} \times \text{I}|\text{A})$, and $r(\text{GD} \times \text{I}|\text{A})$. To explore which of these was most important in driving variation among the 14 studies in the strength of the SGDC, I conducted a stepwise multiple regression analysis. The four bivariate correlation coefficients and all two-way interactions were included as candidate variables for predicting SGDC in the model, with $P < .05$ allowing entry into the model (SAS PROC REG, SAS Institute, Cary, N.C.).

Results and Discussion

The species-genetic diversity correlation (SGDC) was generally positive, although its magnitude varied considerably among systems. In 13 of the 14 data sets, a positive SGDC was found, with five of these significant at $P < .05$ and an additional three significant at $P < .1$ (figs. 1, 2; see app. B in the online edition of the *American Naturalist*). The median and weighted mean correlation coefficients were 0.63 and 0.56 , respectively, and the weighted mean correlation

was significantly >0 ($t = 8.1$, $P < .0001$). For each major taxon (birds, reptiles, mammals, and plants), at least one correlation >0.6 was found. Thus, despite a myriad of factors that can potentially influence species diversity and genetic diversity, it appears that such factors act in sufficient parallel at the two levels to produce correlated patterns that generalize across taxa and archipelagos. The SGDC hereby joins a number of other general patterns, such as the species-area, species-energy, and species-latitude relationships, whose examination forms the basis for understanding global biodiversity (Gaston 2000).

The mean partial correlation between species diversity and genetic diversity was significantly >0 when controlling for area (weighted mean $r[\text{SD} \times \text{GD}|\text{A}] = 0.26$, $t = 2.5$, $P = .01$), isolation (weighted mean $r[\text{SD} \times \text{GD}|\text{I}] = 0.45$, $t = 5.8$, $P < .0001$), or both (weighted mean $r[\text{SD} \times \text{GD}|\text{A}, \text{I}] = 0.17$, $t = 1.89$, $P = .04$; see app. B; see also fig. 2). However, $r(\text{SD} \times \text{GD}|\text{A})$ was significantly lower than $r(\text{SD} \times \text{GD}|\text{I})$ (mean difference = 0.25 , $t = 2.45$, $P = .03$). The strong reduction in the magnitude of the SGDC when area was controlled for indicates that island area was the dominant variable with parallel effects on species diversity and genetic diversity in these studies. Because multiple measures of isolation were initially tested as predictors of diversity and the best one was then selected for further analysis, the lack of a strong isolation effect is probably quite robust. Whether the particular processes through which area influences diversity (e.g., extinction/drift or habitat diversity/diversifying selection) are of equal importance at the two levels of diversity remains an open question. In addition, the persistence of significant positive SGDCs in the partial correlation analyses suggests that both levels of diversity are sometimes influenced in parallel by processes unrelated to island area or isolation. Thus, the parallels between community ecology and population genetics extend beyond the analogy described for the theories of MacArthur and Wilson (1967) and Sewall Wright (1940). This opens a broad scope of opportunities, both theoretical and empirical, for further exploring the correlates and causes of the SGDC.

Because strong, positive species-area relationships are virtually universal, when genetic diversity is also positively correlated with island area, a positive SGDC obtains (fig. 2). In the stepwise multiple regression analysis predicting variation among studies in the magnitude of the SGDC, the only significant predictor variable was the partial correlation of genetic diversity and area, $r(\text{GD} \times \text{A}|\text{I})$. The weighted mean $r(\text{GD} \times \text{A}|\text{I})$ was 0.46 , and this variable alone explained 75% of the variance among studies in the magnitude of the SGDC ($P < .0001$; fig. 3). It is important to note that this does not mean that the species-area correlation is somehow less important than the genetic diversity–area correlation in producing SGDCs; however,

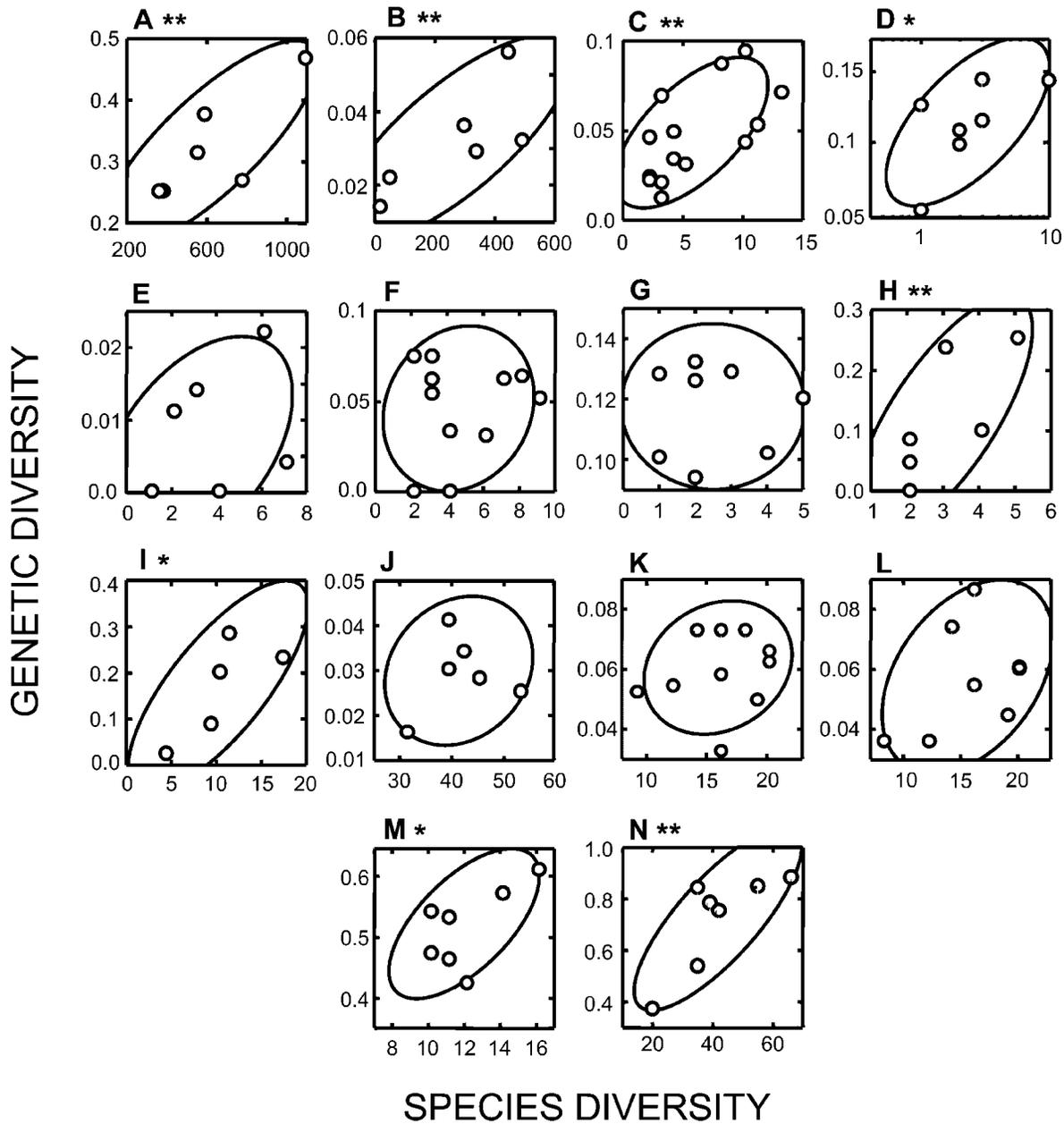


Figure 1: Relationships between species diversity and genetic diversity in 14 studies on oceanic islands (letters correspond to those in table 1). Gaussian confidence ellipses (drawn in SYSTAT version 7.0, SPSS, Chicago) indicate the direction of covariance between the two variables (by their orientation) and the strength of the relationship (by their breadth). Asterisks indicate significant correlations (one asterisk, $P < .1$; two asterisks, $P < .05$).

because there is so little variation in the magnitude of $r(\text{SD} \times \text{A}|\text{I})$ (it is always strong), variation in the magnitude of the SGDC is explained largely by variation in $r(\text{GD} \times \text{A}|\text{I})$. The partial correlation of species diversity with area, $r(\text{SD} \times \text{A}|\text{I})$, was strongly positive in all studies (weighted mean = 0.87), and the partial correlation of

isolation with species diversity, $r(\text{SD} \times \text{I}|\text{A})$, tended to be negative (weighted mean = -0.45) though quite variable among studies (fig. 2). There was no consistent correlation between genetic diversity and isolation (weighted mean $r[\text{GD} \times \text{I}|\text{A}] = -0.03$; fig. 2).

Because the magnitude of the SGDC ultimately depends

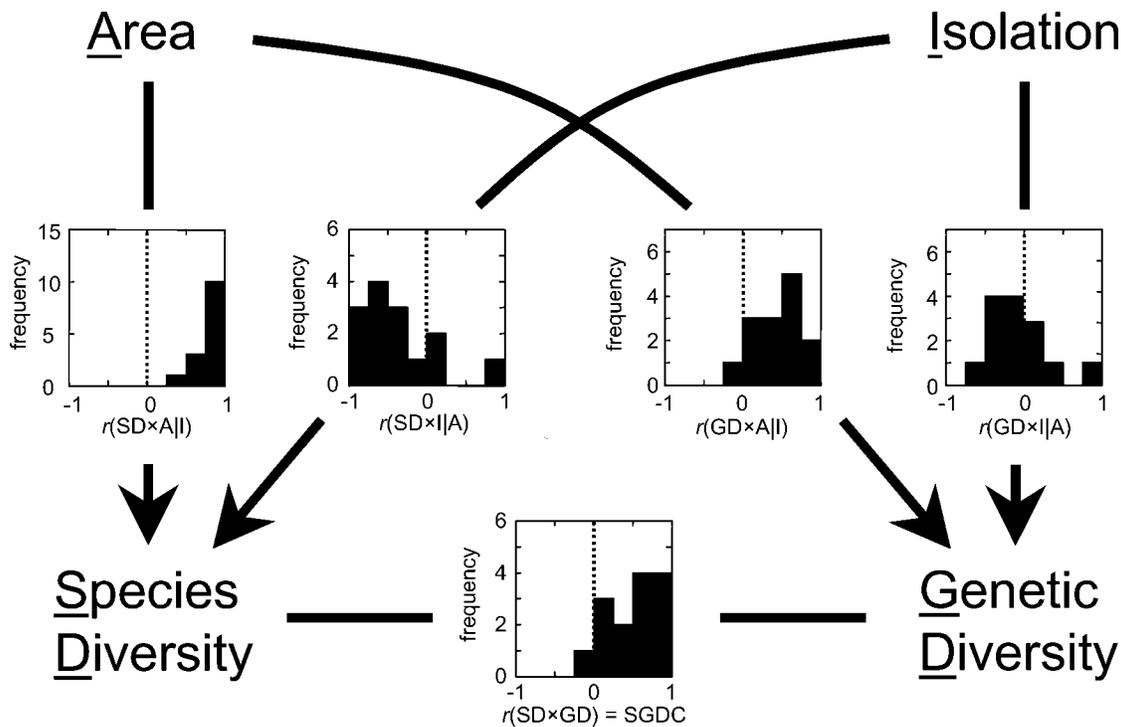


Figure 2: Empirical data on the influence of island area (A) and isolation (I) on species diversity (SD), genetic diversity (GD), and the species-genetic diversity correlation (SGDC). Histograms display the frequency distributions ($n = 14$) of (partial) correlation coefficients between the two variables at either end of the arrow.

on the strength of $r(GD \times A | I)$, the characteristics of the species used in genetic analysis (e.g., dispersal ability, abundance) should be critical to determining the strength of the SGDC. For example, high gene flow among islands may prevent genetic drift from reducing diversity in small populations. To explore this issue, it is tempting to look at differences among taxa (e.g., dispersal capacity is high in birds vs. low in plants), but for the most part different taxa were sampled on different archipelagos, which invalidated such comparisons. Even where there are data sets for multiple taxa (Galápagos and Canary Islands), the individual islands on which the two taxa were sampled were not the same. An in-depth consideration of processes underlying the SGDC is beyond the scope of this note, but as more data accumulate on patterns of island diversity, comparative analyses of the SGDC among taxa with different traits may prove a promising avenue of research.

Some evidence suggests that the generality of the SGDC extends beyond true islands to include habitat islands in naturally fragmented landscapes. For nine discrete wetlands in subarctic Canada sampled by Vellend and Waterway (1999), there was a strong positive correlation between the number of vascular plant species and allozyme heterozygosity in the sedge *Carex rariflora* ($r = 0.81$,

$P = .004$). Among five montane headwater streams in Panama, the number of frog species correlated positively with mtDNA haplotype diversity in a Neotropical glass frog, *Centrolenella prosoblepon* ($r = 0.65$), although the correlation was not significant ($P = .12$; J. M. Robertson and K. R. Lips, personal communication). In Frankham's (1996) review, positive correlations between genetic diversity and area (suggesting the likelihood of positive SGDCs) were listed for two species of bird among natural patches of cloud forest in Mexico ($r = 0.20$ and 0.60 ; Peterson et al. 1992) and for one butterfly species among montane habitat patches in southern France ($r = 0.83$; Descimon and Napolitano 1993). To my knowledge, the only convincing example of a significant negative SGDC is for 27 populations of *Desmognathus fuscus*, among which H_0 decreased from about 0.06 when only one congener was present to <0.01 when four congeners were present (Karlin et al. 1984). These data suggest that naturally fragmented habitats show a pattern similar to that for true islands, with a generally positive, but quite variable, SGDC. Whether the SGDC applies to landscapes fragmented by human activity is an open question for empirical testing.

The strong similarities between theories of species diversity and genetic diversity are well recognized. As a point

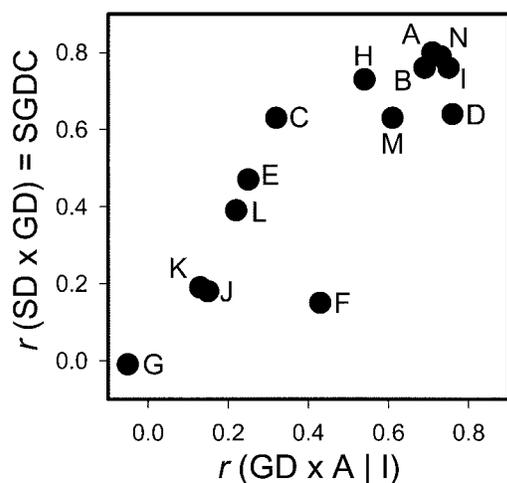


Figure 3: Relationship between the partial correlation of genetic diversity (GD), with area (A) controlling for isolation (I), $r(\text{GD} \times \text{A} | \text{I})$, and the species-genetic diversity correlation (SGDC). Letters correspond to those in table 1 and figure 1.

of departure, study of the SGDC focuses attention on the points of contact between the processes that influence both levels of diversity (see also Amarasekare 2000) and calls for a cross-disciplinary approach to biodiversity research. Unified models that address both levels of diversity simultaneously are now needed to understand the factors that drive variation among systems in the strength of the SGDC.

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