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MULTIPLE SOURCE POOLS AND DISPERSAL BARRIERS FOR GALÁPAGOS PLANT SPECIES DISTRIBUTION

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Abstract. We reexamined geographic factors explaining the number of plant species on islands in the Galápagos Archipelago. We hypothesized that plant species richness (S) was related to the number of source pools and that plant species dispersal preferentially followed direct, oceanic pathways. To test different dispersal pathways from multiple source pools, the total number of islands within a given dispersal radius (i) was posed as the sum of the number of line-of-sight islands (C_i) and of the number of islands without line-of-sight connection (B_i). In partial regression analyses, controlling for nearest island area (A_2) and for recipient island elevation (E) and area ($\ln A$), C_i and $C_i \times E$ were found to be positively correlated with S in the Galápagos for nearly all dispersal ranges from 10 km to 419 km (maximum inter-island separation). In contrast, $B_i \times E$ was negatively correlated with S at the longest dispersal ranges. The connectivity index, C_i , multiplied by elevation, E , explained more variation in S in the Galápagos than prior regression models using additive forms of E , $\ln A$, A_2 , and isolation from the central island. Using the variables $C_i \times E$ and $\ln A$, multiple-regression models explained >90% of the variance in both endemic and total plant species richness in the Galápagos Archipelago.

Key words: connectivity and species number; dispersal barriers, plant; elevation barriers to dispersal; extinction; Galápagos Archipelago; habitat diversity; immigration; island biogeography; oceanic pathways of plant dispersal; plant species richness; source pools and plant species richness; species dispersal in archipelagos.

INTRODUCTION

The number of species (S) present on an island has been depicted as a state variable having inputs of new species by immigration and outputs of occupant species by extinction. The rates of immigration and extinction are typically depicted as functions of S , the island area (A) and the distance (D) of the island from sources of new species (Pielou 1979). Immigration rates decrease with D and S and increase with A . Extinction rates decrease with A and increase with S and D . S has been hypothesized to approach an equilibrium value at which the immigration rate equals the extinction rate (Preston 1962, MacArthur and Wilson 1967, Brown and Lomolino 1989).

Estimation of S from geographic factors in archipelagos has been a focus of ecological studies for decades (Hamilton et al. 1963, Lomolino 1986). Generally, A has been found as the most significant determinant of S . Indices of isolation and/or additional measures of habitat diversity (such as elevation), however, have also been found significant (Johnson and Raven 1973, Wilcox 1978, Dueser and Brown 1980, Heaney 1984). Geographic isolation has been shown to affect both species richness and composition (Power 1975, Kadmon and Pulliam 1993).

The Galápagos Archipelago has been a test site for

ideas related to island biogeography theory. Because it is a relatively clumped and isolated archipelago, differential effects of D from the South American mainland on individual islands are generally considered negligible. Plant species number has been repeatedly analyzed using multiple regression on geographic measures such as island area (A), elevation (E), area of the nearest island (A_2), and isolation distance (D) (Hamilton et al. 1963, Johnson and Raven 1963, Simpson 1974, Connor and Simberloff 1978, van der Werff 1983), with E and $\ln A$ most correlated with total and endemic species number.

Multiple source pools

We hypothesize if a recipient island is within species dispersal range of more than one source island, additional source(s) of new individuals should increase the immigration rate and decrease the extinction rate. Any source *within* dispersal range should potentially contribute propagules directly to the recipient island. As a result, each additional source island within dispersal range increases the probability of new and direct arrivals on the recipient island. That is, the immigration rate should increase with the number of source islands. An increasing number of immigration sources should also reduce the extinction rate via the rescue effect (Brown and Kodric-Brown 1977). Studies have shown, for example, that patch connectivity may reduce the extinction rate (Fahrig and Merriam 1985). At equilib-

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TABLE 1. Geographic variables used to predict number of total species (S_t) and endemic species (S_e).

Island	$S_t^{\dagger, \ddagger}$	S_e^{\S}	A^{\S} (km ²)	E^{\dagger} (m)	A_2^{\S} (km ²)	C_{50}	B_{50}	C_{125}	B_{125}	C_{419}	B_{419}
Baltra	58	23	25.09	150	1.84	8	3	14	12	16	12
Bartolomé	31	21	1.24	109	572.33	6	3	9	15	11	17
Caldwell	3	3	0.21	114	0.78	3	2	10	12	11	17
Champion	25	9	0.10	46	0.18	4	1	14	8	16	12
Coamaño	2	1	0.05	10	903.82	2	6	12	13	12	16
Daphne Major	28	11	0.34	10	1.84	7	3	11	14	13	15
Darwin	10	7	2.33	168	2.85	1	0	1	0	17	11
Eden	8	4	0.03	10	17.95	6	5	9	16	9	19
Enderby	2	2	0.18	112	0.10	5	0	17	5	18	10
Española	100	26	58.27	198	0.57	2	0	13	3	19	9
Fernandina	160	35	634.49	1494	4669.32	1	0	1	12	3	25
Gardner 1	40	17	0.57	49	58.27	2	0	12	1	21	7
Gardner 2	5	4	0.78	227	0.21	4	1	15	7	18	10
Genovesa	41	19	17.35	76	129.49	1	0	12	2	21	7
Isabela	435	89	4669.32	1707	634.49	7	1	19	3	25	3
Marchena	47	23	129.49	343	59.56	2	0	11	4	17	11
Onslow	2	2	0.01	25	0.10	4	2	14	8	16	12
Pinta	165	37	59.56	777	129.49	1	0	9	4	16	12
Pinzon	117	33	17.95	458	0.03	9	2	16	8	18	10
Las Plazas	21	9	0.23	10	25.09	4	3	14	10	15	13
Rabida	75	30	4.89	367	572.33	8	1	14	9	15	13
San Cristóbal	329	65	551.62	716	0.57	3	0	14	4	22	6
San Salvador	282	81	572.33	906	4.89	9	0	17	6	20	8
Santa Cruz	481	95	903.82	864	0.52	14	0	25	1	27	1
Santa Fé	70	28	24.08	259	0.52	4	2	16	8	17	11
Santa Maria	288	73	170.92	640	0.10	7	0	17	5	20	8
Seymour	46	16	1.84	100	25.09	8	2	14	11	17	11
Tortuga	16	8	1.24	186	17.95	3	0	11	9	15	13
Wolf	22	12	2.85	253	2.33	1	0	1	0	19	8

Notes: Geographic variables are defined as follows: A = area of island, A_2 = area of nearest island, B_i = number of islands without line-of-sight connection within a radius of i km, C_i = number of islands directly connected within a radius of i km, and E = elevation.

\dagger Connor and Simberloff (1978).

\ddagger van der Werff (1983).

\S Johnson and Raven (1973).

rium, the presence of multiple source pools should yield a higher S .

Isolation of individual Galápagos islands has been represented by variables including distance to nearest island, distance to the central island of the archipelago, and distance to Ecuador or larger islands such as Santa Cruz or Isabela (Johnson and Raven 1973, Simpson 1974). Although previous regression models have included up to three additive single-distance isolation terms, no prior independent variable has accounted for the effect of multiple sources on the probability of immigration for each island. As Connor and Simberloff (1978:221) noted on existing single-distance approaches to account for the effect of isolation in predicting species number in the Galápagos Islands, "the correlation between the frequency of immigration or 'immigration rate' and isolation is vitiated by multiple variable-sized source pools . . ."

Elevational barriers to dispersal

Over long distances, intervening islands with suitable habitat may provide stepping stones that facilitate plant species dispersal (MacArthur and Wilson 1967). In the Galápagos, however, we hypothesize that tightly clumped, high-elevation islands may provide barriers to dispersing plants. The Galápagos are of relatively

recent volcanic origin, with larger islands characterized by elevations up to 1707 m. Average peak elevation among islands is 358 m (Table 1). As a result of steep volcanic landforms and climatic effects, habitat conditions for plant establishment vary greatly with elevation (van der Werff 1983). We hypothesize that widely varying habitat conditions along elevational gradients inhibit the stepping-stone effect, as dispersal throughout, or across, a given island might be precluded due to large shifts in moisture, temperature, or edaphic conditions along elevational gradients.

The Galápagos have received most plant-species introductions by avifaunal transport (up to 60%), including fruits, seeds, or vegetative disseminules carried internally or attached externally (Porter 1976). Other significant mechanisms of plant-species introduction occur via wind (4–31%) and oceanic drift (9–23%) (Carlquist 1974, Porter 1976). These proportions contrast with locations where water-borne transport is the most important dispersal mechanism, such as the Great Lakes (Morton and Hogg 1989). Dispersal by passive mechanisms, such as via wind and water, should follow direct, oceanic connections, with islands forming barriers to further plant-propagule movement (Morton and Hogg 1989).

For active transport via avifauna, islands with sig-

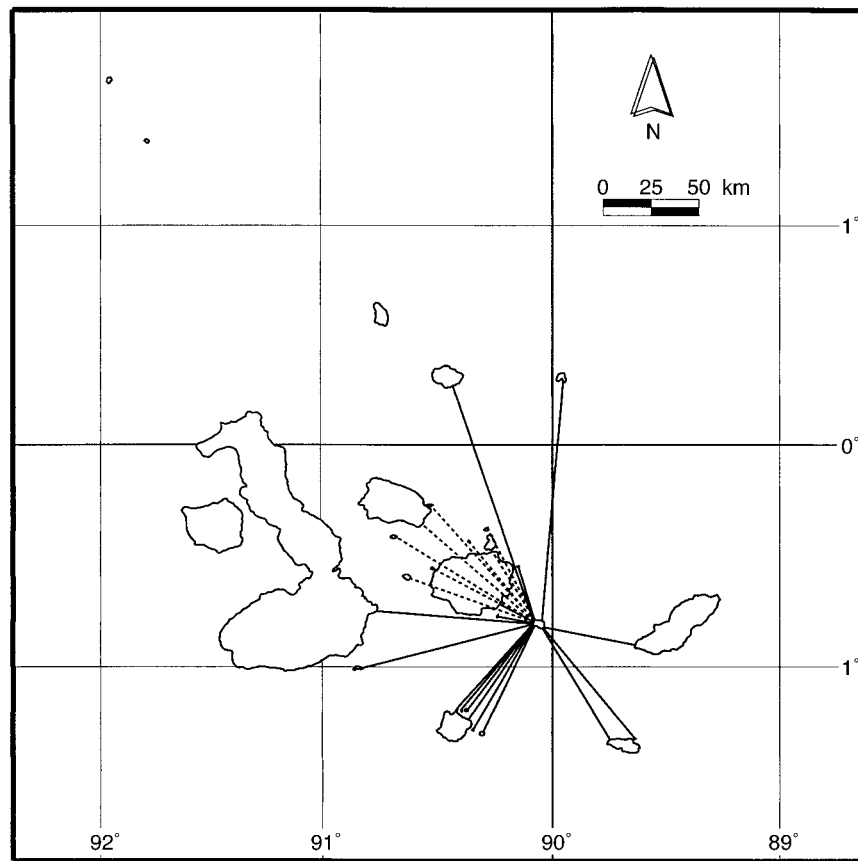


FIG. 1. The Galápagos Archipelago, including an example of the connectivity (C_i) and barrier (B_i) indices for a dispersal range (i) of 125 km for the island Santa Fé. Solid lines represent line-of-sight connections with source islands; dashed lines represent barred islands, or islands without line-of-sight connection.

nificant elevations may constrain avian movement and thus dispersal of plant propagules either via egestion or physical detachment after flight. Avian species in archipelagos may differ in dispersal characteristics and with isolation (Power 1975, Diamond et al. 1976). High terrain constitutes physical boundaries for many species, constraining home ranges. While varying habitat and energy requirements among species affect flight paths, direct connections among islands should help account for flight corridors. Plant dispersal via avian transport thus would also follow direct, oceanic connections.

We propose a simple index of connectivity (C_i) to help account for plant-species dispersal in the Galápagos. C_i tallies the number of source islands that are directly connected, i.e., where a straight, line-of-sight, oceanic path exists between source and recipient islands (i.e., nodes, [Chen 1971]), to the recipient island at sea level within some radial dispersal distance i (Fig. 1). We use C_i to represent the degree of connectivity of each island to source islands within a given dispersal range (i). The index C_i assumes equal influence of directly connected source pools; that is, C_i is independent of differential contributions from source pools related

to source-island size, elevation, or distance from the source island within the radial distance. To test this index, we pose the total number of islands (N_i) within a given dispersal radius (i) as the sum of the number of line-of-sight islands (C_i) and of the number of islands without line-of-sight connection (B_i). We report results of regression analyses using C_i as a measure of the effect of multiple source pools for both total (S_i) and endemic (S_e) plant species number in the Galápagos Archipelago.

METHODS

We used geographic variables from prior studies as well as indices of multiple sources described above. These variables included area (A) and elevation (E) of a recipient island, distance to nearest island (D_1), distance to the central island, Santa Cruz (D_2), and area of adjacent island (A_2) (Johnson and Raven 1973, Connor and Simberloff 1978). Total number of islands (N_i), connectivity indices (C_i) and barrier indices (B_i) were determined for dispersal ranges of $i = 10, 20, 30, 40, 50, 75, 100, 125, 150, 175, 200, 300,$ and 419 (maximum inter-island separation) km (Table 1). Distance and connectivity among islands were measured from

TABLE 2. Pearson correlation-coefficient matrix for the dependent variables S_t (total species richness) and S_e (endemic species richness) plus independent geographic variables from prior studies and new independent variables that account for multiple source pools. Significant correlations ($P < 0.05$) are shown in bold.

	S_e	E	$\ln(A)$	D_1	D_2	A_2	C_{50}	C_{125}	C_{419}	$C_{50} \times E$	$C_{125} \times E$	$C_{419} \times E$
S_t	0.98	0.81	0.81	0.00	-0.17	0.10	0.50	0.51	0.57	0.89	0.91	0.90
S_e		0.79	0.85	0.00	-0.18	0.07	0.53	0.51	0.57	0.89	0.90	0.88
E			0.82	0.01	0.01	0.53	0.20	0.13	0.20	0.74	0.79	0.83
$\ln(A)$				0.25	0.06	0.25	0.23	0.22	0.43	0.67	0.72	0.75
D_1					0.61	-0.12	-0.50	-0.38	0.23	-0.22	-0.10	0.01
D_2						0.05	-0.62	-0.70	0.06	-0.26	-0.22	-0.09
A_2							-0.21	-0.41	-0.57	0.02	-0.03	0.02
C_{50}								0.70	0.32	0.68	0.53	0.40
C_{125}									0.61	0.61	0.59	0.46
C_{419}										0.58	0.62	0.60
$C_{50} \times E$											0.95	0.90
$C_{125} \times E$												0.98

Notes: Independent geographic variables from prior studies: A = area of island, A_2 = area of nearest island, D_1 = distance to nearest island, D_2 = distance to the central island (Santa Cruz), and E = elevation. New independent variables: C_i = connectivity index for dispersal radius of i km (i.e., number of source islands with line-of-sight connection within a radius of i km), $C_i \times E$ = interaction term of connectivity index and elevation for dispersal radius of i km.

operational navigation charts (ONC M-24 and L-25 [Defense Mapping Agency, Saint Louis, Missouri, USA], January 1990), at scale 1:1 000 000. Measurement error at this scale was ~ 1 km. N_i , C_i and B_i were used alone and combined with measures of recipient-island habitat diversity, e.g., $C_i \times E$ and $C_i \times A$.

Although Galápagos flora are constantly being updated (e.g., Adersen 1989), for continuity with past regression analyses we used total species richness (S_t) from Connor and Simberloff (1978), as updated by van der Werff (1983). We used endemic species richness (S_e), where endemism is for the entire archipelago, from Johnson and Raven (1973). We determined correlations among geographic variables and plant species number. Partial regression analyses were used to test relative contributions of multiple source indices, partialling out previously used geographic factors (E , $\ln A$, A_2) that were most correlated with plant species number. Stepwise multiple-regression analyses were performed to determine best-fitting predictor equations, with $P = 0.05$ as selection and deselection criteria. In multiple-regression analyses, predictor variables included variables from prior studies (A , $\ln A$, E , $\ln E$, A_2 , D_1 , D_2) plus C_i , B_i , N_i , for all dispersal ranges measured, as well as interaction terms (e.g., $C_i \times E$, $C_i \times A$).

RESULTS

Simple Pearson correlations showed positive relationships between either total species richness (S_t) or endemic species richness (S_e) and the interaction term of connectivity (C_i , where i is the radial dispersal distance) and elevation, $C_i \times E$ (Table 2). Additionally, while single-source measures of distance (to nearest island, D_1 , to central island [Santa Cruz] D_2) were uncorrelated with species richness (S), the connectivity index (C_i) was correlated with S beyond a 10-km dispersal range. In partial correlations with S_e , controlling for elevation (E), area ($\ln A$), and area of the nearest island (A_2), C_i remained correlated with S_t for nearly

all dispersal ranges (Fig. 2a). The total number of source islands (N_i) was correlated with S_t over a shorter dispersal range and with a consistently lower correlation strength than C_i , and the index of unconnected or barred islands (B_i) was not correlated with S_t for any dispersal range (Fig. 2a). Partial correlation between S_t and $C_i \times A$, controlling for E , $\ln A$, and A_2 , showed no relationship, while partial correlation between S_t and $C_i \times E$ showed a positive relationship for all dispersal ranges except $i = 200$ km (Fig. 2b). In contrast, partial correlations between S_t and $B_i \times E$ showed a negative correlation at dispersal ranges ≥ 300 km.

Despite the update from van der Werff (1983), multiple-regression models based only on prior geographic predictor variables remained consistent with prior regression results, in terms of both predictor variables and coefficients of determination (Table 3). Prior additive models explained 64–79% of the variance in endemic and total species number. In contrast, the interaction term between connectivity and recipient-island elevation ($C_i \times E$) alone explained at least 79% of the variance in either endemic or total plant species number. Regression models that included recipient-island area ($\ln A$) and $C_i \times E$ at multiple dispersal ranges explained $>90\%$ of the variance (Table 3).

DISCUSSION

While prior single-distance measures were uncorrelated with plant species richness, S , an index of multiple sources within dispersal range, C_i , was found positively correlated with S_t (total species richness) in the Galápagos Archipelago for dispersal ranges from 10 km to 300 km (Fig. 2a). Moreover, a measure of multiple sources (C_i) multiplied by elevation (E), a correlate of habitat diversity, explained more variation in S in the Galápagos than prior regression models (Table 3) that used additive forms of E , $\ln A$, (A = area of island), A_2 (area of nearest island), and isolation from the central island (D_2). While area ($\ln A$) yet claimed a

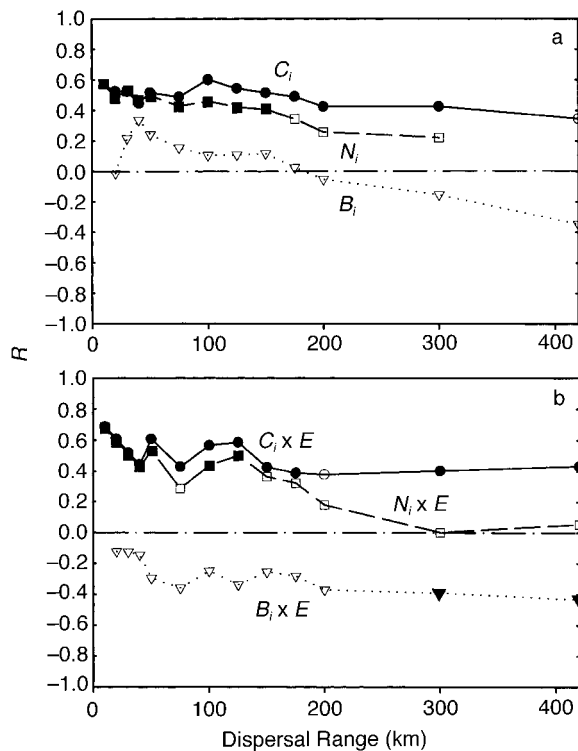


FIG. 2. Partial correlations, R , between multiple source indices and total plant species number (S_i) in the Galápagos Archipelago, where variation due to elevation (E), area of island ($\ln A$), and area of nearest island (A_2) are all controlled. Solid symbols show significant correlations ($P < 0.05$) for: (a) Partial correlations between S_i and multiple-source indices of total number of islands (N_i), island connectivity (C_i), and island barriers (B_i), within dispersal range i ; (b) Partial correlations between S_i and multiple-source indices multiplied by elevation of recipient island ($N_i \times E$, $C_i \times E$, and $B_i \times E$).

significant portion of the variance in species number, $C_i \times E$ explained more variance than either area or elevation alone at any dispersal distance.

In addition to disregarding effects of multiple sources and dispersal barriers, no previous Galápagos flora study addressed interactive effects of the factors; i.e., in prior studies all terms in the analyses were additive. Using additive terms requires an assumption of independence among predictor variables (Martin 1981). The connectivity index, C_i , was very simple, and was found independently correlated with S (Fig. 2a). Our results further show that an interdependence existed between a variable of dispersal sources (C_i) and a variable of habitat diversity (E) in determining S (Fig. 2b). van der Werff (1983) showed that elevation differences on islands in the Galápagos corresponded to xeric plant habitat in lowlands and mesic plant habitat in middle-to-higher elevations primarily due to climatic interactions with landform. The results here indicate that habitat diversity on elevational gradients, combined with direct, interisland pathways of dispersal,

TABLE 3. Multiple stepwise regression results for numbers of total plant species (S_t ; Connor and Simberloff 1978, van der Werff 1983) and for numbers of endemic plant species (S_e ; Johnson and Raven 1973) in the Galápagos Archipelago.

Dependent variable	Independent variables†	Adjusted R^2
S_t	E	0.647
	E, A_2	0.793
	$C_{125} \times E$	0.826
	$C_{125} \times E, \ln(A)$	0.873
	$C_{125} \times E, \ln(A), C_{10} \times E$	0.899
	$C_{125} \times E, \ln(A), C_{10} \times E, C_{75} \times E$	0.935
S_e	$\ln(A)$	0.717
	$\ln(A), D_2$	0.763
	$C_{50} \times E$	0.786
	$C_{50} \times E, \ln(A)$	0.905

Notes: For both S_t and S_e , prior best-fitting regression models are shown, followed by improved models from the present study. All independent variables shown below were significant in partial F tests ($P < 0.05$).

† Defined in Tables 1 and 2.

provide the strongest explanation for plant-species dispersal patterns.

The most correlated dispersal range in this study was 125 km, which is close to the mean interisland distance in the Galápagos Archipelago (112 km). We found that while connectivity variables (C_i or $C_i \times E$) were positively correlated with the number of both endemic and total species for all dispersal ranges, an index of island barriers combined with elevation ($B_i \times E$) was negatively correlated with S for the longest dispersal ranges (Fig. 2b).

These results show that multiple source pools can have a significant effect on species number in archipelagos, by either increasing immigration of new species or decreasing extinction, or by both processes simultaneously. These results also indicate that oceanic pathways in relatively tightly clumped and high-elevation archipelagos can play an important role in plant dispersal. These results further suggest that habitat changes along elevation gradients on islands in the Galápagos Archipelago generally form barriers, rather than stepping stones, to plant species dispersal.

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