



Analysis of plant species diversity with respect to island characteristics on the Channel Islands, California

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Abstract

Aim Species richness of native, endemic, and exotic plant groups is examined relative to island area, disturbance history, geological history, and other physical characteristics. Of particular interest are the biogeographic factors that underlie (a) differences in species-area and species-isolation relationships between plant groups; and (b) adherence or departure of individual islands and/or plant groups from expected patterns.

Location The eight Channel Islands lie along the continental margin between the U.S./Mexico border and Point Conception, CA. They range in size from 2.6 to 249 km², and are located from 20 to 100 km off the coast. The islands are known for their high degree of plant endemism, and they have undergone a long history of human occupation by indigenous peoples, followed by over a century of intensive grazing and other biotic disturbances.

Methods The study is based on linear regression and residual analysis. Cases where individual islands and/or specific plant groups do not adhere to patterns expected under species-area and species-isolation paradigms, are evaluated with respect to other island characteristics that are not captured by considering only island size and isolation.

Results All three plant groups exhibit strong, positive relationships between species richness and island size. For native species, the variance that remains after consideration of island size is largely explained by island isolation. For exotic species, residuals from the species-area relationship are unrelated to isolation. For endemic species, residuals from the species-area relationship are negatively related to isolation. Several islands are outliers for endemic and exotic species, for which richness values are not explained by either island area or isolation.

Main conclusions Species-area and species-isolation relationships for native, endemic, and exotic plant groups differ in accordance with hypothesized differences in the biogeographic factors that govern species diversity for these three groups. Most notably, endemic richness increases with isolation, suggesting the influence of this variable on processes of speciation and relictualism. These general relationships persist despite a long and varied history of human activity on the islands. Analysis of residuals suggests that deviations from expected patterns correspond to island-specific biogeographic factors. It is hypothesized that primary among these factors are land-use history, island environmental characteristics, and community-type richness.

Keywords

California Channel Islands, species richness, plant diversity, island biogeography.

INTRODUCTION

The positive correlation between area and species richness is well-established (Williams, 1943; Wilcox, 1980; Schoener &

Schoener, 1981; Rydin & Borgegard, 1988). Numerous studies demonstrate the stability of this relationship on mainland study sites, on different island groups and for various taxonomic categories (Darlington, 1957; Johnson *et al.*, 1968; Barbour & Brown, 1974; Lomolino *et al.*, 1989). The negative correlation between island isolation (distance from the mainland) and species richness, although not as strong, is also well documented

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(Lack, 1970; Ricklefs, 1977). These relationships, however, do not completely explain patterns of island diversity. Other biogeographic factors and processes are also important.

This research begins with an assessment of species-area and species-isolation relationships on the California Channel Islands for three groups of plant species: native, endemic, and exotic. The results are evaluated relative to expected roles of island area and isolation in governing diversity patterns for the three species groups. Of particular interest is the resilience of species-area and species-isolation relationships in the face of a long history of human occupation. Certain islands and species groups have richness values that deviate from expected patterns. These cases allow the development of hypotheses regarding the roles of other biogeographic factors, including disturbance history, geological history, and environmental heterogeneity.

The California Channel Islands offer an excellent setting for analysing the processes that underline patterns of species richness. The islands exhibit considerable variability in size, degree of isolation, geological history, topographic characteristics, prehistoric occupation, and modern land use. Additionally, the geology, biology and human occupation of the Channel Islands are well studied. Thus, the information for a biogeographical synthesis of the processes that structure species richness patterns on these islands is available. This information is used to posit hypotheses regarding the adherence or departure of islands and groups of species from patterns expected under species-area and species-isolation paradigms.

BACKGROUND

The tendency of species richness to increase with area has proven remarkably consistent for a range of organismal groupings, and in numerous geographical settings (Gould, 1979; Wilcox, 1980; Schoener, 1988). This relationship has particular value in studies of island biota, and plays a major role in the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), providing a structure for integrating the factors of island size and island isolation with the processes of colonization and extinction.

The species-area relationship on islands is attributed to a small set of ecological factors (Wilcox, 1980). First, area, to the extent that it is positively related to environmental variability, is a surrogate for habitat diversity (Maly & Doolittle, 1977). A large area provides a greater array of habitats than a small area within the same macro-environmental setting, thereby supporting a greater number of species (Power, 1972; Johnson, 1975). Other factors, such as topographic complexity, are also important determinants of habitat diversity, so island area is not a perfect surrogate (Hamilton *et al.*, 1963; Fox, 1983; Haila, 1983). Second, a larger area provides sufficient range for a more diverse group of organisms than a small area (Brown, 1971) although the relevance of this circumstance is clearer for animals than it is for plants. Third, larger areas can support larger populations, thus reducing the likelihood of extinction due to chance events (Pielou, 1975; Maly & Doolittle, 1977).

Species richness is also influenced by island isolation (MacArthur & Wilson, 1967; Diamond, 1973; Lomolino

et al., 1989; Alder & Dudley, 1994). Since species differ in the maximum distance over which they can disperse, islands that are near the mainland will potentially receive propagules from more species than will distant islands (Wilcox, 1978; Rosenzweig, 1995). Likewise, a near island will receive more propagules from any particular species, thus increasing the likelihood that some subset of these propagules will establish a population, and that dwindling populations will be rescued from extinction. Distance, however, may not completely account for isolation from the mainland (Lomolino, 1994). For example, intervening islands can act as species source areas; patterns of ocean and atmospheric circulation can facilitate or inhibit dispersal; historical land bridges may have provided pathways for colonization; and historical inundation may have eliminated entire biota. Additionally, the probability that an island has been colonized by a given species is related to the island's duration above water (Brattstrom, 1990).

California Channel Islands

The four northern Channel Islands stretch west to east from Point Conception to Ventura, California. They are separated from the mainland by the Santa Barbara Channel (Fig. 1). The northern islands are close to the mainland and tightly clustered, with no more than 9.6 km separating any two adjacent islands. The four southern islands are separated from the mainland by the San Pedro Channel, and stretch roughly from Ventura to San Diego, California (Fig. 1). They are more remote and scattered than the northern group. The narrowest gap separating any of the southern islands is 34 km between Santa Catalina and San Clemente.

A large body of research exists on the biology, climatology, geology, human history and natural history of the Channel Islands. Much of this work is either found or referenced in the proceedings from a set of multidisciplinary symposia dedicated to the study of the islands (Philbrick, 1967; Power, 1980; Hochberg, 1993; Halvorson & Maender, 1994).

Philbrick & Haller (1977) described twelve plant communities on the Channel Islands. The most dominant include *southern coastal dune*, *coastal bluff*, *coastal sage scrub*, *island chaparral*, *valley/foothill grassland*, *southern coastal oak woodland*, and *island woodland*. The smaller islands sustain fewer of these communities than the larger islands. For example, Anacapa and Santa Barbara Islands (the smallest two) support only the coastal communities and *valley/foothill grassland*. The two largest islands, Santa Cruz and Santa Rosa, support most of the twelve communities (Philbrick & Haller, 1977).

Fire on the islands is rare, with only three lightning-caused fires reported in the last 140 years (Carroll *et al.*, 1993). It is unclear whether this is typical of historical fire regimes, but low fire frequency may have implications for species that require heat-scarring or exposure to char in order to germinate. Such species are common in the Mediterranean-type vegetation that occupies the islands, although Carroll *et al.* (1993) showed that insular populations of several prominent chaparral species are much less dependent on fire treatment for germination than their mainland counterparts.

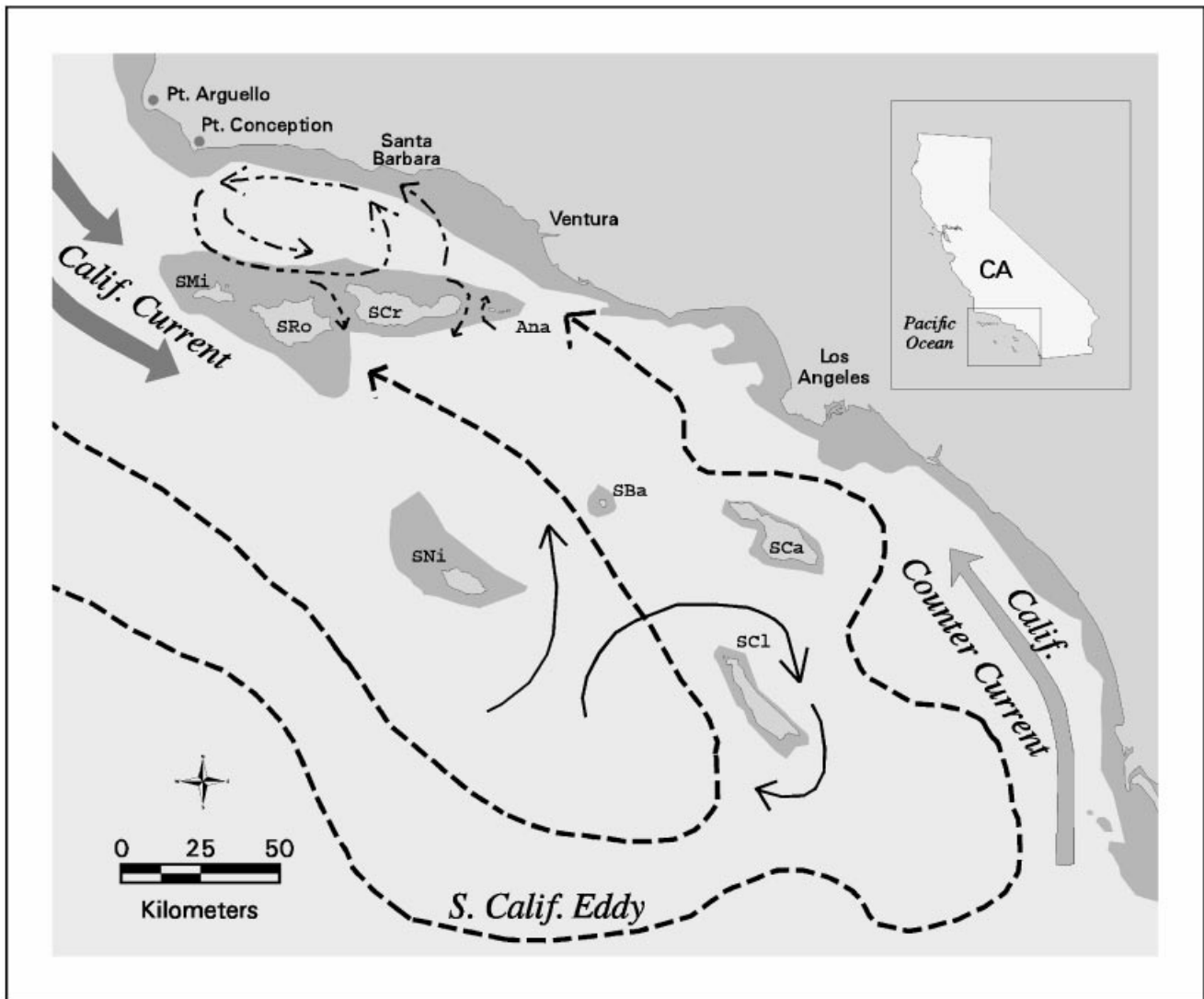


Figure 1 Channel Islands and adjacent mainland. The intermediate grey tone surrounding each island approximates the extent of the islands at sea level minima (17,000–18,000 yr BP). The large southward pointing arrows (dark) represent the California Current. The large northward pointing arrow (grey) indicates the California Counter Current. The large dashed lines indicate the Southern California Eddy. The small dashed lines indicate a small eddy flow in the Santa Barbara Channel. Island codes are as follows: SMi, San Miguel; SRO, Santa Rosa; SCr, Santa Cruz; Ana, Anacapa; SNI, San Nicolas; SBa, Santa Barbara; SCa, Santa Catalina; SCl, San Clemente. (Modified and combined from Seapy and Littler, 1980 and Browne, 1994)

Climate

The climate of the Channel Islands is highly maritime, within a broader-scale Mediterranean-type climatic regime (Philbrick & Haller, 1977). The winters are cool and wet, with most precipitation between November and April (Major, 1977). Summers are warm and dry. There is some variability in climate between the islands, however, measurements are inconsistent in terms of elevation, coastal proximity, and other factors, rendering reported averages and interisland comparisons unreliable. This is especially problematic for the larger islands which exhibit strong gradients in precipitation, temperature and wind speeds. Mean July temperature ranges from about 15°C on San Miguel to 19°C on Santa Catalina.

Annual precipitation ranges from roughly 17 cm on San Nicolas to 52 cm on Santa Cruz (Philbrick & Haller, 1977; Schoenherr *et al.*, 1999). North-west winds blow strongly throughout much of the year. San Miguel, Santa Rosa, San Nicolas, and Santa Barbara, in particular, experience strong winds over a large proportion of their surfaces.

Ocean circulation

The climate of the Channel Islands is influenced by the general ocean circulation patterns in the Southern California Bight. Current dynamics are dominated by convergence of the California Current and the California Counter Current (Fig. 1) and are modified by complex bottom topography, shoreline

morphology and the presence of the islands (Browne, 1994). The cold, southward flowing California Current is pushed offshore just west of the northern Channel Islands at Points Arguello and Conception. The release of the coastal waters from the influence of the California Current, in combination with the California Counter Current, admits a large scale, counterclockwise flow (Southern California Eddy) which influences the entire Channel Island system (Browne, 1994; Engle, 1994) (Fig. 1). The southward flowing limb of the Southern California Eddy is held outside the Santa Barbara and San Pedro channels, and brings cold water to the more oceanward islands such as San Nicolas and San Miguel.

Marine geographic history

Until recently, the four northern islands were thought to have once been joined to the mainland along the axis of the Santa Monica Mountains, of which they are a westward marine extension (Fig. 1) (e.g. Valentine & Lipps, 1967). Recent marine geological data, combined with reconstructions of sea level fluctuations, tectonics, and eustatic dynamics, have produced no evidence of such a land bridge (Junger & Johnson, 1980; Vedder & Howell, 1980). However, during sea level minima (120 m below the present level at roughly 18,000 yr BP) the northern islands were joined together, and the distance between the landward extent of this large platform and the mainland (at Port Hueneme) may have been as narrow as 6 km (Fig. 1). There were no connections among the southern islands, or between the southern group and the northern group, but the extent of all islands was greater than at present (Junger & Johnson, 1980; Vedder & Howell, 1980).

Human history

Native Americans inhabited the Channel Islands beginning at least 6000 yr BP (Wenner & Johnson, 1980). Permanent settlements existed on most islands, and canoe travel between all islands and the mainland was common. By the mid-1800s these populations were eliminated by European colonists and their accompanying diseases. Wenner & Johnson (1980) suggest that insects and animals were introduced either as pets (e.g. The island fox and island spotted skunk) or as stowaways on canoes, for example in the transport of food supplies to the islands. Some plants that are now considered natives may also have been introduced from the mainland by indigenous occupants (Wenner & Johnson, 1980; Junak *et al.*, 1995) and could have outcompeted some island natives and endemics, leading to their extinction. It is possible that indigenous people directly caused some floral extinctions.

Johnson (1980) suggests that fire use by native people played a role in vegetation removal and exposure of soil to erosional forces. In addition, indigenous people may have influenced island fire regimes to an extent that impacted the success rate of individual species, or the viability of different community types. Such activities may have been intentional, for example to stimulate germination of favoured food species such as *Salvia columbariae*, a refractory seeder (Junak *et al.*, 1995).

Fishing crews and marine mammal hunters traveled the waters of the Santa Barbara and San Pedro Channels from the 18th to 20th centuries (Schwartz, 1994). Aside from

their possible role as unintentional vectors for propagule transport, these occasional occupants also planted small gardens for food, which included non-native species.

The most significant modern impacts on Channel Island flora have been commercial ranching of grazing livestock, and feral populations of abandoned domesticates (Halvorson, 1994). Poor grazing management resulted in the continual decimation of island flora between the mid-19th and mid-20th centuries (Johnson, 1980; Halvorson, 1994). Grazing of vegetation often was nearly complete, including consumption of all new foliage, shrub and tree bark, and plant roots. Severe drought, which occurs periodically in the region, amplified the defoliation process, pushing overpopulated grazers onto the most marginal areas and forcing them to consume the least palatable vegetation (Johnson, 1980; O'Malley, 1994). By reducing vegetative cover, excessive grazing not only reduced or modified shrub communities, but also increased exposed soil, permitting accelerated erosion rates (Minnich, 1980).

Numerous observations from the early 1800s suggest that the islands were far more lushly vegetated than at present, with nearly complete coverage by grasses, shrubs, trees, and cactus (Johnson, 1980; Minnich, 1980; Philbrick, 1980). By the late 1800s, most accounts described the islands as defoliated and barren (Halvorson, 1994; Schwartz, 1994). For example, prior to 1863, San Miguel Island was lushly vegetated. By 1870, after a severe drought led to massive livestock starvation, the island was described as completely defoliated (Johnson, 1980; Roberts, 1991). Similar observations are made regarding the other islands, especially San Nicolas, which by the late 1800s was typically referred to as desert-like (Johnson, 1980). Ranching may thus have directly caused local extinctions, as well as facilitating the success of more aggressive introduced species.

Several of the islands have been under military management during some period of the 20th century. On San Clemente and San Nicolas, this has involved numerous personnel, cultivation, waste management, and military exercises. In addition, the military has repeatedly seeded both of these islands with exotic grasses for erosion control and grazing. Santa Catalina has been a popular resort island for nearly 100 years, with continuous human traffic to and from the mainland.

Speciation and relictualism

Insular endemics are treated as a separate group in this analysis. These include species that evolved in place, as well as relictual species that are now extinct on the mainland. There is some debate about the relative roles of speciation and relictualism among the Channel Island endemic flora. Raven (1967) invokes both processes to explain the large number of endemics on San Clemente, suggesting that the island's isolation and duration above sea level may have led to relictualism in the face of mainland range collapse, and to speciation due to lack of gene flow from the mainland or other islands. The process of relictualism is also documented by the discovery of at least eleven species, once considered island endemics, in isolated pockets on the California mainland (Philbrick, 1980). Other endemics, including prominent

Table 1 California Channel Island characteristics and plant species richness data (from Junak *et al.*, 1995).

Island	Area (km ²)	Dist. (km)	Native	Endemic	Endemic %	Exotic	Exotic %	Total
Santa Barbara	2.6	61	88	14	11	44	33	132
Anacapa	2.9	20	190	22	8	75	28	265
San Miguel	37.0	42	198	18	7	69	26	267
San Nicolas	58.0	98	139	18	7	131	48	270
San Clemente	145.0	79	272	47	13	110	28	382
Santa Catalina	194.0	32	421	37	6	185	30	604
Santa Rosa	217.0	44	387	42	9	98	20	485
Santa Cruz	294.0	30	480	45	7	170	26	650

insular species such as *Lyonothamnus floribundus* (an endemic genus) and *Quercus tomentella*, are present in mainland fossil remains (Philbrick, 1980).

There is also evidence for endemism resulting from evolution in place, especially in the context of hybridizing complexes for woody plants, and saltational speciation for annual species (Raven, 1977). Philbrick (1980) identifies several species that exhibit consistent differences between island and mainland populations, and between different island populations, suggesting genetic drift and divergence among island populations that receive little gene flow from the mainland. Notable 'evolutionary' trends among island plants as compared to their mainland counterparts include (Mulroy, 1976; Philbrick, 1980; Carroll *et al.*, 1993; Davis & Junak, 1993): pink flower colouration (where mainland flowers are yellow or red); highly variable leaf morphology (greater between islands than within islands); greyish foliage (e.g. *Lyonothamnus* sp. and *Heteromeles* sp.); gigantism of shrubs, leaves, or fruits (e.g. *Eriogonum* sp., *Dendromecon* sp., *Ceanothus* sp.); prostration (e.g. *Eriogonum* sp., *Artemisia* sp., and *Adenostema* sp.); hybridization (e.g. *Cercocarpus* sp., *Ceanothus* sp., *Malacothrix* sp., *Opuntia* sp.); and reduced fire requirement for germination (e.g. *Ceanothus megacarpus*, *Lotus scoparius*).

METHODS

The Channel Island flora has been assembled from collections dating to the mid-1800s (e.g. Greene, 1878; Brandegee, 1890; Eastwood, 1941; Munz, 1959; Raven, 1963; numerous others). The species richness data used in this analysis (Table 1) are from *A flora of Santa Cruz Island* by Junak *et al.* (1995). Nomenclature follows *The Jepson manual* (Hickman, 1993) and Junak *et al.* (1995). Native, endemic and exotic species are treated separately in this analysis because the processes and factors that underlie species richness in these three groups differ and should result in different richness patterns.

The analysis is organized around four hypotheses:

H1: *Native, endemic, and exotic plant taxa all increase in richness with island size.*

H2: *Richness of native species decreases with distance from the mainland.*

H3: *Richness of endemic species increases with distance from the mainland.*

H4: *Richness of exotic species is not related to distance from the mainland.*

Simple linear regressions are used to characterize relationships between island characteristics (area and isolation) and species richness (Table 1). The species-area relationships are best summarized by linear models rather than the usual log models. This is probably because the threshold in island size at which the slope of the relationship between area and richness begins to decline is not met by the largest of the Channel Islands.

For each plant group, residual values are extracted from the regression models that relate species richness to island area. The residuals are analysed to identify relationships between model error and island characteristics. This analysis provides a baseline for discussing outliers in terms of island histories and environmental conditions.

The relationship between species richness and island distance from the mainland is evaluated both by analysing the residuals, as described above, and by considering species richness in each plant group as a proportion of the total number of species on each island. These proportional values are then modelled using island distance as the independent variable. This approach highlights islands that have a disproportionately high or low number of endemic and/or exotic species.

RESULTS

Species-area (H1)

Species richness is positively correlated to island size for each group of plant species; native, endemic, and exotic (Table 2 and Fig. 2). The species-area relationships are particularly

Table 2 Regression summaries for species richness regressed on island area.

	Coefficient	Standard error	t-value	P > t
Native species: $r^2 = 0.90$				
β_0	118.93	27.39	4.34	0.01
Area (km ²)	1.35	0.19	7.25	0.000
Endemic species: $r^2 = 0.81$				
β_0	16.44	3.60	4.56	0.004
Area (km ²)	0.12	0.025	5.015	0.002
Exotic species: $r^2 = 0.57$				
β_0	68.07	19.42	3.50	0.013
Area (km ²)	0.37	0.13	2.82	0.031

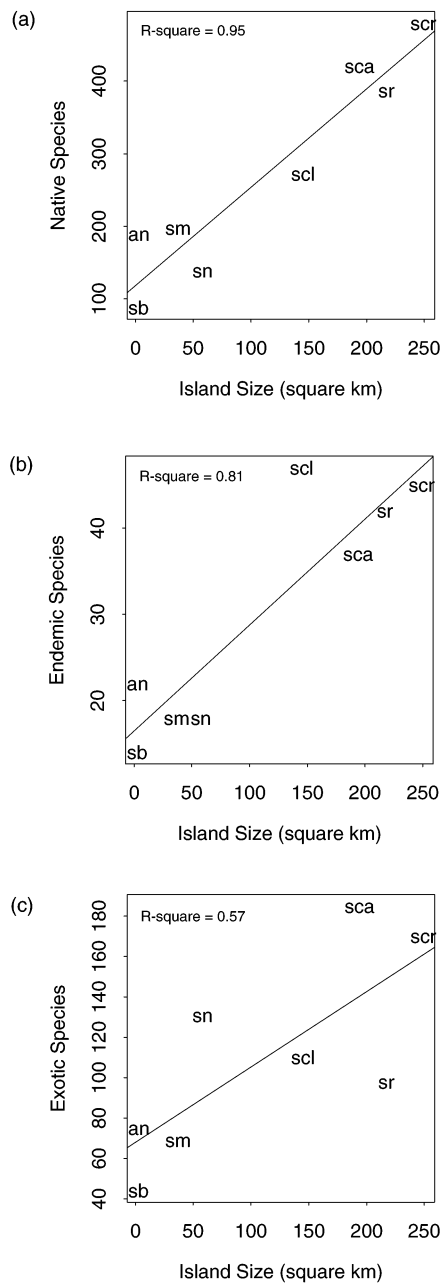


Figure 2 Relationships between island area and species richness for native species (a), endemic species (b), and exotic species (c). sm, San Miguel; sr, Santa Rosa; scr, Santa Cruz; an, Anacapa; sn, San Nicolas; sb, Santa Barbara; sca, Santa Catalina; scl, San Clemente.

strong for natives and endemics (r^2 -values of 0.90 and 0.81, respectively). The species-area relationship is weakest for exotic species ($r^2 = 0.57$).

Species-isolation (H2, H3 and H4)

Despite the strength of size as a predictor of native species richness, the model overpredicts richness for the most

Table 3 Regression summary of the residuals of species-area relationships on distance for native species.

Natives: $r^2 = 0.82$	Coefficient	Standard error	t -value	$P > t $
β_0	78.66	16.78	4.69	0.003
Distance (km)	-1.55	0.29	-5.23	0.002

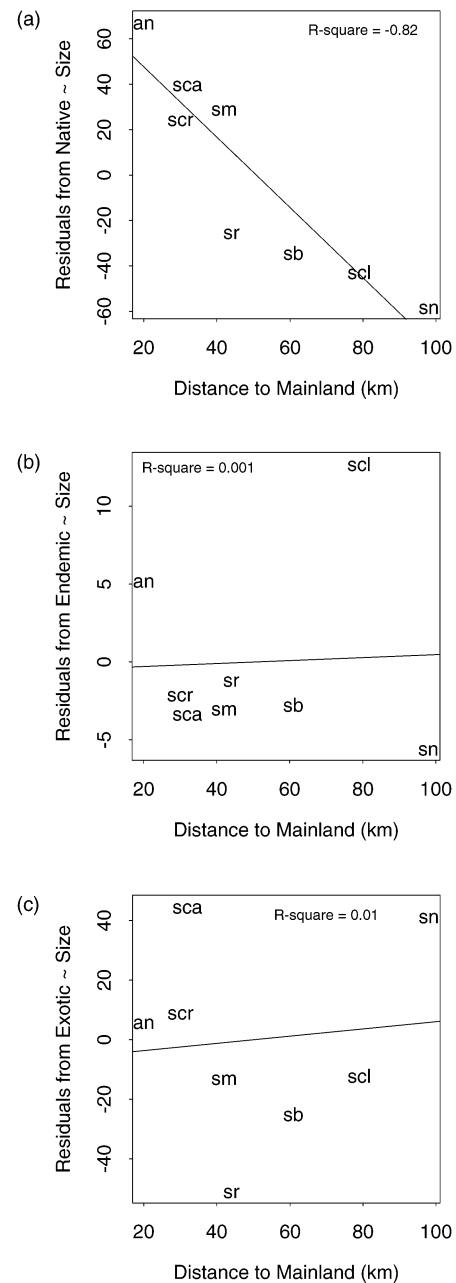


Figure 3 Relationships between the residuals from the models of species richness on island area, and island distance from the mainland, for native species (a), endemic species (b), and exotic species (c). Sm, San Miguel; sr, Santa Rosa; scr, Santa Cruz; an, Anacapa; sn, San Nicolas; sb, Santa Barbara; sca, Santa Catalina; scl, San Clemente.

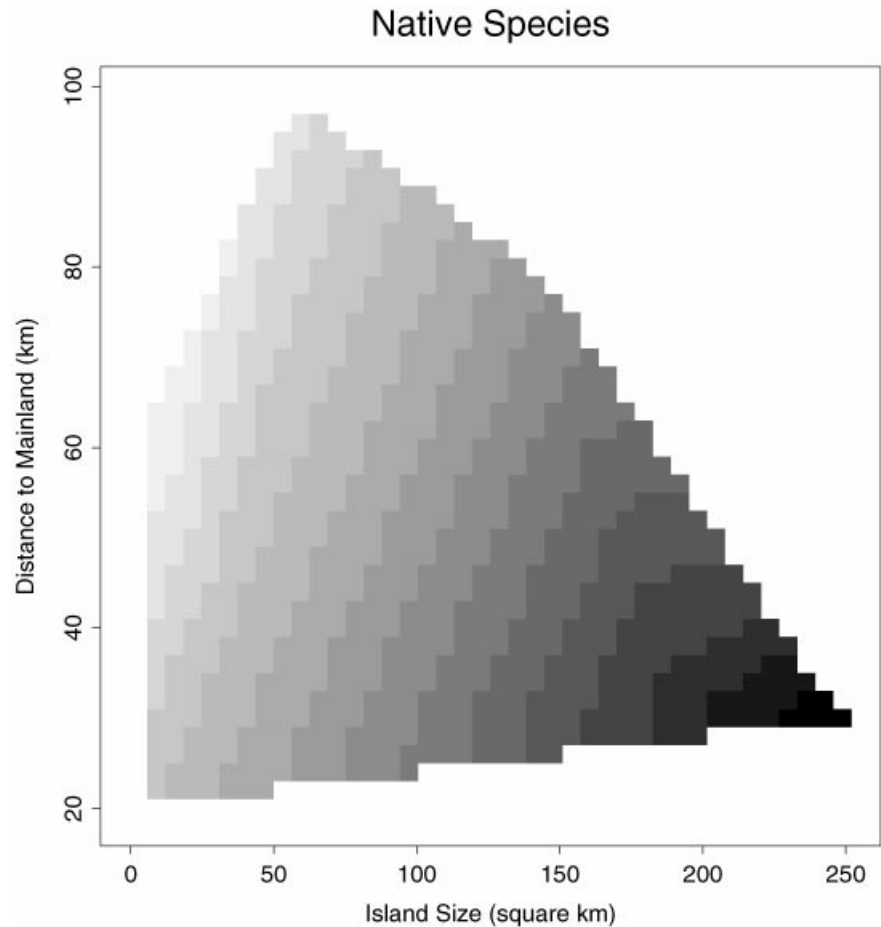


Figure 4 Surface showing the response of native species richness to both island area and island distance. Richness increases from light tones to dark tones.

distant islands (Santa Rosa, Santa Barbara, San Clemente, and San Nicolas) and underpredicts richness for the near islands (Fig. 2a). The strength of this distance effect is illustrated by plotting the residuals from the regression line in Fig. 2(a) against distance (Table 3 and Fig. 3a). For native species, most of the variance in richness that is not explained by island size, is explained by distance from the mainland ($r^2 = 0.82$) (Table 3).

The relationship of native species richness to island size and island isolation, taken together, shows that richness is more strongly associated with island size than island distance (Fig. 4). The parallel contours that run from the upper right to the lower left of Fig. 4 suggest the trade-off between island size and distance that is necessary to maintain a constant richness for native species.

The distance/residual relationships for endemic and exotic species are weak (Fig. 3b,c). San Clemente has eleven more endemics, and San Nicolas has six fewer endemics than expected based on their respective sizes (Figs 2b and 3b). Santa Catalina and San Nicolas both have roughly 40 more exotic species than expected given their size (Figs 2c and 3c). Conversely, Santa Rosa and Santa Barbara have unusually low richness of exotic species (about fifty and thirty fewer than expected, respectively) (Fig. 3c). None of these residuals

are explained by isolation from the mainland (Fig. 3b,c), which suggests that other factors must be important.

The influence of isolation on endemic and exotic richness is evaluated further by examining the number of species in each of these groups as a proportion of the total number of species on each island. Contrary to expectations, there is a strong relationship between exotic proportion and distance, and a weak relationship between endemic proportion and distance (Fig. 5a,b, respectively). However, San Nicolas Island is an outlier in both cases. After removal of San Nicolas the modelled relationships shift toward expected patterns (Table 4; Fig. 5c,d). The relationship between exotic proportion and distance becomes insignificant, and the relationship between endemic proportion and distance becomes strong and positive ($r^2 = 0.78$).

DISCUSSION

Species-area (H1)

All categories of plants increase in richness with island size. This shows that (a) the Channel Islands adhere to the species-area relationship despite a long history of disturbance due to human activity; and (b) this relationship exists across species

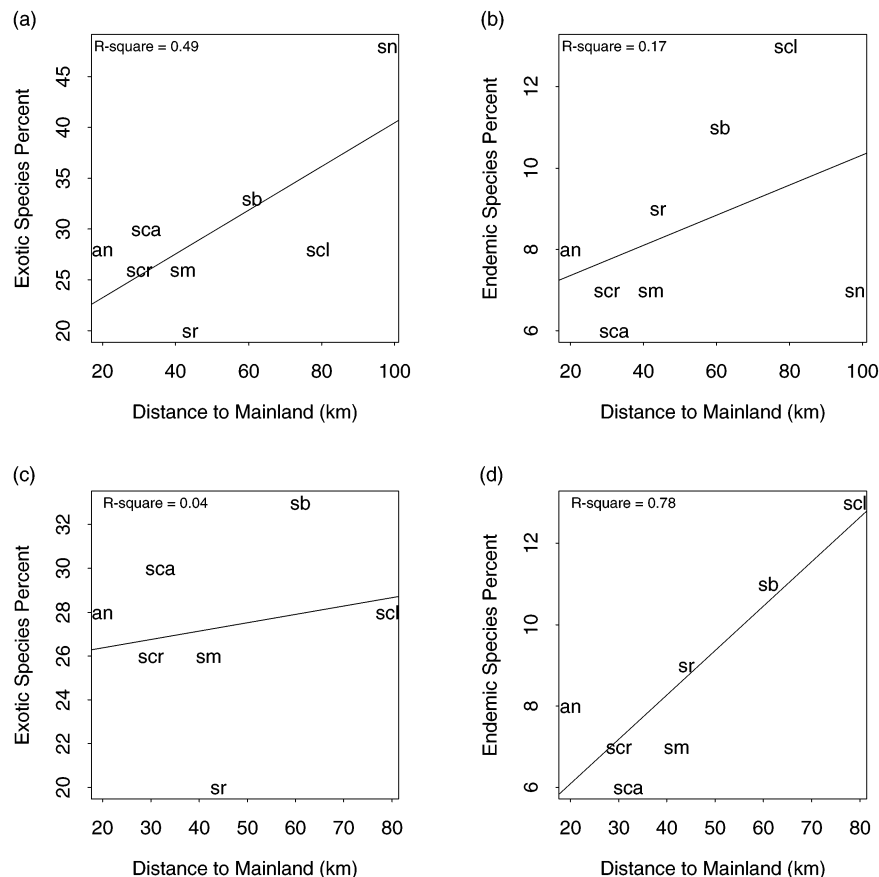


Figure 5 Relationships between species percent and island distance from the mainland for exotic species (a and c) and endemic species (b and d). The outlier (San Nicolas Island) is removed in (c) and (d). Sm, San Miguel; sr, Santa Rosa; scr, Santa Cruz; an, Anacapa; sn, San Nicolas; sb, Santa Barbara; sca, Santa Catalina; scl, San Clemente.

Table 4 Regression summaries for species-isolation relationships of endemic percentage and exotic percentage.

	Coefficient	Standard error	<i>t</i> -value	<i>P</i> > <i>t</i>
Endemics—outlier removed: $r^2 = 0.78$				
β_0	3.91	1.25	3.12	0.03
Distance (km)	0.11	0.03	4.17	0.01
Exotics—outlier removed: $r^2 = 0.04$				
β_0	25.60	4.20	6.10	0.002
Distance (km)	0.038	0.09	0.44	0.68

groups despite differences in the processes and factors that govern diversity for these groups. Considering the documented and potential impact of humans on Channel Island native and endemic species, the strength of the species-area relationships for these groups is remarkable, especially given that many species may have been eliminated or introduced by humans prior to systematic botanical surveys, which did not begin on the Channel Islands until the mid-to-late 1800s (Kellogg, 1854; Greene, 1878).

The disturbance factors that are likely to have influenced species richness on the Channel Islands are summarized below. These factors primarily relate to rates of colonization and extinction. The prehistoric factors are probably minor relative to the impacts of 19th and 20th century land-use practices: (1) extinctions due to prehistoric inhabitants and their landuse practices; (2) introductions and extinctions by

early explorers, and fishing and hunting fleets; (3) extinctions, and facilitation of exotics due to overgrazing combined with severe drought; (4) construction for modern human activities such as tourism and military management; (5) modification of fire regimes; and (6) introduction of exotics, including intentional planting for erosion control and fodder.

Consideration of groups of species that transcend community types is somewhat problematic because communities differ in their inherent potential for species richness. In addition, communities differ in terms of their susceptibility to disturbance. For example, establishment and dominance of introduced grasses may have been facilitated by overgrazing of the now rare and depauperate populations of native grasses in the *valley/foothill grassland* community (Minnich, 1980). Species associated with the *coastal sage scrub* community (CSS), including endemic species of *Eriogonum*, are especially

Table 5 Number of insular endemics on the Channel Islands by endemic type. There are forty-three single island endemics. Thirteen endemics are shared only on the southern islands. Nineteen are shared only on the northern islands. Twenty-three are shared between the northern and southern island groups. There are roughly ninety-eight endemic species on the Channel Islands (Raven, 1967).

Island	Single Island	Southern Islands	Northern Islands	Channel Islands
Anacapa	1	NA	8	11
Santa Cruz	8	NA	18	21
San Miguel	0	NA	8	4
Santa Rosa	4	NA	16	18
Santa Barbara	3	5	NA	5
Santa Catalina	7	10	NA	18
San Clemente	17	12	NA	7
San Nicolas	3	6	NA	7

sensitive to grazing due to their short stature. Consequently, CSS is now largely restricted to areas that are inaccessible to sheep and goats. Large stands of *Opuntia* sp. have taken over areas that supported CSS species prior to grazing. Likewise, refractory seeders, common in *coastal sage scrub*, and *island chaparral* may be disproportionately affected by changes in the fire regime.

At the species level, specific cases of extinction due to grazing on the Channel Islands may be indicative of a common impact that is not well documented. For example, prior to grazing, *Lavatura assurgentiflora* (a small tree) grew in large, unbroken groves on Santa Barbara, San Clemente, and San Nicolas (Lyon, 1886; from Philbrick, 1980). Only occasional scattered individuals remain. According to Philbrick (1980), *Munzothamnus*, an endemic genera from San Clemente is dwindling and twenty-one insular endemics have been eliminated or drastically reduced on at least some of the islands. Among these, *Mahonia pinnata insularis* is extinct on Santa Rosa and Anacapa, and barely present on Santa Cruz. *Dudleya candelabrum* is dwindling on Santa Cruz and Santa Rosa. *Cercocarpus betuloides traskulae* is represented by only a few individuals on Santa Catalina. Three species of *Mimulus* are probably extinct and two single island endemics on San Nicolas (*Phacelia cinerea* and *Lycium verrucosum*) are near extinction (Daily, 1997).

Some species can recover from low or undetectable populations once environmental pressure is removed. For example, *Dudleya traskiae* has begun to expand its range on Santa Barbara Island following the removal of rabbits by the National Park Service (Schoenherr, 1992).

The species-area relationships are strong despite a long history of disturbance and its potential to alter extinction and colonization rates. This is true even for exotic species, a group that is not governed by the same extinction and colonization processes as natives and endemics, but rather is influenced by the degree and type of human activity. These results suggest that species richness, as it is related to area, may be more a function of habitat diversity than extinction and colonization rates *per se*. A similar argument was made by Westman (1983) based on analysis of plot-level species richness data from the four inner Channel Islands. Alternative explanations are that human-caused extinctions have impacted all the islands equally in proportion to their size (or original floral richness); that the number of human-caused extinctions is insufficient to impact the basic species-area relationship; or that species richness

is largely determined by rare species that occupy well-protected sites.

Species-isolation

Increased distance from the mainland should decrease the chance of dispersal, thereby reducing gene flow and the probability of colonization. As such, it is not surprising that the effect of isolation in this study is strong for native species, whose chances of propagule dispersal are directly affected by distance.

The link between endemic species and island isolation is somewhat more complex. Isolation, founder effects, and small, insular populations may favour adaptive radiation, saltation, and speciation. Interisland and mainland gene flow would weaken such effects. In this context, a positive relationship between endemic richness and isolation is anticipated. These processes might also help explain the smaller number of shared endemics among the scattered and isolated southern islands relative to the northern island group (thirteen *v.* nineteen, Table 5). The fact that the southern group contains more single island endemics than the northern group (thirty *v.* thirteen, Table 5), despite the much greater total area of the northern group, probably relates to the fact that the northern group is not only tightly clustered, but was once joined as a single island, whereas the southern group has never been interconnected.

After removing San Nicolas Island as an outlier, the proportion of endemic species is strongly related to distance from the mainland. This corresponds to expected relationships, presuming a linkage between isolation and gene flow and its relevance for processes of speciation and relictualism. The proportion of exotic species is not related to distance from the mainland (also after removing San Nicolas). Introduction of plant species by humans is facilitated by almost immediate access to the islands via boat or plane. In addition, numerous species have been intentionally introduced for grazing and other purposes that are more related to human land-use history than to isolation from the mainland. Distance is thus a negligible effect for introduced species.

Individual islands

The treatment of San Nicolas as an outlier warrants discussion. Raven (1967) cited lack of habitat diversity as a possible explanation for the paucity of species on San Nicolas. It is

the most exposed and desert-like of the islands, experiencing strong NW winds (average 14 knots) nearly every day of the year, and receiving an average of only 17 cm of rain annually (compared to 52 cm on Santa Cruz) (Schoenherr *et al.*, 1999). The flat-topped island has large sand dunes on the western part, and extensive badlands on the south side. Between 1857 and the beginning of military occupation, San Nicolas was intensively and continuously grazed by sheep (Schwartz, 1994). The unusually high number of exotics on the island may also play some role in the low endemic richness through processes of competition and replacement. Finally, it is possible that some endemics were exterminated before Eastwood's 1897 visit (the first botanical visit to San Nicolas) or before complete taxa were catalogued (Raven, 1967).

Despite these factors, San Nicolas is comparable in terms of average climate, grazing history, and military history, to San Clemente, an island with far greater endemic richness, even after accounting for its greater size. There are several possible explanations for this incongruity.

According to Philbrick & Haller (1977) San Nicolas sustains only four community types (*southern coastal dune*, *coastal sage scrub*, *valley/foothill grassland*, and *coastal marsh*), a level of community-type diversity that is more typical of the smallest islands. San Clemente, in contrast, sustains these four as well as *island woodland*, *coastal bluff*, and *maritime cactus scrub*. These differences in community-type richness may be due to lower habitat diversity on San Nicolas, which in turn could relate to its smaller size and/or its lower elevation. San Nicolas is only 277 m in elevation, lower than Anacapa, an island that is 1/20th the size of San Nicolas. Conversely, San Clemente is 600 m in elevation, much higher than Santa Rosa, an island that is 1.5× larger. Also, at 600 m, San Clemente is over twice as high as San Nicolas, enough of a topographic difference to produce greater spatial variability in precipitation, wind, temperature, and fog regimes.

Finally, San Nicolas is the most remote of the Channel Islands by a considerable margin (45 km from its nearest neighbour, Santa Barbara Island) and may lie beyond a critical threshold for dispersal of some southern island endemic species.

The large number of exotics on Santa Catalina and San Nicolas may relate to the unusual intensity of human activities on these two islands: development, tourism, and extensive grazing in the case of Santa Catalina, and a long history of grazing and military activity in the case of San Nicolas. Conversely, the low number of exotics on Santa Barbara and Santa Rosa may be due to their relative lack of disturbance. Santa Barbara Island is uninhabited and has been less aggressively grazed and less frequently visited than the other islands. Santa Rosa was privately owned, and subjected to a lower impact grazing regime than the other islands (Schoenherr, 1992).

Other factors

As a function of island area, native species richness is under-predicted for the four islands that are nearest the mainland,

three of which are northern islands, and one of which is a southern island (Santa Catalina). It is possible that diversity is higher on the northern islands not because they are nearer to the mainland, but because of their history as one large island. This explanation, however, fails to account for the over-prediction on the other northern island (Santa Rosa) and the under-prediction on the southern island (Santa Catalina). Island distance is a more consistent explanatory factor for the patterns of under- and over-prediction.

The above interpretation of species richness patterns have ignored the possibly critical issue of species equilibrium on the islands. The islands may be at different stages relative to their respective equilibria, if such exists, because their histories have differed, their characteristics differ, and their characteristics have varied differently over time. The question of individual island status relative to their equilibria is not answerable at present because of uncertainty regarding their histories and characteristics, how these may influence equilibrium, and how long it might take these islands to reach equilibrium.

In addition, the scale of this analysis precludes the explicit treatment of basic ecological principles that are known to be relevant for species diversity. It is a complex task to integrate the numerous factors that might affect species diversity when large numbers of species are involved. In addition, the relevant characteristics are not known for all species. For example, specific habitat constraints, species interactions, selection pressures, genetic characteristics, and the relative abilities of species to disperse across an ocean barrier are not known. These are all important for species diversity, but cannot be practically accommodated for a study at this scale.

CONCLUSIONS

The species-area and species-isolation models are used as a basis from which to suggest more specific biogeographic factors that influence patterns of species diversity. These relationships are evaluated for different species groups, for which the biogeographic processes governing species richness differ, and in a setting that has undergone intensive human disturbance over a long period of time.

Several patterns emerge from this analysis. First, the classic island biogeographic patterns of species-area and species-isolation hold, despite massive disturbance on the islands. This suggests that (a) disturbance has not significantly altered species richness in native or endemic plant groups; (b) disturbance has altered richness in these groups, but in a way that is proportional to island size, or 'original' species richness; or (c) disturbance has had different consequences for extinction on the different islands, but the continuing strength of the species-area relationship, despite disturbance, suggests that area primarily serves as a surrogate for habitat diversity, rather than modern extinction rate *per se*. Second, certain islands do not adhere to the classic patterns for certain plant groups. These cases are hypothesized to correspond primarily to land-use history, environmental characteristics, and community-type richness.

This analysis is orientated toward positing hypotheses about the factors and processes that underlie current patterns of plant diversity on the islands. There is little reliable data on prehistoric flora of the islands that are sufficiently complete to infer past community or ecosystem characteristics. Furthermore, it is unknown to what extent indigenous people altered island flora, or to what extent grazing has caused extinctions, reduced population sizes, or facilitated non-native plant species. It is also unknown whether these various impacts evenly affected native vs. endemic species, or whether they affected some community types more than others.

However, some key events in island history are known: they were occupied by Native Americans for at least six thousand years, they were intensively grazed for over a century, they have been exposed to exotic species and introduced fauna, the northern islands were joined in the late Pleistocene, but not connected to the mainland. This paper attempts to identify those current and historical factors that are known about the islands and that are potentially informative regarding present day patterns of island plant diversity at the scale of the whole island group. From this point, one can then attempt to evaluate more closely some of these hypotheses regarding variability in Channel Island plant diversity.

ACKNOWLEDGMENTS

Early drafts of this manuscript were thoughtfully considered by Rachel Hochman, Ross Meentemeyer, and Rebecca Vidra. Two anonymous reviewers provided valuable comments on the manuscript.

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