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Nested communities, invasive species and Holocene extinctions: evaluating the power of a potential conservation tool

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Abstract General ecological methods and models that require a minimum amount of information yet are still able to inform conservation planning are particularly valuable. Nested subset analysis has been advocated as such a tool for the prediction of extinction-prone species and populations. However, such advocacy has not been without skepticism and debate, and in the majority of published examples assessing extinction vulnerability, actual extinctions are based on assumptions rather than direct evidence. Here, we empirically test the power of nested subset analysis to predict extinction-prone species, using documented Holocene insular mammal extinctions on three island archipelagos off the west coast of North America. We go on to test whether the introduction of invasive mammals promotes nestedness on islands via extinction. While all three archipelagos were significantly nested before and after the extinction events, nested subset analysis largely failed to predict extinction patterns. We also failed to detect any correlations between the degree of nestedness at the genus-level with area, isolation, or species richness and extinction risk. Biogeography tools, such as nested subset analysis, must be critically evaluated before they are prescribed widely for conservation planning. For these island archipelagos, it appears detailed natural

history and taxa-specific ecology may prove critical in predicting patterns of extinction risk.

Keywords Baja · Biogeography · California · Islands · Introduced mammals · Natural history · Nested subset analysis · Mexico

Introduction

Conservation planning and policy often demand that decisions about the fates of specific species and communities be made on the basis of a limited amount of information, gathered in a limited amount of time (Soulé 1985). As a result, ecologists have sought organizing principles of ecology that can be broadly applied to conservation problems (Doak and Mills 1994; Soulé and Terborgh 1999). General methods and models that can be applied to a variety of conservation scenarios, require a minimum of information, and provide critical predictions are especially valuable. At the top of the list of such key predictions are the immediate and medium-term vulnerability to extinction of populations and species (Terborgh and Winter 1980; Doak and Mills 1994). Since its initial application by Patterson and Atmar (1986), the use of nested subset analysis of species occurrence patterns has become an increasingly common tool in community ecology and many have advocated its use in conservation planning, particularly in reserve design and predicting species susceptibility to extinction (Patterson 1987; Cutler 1991; McDonald and Brown 1992; Fleishman et al. 2000; Kerr et al. 2000; Fleishman and McNally 2002; and many others). However, such advocacy has not been without substantial skepticism, concern, and debate (Quinn and Harrison 1988; Simberloff and Martin 1991; Doak and Mills 1994; Skaggs and Boecklen 1996; Boecklen 1997). Here, we investigate the relationship between nestedness patterns and extinction risk, using data on the mammalian faunas

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and extinction patterns of three island groups off the coasts of California, USA, and Baja California, Mexico.

A perfect nested pattern results when all species that occur on islands (or habitat fragments) containing n species also occur on all islands (fragments) containing $n+1$ species (Darlington 1957; Patterson and Atmar 1986). Many, if not most, islands or fragments are significantly nested in a statistical sense; however, few are even close to perfectly so (Wright et al. 1998). Similar to how species compositions of islands/fragments can be nested, incidence distributions of individual species can also be nested. Thus, both sites (islands/fragments) and species can possess nested qualities. Studies of nestedness have evolved from the elucidation of patterns and the refinement of statistical models to exploring the mechanisms that generate such patterns (Patterson and Atmar 1986; Patterson 1987; Cutler 1991; Atmar and Patterson 1993; Lomolino 1996; Wright et al. 1998). Both abiotic and biotic processes have been implicated in generating nested distributions, including area, selective extinction, differential colonization, environmental variables, distribution of resources, and anthropogenic disturbance (Cook and Quinn 1995; Lomolino 1996; Wright et al. 1998; Fernandez-Juricic 2002; Hecnar et al. 2002).

Nestedness analysis is often portrayed as a tool to predict the order in which extinctions are likely to occur at a suite of sites in response to habitat reduction, fragmentation, or other types of disturbance (Bolger et al. 1991; Cutler 1991; McDonald and Brown 1992; Kerr et al. 2000). The general idea behind these predictions is that populations that are close to the predicted edge of likely occurrence on a particular island are more at risk of extinction, particularly as the nestedness of a system decreases or species or population turnover (i.e., extinction) increases (Atmar and Patterson 1993). However, such predictive power is based on inferred extinctions (e.g., faunal relaxation of Pleistocene land-bridge islands), and these hypothesized extinctions rely on a number of assumptions that are not necessarily valid (Simberloff and Martin 1991; Skaggs and Boecklen 1996). Further, the presence of a nested pattern does not necessarily implicate ordered extinction probabilities. Differences in colonization ability, among other possible factors, can also lead to such a pattern (Darlington 1957; Kadmon 1995). While the interacting effects of area and disturbance on extinction risk has a long history (Diamond 1972; Terborgh 1974), in an alarming fraction of published examples assessing extinction vulnerability, evidence of patterned extinctions are based on statistical extrapolations with questionable assumptions, rather than direct evidence. Furthermore, direct observations of idiosyncratic species loss and subsequent species interactions with fragmentation suggest that such assumptions may not be valid (Terborgh et al. 1997).

Here, we empirically test the relationship between predicted extinction risks from nestedness analyses and the actual extinction and endangerment status of populations. Specifically, we test the power of nested subset

analysis to predict the relative extinction risks of different species and populations, using documented Holocene insular mammal extinctions on islands off the west coast of North America. Given the large role invasive species play in global extinctions (Groombridge et al. 1992) and their complex interactive effects with biodiversity (Vivrette and Muller 1977; Vitousek and Walker 1989; Roemer et al. 2002), we also ask whether extinctions caused by introduced species strengthen or weaken nestedness patterns, as has been inferred elsewhere (Hecnar and McCloskey 1997). At the core of this paper is an attempt to evaluate whether biogeography tools, such as nested subset analyses, are useful in predicting species endangerment, or whether knowing the autecological details of a species and their community interactions is necessary to correctly gauge risks of extinction and endangerment.

Methods

Study system

This study includes data on nonvolant mammals (all those but bats) on islands off the coasts of central California, USA south to the tip of Baja California, Mexico, including the Gulf of California (Fig. 1). Islands were

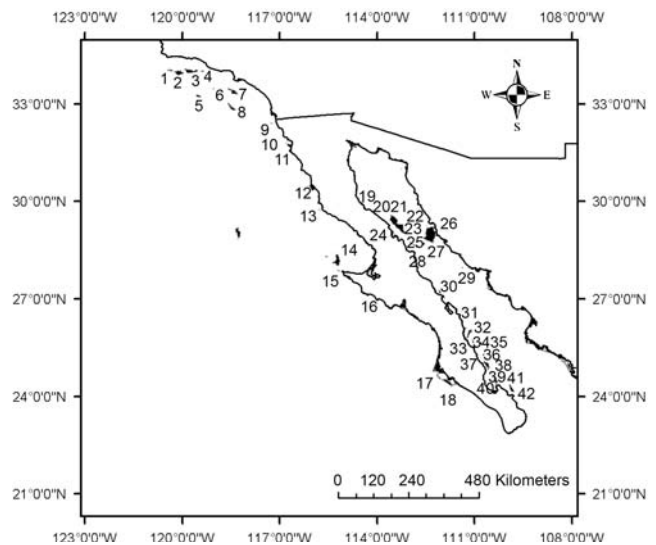


Fig. 1 Three island archipelagos off the coasts of California, USA and Baja California, Mexico. **California:** 1 San Miguel, 2 Santa Rosa, 3 Santa Cruz, 4 Anacapa, 5 San Nicolas, 6 Santa Barbara, 7 San Catalina, 8 San Clemente, **Baja California-Mexico:** 9 Coronado North, 10 Coronado South, 11 Todos Santos South, 12 San Martin, 13 San Geronimo, 14 Cedros, 15 Natividad, 16 San Roque, 17 Magdalena, 18 Margarita, **Gulf of California-Mexico:** 19 Willard, 20 Granito, 21 Meija, 22 Angel de la Guarda, 23 Estanque, 24 Smith, 25 Salsipuedes, 26 Tiburon, 27 Turner, 28 San Lorenzo, 29 San Pedro Nolasco, 30 San Marcos, 31 Carmen, 32 San Jose, 33 Danzante, 34 Montserrat, 35 Santa Catalina, 36 Santa Cruz, 37 San Diego, 38 Animas, 39 San Jose, 40 San Francisco, 41 Espiritu Santo, 42 Cerralvo. Only islands included in the analysis are shown; island names correspond with numbers

broken into three groups according to location, biogeographical history, and island type (oceanic or land-bridge). The California Channel Islands (henceforth, *California*) have not been connected to mainland California during the Quaternary, while the islands off the Pacific side of Baja California (*Baja*) were connected to the Baja peninsula during the Pleistocene (Junger and Johnson 1980; Case et al. 2002). Due to the small number of oceanic islands in the Gulf of California, only islands (henceforth, *Gulf*) that were connected either to the Baja peninsula or mainland Mexico during the Pleistocene are included in the analysis (Case et al. 2002). For all archipelagos, only islands with native mammals present historically were included. Overall, each island group shares a common biogeographic history, a shared ancestral species pool, and to a certain extent similar environmental gradients, all assumptions of nested subset analysis (Atmar and Patterson 1993).

The insular mammal fauna of western North America is well studied (Huey 1964; Alvarez-Castaneda and Patton 1999; Lawlor et al. 2002). The majority of these islands have a documented history of introduced mammals, resulting in several recent extinctions. Seabirds and nonvolant mammals have suffered the greatest impact; here we concentrate on the latter. While up to seven species of exotic mammals occur on some islands in the region, feral cats (*Felis catus*), and to a lesser extent non-native rats (*Rattus* spp.) are responsible for the majority of extirpations and extinctions (Table 1; Tershy et al. 2002; Wood et al. 2002). Other introduced mammals, including European rabbits, goats and pigs, have also had detrimental indirect impacts (Coblentz 1978; Moran 1996; Donlan et al. 2002; Roemer et al. 2002). Prompted by these losses, regional island conservation programs are underway that document and remove invasive mammals from islands off California (Halvorson 1994; Schuyler et al. 2002; Donlan and Comendant 2003) and Mexico (Tershy et al. 2002; Donlan et al. 2003).

At least 21 mammal extinctions or extirpations have occurred from the islands included in our study (henceforth we refer to all local population losses as extinctions). All the extinctions on the Baja and Gulf archipelagos are recent (in last 50 years), and all but one (10/11) can be attributed wholly or partially to the presence of introduced predators (see Table 1 and references therein). In contrast, of the 11 extinctions on the California Islands, nine took place earlier in the Holocene and thus their causes are less clear (11,000 YrBP–1800s; Table 1). These early Holocene extinctions, as well as those of a number of avian and non-avian reptiles, are coincidental or occur after the arrival and establishment of Native Americans on the Channel Islands (12,020–10,700 YrBP; Orr 1968; Guthrie 1993). The early Holocene (or Late Pleistocene) extinction of two species of *Peromyscus* (*P. nesodytes* and *P. anyapahensis*) were replaced by congeners (*P. maniculatus* ssp.), the latter possibly introduced by Native Americans (Guthrie 1993). The dwarf mammoth, *Mammuthus exilis*,

occurred on Santa Rosa, Santa Cruz, and San Miguel Islands beyond the limit of radiocarbon dating (41,000 YrBP). Prior to *c.* 13,000 YrBP, all three islands, along with Anacapa Island, formed the larger island, Santarosae (Agenbroad 2001). Mammoth populations survived after the inundation of Santarosae and the forming of the current islands, with the youngest bone being dated at 11,030 RCBP (radiocarbon years, L. Agenbroad, personal communication), and thus they were included as three separate populations in the analysis. A single tooth of *M. exilis* has been reported from San Nicolas Island; however, it is excluded from the analysis due to doubts of the validity and origin (e.g., human transport) of the fossil (L. Agenbroad, personal communication). The records of *M. exilis* on the other islands are based on multiple specimens (Agenbroad 2003a; b).

In our analysis, we also include as extinctions two insular species that are only remotely likely to still exist. On the small island of Turner (189 ha), *Neotoma varia* has not been documented since 1977, despite at least two trapping efforts; however, a specific survey has been recommended to confirm extinction (Alvarez-Castaneda and Ortego-Rubio 2003). On Santa Catalina Island, *Sorex ornatus willetti* was last collected in 1983. This shrew is likely extinct due to habitat destruction from introduced herbivores and predation from feral cats (Williams 1983; Collins and Martin 1985). We repeated all analyses described below twice, counting three other endangered populations as either extant or extinct. The island fox (*Urocyon littoralis*), endemic to the California Channel Islands, is endangered or extinct on five of the six islands it occurs: extinct in the wild with captive populations on San Miguel and Santa Rosa Islands and endangered on Santa Catalina, Santa Cruz, and San Clemente Islands due to the apparent competition induced by introduced pigs, introduced disease, and mismanagement (Roemer and Wayne 2003; Roemer et al. 2004).

Nested subset analysis

Nested subsets analysis is based on a matrix of occurrences of species (or, as here, genera: see below) on different islands. In these matrices, each cell indicates either the occurrence or absence of a species on a particular island. Species are ordered from those with the most to the least number of occurrences, while islands are ordered from most to least species rich. This results in a matrix with solid occurrences in the upper left, and no occurrences in the lower right. The strength of this pattern of discrete blocks of occurrences and non-occurrences in the matrix, as opposed to a random array of occurrences, indicates the degree of nestedness.

We performed six nested subset analyses for native mammals, using separate analyses for historical and current species occurrence data for each of the three island groups. Species presence/absence data for both

Table 1 Species and subspecies of nonvolant mammals considered extinct (E) or likely extinct (LE) on islands off the west coast of North America

Island group	Extinct taxon	Cause	Est. date	Ref.
<i>Baja CA Pacific–Land-bridge</i>	<i>Peromyscus maniculatus cineritus</i>	C/R	R	Alvarez-Castaneda and Cortes-Calva 1996; Donlan et al. 2000
San Roque (E)	<i>Neotoma martinensis</i>	C	R	Cortes-Calva et al. 2001
San Martin (E)	<i>Neotoma anthonyi</i>	C	R	Donlan et al. 2000; Mellink 1992
Todos Santos (E)				
<i>CA Channel Islands–Oceanic</i>				
San Miguel (E)	<i>Mammuthus exilis</i> ^a	UN	11,030 YrBP	L. Agenbrood, pers. comm.
San Miguel (E)	<i>Microtus</i> sp. nov.	UN	11,000 YrBP	Guthrie 1993
San Miguel (E)	<i>Spilogale gracilis</i> ^b	UN	Late 1800s (?)	Walker 1980
San Miguel (E)	<i>Sorex ornatus cf. willetti</i> ^c	UN	1,000 YrBP–1800s	Guthrie 1993
San Miguel (E)	<i>Peromyscus nesodytes</i>	UN	8,000 YrBP	Guthrie 1993; Walker 1980
San Miguel (E)	<i>Urocyon littoralis littoralis</i> ^d	P	R	Roemer et al. 2002, 2004
Santa Catalina (LE)	<i>Sorex ornatus willetti</i> ^e	UN	R	Williams 1983; Collins and Martin 1985
Santa Cruz (E)	<i>Mammuthus exilis</i> ^a	UN	11,030 YrBP	L. Agenbrood, pers. comm.
Santa Rosa (E)	<i>Mammuthus exilis</i> ^a	UN	11,030 YrBP	L. Agenbrood, pers. comm.
Santa Rosa (E)	<i>Peromyscus nesodytes</i>	UN	LP	White 1966
Santa Rosa (E)	<i>Urocyon littoralis santarosae</i> ^d	P	R	Roemer et al. 2002, 2004;
Anacapa (E)	<i>Peromyscus anyapahensis</i>	UN	LP	White 1966
<i>Gulf of California–Land-bridge</i>				
San Pedro Nolasco (E)	<i>Peromyscus pembertoni</i>	R	R	Alvarez-Castaneda and Ortega-Rubio 2003
Coronados (E)	<i>Neotoma bunkerii</i>	C	R	Alvarez-Castaneda and Ortega-Rubio 2003; Smith et al. 1993
Granito (E)	<i>Peromyscus guardia harbitsoni</i>	R	R	Alvarez-Castaneda and Ortega-Rubio 2003; Mellink et al. 2002
Mejia (E)	<i>Peromyscus guardia mejia</i>	C	R	Alvarez-Castaneda and Ortega-Rubio 2003; Mellink et al. 2002
Estanque (E)	<i>Peromyscus guardia subsp.</i>	C	R	Mellink et al. 2002
San Jose (E)	<i>Dipodomys insularis</i>	C	R	Alvarez-Castaneda and Ortega-Rubio 2003;
Montserrat (E)	<i>Chaetodipus baileyi fornicatus</i>	C	R	Alvarez-Castaneda & Cortes-Calva 2002
Turner (LE)	<i>Neotoma varia</i> ^f	UN	R	Alvarez-Castaneda and Ortega-Rubio 2003; Bogan 1997

Likely causes and estimated date of extinction are shown (C cats, R rats, P pigs, UN Unknown, LP Late Pleistocene, R 1950-present).

Other approximate or ranges of dates during the Holocene range from 11,000 YrBP to the late 1800s

^aEstimated date of extinction on all three islands are based on the youngest radiocarbon date of pooled specimens

^bBased on a fossil cranium and unpublished field notes of trapped skunks ~1893

^cAbundant in the fossil record; may have gone extinct sometime in the 19th century due to land transformation by introduced sheep overgrazing

^dExtinct in the wild; captive populations exist

^eLast specimen collected in 1983; extinction may be due to habitat destruction from introduced herbivores and cats

^fSingle specimen trapped in 1977, despite trapping efforts in 1976 and 1997 (536 trap-nights) and small island size

native and exotic mammals, as well as geographical data, were obtained from a regional conservation database (Donlan et al. 2000) and published literature (Guthrie 1993; McChesney and Tershy 1998; Alvarez-Castaneda and Patton 1999; Case et al. 2002; Alvarez-Castaneda and Ortega-Rubio 2003). Given the presence of congener endemic species/subspecies that are arguably ecological analogs, all analyses were conducted at the generic level. A total of 19 genera occur or occurred on 42 islands in our study area, with only seven islands harboring two species within the same genus (all *Peromyscus* and *Chaetodipus*). In four of these cases, one of the conspecifics is now extinct. The strength of the nestedness pattern for each occurrence matrix was evaluated using the methods of Atmar and Patterson (1993, 1995), with “temperature” (T, 0° indicating complete disorder) giving a relative measure of nestedness compared to a null model estimated using a Monte Carlo simulation (1,000 iterations). This method arranges the island-species matrix to minimize the unexpectedness of occurrences. This index is matrix-size independent, allowing for spatial and temporal comparisons (Patterson and Atmar 2000). In particular, we use the temperature before and after Holocene extinctions to determine the impact of extinctions caused by introduced species on the strength of nestedness patterns.

We estimated risk of extinction using two approaches, both of which have been advocated in the literature (Kerr et al. 2000; Patterson and Atmar 2000; Hecnar et al. 2002). First, we compared the recent extinctions of populations to their position in the historical occurrence matrix. Patterson and Atmar (2000) suggest that the populations near the boundary line between largely unoccupied and mostly occupied cells are at the greatest risk of extinction; further, the nestedness temperature method calculates the probability of each matrix cell being occupied, thus quantitatively assessing the stability of various populations. To test qualitatively for an association between extinction and these risk measures, we categorized risk estimates as high or low, using a conservative probability occurrence (< 50%) as indicating high risk. To test quantitatively for an association between extinction and predicted risk, we performed a logistic regression of risk score (i.e., median of the range of probability of occurrence outputted by the nested analyses, see Fig. 4), archipelago, and their interaction on extinction versus persistence of populations. To test more generally whether there were any deviations in distributions of the risk ratings between extinct and extant populations, we also used Kolmogorov-Smirnov two-sample tests for data from each archipelago, and overall. Note, however, that risk values for each matrix cell depend on the entire pattern of occurrences. Thus, these values are not independent and statistical results based upon them should be viewed with some caution.

Second, we asked whether the strength of historical nestedness for individual genera correlated with extinc-

tion. For each genus and island group, we first separately evaluated whether occurrence patterns were well ordered by area, isolation (i.e., distance from mainland), or species richness. For each of these ordering variables, we produced a vector of occurrences/non-occurrences and used a Wilcoxon two-sample rank-sum statistic test (i.e., Mann-Whitney *U*-test) to assess orderedness, or nestedness (Simberloff and Martin 1991). To compare among genera and across archipelagos, we report the chi-square approximation (1 d.f.) and respective probabilities rather than the magnitude of the *U*-score, given that the latter is sample size dependent (Zar 1996). To ask if the degree of ordering predicts extinction risk, we report Spearman rank correlations between the nestedness scores of genera (i.e., chi-square test statistic) and the fraction of original populations that have become extinct, for each island group and ordering variable. Statistical analyses were conducted in Systat 10.0 and SPSS 11 with an α -level=0.05 (Wilkinson 1998; SPSS 1999).

Results

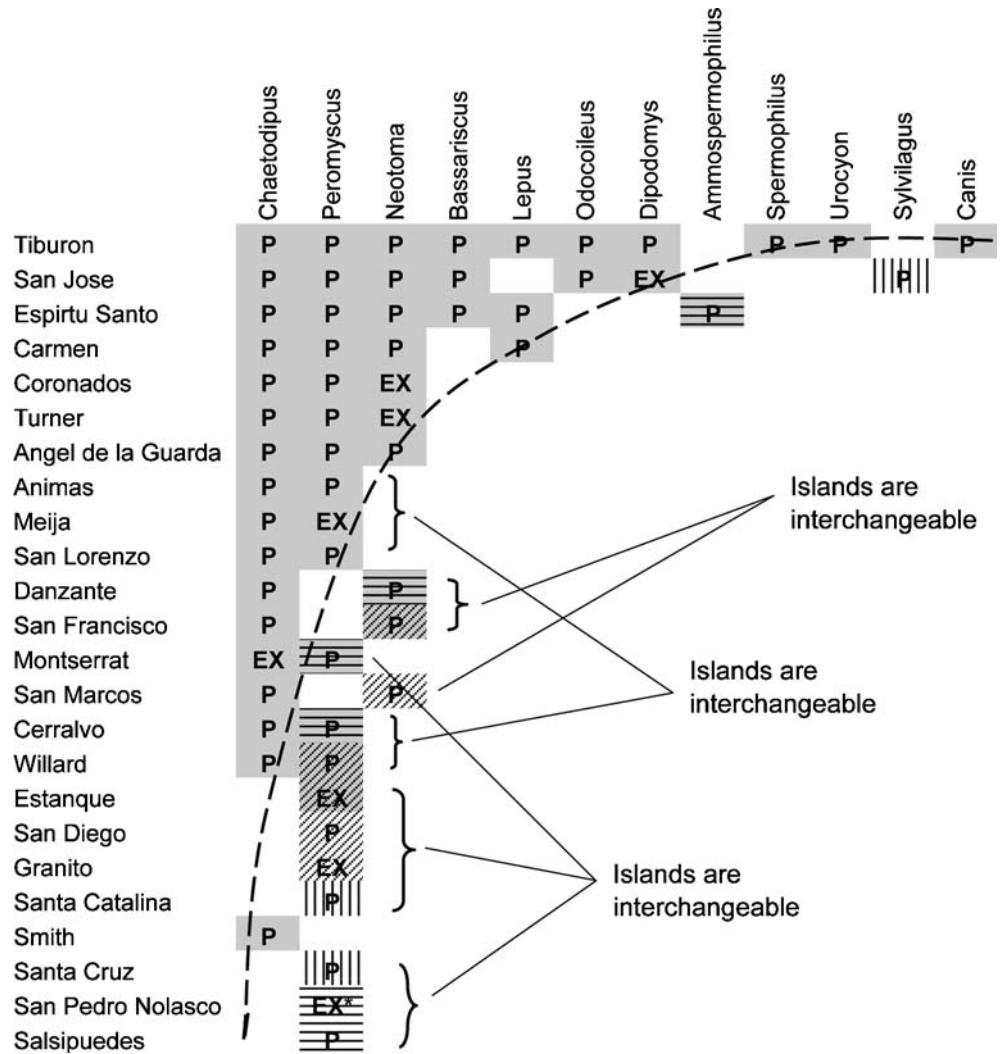
Mammals in all island groups exhibited significant nestedness before and after recent extinctions (Table 2). Historically, California and Gulf islands were more nested than Baja islands; while the Gulf islands are presently more nested than Baja and California islands (Table 2). However, nestedness was similar on all archipelagos. Extinctions resulted in inconsistent changes in nestedness for the three island groups. The California and Baja island groups decreased slightly in nestedness, while the Gulf islands hardly changed as a result of extinctions (Table 2). There was no clear pattern between introduced species, extinction, and nestedness. All but one extinction on the Gulf islands (7/8) were caused by introduced predators, resulting in little change in degree of nestedness, and all three extinctions on the Baja islands (3/3) were caused by introduced predators, resulting in a slight decrease in nestedness (Tables 1 and 2). The twelve extinctions on the California Islands, for many of which the cause is uncertain

Table 2 Nestedness of nonvolant mammal communities on islands off the Pacific coast of North America before and after recent mammal extinctions

	Historical	Current
Land-bridge		
Baja	9.06 (0.009)	10.8 (0.02)
Gulf	6.84 (<0.001)	6.75 (<0.001)
Oceanic		
California	6.26 (0.001)	8.10 (0.02)

Islands are broken into oceanic and land-bridge, the latter being connected to the mainland during the Pleistocene. The lower the index (Atmar and Patterson’s Temperature) the more nested the community; p-values in parenthesis are the result of a null model comparison via a Monte Carlo simulation (1,000 iterations)

Fig. 3 Nested nonvolant mammal communities on land-bridge islands in the Gulf of California, Mexico. *P* indicates species presence, *EX* extinctions, and *EN* endangered taxa. *EX** indicates an extinction, but a congener remains extant. The dotted line illustrates the boundary layer. Certain islands are interchangeable in the arranged matrix due to identical species presence. Shaded boxes indicate probability of occurrence (see Fig. 2 caption)



were ordered by species richness and area. *Lepus* was significantly nested when islands were ordered by species richness. On the California Islands, only *Urocyon* was significantly nested (ordered by species richness, area, and isolation). In the Gulf of California, a number of rodent genera (*Chaetodipus*, *Neotoma*, *Peromyscus*, and *Dipodomys*), and *Odocoileus* and *Bassariscus* were nested when ordered by one or more of the variables. None of the ordering variables (island richness, distance or size) correlated with the fraction of extinctions across genera (Table 3). When the island archipelagos were pooled, ordering by species richness produced a significant weak correlation with extinction ($S_r = 0.50$, $P = 0.03$), while ordering by the other variables showed no correlation with risk (Table 3).

Discussion

On the islands off the west coast of California and Mexico, where recent mammal extinctions are well documented, nested subset analysis does a poor job of

predicting observed extinctions. We could not find any statistically significant predictions of extinction risk. The utility of nested analysis in providing insights into nature reserve design and predicting extinction risk has been debated (Patterson 1987; Simberloff and Martin 1991; Doak and Mills 1994; Boecklen 1997; Fleishman et al. 2000; Patterson and Atmar 2000; Fleishman et al. 2002). However, in the majority (if not all) of past studies, extinction predictions have been inferred from unobserved historical events, such as relaxation events on land-bridge islands formed in the Pleistocene or habitat fragmentation (Patterson and Atmar 1986; Bolger et al. 1991; Soule 1991; Fleishman and Murphy 1999). In this effort to confirm the utility of nestedness predictions with documented extinction data, we come away without any evidence that this methodology can or should be used for predicting extinction risk.

The *temperature* method of Atmar and Patterson (1993, 1995) asserts that the topmost island or fragment in a packed matrix is the most hospitable, while the leftmost species is most resistant to extinction (i.e., holds the widest niche breadth, Patterson and Atmar 2000).

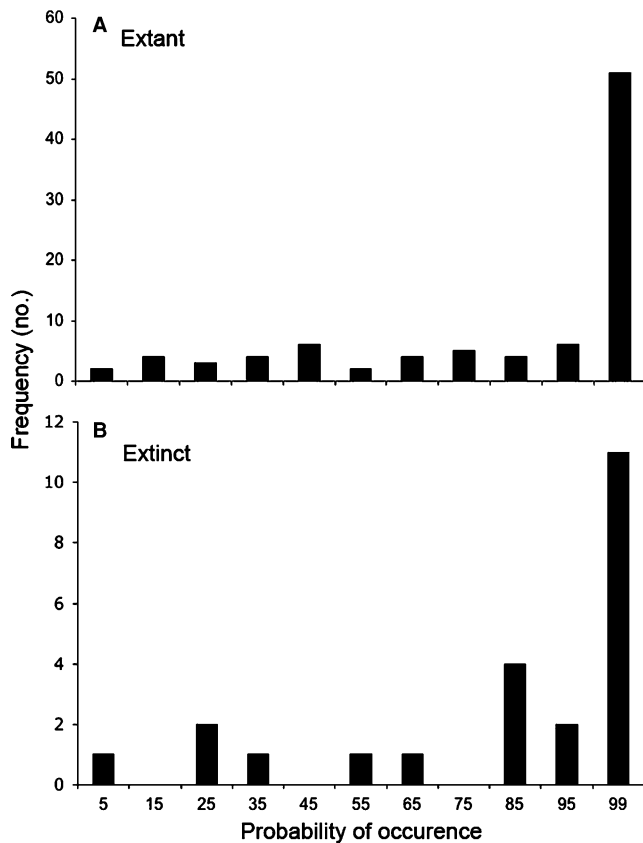


Fig. 4 Distributions of the probability of occurrence from nested subset analysis of **a** extant and **b** extinct populations. Probabilities are reported as median percentages, as outputted from the analysis. No differences exist when populations are pooled across all three archipelagos: Kolmogorov-Smirnov two-sample test, $P=1.00$, $N_{\text{extinct}}=23$, $N_{\text{extant}}=91$

The islands deemed the *most hospitable* in the three archipelagos were Magdalena and Margarita (Baja); San Miguel and Santa Cruz (California); Tiburon and San Jose (Gulf; Figs. 2 and 3). On these islands, eight extinctions have occurred and an additional species is critically endangered (Table 1, Figs. 2 and 3). Of the genera deemed most extinction-resistant (*Peromyscus*, *Neotoma*, *Chaetodipus*, and *Urocyon*), twelve populations have become extinct and three are endangered (Table 1; Figs. 2 and 3). On all three archipelagos, a single taxon occurs on the *least hospitable* islands; of these 15 islands, five have suffered an extinction. On all three archipelagos, several extinct populations were located near the boundary line of occurrence matrices. However, this visual pattern was offset by the presence of other observed extinctions with strong predicted occurrences and the overall poor performance of the analysis to predict observed extinctions. For example, the island fox (*Urocyon littoralis*) is highly endangered or extinct in the wild (Roemer and Wayne 2003; Roemer et al. 2004), while occupancy probabilities from the nested analysis were 97–100%. Of the 23 populations conservatively deemed threatened with extinction, with a probability of occurrence < 50%, only four suffered extinction.

Individual nestedness scores can be useful for determining which species or genera do and do not conform to an observed nested pattern. Taxa differ greatly to the degree they conform to their orderedness of an expected variable such as area or species richness (Table 3; Simberloff and Martin 1991; Hecnar et al. 2002). However, the ability to elucidate a mechanism to explain an observed species occurrence patterns relies on additional biological knowledge such as abundance, habitat requirements, or strength of species interactions. In addition, a species orderedness or lack thereof is a result of a number of possible mechanisms, and these mechanisms hold different conservation implications (Simberloff and Martin 1991). On all three archipelagos, species orderedness differed greatly with some genera being nested across all ordering variables (*Urocyon*), others being significantly ordered with just one variable, and many others showing no ordered pattern. The genus-level degree of orderedness failed to give insight into extinction risks; rather, detailed natural history and ecology are likely to hold the answers to such patterns.

Overall, nested subset analysis provided little qualitative or quantitative insight in predicting extinction risk. A number of prior studies have suggested a link between extinction and nestedness. However, such linkages have been based on inferences of extinction events based on assumptions about Pleistocene relict faunas or fragmentation-induced extinctions rather than direct evidence (Patterson 1987; Bolger et al. 1991; Cutler 1991; Kerr et al. 2000). While species loss may have occurred due to such events, other mechanisms are equally likely such as habitat requirements, colonization, or strong species interactions, and thus could have contributed to the observed species occurrence patterns. In this study with documented extinctions, the majority were not predicted. While a few of the predicted extinctions were corroborated by observed trends, these results could have been attained solely from the information needed to conduct the analysis in the first place. Thus, it appears detailed natural history and taxa-specific ecology may prove critical in predicting even broad-scale patterns of extinction risk (e.g., Bennett and Owens 1997; Owens and Bennett 2000). In our opinion the best approach to making conservation and management decisions is the careful consideration of multiple ecological factors as they apply to individual taxa, rather than the application of a highly general model such as nested analysis. At the least, further research is needed in the utility of nested subset analysis before it is prescribed widely as a useful conservation tool.

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Table 3 Individual orderedness of mammal genera on three island archipelagos

Genus	Baja Islands			California Islands			Gulf Islands		
	Rich	Area	Isolation	Rich	Area	Isolation	Rich	Area	Isolation
<i>Ammospermophilus</i>							0.1	0.8	0.1
<i>Bassariscus</i>							2.7	5.6*	2.7
<i>Canis</i>	2.2	0.7	0.7				2.2	2.7	2.2
<i>Chaetodipus</i>	6.5**	5.7*	0.3				13.4**	7.8**	7.5**
<i>Dipodomys</i>	2.2	0.75	0.3				2.8	4.7*	2.8
<i>Lepus</i>	5.0*	2.4	0.1				2.2	4.8*	2.2
<i>Microtus</i>				2.4	0.4	0.4			
<i>Mammuthus</i>				3.3	1.8	1.8			
<i>Neotoma</i>	7.8**	3.9*	17.0				4.8	5.8*	4.8*
<i>Notiosorex</i>	0.3	0.03	0.2						
<i>Odocoileus</i>	3.3	4.3*	0				2.8	4.7*	2.8
<i>Ovis</i>							2.2	2.7	2.2
<i>Peromyscus</i>	NI	NI	NI	NI	NI	NI	3.8*	0.1	3.8*
<i>Reithrodontomys</i>				1.8	2.7	2.7			
<i>Sorex</i>				3.4	0	0			
<i>Spermophilus</i>				0.7	0.4	0.4	2.2	2.7	2.2
<i>Spilogale</i>				3.3	0.4	1.8			
<i>Sylvilagus</i>	0.8	2.5	2.4				0.6	1.8	0.6
<i>Thomomys</i>	2.2	1.4	2.4						
<i>Urocyon</i>				4.1*	4.0*	4.0*	2.2	2.7	2.2
Spearman Rank									
Correlation (S_r)	0.65	0.29	0.71	0.56	-0.37	-0.37	0.55	-0.01	0.55
Bonferroni P value	0.34	1.0	0.19	1.0	1.0	1.0	0.32	1.0	0.32
N	9	9	9	7	7	7	13	13	13
Archipelagos pooled									
S_r	0.50	-0.17	0.13						
Bonferroni P value	0.03	1.0	1.0						
N	29	29	29						

Ordering variables include mammal species richness, island area, and isolation (i.e., distance to nearest mainland). Wilcoxon two-sample rank-sum tests were used and the chi-square approximation values (1 df) are reported; statistical significance is shown with **($P < 0.01$) and *($P < 0.05$). *Peromyscus* spp. were not included

(NI) in the analysis on the Baja and California archipelagos since they occur on every island. Spearman rank correlations (for each archipelago and for all islands pooled) are shown between chi-square statistics and fraction of original populations that are now extinct in each genera

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