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Sampling procedures and species estimation: testing the effectiveness of herbarium data against vegetation sampling in an oceanic island

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Keywords
Guadalupe Island; Herbarium specimens; Richness estimation; Sampling process; Species-abundance distributions

Nomenclature
Moran (1996); Little (2006) for the Guadalupe cypress

Abbreviations
CAS, California Academy of Science Herbarium; DS, Dudley Herbarium, California Academy of Science; SD, San Diego Natural History Museum Herbarium; UC, University of California Herbarium

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Abstract

Questions: What is the relationship between species assemblages in herbarium collections and species abundances in the field, and how trustworthy are herbarium data in vegetation science?

Location: Guadalupe Island, Baja California, Mexico.

Methods: We compared species-abundance distribution and evenness in 110 vegetation plots in Guadalupe Island against data from four herbaria. We tested whether the relative frequencies derived from herbarium specimens differed significantly from species frequencies in the field. We compared the rarefaction curves for both field and herbarium data sets, and tested whether taxonomic collectors accumulated new species at a higher rate than that observed in ecological plot sampling.

Results: At any given sampling effort, the total number of observed species was higher in herbarium data. The relative abundance of common species in the field was higher, and the evenness of the distribution was lower, than in herbarium data. There was no significant correlation between species abundances in the field and in the herbaria. By selectively targeting rare species, collectors accumulate previously unseen species much faster than through ecological sampling.

Conclusions: Because collectors aim for the rarer species and avoid the more common ones, the relative abundance of species in herbarium collections cannot be interpreted as a predictor of their true abundance in the field. Any statistical procedure that requires the sample to be representative of the true abundance distribution is likely to show errors when applied to herbarium data. However, because collectors actively search for rare species their rate of species accumulation is higher and their floristic lists are more complete than those obtained through ecological field sampling.

Introduction

Natural history museums, herbaria and other biological collections have historically been repositories of taxonomic, evolutionary and biogeographic information. Information from these collections, often in the form of electronic databases, is frequently used to test hypotheses on species distributions and vegetation science because it has important advantages, described below.

Quantity and accessibility

Collections contain, in total, one of the best sources of information on past and present biodiversity (Krishtalka & Humphrey 2000; Suárez & Tsutsui 2004) and their electronic accessibility is rapidly growing (e.g. the Global Biodiversity Information Facility – GBIF: http://www.gbif.org; Consortium of California Herbaria: http://ucjeps.berkeley.edu/consortium/; Australia's Virtual Herbarium:

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http://www.cpbr.gov.au.avh; the Southwest Environmental Information Network – SEINet: http://swbiodiversity.org/seinet/index.php; Red Mundial de Información sobre Biodiversidad – REMIB: http://www.conabio.gob.mx/remib/doctos/remib_esp.html).

Taxonomic confidence and updating

Collections contain information assembled by experienced taxonomists in the form of well-identified specimens (Kress et al. 1998; Funk et al. 1999; Ponder et al. 2001; Petersen & Meier 2003) whose taxonomic status is regularly checked by specialists and which remain available for validation in the future, a trait that is essential to the integrity of taxonomic knowledge (Cotterill 1995).

Wide temporal scale

While a single sample taken by an ecologist interested in species richness at a particular site only provides a snapshot at one point in time, museum collections are assembled over long periods, making temporal fluctuations in relative abundances less likely to influence species richness estimates (Petersen & Meier 2003). Furthermore, a major strength of natural history collections is the potential to determine change in species richness through time, especially at regional and continental scales (Guralnick & Van Cleve 2005).

Wide geographic scale

In studies involving broad-scale gradients in species richness, plot sampling can be labour-intensive and time-consuming. The use of museum collections for studying broad-scale geographical patterns allows the researcher to take advantage of the efforts of other collectors. This approach will probably become more important and common as more and more herbarium information becomes readily available in electronic database form.

In a previous paper on plant richness estimation on Guadalupe Island (Garcillán et al. 2008), we showed how the temporal effect captured by herbarium data gave higher species richness estimation (218 species) than systematic field data over the entire island (187 species). We proposed that the two types of estimation were calculating two different types of diversity – historic and current diversity, respectively (Garcillán et al. 2008).

A fundamental problem remains, however, for the vegetation ecologist when using herbarium specimens – that of the non-random nature of the herbarium data. Indeed, vegetation analysis based on information derived from non-random, i.e. opportunistic or targeted, plant collecting can introduce several biases (temporal, geographic and taxonomic) into the research data set. These potential sources of error must be taken into account when interpreting results derived from collection data, chiefly because the species abundance distribution in the herbarium data sets may differ substantially from that in the field (Ponder et al. 2001; Petersen & Meier 2003; Crawford & Hoagland 2009).

To analyse how the taxonomic bias due to directed sampling for herbarium specimens affects the estimated relative abundance of individual species and the abundance distributions of the floristic species set, we compared herbarium data for Guadalupe Island (1875–2000) with a field database obtained from an extensive field survey done in May 2004. We tested the hypothesis that the taxonomic bias caused by the rarity or endemicity status of the species can affect the collectors' preferences and the relative abundance distributions of species in herbarium databases.

Methods

Study area

Guadalupe is an oceanic island of about 250 km^2, located approximately 260 km off the coast of the Baja California peninsula, Mexico (Moran 1996). Goats were introduced to the island by sailors in the mid-nineteen century, and since then the native flora and plant communities of the island have been devastated by overgrazing (three islets always remained goat-free). Since 1875, when Edward Palmer made the first botanical collections on the island, there have been 218 different plant species documented on Guadalupe Island (Moran 1996; Rebman et al. 2002; León de la Luz et al. 2003). Due to overgrazing, 31 species are supposed to have become extirpated from the island (locally extinct), 21 of which were native to the region. At present there is an estimated total of 187 vascular plant species on Guadalupe (five additional species survive on the surrounding islets; Moran 1996; Rebman et al. 2002; León de la Luz et al. 2003). A collaborative governmental and multi-institutional programme was established in 2004 to eradicate the goats, restore the island and manage it as a protected area.

Data collection

Field survey data

As part of a baseline study to monitor the success of the goat eradication programme, we placed 110 transect plots (each 50-m long × 2-m wide) in the main island, and recorded the presence of all vascular plant species within each plot. We divided the island in 45 cells of 1.5′ latitude by 1.5′ longitude, and placed three random transect plots within each cell, ensuring that one plot fell near the centre of the cell and that the other two fell north and south of the first one, at a distance of more than 350 m

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from each other. A total 1173 occurrences were registered and 80 plant species were found (a detailed description of the sampling procedure is given in Garcillán et al. 2008).

Herbarium data

We checked all specimens collected in the main island at four herbaria in California (CAS, DS, SD and UC) that have historically been the main recipients of voucher specimens from floristic expeditions, registering the collection date. After synonyms were eliminated, a total of 191 different species in 1960 specimens was found in the four collections, collected by 50 different collectors in 52 different collecting expeditions.

Estimating taxonomic bias

Relative abundance distributions

For the field data set, we used the percentage of occurrences (number of plots in which each species was found divided by the total of 1173 occurrences) as a measure of relative abundance in the island. For the herbarium data set, we used the number of herbarium specimens for each species divided by the total number of specimens (1960) in the pooled herbarium data set. Using χ^2 analysis, we compared the relative abundance distributions of both herbaria and field data to see if the patterns of rarity and dominance in the herbaria differed from the pattern observed in the field. We also used the standard evenness and Gini indices to estimate the evenness/dominance of herbaria and field abundance distributions. Evenness was calculated as $E = e^{H/s}$, where H is Shannon's index and s is the total number of species collected in the sample (Hill 1973). Gini's index was calculated following Deaton (1997).

Individual species abundance

To explore how rarity/commonness and native status of the species affected their probability of being counted, we compared the relative abundances of species in herbarium and field data. We defined an index of collecting preference $C = h/f$, where f is the relative abundance of the species in the field, and h is the relative abundance of the species in the herbaria. Using χ^2 analysis on the absolute frequencies, we identified species that showed significantly higher frequencies in the field than in the herbaria ($C < 1$), and species had significantly higher frequencies in the herbaria than in the field ($C > 1$).

Accumulation process

For the field data, we constructed a presence/absence matrix of 80 species × 110 plots with a total of 1173 occurrences. In the case of herbaria data, we sorted chronologically the 1960 specimens and grouped them into 196 sequential groups of ten specimens each. We then constructed a frequency matrix of 191 species × 196 groups of ten, time-ordered, specimens. Each cell contained, for each species, the number of specimens for which the species was represented in a given chronological group of ten (see Garcillán et al. 2008). Rarefaction curves were computed for both data sets using the analytical procedure in EstimateS 8.0 (Colwell 2006). We compared the rarefaction curve of species as a function of occurrences, for the historic herbarium data, against the rarefaction curve based on plots for the field data.

The effect of individual collectors

In order to test the effect that the preference of individual collectors could have on the species assemblages derived from herbarium data, we plotted a species-versus-specimens graph for all the collectors that have worked in the island, and compared the resulting data cluster against the rarefaction curve for the field plots, which we took as our null model representing the rate at which a researcher doing a plot-based ecological survey accumulates species records.

Results

The cumulative number of species found was higher in herbarium data than in field survey: we obtained 191 different species from the herbaria (23.6% of which were non-native), and counted only 80 different species in the field survey (37.5% of which were non-native). The 191 species contained in the four herbaria represent 87.6% of the total 218 species historically recorded for the main island. In contrast, during the field survey we found only 42.8% of the 187 accepted extant species in the island at that time (Table 1).

Taxonomic bias

Relative abundance distributions

The species-abundance distributions of herbarium and field data showed clear differences in the shape of the curves. Dominance by some species in the field was much higher than that in the herbarium data, both for native and non-native species, and for the pooled data set (Fig. 1a–c). The relative abundance of the most common species in the field was in all cases significantly higher ($P < 0.001$ in the χ^2 tests) than the highest relative abundances in the herbarium and, conversely, the relative abundance of the rarest species in the field was in all cases significantly lower than that of the rare plants in the herbarium. In agreement with this distributional pattern,

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Table 1. Number of species recorded from herbarium specimens and in the field survey; evenness and dominance of the species-abundance distributions for native species, non-native species and for all species pooled together.

	Species assemblages		
	Native	Non-native	All species
Species richness			
Herbaria	146	45	191
Field	50	30	80
Evenness			
Herbaria	0.701	0.751	0.710
Field	0.622	0.671	0.597
Dominance (Gini coefficient)			
Herbaria	0.461	0.417	0.458
Field	0.543	0.501	0.559

the evenness of the distribution was higher in the herbarium data set, both for native and introduced species, and dominance in the species assemblage, indicated by the Gini coefficient, was in all cases higher in the field data sets (Table 1).

Individual species abundance

We found no significant correlation between the relative abundance of individual species in the field and in the four herbaria ($r = 0.14$; $P = 0.06$), indicating that the preference with which species are collected is largely independent of their abundance in the field (Fig. 2). Species whose relative frequency in the field is significantly higher than that in the collections were mostly introduced weeds and a few native, but floristically common, plants. Conversely, the species whose relative frequency in the herbaria is significantly higher than that in the field were all island endemics or species native to the region (see Appendix S1).

The species accumulation process

The comparison of rarefaction curves obtained for herbarium and field data shows clearly that herbarium collectors accumulate new unrecorded species much faster than is achieved by the process of ecological sampling (Fig. 3). Although at first the accumulation rates were similar, the rate at which new species accumulate decreased more rapidly in the plot sampling than in the directed taxonomic search done by herbarium collectors.

The effect of individual collectors

One collector alone (Reid Moran) collected 890 specimens, almost half (45%) of the total 1960 herbarium specimens. His specimens contained 166 of the total 191 species found in the herbaria. The remaining 49 collectors contributed 1070 specimens containing 171 species.

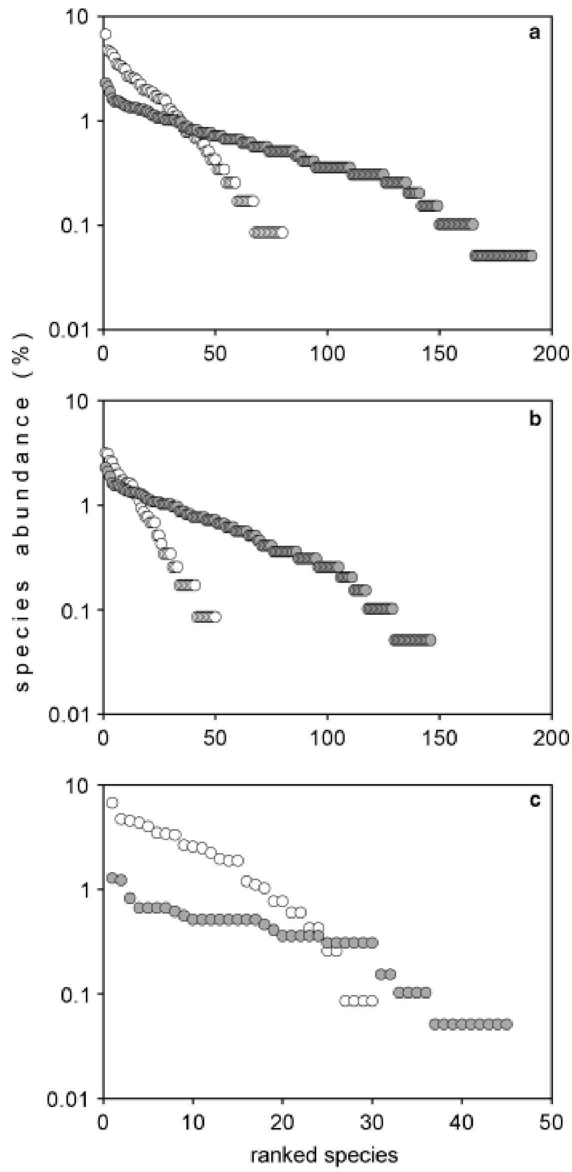

Fig. 1. Ranked abundance distributions of species from the herbaria data set and from the field sampling. (a) All species, (b) native species and (c) non-native species. Grey dots correspond to herbaria abundance distributions and white dots to field abundance distributions. The evenness of the distribution for herbarium data was higher than for field data.

We found that most collectors who had collected < 100 specimens incorporated new species at a similar rate as a researcher doing plot sampling (Fig. 4). In some cases, these "low-numbers" collectors gathered less species than the rarefaction curve predicted, mostly as result of collections taxonomically targeted towards particular research species such as *Pinus radiata* or *Callitropsis guadalupensis*. On

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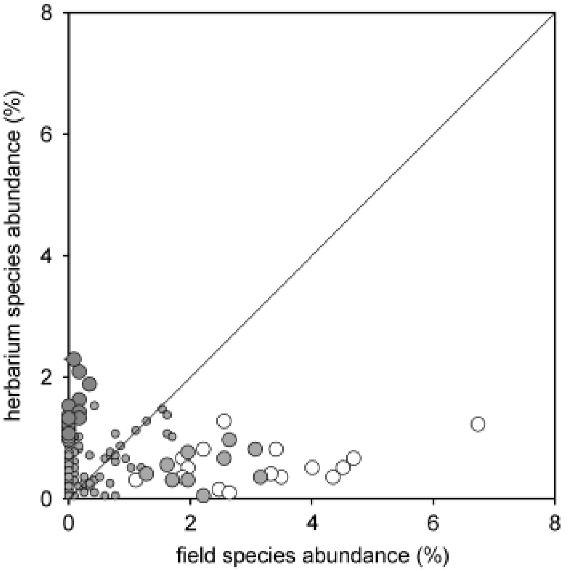

Fig. 2. Relation of single species abundance as derived from herbarium specimens with respect to field data. Large dots correspond to species significantly over-collected or under-collected in the herbaria data set (above or below the diagonal, respectively): White dots show non-native species; light grey dots, native species, and dark grey dots, species endemic to Guadalupe Island or to the California Channel Islands. Small dots correspond to the rest of the species.

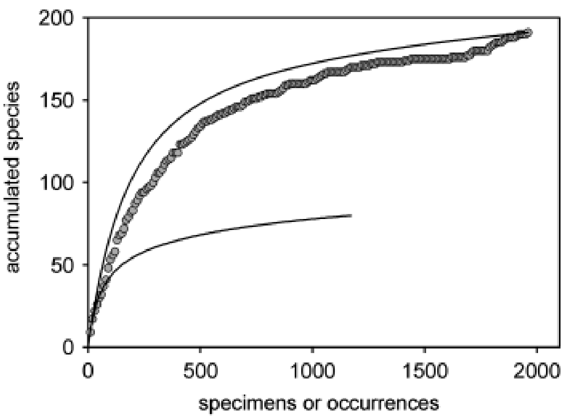

Fig. 3. Species accumulation curves. The grey dots show the herbarium accumulation curve plotted against the sequential number of collected specimens; the black lines show the rarefaction curves for the herbarium and field data sets.

the other hand, the "high-numbers" collectors, who collected with the obvious intent of documenting the island's total biodiversity, gathered significantly more species than could have been recorded through the process of ecological plot sampling, given a similar effort. These active herbarium collectors clearly search for the rarer species and avoid targeting the more common ones.

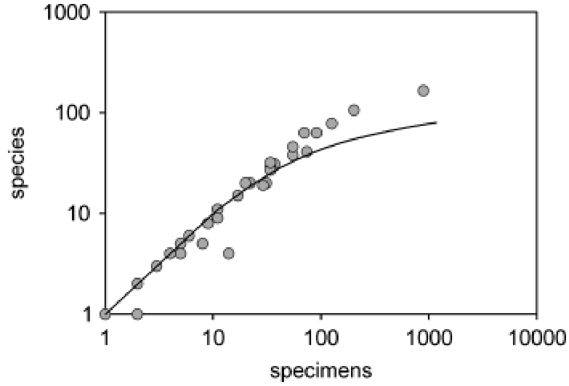

Fig. 4. Relation between the number of recorded species and collected specimens for the 50 individual collectors of herbarium specimens from Guadalupe Island. Both axes are plotted on a log basis. The rarefaction species accumulation curve (black line) from the field plots is given for comparison purposes. In all cases, the more prolific collectors have accumulated species at a rate higher than predicted by the field sampling data, suggesting an active search for taxonomic novelties in their explorations.

Reaffirming this observed trend, we found that there was no correlation between the number of collectors who collected a given species and the estimated abundance of that species in the field ($r = 0.14$, $P = 0.7$); i.e. collectors do not collect specimens in proportion to the species' abundances, but rather search actively for the rarer plants.

Discussion

The main conclusion from this study is that the species abundance distributions of herbaria and field data sets of the same region (Guadalupe Island) differ. Species-abundance distributions observed in the herbaria data set, which has higher evenness, is more equitable and less hierarchical than the distributions observed in the field. Herbarium specimens are not the result of random sampling and can introduce several biases into the floristic data set. In the case of our study on the Guadalupe Island flora, the following sources of bias are relevant.

Availability/completeness

Voucher specimens are often deposited in many different herbaria around the world. Access to different collections and retrieval of specimen information can be a difficult and lengthy process, constrained by the availability of time or funding. For our study, we consulted only four herbaria located in California, containing 191 of the 216 species historically recorded on the island.

Non-random samples

To obtain unbiased estimators of true species richness in a natural community, the sample must accurately reflect the true species-abundance patterns of the community, as species accumulation (rarefaction) curves depend upon relative abundances (the greater the evenness of the relative abundance distribution, the steeper the rarefaction curve; see Colwell & Coddington 1994; Gotelli & Colwell 2001). Being non-random, but rather targeted samples, museum collections fail to meet these statistical requisites and are normally not well suited to estimate total species richness through extrapolation using rarefaction curves or similar statistical procedures (Grytnes & Romdal 2008). In Guadalupe Island the species-abundance distribution, evenness and dominance of the herbarium data set were dramatically different from the values estimated in the field.

Taxonomic bias

Collectors in some groups tend to focus their attention towards rare species, often failing to collect the most common ones. Thus, common species tend to be under-represented and rare species to be over-represented in the collection (the "rare representation" effect, Guralnick & Van Cleve 2005). Museum collections may also have other biases, such as expertise and interests of local taxonomists, avoidance of difficult groups or legally protected taxa or higher collection intensity of conspicuous groups (Rich & Woodruff 1992; Grytnes & Romdal 2008; Crawford & Hoagland 2009). As a result, collections can be a distorted representation of the whole plant community composition (van Gemerden et al. 2005), and information about relative abundance based on museum collections can misrepresent relative abundances in the original community assemblage (Grytnes & Romdal 2008). In Guadalupe Island the taxonomic bias was particularly evident by the over-representation of endemic tree species and by the under-representation of non-native weedy species in the herbaria.

Temporal bias

The long temporal interval normally contained in the museum data can incorporate bias due to unequal sampling effort over time (Crawford & Hoagland 2009), or to the effect of species turnover through time. The long time-span represented in most collections can lead to an over-estimation of species richness for a given area if species turnover in time is not considered. Disturbance can amplify temporal bias through an increase of species turnover due to the local extirpation of (native) species and the arrival of exotic ones. The effect of temporal bias on the Guadalupe Island floristic knowledge is discussed in Garcillán et al. (2008), where we showed that the work of particular collectors such as Reid Moran produced a quantitative leap in the cumulative number of recorded species.

It has been argued that if many different botanists collect over many years in the same area, the inherent biases present in most collections are lowered, creating a sample approaching randomness (Petersen & Meier 2003). This compensation effect, however, is only theoretical and can be difficult to detect in practice. Furthermore, if a single or a few researchers with a given collecting pattern have been active for many years, contributing a disproportionate amount of specimens to the collection, the resulting databases can retain their bias in the collection's data structure for a very long time.

The main fact that can be concluded from our study in Guadalupe Island is that botanical collectors systematically reject some species (normally, the most common and "uninteresting" ones) while actively searching for others (mostly rare species with very restricted distributions). In our study area this pattern was consistent for almost all individual collectors, and in particular for those who have collected a large number of specimens with the intention of doing comprehensive biodiversity surveys.

This selective collection pattern is reflected in the species-abundance distributions observed in the herbarium data set, which has higher evenness, is more equitable and less hierarchical than the distributions observed in the field. In herbarium collections, rare species are over-represented while common species are under-represented, independent of their taxonomic identity, giving the species-abundance distribution a much higher evenness than is actually observed in the field.

As a result, in Guadalupe Island the abundance of individual species in the herbarium data sets was found to be largely uncorrelated with their abundance in the field. Native species that are rare in the field may be common in the collections, as most collectors prefer collecting these micro-endemic or demographically rare plants to collecting widespread, cosmopolitan species. For this reason, the relative abundance of a species in the herbarium collections cannot be interpreted as a predictor of its true abundance in the field.

It is clear, then, that relative abundance in herbarium collections cannot be regarded as an estimate of the true species-abundance in the field. Hence, any statistical procedure that demands that the sample be representative of the true species-abundance distribution in the field, such as rarefaction curves, is likely to show errors when applied to herbarium data.

On the other hand, a rare and unrecognized merit of herbarium data shows up very clearly in the Guadalupe species set: because most collectors actively search for rare species, the rate of species accumulation in targeted taxonomic collecting is much higher than that observed

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in ecological field sampling following a systematic or a random design. It is a well-known fact in ecology that the number of species in a sample is a biased under-estimate of the true species richness, as many of the rarer species commonly fail to fall in a given sample and the resulting data will thus provide an under-estimation of the true floristic richness of a site. Many statistical methods have been devised to quantify and correct this bias (Lande 1996), but the fact remains that while it is possible to estimate the number of "unseen" species, it is not possible to estimate their taxonomic identity. The question is important because it is often in these rare species where the highest conservation interest lies.

Thus, for many ecological or biogeographic studies in which the main interest lies in analysing diversity patterns, and for many other studies that are geared towards the conservation of rare and endangered species, targeted taxonomic collecting and data derived from herbaria may provide a more useful, practical and reliable alternative than systematic or random ecological sampling.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of species whose relative abundance in the field or in herbarium data are significantly higher than expected. *f*/*h* is the ratio between relative abundance in the field and in the herbarium. Species are classified according to their degree of endemicity: E1, endemic to Guadalupe Island; E2, endemic to the California Channel Islands and Guadalupe Island; N, native; and X, non-native species.

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