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COLONIZERS, WAIFS, AND STOWAWAYS: ARRIVAL OF NEW PLANT SPECIES ON SANTA BARBARA ISLAND OVER A 30-YEAR PERIOD

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Abstract—Santa Barbara Island is a small island with an extensive history of botanical exploration. We report on floristic studies on the island that have spanned the last three decades, covering the period since the removal of introduced European rabbits from the island. In aggregate, these studies have surveyed this small island thoroughly, and have recorded a significant percentage of additions to the island flora. Over the course of this period, 32 plant species have been recorded that are new to Santa Barbara Island. Just over half of these are non-natives. A few of the new species, such as *Baccharis emoryi*, have only been found on the island as single, non-persisting individuals. Most of the non-natives were first recorded in the Landing Cove area of the island, along trails, or in other locations that suggest they were inadvertently transported to the island by people. Of the native species, nine are composites (family Asteraceae), and all appear to have arrived on their own. Particularly noteworthy is the genus *Pseudognaphalium*, previously unknown from Santa Barbara Island, but which is now represented by four species there (three native and one non-native). These results have implications both for management of invasive weeds, and in furthering our understanding of island biogeography. From the management standpoint, understanding where and how non-native plants arrive is an important step to limiting future, unwanted colonizers.

INTRODUCTION

The California Channel Islands have been the focus of a wide range of island biogeography studies, including analyses of 'turnover' rates and species richness patterns in birds (Diamond and Jones 1980; Lynch and Johnson 1974; Power 1976), species numbers and species—area relationships of amphibians and reptiles (Savage 1967; Wilcox 1980), species distribution and colonization of insects (Powell 1981, 1994), and biogeographic patterns of marine invertebrates and near-shore fish species (Pondella et al. 2005; Seapy and Littler 1980). In this way, studies on the Channel Islands have contributed to knowledge of regional faunal patterns, and also to more general questions of island colonization and community processes.

Compared to animal species, plants have been relatively neglected in studies of colonization on the California Channel Islands. Most studies of plants on the Channel Islands have focused on floristics and species diversity, including inter-island comparisons (e.g., Junak et al. 1995; Moody 2000; Oberbauer 2002; Raven 1967), patterns of endemism (Philbrick 1980), and effects of introduced herbivores such as sheep, goats, and pigs (e.g., Coblentz 1980; Hobbs 1980; Klinger et al. 1994; Peart et al. 1994). Floristic studies, which frequently make comparisons to other islands and nearby mainland floras, provide presumptive information on patterns of colonization, or at least successful establishment. Carlquist (1974) included San Clemente Island in the Channel Islands group in a comparison of different oceanic islands in relation to presumed colonization modes. However, there have been no previous studies that have directly examined current colonization patterns on any of the California Channel Islands.

Until recently, most studies of island colonization by plants have looked at devastated islands or newly formed islands. The most well-known of these include Krakatau, which was largely destroyed by volcanic eruption in 1883, and has slowly reformed. The island of Surtsey rose from the ocean off of Iceland in November 1963, and the arrival and spread of plant species on this new island have been followed since that time (e.g., Fridriksson 1987). However, colonization of barren, newly

formed or devastated islands is quite different from colonization of islands that have well-established plant communities. These latter islands have a more or less well-developed soil cover which is largely lacking on new islands, and potential colonizers face competition from established plant species. There have been very few studies (with the notable exception of Cody 2006) that have examined plant species colonization under such conditions. In this paper, we present another study of patterns of species arrival and colonization in an established island flora, on Santa Barbara Island, a small, comparatively isolated island in the California Channel Islands. We specifically describe and evaluate colonization rates and taxonomic patterns of both native and non-native vascular plants that have arrived on the island in the last 35 years.

STUDY AREA

Santa Barbara Island is located in the center of the Channel Islands group off the coast of southern California. It is a small island, measuring about 2.6 sq km in area, and is 62 km from the nearest point on the mainland coast. The nearest neighboring island is Santa Catalina, 38 km to the east. Santa Barbara Island is primarily volcanic, with thin layers of marine sediments. Topographically, the island has a series of low terraces, with small peaks at the north and south ends of the island. The highest point on the island is Signal Peak, at 193 m. Sheer cliffs bound much of the north, west, and part of the south sides of the island. Santa Barbara Island would have been completely submerged at high sea levels during the latter part of the Pleistocene, so the island's current biological history is presumed to be limited to within the last 100,000 years (Vedder and Howell 1980).

Coastal southern California has a Mediterranean climate, with mild winters and warm to hot summers, and most precipitation occurring as winter rains. On the offshore islands, particularly small islands like Santa Barbara, summer high temperatures and winter lows are strongly moderated by the surrounding ocean, so that seasonal temperature variation is comparatively low (Dunkle 1950; Philbrick 1972). On Santa Barbara Island, monthly average high temperatures range from 16°C in December and January to 23°C in August (Fellers and Drost 1991). Average annual precipitation has been reported from 22.7 cm (Fellers and Drost 1991) to about 30 cm (Dunkle 1950). Prevailing winds are from the west-northwest (Dunkle 1950; Philbrick 1972). Of possible significance to this study, however, are seasonal, strong east to northeast winds ("Santa Ana winds") that blow from the mainland out over the Southern California Bight at times during the fall and winter.

Like all of the Channel Islands, Santa Barbara Island has a long history of human impacts on the flora, ranging from introduced grazing animals to clearing and tilling for farming. Goats were recorded on the island as early as 1846, and farming families later brought sheep and other domestic animals (Philbrick 1972). European rabbits (*Oryctolagus cuniculus*) were introduced in the early 1900s, and at times increased to high numbers and caused severe declines in the native vegetation of the island (Sumner 1958, cited in Philbrick 1972). Larger grazing animals were taken off the island when grazing ceased in the late 1920s. European rabbits were successfully removed from the island by the National Park Service in 1981 (Junak et al. 1993; McChesney and Tershy 1998).

Visitation to the five islands that make up Channel Islands National Park is moderate, with approximately 30,000 visitors recorded in 2006. Santa Barbara Island receives fewer visitors than most of the other islands, because there is limited commercial transport to and from the island. In 2008, there were 332 visitors to the island via commercial tour boat (annual park visitor statistics, C. Leon., Channel Islands National Park, personal communication). Particularly during the summer, limited numbers of small private boats anchor at the island. Most of these come from the Los Angeles/Long Beach harbors on the California mainland or from Catalina Island.

Several features of Santa Barbara Island make it a good study site to examine species arrival and colonization. It is small and topographically simple, and most of the island is easily surveyed. Steep cliffs on parts of the north and south sides are the only areas that cannot be accessed to survey on foot. The vascular flora is limited, numbering just over 130 taxa. Most of the vegetation on the island is low coastal scrub and annual grassland, and is relatively open and easy to traverse (Philbrick 1972). The

tallest (up to 2–3 m high) and densest vegetation is in some of the small canyons on the east side of the island. The flora of the island is also relatively well-studied. In addition to our own observations, we had the benefit of observations and collections by many National Park Service staff and visiting researchers over the course of this study.

Documented studies of the Santa Barbara Island flora began in the 1860s, though most work on the island dates from the early 1900s. At least 25 botanists, collectors, and observers have visited Santa Barbara Island (Junak et al. 1993). Particularly important studies include those of the Los Angeles County Museum Channel Islands Biological Survey, from 1939 through 1942. The botanical portion of this study was led by Meryl B. Dunkle, and culminated in the first comprehensive floristic list for Santa Barbara Island (Dunkle 1950). This was followed by studies conducted by staff of the Santa Barbara Botanic Garden, particularly Ralph Philbrick and associates. This work led to a detailed, revised flora for the island (Philbrick 1972), which provided the baseline for the study described here.

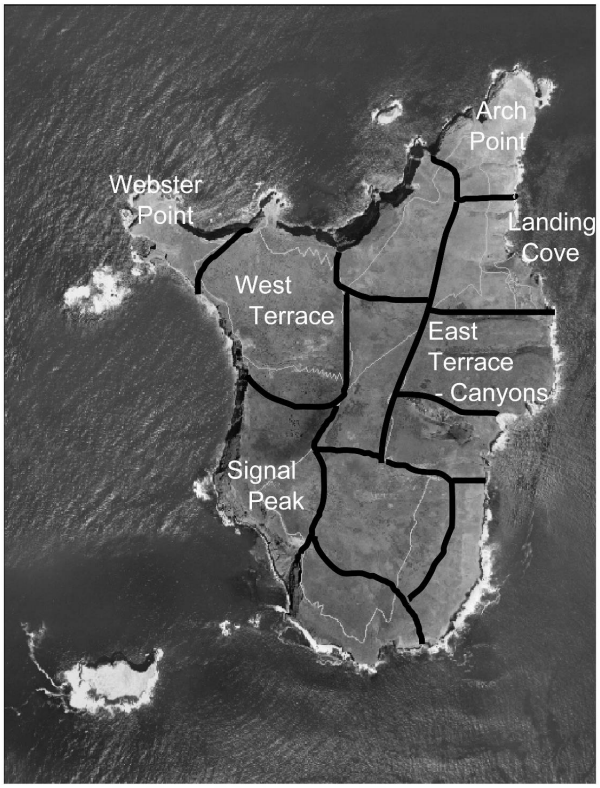

Figure 1. Santa Barbara Island, California, showing place names and the series of zones used in surveying for new vascular plant species.

METHODS

Our field surveys may be broken down into two general, complementary types. Junak conducted targeted searches around the island, looking for rare and unusual species. These observations were generally directed toward particular rare native species and habitats, but all species seen were noted. He also visited and read widely scattered permanent vegetation transects from 1978 through 2000 (e.g., Halvorson et al. 1988; Hochberg-Junak et al. 1983; Johnson and Rodriguez 2001; Corry and McEachern 2009). Drost added to these targeted searches with systematic surveys covering the entire island. For this purpose, the island was divided up into a number of zones (Fig. 1), and each zone was visited at repeated intervals (average of two to three visits per year). The zones were searched by walking through each defined area in a series of parallel lines spaced approximately 5 m apart, to ensure complete and uniform coverage of the entire area. New or unusual species were noted, and vouchers were collected or photographs taken. In the case of new native plants that were evidently rare (in some cases, single individuals), we limited voucher material to a small piece of the plant. In line with Channel Islands National Park management practice, we intentionally removed non-natives to the extent that we could.

We include as the time span of this study the period from Philbrick's (1972) flora up through 2007—a span of 35 years. Although we include observations from this entire time period and base our analyses on this interval, the most intensive fieldwork was during the period 1978 through 2000. Thus, field observations began while rabbits were still present on the island and continued after the last rabbit was removed in 1981. Junak and others from the Santa Barbara Botanic Garden and Santa Barbara Museum of Natural History conducted a detailed survey of the island's natural resources in 1978 and 1979, including mapping vegetation communities and the distribution of rare species (Hochberg et al. 1979; Hochberg-Junak et al. 1983). Junak spent 60 days on the island between June 1978 and April 2004, mostly during the spring months. During the 1980s, Drost spent over 900

days engaged in fieldwork on Santa Barbara Island, including observations on plants over the entire island. From 1981 through 1983, he averaged over 200 days per year on the island, in all months of the year. From 1984 through 1988, he spent from 30 to 80 days on Santa Barbara, from spring through early fall. Since that time, he has continued fieldwork on the island on an occasional basis, primarily in spring and early fall.

New species arrivals (and, in a few instances, changes in distribution and abundance of existing species) were determined with reference to the baseline provided in Philbrick (1972). We mapped the distribution of new species occurrences on the island, and noted habitat and location of new species in relation to trails, the National Park Service campground and visitor contact station, and other features and areas of human influence. Based on the total number of new species found, we calculated minimum arrival rates over the span of the study, for all species combined, and for native and non-native species separately. We specifically compare and contrast new native arrivals with new non-natives, with respect to taxonomic composition, spatial patterns on the island, and other aspects of species biology.

Throughout this paper, we refer to "native" species to mean plants that are native to the flora of California. In some cases, native mainland species may have arrived on the islands with human assistance, or may have spread on the mainland to an extent that they were then able to spread to offshore islands. For that reason, these species might be considered non-native in terms of the island flora. These distinctions are difficult to make with certainty, and we have not attempted to sort out such species for the purposes of this paper.

RESULTS

Between 1973 and 2007, we recorded a total of 32 species new to the flora of Santa Barbara Island (Table 1), including taxa documented by Junak et al. (1993) and taxa listed in Appendix A. These represented 11 plant families, two of which (Oleaceae and Tropaeolaceae, both non-native) were new to the flora of the island. One native species, the bush sunflower, *Encelia californica*, was probably missed in previous surveys as it was

Table 1. New vascular plant species found on Santa Barbara Island, California, during surveys from 1972 to 2007. Plant families are in alphabetical order, with dicots first and then monocots, and species are listed alphabetically within families. Non-natives species are noted by *.

Apiaceae
Apiastrum angustifolium
Asteraceae
Baccharis emoryi
* *Conyza bonariensis*
Conyza canadensis
Conyza coulteri
* *Cotula australis*
Encelia californica
Filago arizonica
Filago californica
* *Hedypnois cretica*
Pseudognaphalium biolettii
Pseudognaphalium californicum
Pseudognaphalium canescens
* *Pseudognaphalium luteoalbum*
Caryophyllaceae
* *Herniaria hirsuta ssp. cinerea*
* *Polycarpon tetraphyllum*
* *Spergularia bocconii*
Spergularia salina
Chenopodiaceae
Monolepis nuttalliana
Fabaceae
* *Melilotus indicus*
Hydrophyllaceae
Eucrypta chrysanthemifolia
Oleaceae
* *Olea europaea*
Primulaceae
* *Anagallis arvensis*
Solanaceae
* *Lycopersicon esculentum*
Nicotiana clevelandii
Solanum douglasii
Tropaeolaceae
* *Tropaeolum majus*
Poaceae
* *Agrostis viridis*
* *Cynodon dactylon*
* *Lolium multiflorum*
* *Poa annua*
* *Schismus arabicus*

found on the remote, difficult-to-access cliffs on the south side of Signal Peak. We found a total of five large, spreading individuals of this shrub that appeared to be quite old, suggesting they were relict survivors from periods of intense grazing on the island. As far as we know, this steep cliff on the south side had not been previously accessed by other observers and collectors. Among the non-native species, the European olive (*Olea europaea*) represents a special case as well. It was obviously an intentionally planted individual, placed in lower Cave Canyon with the bottom half of a plastic milk jug still encasing the roots and soil (we removed this plant in its entirety). Neither *Encelia* nor *Olea* are included in the following analyses.

Not counting *Encelia* and *Olea*, the 30 new species include 14 natives and 16 non-natives. The native species represented six families, but were dominated by the family Asteraceae, with eight species in four genera (Table 2). The only other family with more than one native species was Solanaceae, with two taxa. Among non-native plants, the 16 species comprised 8 families. The largest of these was Poaceae, with five new species. This was followed by Asteraceae (four species) and Caryophyllaceae. Including both native and non-native species, the family-level taxonomic composition of new species was significantly different from the composition of the pre-existing flora of the island (Chi-square, p=0.044 for the six largest families). Some genera were represented by more than one new species for the island. Particularly noteworthy in this regard is the genus *Pseudognaphalium*, with four species (three native and one non-native; see Figs. 2a and 2b). Prior to this study, *Pseudognaphalium* had not been reported from Santa Barbara Island. *Conyza*, with three species (two native and one non-native) found since Philbrick's (1972) flora, is also a new genus for the island.

Table 2. Taxonomic breakdown of new native and non-native vascular plant species found on Santa Barbara Island, California, between 1972 and 2007.

Family	Native	Non-native
Apiaceae	1	--
Asteraceae	8	4
Caryophyllaceae	1	3
Chenopodiaceae	1	--
Fabaceae	--	1
Hydrophyllaceae	1	--
Oleaceae	--	1
Poaceae	--	5
Primulaceae	--	1
Solanaceae	2	1
Tropaeolaceae	--	1

Many of the new species were first recorded as single individuals. Of the 30 total new species, 6 (20%) were single individuals. There was a trend for native species to be found as single plants, compared to non-natives, which were usually found as multiple individuals (Fisher Exact Test, p=0.072). Among native species, 5 of 14 new species (over 1/3 of the total) were single plants, including *Baccharis emoryi*, *Eucrypta chrysanthemifolia*, *Nicotiana clevelandii*, *Pseudognaphalium californicum*, and *Solanum douglasii*. Among non-natives, only *Tropaeolum majus* was represented by a solitary individual. In spite of intensive searches, we were unable to find additional individuals of any of these species in the year they were first found, and only one (*Pseudognaphalium californicum*) has persisted and spread on the island. Other species, such as *Conyza coulteri* (Fig. 2c), have been found as a very few individuals in different years.

Location and Fate of New Species

We noted clear differences between native and non-native species in terms of where new arrivals were first seen on Santa Barbara Island. Among non-natives, 9 of 16 were first found along the trail in Landing Cove canyon or in the adjacent campground/residence area—where people arrive at the island, unload supplies, and spend most of their time (Fig. 3). Four of the remaining seven species were found along the main foot trails that cross the island. Native species, on the other hand, were found scattered in a variety of habitats over most of the island (Fig. 4). Only two native species were associated with trails or other human facilities: *Monolepis nuttalliana*, first seen in disturbed soil along a trail above Landing Cove, and *Nicotiana clevelandii*, found along a trail at the south end of the island. Other native species were found in native shrub and shrub-grassland communities on the east terrace and around the canyons on the east side of the island, and in native shrub communities on the

Figure 2. New plant species documented on Santa Barbara Island, California. a) *Pseudognaphalium biolettii* is one of four species of *Pseudognaphalium* documented on the island (photo from north of head of Graveyard Canyon). b) *Pseudognaphalium californicum* was first recorded as a single individual, but has persisted (photo of first individual found, along south rim of Middle Canyon). c) *Conyza coulteri* has been found as a few widely scattered individuals, which may represent repeated arrivals at the island (photo from sea slope north of Landing Cove).

west slope and terrace. The north and west points of the island, with their shallow, rocky soil, were notable for their lack of new plant species.

Approximately half of the new plants we recorded on Santa Barbara Island have established at least a temporary foothold on the island (i.e., they have persisted for more than one generation). Among the native species, 7 of the 14 new species are known to be persisting (*Apiastrum angustifolium*, *Conyza canadensis*, *Filago californica*, *Monolepis nuttalliana*,

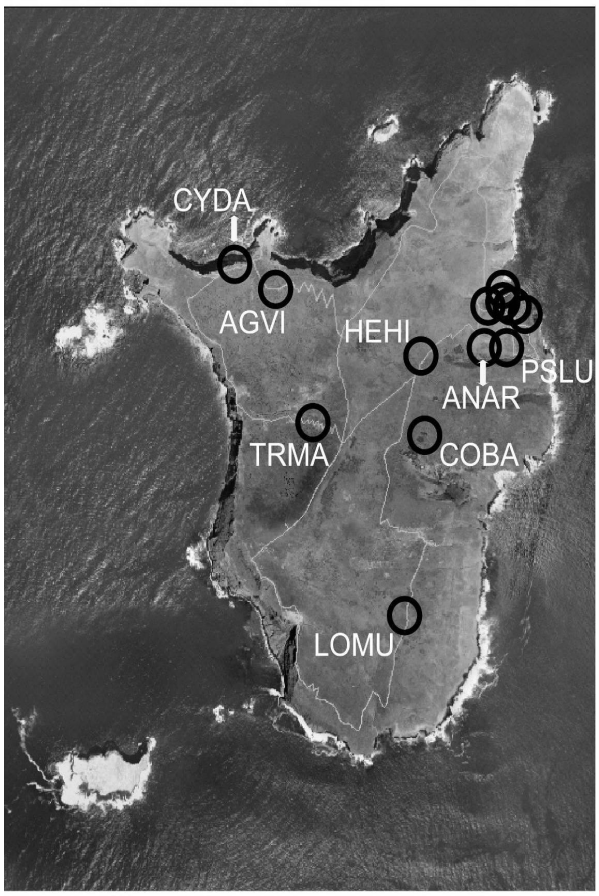

Figure 3. Locations where 16 new non-native plant species were first recorded on Santa Barbara Island, California, during surveys from 1973 through 2007. Eight species were found along the upper Landing Cove trail and north end of the visitor center building (cluster of overlapping circles towards upper right): *Cotula australis*, *Hedypnois cretica*, *Lycopersicon esculentum*, *Melilotus indicus*, *Poa annua*, *Polycarpon tetraphyllum*, *Schismus arabicus*, and *Spergularia bocconii*. Other abbreviations are: AGVI, *Agrostis viridis*; ANAR, *Anagallis arvensis*: COBA, *Conyza bonariensis*; CYDA, *Cynodon dactylon*; HEHI, *Herniaria hirsuta*; LOMU, *Lolium multiflorum*; PSLU, *Pseudognaphalium luteoalbum*; TRMA, *Tropaeolum majus*. The location of a single, intentionally planted individual of *Olea europaea* is not plotted.

Pseudognaphalium bicolor, *Pseudognaphalium californicum*, *Spergularia salina*). Among the non-natives, as many as 7 of 16 species have persisted over multiple years (*Conyza bonariensis*, *Cotula australis*, *Melilotus indicus*, *Poa annua*, *Pseudognaphalium luteoalbum*, *Schismus arabicus*, *Spergularia bocconii*). One questionable case is *Melilotus indicus*, which may have been introduced more than once. A small introduction was thought to have been eradicated after it was first found in 1982. This conspicuous species was not seen again for 12 years, when it was found along the main trail on the east terrace. In spite of their persistence, spread of most recently arrived non-native species has been limited so far. Only *Schismus arabicus* has spread widely, from near the north end of the island at Landing Cove to the south end of the island.

DISCUSSION

We believe that survey coverage was intensive enough to detect nearly all new plant species that reached flowering stage on Santa Barbara Island. Coverage of the island was more limited between 1973 and 1977 and between 1994 and 1997, but between 1978 and 1993, and again between 1998 and 2000, one or both authors conducted extensive searches over the island at multiple times during the growing season. The number of species represented by single individuals, found only once and not seen in any other year, is one indication of the thoroughness of coverage. Likewise, almost all of the species that were recorded for the first time appeared to be new arrivals. Few of them are very small, cryptic, or otherwise likely to have been overlooked. Many of them, in fact, are comparatively large, conspicuous species that can be recognized over much of the growing season. With one exception, none of the new species were found in inaccessible or infrequently visited areas. *Encelia californica*, found on the steep sea cliffs on the south side of the island, is the only "new" species that was probably a relict survivor that had been overlooked by earlier observers.

There were clear taxonomic patterns among new species that arrived on the island. Among native plants, new arrivals were dominated by members of Asteraceae (Table 2). Among the non-natives, Asteraceae, Poaceae, and Caryophyllaceae

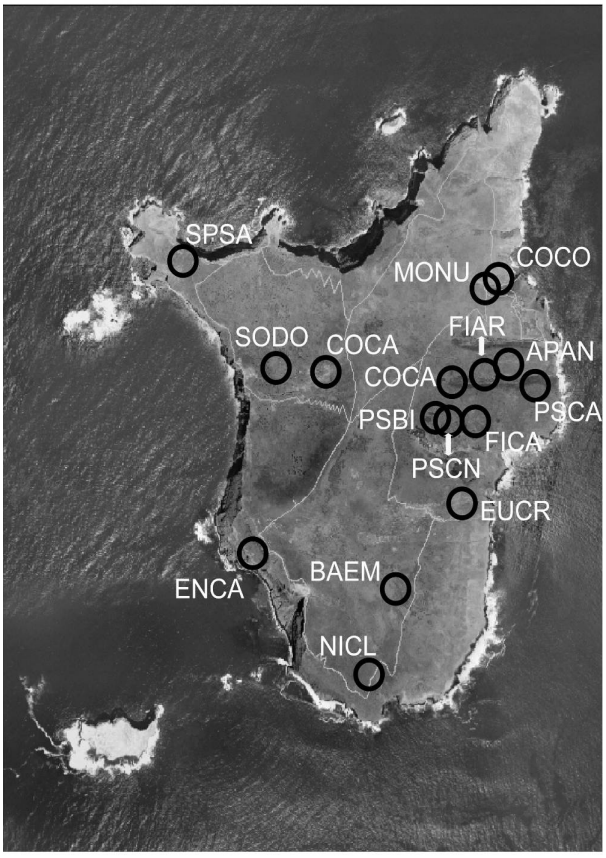

Figure 4. Locations where 15 new native plant species were first found on Santa Barbara Island, California, between 1973 and 2007. Abbreviations are: APAN, *Apiastrum angustifolium*; BAEM, *Baccharis emoryi*; COCA, *Conyza canadensis* (first found in two different locations); COCO, *Conyza coulteri*; ENCA, *Encelia californica*; EUCR, *Eucrypta chrysanthemifolia*; FIAR, *Filago arizonica*; FICA, *Filago californica*; MONU, *Monolepis nuttalliana*; NICL, *Nicotiana clevelandii*; PSBI, *Pseudognaphalium biolettii*; PSCA, *Pseudognaphalium californicum*; PSCN, *Pseudognaphalium canescens*; SODO, *Solanum douglasii*; SPSA, *Spergularia salina*.

contributed multiple species (Table 2). These taxonomic patterns reflect at least in part the dominant modes of dispersal of these plants. Carlquist (1974) included San Clemente Island in the southern California Channel Islands as part of an analysis of probable modes of dispersal contributing to island floras. His analysis is based on the native island flora, and a subjective evaluation of the means of dispersal by which propagules of each native species probably reached the island. Categorized in this way, the new native species that we documented on Santa Barbara Island present a distinctly different picture (Table 3). Particularly

Table 3. Comparison of probable dispersal modes for recent native plant arrivals on Santa Barbara Island, versus modes hypothesized for the flora of San Clemente Island (see Carlquist 1974).

	Santa Barbara		San Clemente
Mode	Number	Percent	Percent
A	8	57	18
BB	1	7	10
BI	1	7	40
BM	2	14	18
BV	2	14	5
DF	0	0	7
DR	0	0	1

Codes (after Carlquist 1974): A - aerial; BB - birds, seeds adhering with barbs, bristles, etc.; BI - birds, internal (fruits eaten by birds); BM - birds, seeds in mud on feet; BV - birds, seeds adhering by viscid coating; DF - drift / frequent (seeds capable of floating); DR - drift / rare (seeds arriving via rafting).

noteworthy in our results are the large number of wind-dispersed species (all of them Composites) on Santa Barbara Island, relative to the low percentage indicated for the San Clemente flora by Carlquist. Likewise, the largest component of the San Clemente flora is represented by plants with fruits that are eaten by birds and transported by them internally. The only new species on Santa Barbara Island that fits in this category is *Solanum douglasii*, which has a fleshy fruit eaten by birds.

Carlquist (1974) notes that presumed modes of transport are poorly studied and difficult to verify, so any such assessment has a measure of subjectivity. As a specific example among the new arrivals on Santa Barbara, the *Filago* species have some achenes with pappus and some achenes without (Hickman 1993). Even on the achenes with a pappus, however, the plumes are deciduous. Hence, the two *Filago* species may typically disperse to a greater extent by adhering to the feathers of ground birds, or by being transported in mud on the feet of birds.

The differences between our results and those of Carlquist (1974) are probably to be expected, however. Carlquist's analyses reflect the cumulative results of tens of thousands of years of colonization, competition, local extinction, and adaptation to the island environment. The shorter-term results for Santa Barbara Island represent species that disperse easily but may not become permanently established on the island. General studies of seed dispersal indicate that species with small seeds and high dispersal ability are good colonizers, but frequently do not persist for long in the face of competition (Howe and Smallwood 1982). The number of species that showed up briefly on Santa Barbara and then disappeared appears to reflect this pattern.

All of the new grass arrivals were non-native species. The lack of recent colonization by native grass species stands out (Table 2), given that grasses make up a high percentage of the native flora of the Channel Islands (e.g., 9.3% on Santa Barbara Island, Junak et al. 1993; 9.6% on San Nicolas Island, Junak 2008). Known or suspected modes of transport for the relatively large, heavy seeds of most grasses include rafting or water transport for strand grasses (e.g., Carlquist 1974) and transport of florets adhering to the feathers of birds or fur of mammals. However, because of the wholesale shift of grasslands in much of California to non-native annual species, the relative lack of native colonizers may be due to much-reduced mainland and near-island sources of propagules. On the other hand, many abundant introduced grasses have spiny awns and are effectively transported in the clothing and shoes of humans.

The Santa Barbara Island flora is surprisingly dynamic. Counting both native and non-native species, there have been approximately 0.85 new species per year over the span of this study. Broken down, this is 0.4 native and 0.45 non-native species per year. As already noted, many of these were represented by single individuals that did not persist. Any such waifs that were missed would increase the calculated arrival rates (on the other hand, if any "new" species were present but were simply missed by earlier surveys, the rates would be lower).

In comparison, Philbrick (1972) found a total of 20 new species since Dunkle's (1950) list. He considered that 5 of these, because they are inconspicuous or taxonomically difficult, may have been overlooked by earlier botanists. The remaining 15 species consisted of 8 natives and 7 non-natives. Over a 22-year period, this equates to 0.68 new species per year, or 0.36 native species, and 0.32 non-natives per year. By calculating annual rates, we do not mean to imply that arrival of new species on the island is expected to be constant. A variety of

factors such as rainfall, relative frequency of offshore winds from the mainland, and possibly reduced herbivory since the removal of European rabbits, may influence the probability of plant propagules reaching the island and successfully germinating and growing to maturity.

Considering other island systems, there are no perfect comparisons for our estimates of arrival rates on Santa Barbara Island. Differing island size, distance from mainland, latitude, composition of potential source floras, and successional state of the island flora all probably affect colonization rates. Nonetheless, comparisons with studies on other islands provide points of reference. The islands studied by Cody (2006) in Barkley Sound, British Columbia, have established floras, but they are generally much smaller (most much less than 1 km^2), and closer to mainland sources (< 1 km to about 8 km). Arrival rates on these islands ranged up to 2 species per year or more. The island of Surtsey off of Iceland is the closest to Santa Barbara in size (maximum of 2.7 sq. km, but now shrinking due to erosion) and distance from mainland (33 km), but it is a very new island (risen from the sea less than 35 years ago) and is at a much higher latitude. Early colonization rates were on the order of 1/year (Fridriksson 1987), but rates have increased to the order of 2–5 /year. Finally, the island of Nishino-shima is smaller (about 0.22 sq km) and much farther from the mainland (ca. 1000 km south of Japan). It has a measured colonization rate of 0.1/year (Abe 2006).

Non-native Plants

Carlquist (1974) and Cody (2006) note that islands may be particularly prone to invasion by non-native plants, owing to their relatively depauperate floras. However, although theoretical studies all indicate that lower diversity should be associated with higher invasibility, and some experimental studies have also supported this, observational studies based on species lists suggest that areas with higher native diversity have higher numbers of non-native species (Levine and D'Antonio 1999). A more important and more consistent predictor of whether invaders establish on a site where they arrive may be disturbance—both natural and human-caused. Santa Barbara Island and the other Channel Islands have all experienced moderate to severe disturbance since being occupied by people. The fact that almost all non-native species have first been found along trails and around areas of human activity might also reflect continued disturbance of areas along trails and around buildings and other human-use facilities.

On the other hand, in a study of non-native plants on coral cays in the Great Barrier Reef region of Australia, Chaloupka and Domm (1986) found that the proportion of the flora represented by non-natives was correlated with frequency of human visitation. They further concluded that this was due to inadvertent human transport of non-native plant propagules ("anthropochory"), as opposed to habitat disturbance by humans that subsequently allowed colonization by wind or other mechanisms. New non-natives on Santa Barbara Island were not distributed widely on trails, cleared areas, and other human-disturbed habitats across the entire island. Rather, they were heavily concentrated in those areas of highest human traffic and initial entry onto the island, at Landing Cove and around the ranger station and campground. In agreement with Chaloupka and Domm (1986), this suggests that direct human transport of seeds and other propagules, rather than disturbance and opening of potential habitat, is mainly responsible for colonization by non-native species.

The locations where non-native plants were found (Fig. 3) also presents clear implications for management of invasive species. Nine of the new non-native species were found in the Landing Cove/residence/campground area. Three of these were along the upper part of the Landing Cove trail, and three were found at the north end of the National Park Service visitor center, just beyond the top of the Landing Cove trail. Most of the remaining non-natives were found immediately along main visitor trails. Control of non-native plants is a high priority in protected areas. It is generally considered that the most important thing that can be done to stop invasion of exotic species is to detect them early, before they have a chance to spread widely and increase in numbers (e.g., Myers et al. 2000; Simberloff 1997). On the Channel Islands, regular surveys of the main visitor access areas (e.g., the Landing Cove area and main trails on Santa Barbara Island) would be a simple and cost-effective means of early detection of new non-natives. Islands have the obvious added advantage that it is easier to

control initial invasions and prevent reintroductions than it is in mainland settings (Brockie et al. 1988; Simberloff 2002).

Relationship to Vegetation Recovery

Introduced European rabbits formerly occurred on Santa Barbara Island, and prior to that, the island was farmed and grazed (Philbrick 1972; Junak et al. 1993). High rabbit numbers in the 1950s and a fire that burned most of the east side of the island in 1959 probably severely reduced and possibly eliminated some species. Paired photos taken in 1939–1940 and again in 1970 document persistent changes related to past disturbance of the island's vegetation, particularly in the reduction in cover and stature of native plant species (Philbrick 1972). Since the last rabbits were removed from the island in 1981, there have been conspicuous increases in the numbers and extent of some native shrubs on the island (Clark and Halvorson 1990; Corry and McEachern 2009).

Moody's (2000) analysis indicated that the number of native species on Santa Barbara Island was lower than expected, based on island size. It is possible that the combination of grazing, heavy browsing and digging by periodically very large populations of rabbits, and the 1959 fire reduced the number of plant species to a level from which the flora is still recovering. Clearly, new native plant species continue to arrive on the island. The effects of rabbits, past cultivation, and fire may also have influenced the observed colonization rate by opening up areas where colonizing species, especially invasive non-natives, could become established. Much of the east side of the island is still covered by a mix of exotic annual grassland and open badlands.

In contrast to some of the island endemic plants on Santa Barbara Island, which appear to have increased substantially since the removal of human disturbance (most recently, feral rabbits), the spread of newly established native colonizing species has been slow. *Pseudognaphalium californicum* and *P. biolettii* are still confined to scattered small areas in and around the canyons on the east side of the island, mostly in association with cactus patches. *Apiastrum angustifolium* is found on limited portions of the island's east terrace, in mixed grass – shrubland. Some other species noted by Philbrick (1972) also appear to be spreading very slowly. Philbrick found only a single individual of the large shrub *Baccharis pilularis* in his surveys. Eight individuals were noted by Junak in 1982 and 1983 (Junak et al. 1993), and a total of 11 were found in a reconnaissance of the entire island in 1998 (Drost, unpublished notes). Clearly the arrival and successful germination of a colonizing plant species on an island is just the first step in a long process.

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Appendix A. Additions to the known flora of Santa Barbara Island, California, since the publication of "A revised flora of Santa Barbara Island" (Junak et al. 1993). Included here are details of observations of previously unrecorded species, including herbarium specimen records, and descriptions of important changes in status or distribution of species on the island. Herbarium voucher specimens have been deposited at the Santa Barbara Botanic Garden (SBBG) unless otherwise noted.

Asteraceae

Filago arizonica A. Gray. Localized population on open south-facing slope along north rim of Middle Canyon, elevation ca. 160 ft, April 6, 2000, *Junak SB-179*; scattered on south-facing slope along north rim in central portion of Middle Canyon, elevation ca.170 ft, April 6, 2000, *Junak SB-183*.

Hedypnois cretica (L.) Dum.-Cours. Localized population of three individuals along trail at Landing Cove, just downhill from bench at switchback, elevation ca. 120 ft, June 7, 1999, *Junak SB-170*. This non-native taxon is also known from Santa Catalina Island and San Clemente islands. It has spread very rapidly, especially along roads, during the last decade on Santa Catalina Island.

Brassicaceae

Brassica nigra (L.) W.D.J. Koch. Along trail near NPS Ranger Station, 1995 or 1996, *Chaney s.n.* (SBBG 117128). Possible reintroduction to the island. Identification of this taxon is tentative as records are based on sterile specimens which may in fact be *Hirschfeldia incana* (L.) Lagr.Foss. Only known previous collection was by Dunkle in 1940. This conspicuous species was not seen during intensive surveys in 1981–1989, but was found again by NPS staff in 1995 or 1996. All individuals seen were removed.

Caryophyllaceae

Herniaria hirsuta L. var. *cinerea* (DC.) Loret & Barrandon. Rare in new gravel along trail to saddle, between Cave and Middle canyons, elevation ca. 420 ft, April 16, 1994, *Junak SB-109*. This non-native taxon has now been found on San Miguel, Santa Rosa, San Nicolas, Santa Catalina, and San Clemente islands as well (Junak 2008).

Polycarpon tetraphyllum (L.) L. Localized population on disturbed north-facing slope near top of Landing Cove trail, elevation ca. 130 ft, June 1, 1999, *Junak SB-146*. This non-native taxon has now been found on all of the California Channel Islands except San Nicolas and San Clemente.

Fabaceae

Melilotus indicus (L.) All. After its original discovery and targeted eradication efforts in the early 1980s, this conspicuous species was not seen again from 1985 through at least 1989, in spite of intensive surveys across the island. It may have been reintroduced with imported gravel and sand in 1994 and perhaps again in 1999. Scattered plants in new gravel along trail to saddle, between Cave and Middle canyons, elevation ca. 420 ft, April 16, 1994, *Junak SB-110*; two plants found on introduced sand at helicopter pad near ranger station above Landing Cove, elevation ca. 170 ft, June 7, 1999, *Junak SB-169*.

Oleaceae

Olea europaea L. At base of north-facing slope in lower Cave Canyon, near mouth; in milk jug 'pot' buried in ground, among Coreopsis. This obviously intentionally planted individual was removed in its entirety. A specimen was not kept.